Bulletin of the Museum of Comparative Zoölogy

AT HARVARD COLLEGE

Vol. XC, No. 1

STUDIES OF NEOTROPICAL ANT-PLANTS
AND THEIR ANTS

BY WILLIAM MORTON WHEELER

WITH FIFTY-SEVEN PLATES

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
October, 1942
No. 1.—Studies of Neotropical Ant-Plants and Their Ants

CONTENTS

Part I. The Neotropical Ant Plants.

Chapter 1. The Myrmecophytes of the Genus Cordia
   A. The Cordias of the Section Physoclada
   B. The Cordias of the Section Gerasanthus

Chapter 2. Observations on Triplaris
   A. Historical
   B. Triplaris surinamensis Cham. and Schl.
   C. Triplaris americana Linné
   D. Triplaris auriculata Meisner

Chapter 3. Observations on Tachigalia

Chapter 4. Observations on Cecropia

Chapter 5. Observations on Rubiaceae and Verbenaceae
   A. Duroia and Remijia
   B. Patima formicaria Johnston
   C. Clerodendron Siphonanthus R.Br.

Chapter 6. The Myrmecophytic Acacias
   A. The Bull-horn Acacias
   B. Acacia cavenia Hooker and Arnott
   C. The African Acacias

Chapter 7. Various Non-myrmecophytic Plants with Ant-inhabited Stems, etc.

Chapter 8. The Epiphytic Bromeliaceae and their Fauna

References

Part II. Neotropical Plant Ants

Part I. THE NEOTROPICAL ANT PLANTS

Chapter 1

THE MYRMECOPHYTES OF THE GENUS CORDIA

The more than two hundred known species of Boraginaceous trees and shrubs of the genus Cordia, distributed over the tropics of both hemispheres, have been divided by botanists into several groups, or sections. Two of these, the Physoclada (Pilicordia) and Gerasanthi, are confined to the Neotropical Region and contain several ant-plants, or myrmecophytes, of unusual interest. The most typical representative of the Physoclada is Cordia nodosa Lamarck of Northern South America.
America, and perhaps the only true myrmecophyte in the Gerasanthus section is *C. alliodora* Ruiz and Pavon, which ranges from Northern Mexico to Bolivia and eastward over the Antilles and portions of Northern South America. The following account is concerned primarily with these two species which I have had abundant opportunity to observe in the field, the former in British Guiana, the latter in Panama.

(A) The Cordias of the Section Physocladia

Professor I. W. Bailey and I found *C. nodosa* to be common, both in the primeval forest and in the second-growth jungle about Kartabo, Kalacoon, Barakara and on Great Batavia Island in the Cuyuni River, British Guiana. This and closely allied species have been frequently described by botanists, notably by Beccari (1884-'86), Schumann (1888), Schimper (1888), Mez (1890) and Ule (1907). Though *C. nodosa* may attain a height of 10 or 12 feet, most of the specimens are small, symmetrical bushes, with verticillate branches, and growing in the shade of tall trees and, on low but not inundated soil. The whole plant, including the stem and the large ovate leaves, is covered with long reddish hairs. As Bailey (1924a) says, the leaves "are alternate, paired or grouped in false verticils of four. The subnodal portion of the stem, subtending each verticel of leaves, is strongly thickened and angular and usually, though not invariably, provided with a long bladder-like swelling. This pouch is jacketed internally as well as externally, by a cuticularized epidermis and numerous trichomes. It subtends the lowermost of the four leaves, in the axil of which is a small apical outlet which is not excavated by the ants. Above this leaf, the thickened and much compressed primary axis gives rise to lateral inflorescences which are inserted in the axils of the three remaining leaves."

There has been much difference of opinion concerning the morphology of these ant-inhabited cauline swellings, which always occur immediately below each node with its verticel of leaves or branches. Schimper believed that the swellings are really the lateral enlargement of the base of the petiole of the lowermost leaf, which is adnate to the main axis. Schumann regarded the inflorescence as terminal and the swellings as cauline rather than as adnate foliar structures. Mez maintained the same opinion in regard to the inflorescence, but interpreted the swellings as formed by lateral invaginations, which he believed to have been originated by small insects living in the lateral
grooves and later to have been inherited as ant-domatia. Bailey (1924) after a careful study of these structures reaches the following conclusion:

"What then is the morphological significance of these extraordinary structures? The hypotheses of Schimper, Schumann and Mez do not afford an adequate explanation of all phases of their ontogenetic and phylogenetic development. Below the subnodal hypertrophy, the stem is of normal structure. Above this level, it rapidly increases in girth. As it does so, the circumference of its concentric layers of epidermal, cortical and fibrovascular tissues becomes correspondingly enlarged, and a commodious internal cavity is concomitantly formed in the dilated core of medullary parenchyma. This chamber, unlike that of the caulinary domatium of other myrmecophytes, is characterized by being jacketed by centripetal layers of epidermal, cortical and more or less rudimentary fibrovascular tissues. There is, in other words, no indication of a compressed stem and adnate petiolar enlargement, nor of an extensive lateral invagination. The centripetal layers of epidermal, cortical and fibrovascular tissues unite with the homologous centrifugal layers only in the apical portion of the wall of the domatium which surrounds the small circular aperture.

"A detailed study of the morphology of the myrmecodomatia, during successive stages of their ontogeny, indicates very clearly that they are hypertrophied portions of the cauline axes, whose medullary cavities are jacketed by layers of invaginating tissues. The invagination does not originate, however, in a longitudinal lateral groove, but in the axil of one of the leaves of the pseudo-apical verticel. As it develops, it produces an elongate-saccate ingrowth of the epidermal, cortical and fibrovascular tissues into the rapidly enlarging core of medullary parenchyma. The absence of even a rudimentary bud in the axil of a leaf which subtends an entrance aperture suggests that this growing point may be concerned in the formation of the invagination. If it is, the invagination may be visualized as the homologue of an ingrowing lateral shoot, and its formation may be likened to what happens when one finger of a glove is retracted so that it ultimately projects inwards instead of outwards. In exceptional cases, invaginations may develop in the axils of two of the leaves of a single verticel." Prof. Bailey figures an abnormal compound domatium of this type. (1924, pl. 7, fig. 8).

It is clear from this account and indeed from the most cursory study in the field that the myrmecodomatia of C. nodosa are preformed structures, which cannot be regarded as galls, or as hypertrophies
produced by insects or fungi. The same statement is undoubtedly true of the corresponding structures in *C. hispidissima* D C.¹ In this species, however, which seems to be common in Amazonas and Bolivia, but was not encountered in the hylæa of British Guiana, the cauline swelling is asymmetrical, that is, one-sided. Bailey, who has studied its structure on materials collected by Dr. Orlando White and Dr. W. M. Mann on the Rio Beni, in Bolivia, finds it to be fundamentally the same as that of *C. nodosa*, though differing in morphological details. "The striking difference in their external form is due to the fact that in the case of the former plants (*hispidissima*), the subnodal enlargement of the stem is unilateral and the basal projection of the trace of the leaf which subtends the entrance aperture is set off from the central cylinder at a much lower level."

*C. hispidissima* has been recently observed by Bequaert (Wheeler & Bequaert, 1929, p. 28) on the Lower Rio Branco, Brazil. In his account of the domatia he agrees with Bailey and states that they contained a "varied fauna". "One swelling contained a book-scorpion (Chelifer) occupying the lowermost portion of the cavity which was enclosed above by a white web-like partition; another was occupied by a medium-sized spider. Other domatia contained small colonies of a Ponerine ant, *Neoponera unidentata* Mayr var. *eburneipes* Wheeler. Each of these colonies consisted of four to six workers, with eggs, larvae and pupae, the last enclosed in cocoons."

Chodat and Carizzo (1920) describe and figure another Cordia (*C. chacoensis* Chod.) from Paraguay, which has true domatia somewhat resembling those of *C. nodosa* and *hispidissima*, though longer and more slender. This Cordia grows in moist places and is of small size like the species of the Section Physocladia. Unfortunately no account is given of the structure of the domatia or of their tenants.

Up to the present time the following ants have been taken in the cauline swellings of *C. nodosa* and *hispidissima* in various parts of South America:


¹Engler and Prantl, IV, 3, 1897, p. 83 recognize only one species, *C. nodosa*, in the section Physocladia and regard *hispidissima* D C. and *miranda* D C. as "wohl von der vorstehenden Art nicht spezifisch verschieden."


(12) *Azteca stanleyi* Forel. In *C. nodosa*. Brazil (J. Huber; Chodat).


(14) *Azteca ulei* Forel var. *cordia* Forel. In *C. nodosa*. Brazil (Ule); British Guiana (Wheeler).


Most of these forms and notably the species of Neoponera, Pheidole, Crematogaster, Solenopsis, Brachymyrnex and Myrmelachista are of infrequent occurrence and found only in single domatia. The same seems to be true of the species of Azteca, but the forms of *Allomerus 8-articulatus* are regular, or obligate tenants. This is certainly the case in *C. nodosa* in British Guiana, where the var. *demerarae* was found
in every one of the plants examined and usually inhabiting all of its
cauline swellings. As the habits of this ant are practically unknown,
I single it out for special consideration.

The genus Allomerus was established by Mayr in 1877 for some
small yellow worker ants taken by Prof. James Trail in Northern
Brazil, presumably in the cauline swellings of Cordia or of some other
myrmecophyte. In 1904 Forel described all three phases of 8-articulatus
taken in Amazonas by E. Ule in the petiolar sacs of Tococa setifer
Pilger and observed that the females and males were of a much
darker color and larger size (6 and 5.3 mm. respectively) as compared
with the workers (1.8 mm.). Misled by a false analogy with the ants
of the genera Solenopsis, Carebara, etc., he surmised that the Allomeri
might be thief-ants. This is clearly disproved by my observations.
The genus, as Emery has shown (Genera Insect., Myrmicinæ, 1921,
p. 188), belongs to the tribe Monomoriini and not to the Solenopsi-
diini, which comprise so many lestobiotic species.

Allomerus 8-articulatus var. demerarae is well known to the native
Indians of British Guiana, who call it the "Kurabelli" (Hohenkerk,
1918). Its colonies are extremely populous, comprising thousands of
workers and many mother queens. Each colony normally occupies all
or most of the cauline swellings of a C. nodosa bush or tree. All the
cavities are connected with one another and with the forest floor by a
peculiar system of galleries or arcades, constructed on the surface of
the plant by the ants and measuring about 5-10 mm. in diameter.
They consist of minute particles of black, agglutinated earth built up
around and supported by the long red hairs above mentioned. A
single gallery starts at the ground and ascends the trunk in a straight
line to the first node, where it ramifies and sends a branch along the
surface of each limb of the verticel. The branching is repeated at
succeeding nodes till each swelling is furnished with a gallery that runs
up its side and terminates at the orifice of the cavity. The minute,
pale, yellow, small-eyed workers are thus enabled to pass under a
continuous carton-like roof and between the stiff hairs which support
it like so many pillars, from their nests in the domatia to the ground
where they forage among the dead leaves. Coccids (Pseudococcus
brevipes) are found in some of the domatia but they are not sufficiently
numerous to provide more than an insignificant portion of the food
required by so large an ant-population. This consideration and the
elaborate construction of the system of galleries show that while the
Cordia furnishes most admirable domatia for the ants, it is by no
means an adequate source of food.
During the rainy season (July to September 1920) I found the cauline swellings full of the Kurabelli brood in all stages, together with many males and winged females. As soon as the swellings on the youngest branches become large enough, deïlated females take possession of them and begin, apparently at once, to lay eggs. And though each incipient swelling usually contains only a single young deïlated female, I have on several occasions found two, three or even four such females, all caring for their eggs or young larvae in common in the same domatium. Unlike most ants, therefore, Allomerus is normally pleometrotic even during the incipient stages of colony formation. After they are reared the broods of these young females undoubtedly become a part of the single large polycladic colony which possesses the whole plant.

It cannot be maintained that the Kurabelli act as an efficient protective body guard for the Cordia, at least so far as man and the larger animals are concerned. When one handles the plant for some time, the workers do indeed swarm over one's clothes and body and for some time keep on stinging, but their stings are so feeble that they produce merely a rather unpleasant itching and that only of parts with very thin epidermis. While it is probable that the Kurabelli may be more efficient in keeping the plant free from certain insects, it should be noted that other Formicidae not infrequently occupy some of the domatia although most of them may be tenanted by Allomerus; and both Professor Bailey and I sometimes found the foliage of such plants considerably damaged by leaf-cutting ants (Atta cephalotes). I have also noticed leaves that had been extensively gnawed by caterpillars. The foliage of one plant tenanted by Allomerus was covered with Cecidomyid galls. The only other insects found associated with C. nodosa were termites, which on one occasion were seen to have a gallery extending up the trunk from the ground and terminating in a cauline swelling which they were occupying.

(B) The Cordias of the Section Gerascanthus

The Cordias of this group, unlike the Physoclada, are tall shrubs or trees, frequently attaining a height of 20 to 60 feet, with gray bark and coriaceous, opaque leaves, covered with dense stellate hairs beneath and sparser hairs of the same type above. The branching, except in young specimens, is much more obscurely verticillate, and though ant-inhabited cauline swellings occur in some of the forms, they are much simpler than those of the Physoclada, being merely
conical, pyriform or turbinate dilatations of the stem beneath and at
the nodes, with large medullary cavity and without a preformed
orifice. The flowers are much more numerous and showy and usually
aggregated in broad, dense panicles or corymb. As a rule, the plants
grow on higher ground, in the campos or more open woods and
thickets and therefore in more xerothermal situations than the
Physocladia.

Chodat and Vischer (1920) recognize seventeen species as belonging
to the Gerascanthus section, but many of the forms are by no means
easy to distinguish, as may be inferred from their remarks: "After a
thorough examination of the flowers of all the species, we have been
unable to discover other characters than those derived from the size
of the organs, the more or less elongate form of the ovary or of the
infraovarian disc, the importance of which is in no respect greater
than that resulting from an examination of the vegetative organs and
the external appearance of the calyces and corollas. The evaluation
of the characters derived from a comparison of the reproductive struc-
tures is rendered difficult by the fact that there is in the Cordias, at
least of this group, a pronounced heterostyly .....................
We are, in fact, dealing with species which are but feebly defined
morphologically and the taxonomy of which will require revision from
time to time as observations in the field increase in number". The
authors call attention to the fact that Schumann (1888) regarded all
the forms of the Gerascanthus section as constituting but a single
species.

Of the seventeen species recognized by Chodat and Vischer, nine
are recorded as certainly possessing cauline swellings and as being
therefore myrmecophilous, namely C. gerascanthus L. and its varieties,
alliodora Ruiz and Pavon, Rusbyi Chodat, Hassleriana Chodat,
glabrata var. orbicularis Chod. and Vischer, longituba Chod. and
Vischer, Chamissoniana Steud., Cuyabensis Manso and Lhotsk. and
gerascanthoides H B K. They failed to detect myrmecophily in C.
hypoleuca D C. and excelsa D C. and in certain large-flowered species
not belonging to the Gerascanthus section, namely insignis Cham.,
nettoana Taubert, Hainkeana Mez and formosa Chod. I may add, in
this connection, that I have failed to find any indications of myrme-
cophily in C. lutea, which is very common in the Galapagos Islands.
It has no cauline swelling and ants merely visit its clusters of showy
yellow flowers for their nectar. The same is true of the beautiful,
vermillion-flowered C. sebestena L., which is common in gardens and
along road-sides in the West Indies.
Among the myrmecophilous species cited by Chodat, *C. gerascanthus* is given as the most widely distributed and best known. He distinguishes three forms or varieties of the plant: *genuina* Chod. (≡*gerascanthoides* Rich. *non* H B K), *Martinicensis* Chod. and *micrantha* Jacq. The first is cited as common in the Antilles (Cuba, Porto Rico, Jamaica, Haiti, St. Thomas, St. John, Antigua, St. Vincent, Trinidad), the second as known from Martinique and Guadalupe, the last from Mexico, Guatemala, Nicaragua, Costa Rica, Panama, Peru and Bolivia. This form has somewhat smaller flowers than the West Indian type (*C. gerascanthus* L. *sens. str.* or *genuina*) and has been cited by authors as *C. gerascanthus* Jacquinii.

This interpretation of *gerascanthus* is not accepted by Dr. I. M. Johnston (1924), of the Gray Herbarium, to whom I submitted specimens of the species I studied in Panama for identification. I quote his remarks on the synonymy of *gerascanthus* and *alliodora*: "In 1910 Urban, Symb. Antil. IV. 516 indicated, that, as then used, the binomial *Cordia gerascanthus* L., was incorrectly applied to the widely distributed tree with canescent, densely stellate calyces, and that the name is properly applicable to the relatively localized species of the West Indies and Southern Mexico which has glabrous or sparsely hisrate calyces and larger flowers, and which was described and current as *C. gerascanthoides* H B K. Ten years later, in his paper on *Cordia Gerascanthus* Chodat, I.c. declared Urban's interpretation of *C. gerascanthus* L. to be incorrect, and used the term in the traditional sense, applying it to the widely distributed plant with stellate calyces. Further examination of this matter has recently been made to determine the correct specific name for use by Dr. W. M. Wheeler in his publications on myrmecophytes. For the convenience of others the results of this study are here put on record. *Cordia gerascanthus* L. is based upon the Jamaican plant which Patrick Browne, I. c., described and figured under the name "Gerascanthus". Browne's illustration, showing only the floral structures, portrays a corolla of large size which has broad short obtuse lobes with conspicuous pinnate veining, a broad saucer-shaped throat, a stocky weakly ribbed calyx, and deltoid calyx lobes. These characters definitely associate Browne's plant with *C. gerascanthoides* H B K. and prohibit the use of the Linnean name for the plant with stellate calyces. It is to be also noted that not only does Grisebach, I. c. cite Browne's figure under "*C. gerascanthoides* H B K.,” but he gives *C. gerascanthoides* H B K as "common in the lowlands and mountains" of Jamaica, and gives the plant with stellate calyces (under *C. gerascanthus* Jacq.) as "rare" on
that island. Browne's plant was not rare, for he speaks of it as follows. "This tree grows in many parts of Jamaica, and is generally esteemed as one of the best timber woods of the island; it rises to considerable height . . . , especially in the lowlands, where it is most common, . . . "It is significant that concerning the Jamaica occurrence of the plant with stellate calyces, Urban, l.c. (under C. alliodora Cham.), comments parenthetically as follows, "fortasse a cl. Wilson introducta ex cl. Stapf. in lit." Since the identity of C. gerascanthoides H B K. and Geranthis Browne is certain from a study of Browne's plate and description, and from distributional considerations, it is evident that Cordia gerascanthus L. is, indeed, improperly applied to the widely distributed plant with stellate calyces. Among its close relatives in the West Indies and Central America, C. gerascanthus L. is readily recognized by its large flowers, saucer-shaped throat, hirsute or glabrescent stout weakly ribbed calyx-tube, and deltoid calyx lobes. It is known only from Cuba!, Isle of Pines!, Jamaical, southern Mexico!, and northern Central America. As Urban, Symb. Ant. IV. 516 (1910) and VIII 574 (1921), has pointed out, Cordia alliodora (R. & P.) Cham. is the correct name for the widely distributed plant with stellate calyces, or in other words, for the one incorrectly current as "C. gerascanthus". Cordia alliodora ranges from Mexico and the West Indies southward along the Andes to Bolivia. A number of critical species, doubtfully distinct from it, have been described from Brazil, adjacent Paraguay and Argentina".

It is clear, therefore, that at least two quite different species of Cordia have been confused in the literature, C. gerascanthus Linn. (=gerascanthus Browne=gerascanthoides H B K=gerascanthoides Griseb.) of the West Indies and C. alliodora R. and P. (=gerascanthus var. micrantha Chodat), distributed from Mexico to Bolivia and also occurring, though apparently not very abundantly, in the West Indies. Now C. alliodora always has preformed domatia whereas these structures do not occur in gerascanthus L. Chodat, who has interpreted all the cauline thickenings in the group of Cordias under consideration as insect galls, has simply obscured and confused the whole subject, because while both species may have occasional stem-galls produced by insects, these galls have nothing to do with the preformed myrmecodomatia which are a conspicuous and constant feature in C. alliodora. This matter will be discussed in greater detail in the sequel. I may add that a very competent dendrologist, Professor J. G. Jack of the Arnold Arboretum, has at my request carefully studied many specimens of gerascanthus L. at the Harvard Botanical Garden
at Soledad, Cuba and reports that he has utterly failed to find the slightest traces of myrmecodomatia in this species.

I admit the possibility, however, that the Panamanian *C. alliodora* may differ varietally from the Peruvian type described by Ruiz and Pavon, for the following reasons: (1.) The original figure represents the flowers accurately but does not show the cauline swelling which should be present at the base of the panicle. Of course, either the draftsman or the authors may have omitted it owing to its resemblance to a gall. (2.) The authors state that the tree blooms in July and August, whereas the Panamanian tree is leafless at that season and blooms in spring. (3.) According to Ruiz and Pavon, the Peruvian Indians use the bark and leaves as a condiment. The bark and foliage of the Panamanian tree seem to have no such properties. (4.) The following peculiarities cited by Ruiz and Pavon, do not apply to the plants I have examined: “Cum hujsusmodi arbores secantur, odorem gravissimum emittunt, et penetrantissimum, qui oculorum aciem perstringit. Corticis recente evulsi odorem valde foetidum vulpis urinae haud multum adsimilem, spirant; postea vero Foli uli etiam Cortex, allium maxime redolent, unde nomen ab Incolis Arbor accepit.” After calling Dr. Johnston’s attention to these considerations, he agrees with me that the plant usually cited as *C. Gerascanthus* Jacquiniius and more recently as var. *micantha* Chodat of that species, may differ from the typical *alliodora*. I quote from one of his letters received February 23, 1924: “In regard to Cordia, I must say that I am unable to give you any thoroughly satisfactory information. The plant which Chodat treats as *Cordia gerascanthus* var. *micantha* is newly published by him, although from Chodat’s citations one might obtain the impression that the trinomial was based upon a name published by Jacquin. Chodat apparently wished to show that his form *micantha* was based upon and included the plant described and figured in his *Stirpium americanarum* 43. t. 175, fig. 16 (1763). Unfortunately, however, Jacquin’s figure shows a flower 17 mm. long, whereas Chodat describes his forma *micantha* as having corollas 1 cm. long. In other words, Jacquin’s plant is the common form growing in the West Indies, and the plant which Chodat describes is the common form of Mexico and Central America. Wright’s plant from Cuba is probably the same form as that figured by Jacquin. I have talked the situation over with the men at the Gray Herbarium and the general consensus of opinion appears to be that Chodat’s forma *micantha* had best be taken as covering the plant described, rather than as being typified by the cited specimen or the reference to Jacquin. With this solution of the
problem I am now inclined to agree. If it is satisfactory to you Chodat’s trinomial will be applicable to your Panamanian form. The situation will undoubtedly lead to confusion since certain workers are inclined to lay more weight on the specimens cited than upon the actual description, and such people would treat Chodat’s trinomial as applying to the large-flowered West Indian form of alliodora. This and other aspects of Chodat’s work on Cordia has led me to believe that it has given more confusion than it can possibly give help. Certainly it has not clarified the classification of that large and difficult genus. Intercategorical priority not being recognized in botany, I can and will describe the Mexican and Central American plant as a geographical variety of alliodora, giving it a new name and one definitely applicable to your plant.” Since this name is not yet published, I am using the specific name alliodora for the small flowered plant, with preformed myrmecomatia and a distribution from Mexico to Bolivia. ¹

The confusion between ‘gerascanthus Linnaeus and alliodora Ruiz and Pavon has, of course, led to confusion in the writings of those who have considered their relations to the ants. I therefore take up in chronological sequence the various authors who have been concerned with the Panamanian species.

One of the earliest, if not the earliest accounts of the relations of ants to Cordia, is that of Ruiz and Pavon (1799), who described and figured C. alliodora (called the “arbol del ajo” an account of its onion-like odor) from Peru under the name Cordana alliodora. They observed that “quædam exiguæ Formicæ quorum punctio acrem intolerabilemque pruriginem diu persistentem excitat, frequenter has arbores infestantes folia devorant, ita ut vix ulla inveniri possint integra.” The first part of this sentence seems to refer to some species of Pseudomyrma, but the latter part is erroneous, since no ants devour foliage, and if it refers to the leaf-cutting Attini, they neither sting nor occupy the cauline swellings of Cordia. Chodat seems to have been led by the remark of Ruiz and Pavon to a peculiar and partly erroneous interpretation of the peculiar carton disseminations (vide infra) in the cauline swellings and of the habits of their ant-inhabitants.

Spruce (1869 [1908]) was also familiar with C. alliodora, which he cites under the name gerascanthus Jacq. He says that “it rises to a stoutish tree 30 to 40 feet, and is throughout fasciculately branched

¹Since this passage was written I find that Standley, in his works both on the Mexican (1924) and Panamanian flora (1928), has accepted C. alliodora as the correct name of the plant which I studied.
(branches 3–5–nate). At the point where the branches divide there is mostly a sac, inhabited by very vicious ants of the tribe called "Tachi" by the Brazilians." These ants are undoubtedly a species of Pseudomyrmica and, in all probability, some form of *Ps. sericea* Mayr or *Ps. gracilis* Fabr.

Seemann (1852–1857), in his early account of the Panamanian flora shows that he was acquainted with *C. alliodora* (cited as *gerascanthus Jacq.*), which, he says, is called "laurel" by the natives, who use its wood in building and cabinet making. Although he records the tree as common on the outskirts of woods in the provinces of Panama and Veragua and as growing as far north as Mazatlan and Acapulco, Mexico, he says nothing about the peculiar cauline swellings and their tenants. The same remark applies to Saldanha da Gama (1874), who cites *C. alliodora* as distributed throughout Brazil and as known under the name "lauro". It is described as a large tree of such rapid growth that it may yield planks in only eight years after germination. The wood is described as odorous, light and nonresistant to moisture and as being used for doors in the interior of houses, lintels, etc. The carpenters who saw it become very thirsty, owing to peculiar properties of the sawdust, and the shavings withdraw so much moisture from the hands that the workmen find it an unpleasant wood to handle. There is nothing in Saldanha da Gama’s description to prove that his *C. alliodora* is identical with the Panamanian species.

Beccari (1884) was the first to give a clear description and figure of the cauline swellings of *C. alliodora* (cited as *gerascanthus*) from Mexico. He mentions the plant as occurring in the Sierra Padro Nolasco, at Talca, Acapulco, etc. The peculiar convoluted or travecular carton in the cavity of each swelling was figured and described, and he noticed the entrance holes made by the ants and the large coccids kept by them on the walls of the cavity. He was also quite clear in regard to the structural differences between the swellings of *alliodora* and those of the Physocladia (*C. nodosa*).

Schumann (1888), after a brief revision of the Cordias of the *gerascanthus* group, confirmed but added nothing to Beccari’s statements concerning the Mexican *alliodora*.

More than twenty years ago Mr. C. H. Tyler Townsend sent me a number of cauline swellings of *alliodora* which he found near Cualata, on the slopes of the Volcan de Colima, Mexico. Referring to his letter of August 6, 1902, I find the following note: "The ant from Cualata which keeps a large red laccanoïd coccid in its nests in swollen joints of the branches of a tree is probably a new species. This is a most striking
instance of the interrelations and mutual dependence of plant, ant and coccid.’’ Professor Forel, to whom I later sent specimens of the ant, described it as *Azteca longiceps* Emery subsp. *patruelsis* (see Pt. II p. 233). The specimens of the caulinaceous swellings and Coccids, still in my collection, are precisely the same as those described below from Panama. They bear the following note in Townsend’s handwriting: “July 25, 1901. Living in hollow cavities in swollen joints of tree growing 12 to 20 ft. high. Cavities in these joints are natural. Ants keep coccids inside. Small hole or holes allow exit of workers only. These holes are sometimes found grown over, the ants having failed to keep them open, in which case the dead ants are found inside. Joints are inhabited all the way from twigs to branches an inch in diameter. The ants bite.”

Pittier (1908) in his work on the economic plants of Costa Rica, cites *alliodora* under the name *gerascanthus* Jacq., with the following note: “The laurel is one of the most important trees of the country as wood for construction. The trunk is straight, with white bark; the leaves are small, entire, elliptical-lanceolate; the flowers white, very fragrant and in large racemes. The wood is rather fine and hard, of a pale chestnut color and easy to work; it is reputed to be incorruptible and is used principally for flooring. The laurel grows on both slopes of the country from sea-level to 1500 m. more or less, but attains greater dimensions on the Atlantic Slope.” Pittier gives the Bribri Indian name of the tree as “dze-ui.”

Ule (1907) observed *C. gerascanthus* Jacq. (evidently *alliodora*) at Tarapoto, Peru, in a rather dry region and, after describing the caulinaceous swellings, remarks that “they make the impression of galls, but are thin-walled and nearly always harbor in their cavities a very vicious species of ant, *Pseudomyrmex sericata* var. *cordiae* Forel.”

Dr. W. M. Mann, while on the Mulford Expedition to Bolivia during 1921–22, made observations on *C. alliodora* (probably var. *boliviana* Chod. & Visch.) and collected ants and other insects in the domatia. These structures are precisely like those of the Central American and Mexican trees.

Bailey (1924), who made a study of the structure of the caulinaceous swellings of *C. alliodora* (cited as *gerascanthus* Jacq.) from herbarium specimens, remarks that “the domatia vary greatly in size, shape and

---

1 According to Boulger (1908) the wood of *C. gerascanthus* L. of the West Indies is known in commerce as “bois de Cypre”, “prince-wood”, “Spanish elm”, “Dominica rose-wood” and “bois de Rhodes” and is “dark brown with dusky, excentric sones, open-grained, soft, durable.” He says that it is used in cabinet-work. According to Mazza and Roig. (1908) *C. gerascanthus* and *gerascanthoides* are called by the Cubans “caba rota”, “palo de rosa”, “palo de rosa del pain.” The wood of *gerascanthoides* is said to be one of the most valued in Cuba, of a dark chestnut color and to be employed in rural carpentry.
distribution in different representatives of even a single species. When present, they are irregularly shaped hypertrophies of the axis of the large diffuse inflorescences or of the transitional region between cauline and floral axes. The lateral entrances or exits are not preformed apertures, as in the Physocladaceae, but evidently are excavated by insects. Furthermore, the domatia are not jacketed internally by invaginated layers of epidermal, cortical, and fibrovascular tissues. As shown in fig. 3, a transverse section of a myrmecodomatium of Cordia Gerascanthus Jacq. (Herbarium J. D. Smith no. 4365), the inflated central cylinder surrounds a large heterogeneous medulla, the large celled, succulent core of which has dried up and has been trimmed away by the ants. In other words, these structures are quite distinct morphologically from the myrmecodomatia of the Physocladaceae, and resemble those of the Ethiopian species of Cuviera and Electronia.

Menozzi (1927) has recently published a few notes on the domatia of C. alliodora (cited as gerascanthus) and their ant-tenants, collected by H. Schmitt in the vicinity of San José, Costa Rica. He figures the domatia and describes the coccids as probably belonging to the genus Cryptostigma, the ants as Crematogaster brevispinosa Mayr, Cryptocerus setulifer Emery and Axteca pittieri Forel.

Standley (1924, 1928) gives a brief but excellent description of C. alliodora. He finds it to be one of the common trees of Mexico and Central America, ranging as far north as Sinaloa, and that "the forks of the young twigs are almost always enlarged by hollow swellings, which afford shelter for fierce ants, hence the name "horniguero."

The fruit is edible. A decoction of the leaves is employed as a tonic and stimulant, especially in the case of catarrh and afflictions of the lungs, and an ointment made with the pulverized seeds has been used in the West Indies as a remedy for cutaneous diseases. The fresh bark is reported to have an odor suggestive of garlic." ¹

The recent study of the Cordias by Chodat, Vischer and Carisso is so much more extensive than that of previous writers and so significant in connection with my own observations that it must be considered in detail. These authors investigated several species in Paraguay (C. glabrata var. orbicularis, Hassleriana, Chamissoniana and longituba and two species, salicifolia and chacoensis, which belong to another

¹The economic value of the tree is indicated by the number of local names which it bears in various parts of its range. These are cited by Standley as "bojón", "bojón blanco", "bojón prieto" (Tabasco); "tambor" (Michoacán); "horniguero" (Michoacán, Guerrero, Oaxaca); "amapa prieta" (Sinaloa); "palo de rosa" (Oaxaca, Cuba, Porto Rico); "palo María" (Guerrero); "laurel" (Panama, Costa Rica, El Salvador, Guatemala, Honduras); "Solera" (Colombia); "laurel macho" (Nicaragua); "caca prieta" (Porto Rico, Cuba); "varea", "caca voja" (Cuba); "canjara", "parrillo" (Venezuela); "arbol del ajo" (Peru); "laurel blanco" (El Salvador); "canalete" (Colombia).
group of forest Cordias related to the Physocladæ). As *gerascanthus* and *alliodora* were not found in that country, they resorted to herbarium material for a knowledge of their peculiarities. For many ecological and morphological details of purely botanical interest the reader may be referred to the first section of the paper by Chodat and Vischer, but the second section, on the myrmecophily of the Cordias of the *gerascanthus* group, calls for fuller discussion. The authors state positively that the cauline swellings are not preformed structures, like those of the Physocladæ, but true galls, which owe their inception to infection by a Chalcidid of the genus *Eurytoma*, according to C. Ferrière's identification. Apparently, only the egg, larva, and pupa of the gall-maker were obtained. In *C. gerascanthus* Jacq. (that is *alliodora*) "the beginning of the infection occurs at the base of the inflorescence or at one of the secondary forks of the latter." And the following remark is added: "We have traced a similar development of this gall in the plant from Guatemala. We were able to ascertain the beginnings of the development of the larva and its morphogenetic action which results in a biomorphosis of rather large dimension." Their Fig. 322 shows a longitudinal section of a young gall with the *Eurytoma* egg at the base of a feeble inflorescence of *C. gerascanthus*. Their Fig. 328 is an enlarged sketch of portions of such a gall containing larvae. Figs. 314a and b, representing similar conditions in *C. globrata* and *longituba*, are quite unlike the typical cauline swellings of *alliodora*. Moreover, the authors confess (p. 179) that they did not follow the ulterior development of the structures in the Paraguayan species. The exit hole of the adult *Eurytoma* is supposed to form the opening through which the ants enter the gall, but no attention is paid to the relatively enormous increase in size of the structure after the minute Chalcidid has deserted it, and neither text nor figures give any clear and convincing account of the eventual developments. The authors do, indeed, describe and figure the fully-formed swelling but they say nothing about the large coccids which were probably present in the specimens they examined and had so vividly impressed Beccari and Townsend. The Genevan botanists figure the convoluted carton mass in the cavity of the fully formed swelling and find it to consist of the pollen and stellate and other hairs of the Cordia, starch grains from the pith, filamentous fungi and bacteria allied to *Leptothrix*. This led them to quote the sentence which I have cited from Ruiz and Pavon and to conclude as follows: "We may therefore regard these structures (i.e. the convoluted masses of carton) as fabricated by the ants themselves with materials from at least two sources: first, the
pollen of the innumerable flowers, second, the agglomerated fragments of lacerated leaves or flowers; third, fungi, perhaps intentionally introduced by the ants (acting as mycetophagous horticultural insects?)." The general results of their study are summarized by the authors in the following paragraphs:

"Thus our investigations establish a new theory of the myrmecophily of Cordia, based on incontestable facts. Observations made by an entomologist in the field will fortunately complete the sketch which we have given of the curious phenomenon, but in the meantime, till these observations are forthcoming, we would call the attention of biologists to the following points:

"Throughout the entire range of species of the section Geráscanthus, from Mexico to Paraguay and from the Guianas to Eastern Peru and Bolivia, we have demonstrated, either in the field (Paraguay) or by examination of herbarium material, the general infection of these plants by ants of the genera Azteca and Pseudomyrma, which establish their fornicaries in these empty galls with materials taken from the host plant. We are not therefore concerned with ants that protect the plants from the leaf-cutters (Atta sexdens), according to the theories of Belt, Mueller and Schimper, since they attack, not the glands of the plant as if they were prepared for the benefit of the ants, as in the case of Cecropia, but essential organs, the pollen and parenchyma of the leaves.

"We fail to see any advantage these trees might derive from the presence of the ants. Their habitual presence on certain species of Cordia clearly shows that these plants which are so widely distributed and so abundant, suffer in no wise essentially from this attack and symbiosis, since it does not jeopardize the existence of the Cordias and is profitable only to the ants. In so far as the Cordias are concerned, there is merely a biomorphogenic reaction."

Chodat and Vischer thought they found confirmation of their general conclusions in their study of the large thorns of the Paraguayan Acacia cavenía, which will be discussed in connection with the Central American Acacias (p. 116), but Fiebring (1909) had previously shown that the cavenía thorns are originally inhabited by Lepidopteran larvae (Tineids). It is difficult to understand why Chodat and Vischer should have regarded their theory as "new." Myrmecologists have long been familiar with the fact that ants are very fond of nesting in the abandoned galls of the most diverse plants, and if the cauline swellings of the Cordias of the Geráscanthus group are nothing but galls, these plants obviously cannot be regarded as myrmecophytes. I trust that
the following observations will demonstrate that the Genevan botanists have reached erroneous conclusions from insufficient data.

I found *C. alliodora* to be a common tree on the Pacific side of the Panama Canal Zone and less abundant on the Atlantic side near Colon. There are many specimens of it on Barro Colorado Island, in Gatun Lake. From Frijoles to Ancon it is often a common component of the second growth jungle, or thickets, and in the clearings, but usually avoids moist spots and seems to show a preference for the slopes of hills. It comes into flower during the last days of February and continues to bloom profusely till about the last of March. During this portion of the dry season the large compact racemes of small white blossoms make the trees conspicuous objects in the landscape (Plate 2). Seedlings and young trees of all sizes can often be found singly or in colonies, especially about clearings and along road-sides, so that the plant can be readily studied in all stages. The largest specimens attain a height of 30 or 60 feet, but flowers are not produced till the tree is about 10 or 15 feet high. While young (below about 4 to 6 feet) it is usually very symmetrical, with the branches coming off in regular whorls at intervals along the straight, slender trunk, so that in this stage it somewhat resembles adult specimens of *C. nodosa*. Later the branches vary much more in length and direction and are less horizontal. Eventually the crown of foliage may be either irregularly pyramidal or, especially when growing in the open, more diffuse and spreading. The trunk and branches are slender and graceful, with moderately smooth, gray bark. The ovate coriaceous leaves are two to four inches long and grayish green, with rough margins. There is considerable variation, however, in the texture and surface of the leaves. The flowers have a strong odor, somewhat like that of decayed urine. They soon turn brown and persist for some time, often till the middle of April, but later fall and the same is true of the stems of the inflorescence though its base, which has a well-developed swelling, or domatium, may remain behind as a dead and dry structure for at least a year. Those who may not care to study the Cordias in the Panamanian jungles will find a number of fine specimens on the hospital grounds, about the reservoirs and in the gardens of private dwellings at Ancon and Balboa. An unusually fine tree nearly 40 ft. high, on the slope of the lower reservoir in Ancon, is shown in Plate 1.

An examination of fully developed trees shows that there is almost invariably an ant-inhabited domatium at each node and that the swellings grow larger successively the nearer they are to the bases of the branches, but the stoutest branches and the trunk exhibit little or
no enlargement in the corresponding regions. Here the domatia persist, nevertheless, but are concealed by a normal and very considerable growth in the thickness of the wood. These masked cauline swellings will be discussed later. It is a singular fact that the adult *C. alliodora* trees lose their leaves during the rainy season when all the other trees of the Panamanian jungle are in full foliage. During July and August the bare trunks and branches stand out as if dead among the dense green foliage of the other trees and the regular arrangement of the domatial swellings at the insertions of the branches becomes conspicuous. These trees could thus be located with the field glasses among the tree-tops visible from the laboratories at Ancon and Barro Colorado Island.

My attention, like that of Chodat and his collaborators, was at first directed to the inflorescences, by finding distinct elongate thickenings of some of the small flower-stems, and I, too, at first took these thickenings to be the initial stages in the formation of the ant-inhabited cauline swellings. In the thickenings I also occasionally found minute maggot-like larvae but did not succeed in rearing the adult insects. They were Hymenopterous and very probably the larvae of the Eurytomid observed by the Genevan botanists, or of some allied species. But most of the enlargements, which are only 2 or 3 mm. in diameter, contain no traces of eggs or larvae and are filled with a uniform and undisturbed mass of brown pith. I am certain, therefore, that they are not galls but merely occasional preformed thickenings of the flower stems, in which the Eurytomids lay their eggs. In other words, these thickenings are strictly limited structures which precede the infection and are not produced by it. The Eurytomid (?) larva simply feed on the pith which happens to be more abundant in the thickenings than in other portions of the flower stems. That these thickenings do not become the true nodal or cauline swellings inhabited by the ants is proved by the fact that they wither and drop off after flowering and cannot therefore produce persistent leaf-bearing branches. True woody galls are, however, occasionally produced on the twigs of the tree by some unidentified insect. One vigorous young tree about 10 ft. high observed Aug. 2, 1924 on Barro Colorado Island had many of these galls, which were regular, ovoidal thickenings of the twigs below the true domatia, quite unlike them in form and about 2 to 3 cm. long and 1 cm. in diameter. They were hard and woody and contained winding passages made by some boring larva. Many of these galls were inhabited by portions of the same *Azteca longiceps* colony that occupied the domatia on the same tree.
In order to ascertain the origin of the cauline swellings it is necessary to investigate the seedlings and young Cordias and the suckers that often grow up from the roots of larger trees that have been felled. These juvenile stages present a very different picture from that described by Chodat and Vischer. The plants are green throughout and actively growing and, as I have stated, very symmetrical in the arrangement and length of their few branches and nodes. Each of the latter is regularly swollen and turbinate and forms a rather thin-walled, green capsule closed on all sides and varying according to its age from 5 to 20 mm. in diameter. The delicate remnants of the pith form an even layer over the wall of its large cavity, which contains no traces of any insect parasite. Nor does the great majority of juvenile trees or suckers contain any ants till they reach a height of about three to five feet. The swellings are so perfectly regular in their arrangement and in position so comparable to those of the Cordias of the Physocladida group and so constantly present, except in the youngest seedlings less than a foot in height and with only the first whorl of leaves, that no botanist and certainly no entomologist, could possibly regard them as galls. Very occasionally there may be no swelling at a node where it might be expected to appear, but this sometimes happens also in the Physocladidae, and such inhibitions of development do not invalidate the general conclusion that the domatia of C. alliodora are quite as certainly preformed structures as those of C. nodosa. Of course, the crucial demonstration that the domatia are preformed can come only from growing the plant from seed under controlled conditions. I made an attempt to accomplish this with seeds sent to Boston by Mr. Zetek, but they failed to germinate in the hot houses of the Bussey Institution, probably because they were sterile.

Except in the domatia at the very base of the inflorescence, which, as previously stated, may persist and dry up when the latter falls off, there is a gradual growth in the thickness of the woody walls and in the size of the enclosed cavity. The series of photographs (Plates 3, 4, 5) show this increase very clearly. The ants perforate and enter the domatia very soon after their walls begin to lignify. I have not been able to follow the details of the invasion, although I have frequently found single young deálated females of various species and notably of Asteca longiceps Emery, either alone or with their first brood of larvaé in the swellings. The perforation or perforations—for there may be several—are always made in the thinner portion of the wall below the node, but there is no regularity in their position. In many cases the opening made by the entering queen closes by growth of the
plant tissues and has to be reopened by the first brood of workers. The continued growth of the domatium after its occupation must be due to the constant irritation produced either by the ants or by the numerous Coccids which attach themselves to the walls of the cavity and sink their delicate mouthparts into the plant tissues. That the Coccids may be the more potent irritants seems to be indicated by the conditions in the various Aphid and Psyllid galls of temperate regions and the Coccid galls of Australia. In the case of C. alliodora, the Coccids may be responsible not only for the irregular shapes assumed by many of the domatia in their later stages, but also for the unequal vigor and growth of the branches at the nodes and the general asymmetry of the older trees (Plate 6, Fig. b).

That the growth of the domatia does not continue indefinitely is shown in longitudinal sections of the nodal regions of the trunk and larger branches of old trees. The cavity ceases to enlarge when it reaches about the size shown in Plate 6, Fig. a, but the layers of xylem in its wall increase so enormously that the external swelling is obliterated. Concomitantly with this growth in the xylem the perforations or entrances to the cavity develop as long tubular galleries which traverse the whole layer of wood. In the section represented in Plate 7, Fig. b, which is slightly less than natural size, there were seven of these galleries which radiated from the chamber and opened on the surface of the bark at points several inches apart. Although even at this stage the cavities may still be inhabited by ants, the Coccids have all disappeared, probably because their food-supply has been completely shut off by the development of the very thick layer of wood between the cavity and the cambium.

The regular development of the swellings, or domatia in C. alliodora and other Cordias with such preformed structures thus presents a very interesting problem to the plant anatomist interested in phylogeny. Attention may be called in this connection to similar structures in at least one other plant in a very different genus, all the other species of which have stems of the normal unswollen type. This is the Polygonaceous genus Eriogonum, which comprises about 100 species in the United States west of the Mississippi. One, however, E. inflatum Torre, has hollow, fusiform swellings at the upper ends of the internodes of the stems and branches. I have observed this plant at Palm Springs, California, in the Mojave Desert at the foot of the San Jacinto Mountains. It is one of the few perennial species of the genus, according to Tidestrom (1925), who cites it as belonging to the "desert areas and hillsides of the Covillae and Artemisia belts" in
Southwestern Utah, Colorado, Nevada, Arizona and California. The swellings are not inhabited by ants, because all the Formicidæ in its desert environment are earth nesting forms. But there is no doubt in my mind that if the plant were to invade the tropics, certain species of stem-inhabiting ants would at once take up their dwelling in its inflations. Under these circumstances the plant would become a regular myrmecophyte like *C. alliodora*.

The following is a list of the ants that have been found associated with *C. alliodora* in Mexico, Central America, Peru and Bolivia:

(1) *Ectatomma ruidum* Roger. Foraging on trunk and foliage. Ancon, C.Z.

(2) *Ectatomma tuberculatum* Oliv. Foraging on trunk and foliage. Barro Colorado Is. C.Z.

(3) *Ectatomma (Gnamptogenys) sulcatum* F. Sm. On trunk. Barro Colorado Is. C.Z.


(5) *Pseudomyrma alliodora* sp. nov. In domatia. Ancon, C.Z.


(9) *Pseudomyrma gracilis* var. *bicolor* Guérin. In domatia. Red Tank, Gamboa and Quebrada de Oro, C.Z.

(10) *Pseudomyrma sericea* Mayr var. *ita* Forel. In domatia, Ancon, C.Z.

(11) *Pseudomyrma sericea* var. *cordæ* Forel. In domatia of *C. alliodora* var. *boliviana*? Ivon Beni & Huachi Beni, Bolivia (W. M. Mann); Bolivia (Bang); Eastern Peru (Spruce).


(13) *Crematogaster acuta* F. In domatia. Barro Colorado Is. C.Z.


(16) *Crematogaster* (Orthocrema) *limata* F. Sm. var. In domatia. Gamboa, C.Z.
(17) *Crema
gaster (Orthocrema) limata* subsp. *parabiotic*
a Forel. In domatia. Red Tank, C. Z.

(18) *Crema
gaster (Orthocrema) limata* subsp. *ludio* Forel. In domatia of *C. alli
dora var. boliviana? Huachi Beni, Bolivia (W. M. Mann).

(19) *Crema
gaster (Orthocrema) sumichrasti* Mayr. In domatia. Quebrada de Oro, C. Z.

(20) *Crema
gaster (Orthocrema) virgula* Forel. In domatia. Red Tank, C. Z.

(21) *Solenop
cis hermione* Wheeler. In domatia. Gamboa, C. Z.

(22) *Solenop

(23) *Solenop
cis piecea* Emery. In domatia of *C. alliodora var. boliviana? Isimama,
Bolivia (W. M. Mann).

(24) *Solenop
cis zeteki* Wheeler. In domatia. Red Tank, C. Z.

(25) *Lepto
thorax (Goniothorax) echinatinodis* Forel subsp. *cordincola*
subsp. nov. In domatia. Red Tank, C. Z.

Barro Colorado Is. C. Z.

(27) *Cryptocer

(28) *Cryptocer
cus (Cyathocepalus) pellens* Klug var. *porrasi* var. nov.
In domatia. Frijoles, Red Tank and Quebrada de Oro, C. Z.

(29) *Atta sexd
dens* L. On foliage. Ancon, C. Z.

(30) *Dolichoder
erus (Monacis) bispinosus* Oliv. In domatia. Red Tank, C. Z.

(31) *Dolichoder
erus (Hypocheila) championi* Forel subsp. *trinidadensis*
Forel var. *taeniatus* Forel. In domatia. Frijoles, C. Z.

C. Z. (a single female).

(33) *Azteca foreli* Emery var. *ysticola* Forel. Running on bark and
nesting in trunk. Ancon, C. Z.

(34) *Azteca instabilis* Emery var. Nesting in trunk. Barro Colorado
Island, C. Z.

(35) *Azteca bicolor* Emery var. Incipient colony in domatium. Ancon,
C. Z.

(36) *Azteca longiceps* Emery. In domatia. Ancon, Red Tank, Frijoles,
Las Cascades, Barro Colorado Is. Agua Clara Reservoir, Gamboa,
Corozal, etc. C. Z.

(37) *Azteca longiceps* subsp. *balboa* subsp. nov. In domatium. Balboa,
C. Z. A single deãlated female.
(38) *Azteca longiceps* subsp. *cordincola* Forel. In "galls" of Cordia. Bolivia (Chodat). In domatia of *C. alliodora* var. *boliviana?* Huachi Beni, Bolivia (W. M. Mann)


(42) *Azteca trigona* Emery. In domatia. Ancon and Las Cascades, C. Z.

(43) *Azteca velox* Forel. In domatia. Ancon and Marajal, near Colon, C. Z.


(46) *Camponotus (Tanaomyrmex) coruscus* F. Sm. Exploring foliage. Ancon, C. Z.


(49) *Camponotus (Myrmobrachys) canescens* Mayr. In domatia. Barro Colorado Is. C. Z.

(50) *Camponotus (Myrmobrachys) brettesi* Forel. In domatia. Ancon C. Z.

(51) *Camponotus (Myrmobrachys) lindigi* Forel. Exploring foliage. Ancon, C. Z.

(52) *Camponotus (Myrmobrachys) brevis* Forel. In domatia. Red Tank, Gamboa, Frijoles, Las Cascades and Barro Colorado Is. C. Z.

(53) *Camponotus (Myrmocladocus) bidens* Mayr. In domatia. Red Tank, C. Z.


Of the 54 different forms in this list 44 were found nesting in the domatia; the remaining 10 were either nesting in the trunk (*Azteca xysticola* and *instabilis*) or in the ground (the species of Ectatomma, Atta, Paratrechina and some species of Camponotus) and merely visited the foliage to attend Aphids or Coccids or to forage for insects. *Atta sexdens* was not seen to cut the leaves, which seem not to be in-
jured by this ant, probably on account of their coarse texture. The
great majority of the domatia tenants occur also in dead twigs of a
great variety of trees and shrubs. Probably only four of the species
listed, namely, *Azteca longiceps* and its subspecies, *A. pittieri* and its
var. *emarginatissquamis*, *Pseudomyrma sericea* and its varieties *ita* and
*cordia*, and *Ps. alliodora*, are to be regarded as obligate tenants of the
plant. Of these *A. longiceps* is the most abundant and occurs in about
85% of the cauline swellings. Forel cites *Pseudomyrma chodatii* as
living in "galls" of *C. longituba* in Paraguay and *Ps. sericea* var.
cordia from an undetermined Cordia. If this plant belongs to the
Gerascanthus section we may say that its members are inhabited by at
least 60 different species, subspecies and varieties of ants. Indeed, the
number is probably much greater, because the ants inhabiting these
Cordias have not been intensively collected, except in a portion of the
Panamanian region.

For the purpose of studying the ants of *C. alliodora* Mr. James Zetek
and I adopted a method, which we also employed successfully, with
obvious modifications, in dealing with other myrmecophytes (Tri-
plaris, Acacia, Cecropia, Clerodendron, Tillandsia). We either cut
down the tree, or when this was impracticable, lopped off large
branches. Then with a pair of strong pruning scissors we cut out the
cauline swellings and carried them in cloth bags to the laboratory,
where they were placed in a large jar. Some chloroform was poured on
the bags and the jar covered till the insects were asphyxiated. The
nodes could then be cut open and their contents examined at leisure.
We found that few of the ants left their nests to die in the bags and
that the swellings, even when they were inhabited by different species,
contained all or nearly all of their regular inhabitants. The preliminary
work of ascertaining the qualitative composition of the *alliodora*
biocenose was so time-consuming that a quantitative or statistical
study of the various species could not be attempted. It is to be hoped
that some future student will feel inclined to undertake such an in-
vestigation at the new tropical laboratory on Barro Colorado Island.

A number of the *alliodora* ants, especially those of the genera
Crematogaster, Leptothorax, Cryptocerus, Tapinoma and Campono-
tus, are very sporadic, occurring in only a few of the swellings on a
tree or branch. *Azteca longiceps* is certainly the common and dominant
tenant in nearly all the localities in which I collected. It usually
occupies most or all of the swellings, especially those at the bases of
the branches, whereas the sporadic species inhabit by preference the
terminal and especially the dead and dried swellings that bore the
inflorescences of the previous dry season. Not only *A. longiceps* and *pittieri* and the varieties of *Pseudomyrina sericea* but also several of the other forms keep living Coccids in their nest-cavities. I here insert a fuller description of the habits of *A. longiceps* as the most typical of the *alliodora* tenants and append brief notes on some of the other ants.

Unlike the larger aggressive Aztecas (*trigona, velox, foreli, instabilis*, etc.) which either make large pendent carton nests on various trees or form compact and populous colonies in their trunks, *longiceps* is a small, timid and rather lethargic ant. This is indicated both by its toleration of other ant-tenants on the same tree and by the fact that I have sometimes cut up Cordias for hours without being bitten more than half a dozen times by the larger workers. The *longiceps* inhabitants of all the domatia on a tree constitute a single polyclad colony, which keeps growing and spreading by successive occupation of the new swellings as fast as they attain the proper size on the developing branches. During March and April the nests contain much brood in all stages together with many males and winged females. The domatia are lined with a thin layer of brownish or blackish substance and contain a black or dark brown mass of carton made up of a network of traveculæ like those constructed by many other Aztecas that nest in plant cavities. This structure, shown in Plates 7 and 8, was seen by Beccari and Chodat and Vischer, but in their figures it is represented as grosser or more massive. It consists of very finely and uniformly triturated and agglutinated particles of wood and pith. I have failed to detect in it any pollen-grains, leaf-fragments or stellate hairs but would not deny that such substances may, perhaps, be occasionally employed by the ants in the confection of the mass. It is obviously a kind of scaffolding which subdivides the original cavity of the domatium into smaller compartments and galleries in which the brood can be spread out and more easily cared for. The mass can be readily removed in its entirety because it is rather feebly attached to the walls of the cavity. Chodat’s and Vischer’s contention that the ants, “dévorent une partie des feuilles et récoltent le pollen” is highly improbable. I have never seen the Aztecas visiting the flowers and they certainly do not devour the leaves. But even if this were true, and if the carton were made of leaf material as these authors maintain, the combined mass of carton in all the domatia on a tree would be too small to represent any serious damage to the plant.

In the spaces surrounding the mass of carton and sometimes almost covering the walls of the cavity are the numerous Coccids among
which at least three kinds or species may be readily distinguished. The
majority are flat Lecanoid forms of a pinkish color and varying con-
siderably in size. Among them may be found small snow-white
Pseudococci, either singly or in clusters and several large subglobular
shining black or red forms belonging to three species of the genus
Cryptostigma.

These Coccids suggest interesting problems and reflections. They
are present in such numbers that they must provide the ants with a
copious supply of honey-dew. That the large subglobular forms
(Cryptostigma) breed in the domatia is indicated by the fact that they
are often found to be filled with eggs and owing to their size are quite
unable to escape to the surface of the plant through the tenuous open-
ing in the walls of the domatia. But whether the coccid colonies are
originally established by young individuals that crawl into the swellings
from the surface of the plant or are carried in by the ants, cannot be
decided without further observation. Judging from what is known of
some other ants (Lasius species, Iridomyrmex humilis, etc.), the latter
alternative would seem to be the more probable. I have seen what I
take to be the male pupae of one of the large Cryptostigma species en-
closed in peculiar flattened, bivalve-like cases, embedded in the central
mass of carton. The Pseudococci are often destroyed by the larvæ of a
small Chalcidid of the genus Blepyrus very much like B. tachigaliæ
Brues which I found infesting Pseudococcus brevipes in the petiolar en-
largements of Tachigalid paniculata Aublet in British Guiana.

There is also in the cavity of each domatium occupied by A. longi-
ceps another singular object which has been overlooked by previous
observers. The funnel-shaped lower end of the cavity is filled with a
small conical plug of moist substance, which can be readily removed as
a coherent mass and on examination proves to have a very complex
structure, consisting of the ejected infrabuccal pellets of the ants,
moulds and innumerable bacteria and Nematode worms. Its more
liquid portion is probably the faeces of the ants and such honey-dew
from the Coccids as happens to drain down the walls of the cavity and
has not been intercepted and imbibed at its source. We may therefore
regard the lowermost funnel-shaped end of the domatia as a
veritable public latrine or cess-pool. The Nematodes have been
studied by Dr. Cobb who informs me that they are unusual from the
taxonomic point of view. The moulds and bacteria which flourish in
the fecal medium of the latrines may afford an interesting study for
some future investigator.

In Mexico the subsp. patruelis and in Bolivia the subsp. cordincola
seem to replace the typical *A. longiceps* as the obligate ants of *C. alliodora*. But even in Panama the typical *longiceps* may be replaced by *A. pittieri*, an ant of very similar appearance and habits. I found this to be the case in a small piece of jungle on the Tumba Muerta Road, near Las Sabanas. According to my observations, *Pseudomyrmex sericea* var. *ita* is much less important as a member of the *alliodora* biocénose. Its colonies are small and usually occupy only a few of the domatia on trees infested with *A. longiceps*. The same is true of *Ps. gracilis* and its var. *bicolor* which are more frequently found in hollow twigs of various trees and shrubs. *Ps. alliodora* is a timid form of rather sporadic occurrence. The older accounts of Ruiz and Pavon and Spruce seem to imply that *Ps. sericea* or other species of the same genus may be abundant and more formidable tenants of the Cordias in certain parts of South America.

The species of Cryptocerus are sluggish, cowardly and harmless. Both of the forms cited above, *setulifer* and *pallens* var. *porrasi* may occupy occasional swellings on trees infested with other ants. They belong to the subgenus Cyathocephalus, the females and soldiers of which have the top of the head peculiarly modified in the form of a large elliptical or suborbicular dish. A swelling occupied by Cryptocerus can be at once recognized by its entrance hole, which unlike that made by the Aztecas and Pseudomyrmex, is large and regularly elliptical instead of being small and round. The mother queen of the incipient colony or in older colonies one of the soldiers, constantly stands guard at the entrance and occludes it with the dish-shaped top of her head. This behavior is exactly like that of Colobopsis, except that in the ants of this subgenus, the portions of the head employed as a door are the truncated, orbicular front and cheeks. In the mother queen and older soldiers of Cryptocerus colonies the cephalic dish has been so persistently used in the manner described, that its concavity is often found thickly incrusted with grayish green foreign matter and thus comes to resemble the dull gray lichen or alga covered bark of the Cordia. The two species of Cryptocerus, like several other ants enumerated in the list on p. 25, are merely inquilines which often nest in the dead twigs and branches of other trees and shrubs.

That *Cordia alliodora* can derive little protection from the numerous ants which it harbors, is obvious from my account of their disposition and behavior. There is further evidence of this inefficiency in the great number of insects and other organisms that infest the foliage and flowers of the plant. Although Mr. Zetek and I devoted much attention to these forms, we were soon convinced that it would require
many months or even years to gain an adequate knowledge of the *allioidora* biocenose and the interrelationships of its numerous components even in so limited an area as the Canal Zone. The following list of species hitherto observed, however, with notes on some of the more interesting forms, will constitute a sufficiently formidable rebuttal of the argument that *C. allioidora* would probably perish in the struggle for existence if it failed to attract and provide quarters for battalions of ants.

*Lepidoptera.* At least six different species of moth caterpillars feed on the leaves of *C. allioidora* and some of them are rather destructive. One is a small leaf-miner of which I have seen only the small blister-like feeding-spots. Of another moth I have seen only the beautiful yellowish, regularly net-like cocoon spun in a folded leaf and containing an empty chrysalis. Three slender green caterpillars belonging to as many different species also remain to be reared and identified by some future observer. One of these larvæ which is fairly abundant bites a big hole in the wall of a young green domatium and hides in its cavity during the day. At night it eats the terminal leaves and spins their remains together about the domatium, leaving its frass among them. This untidy insect is very destructive to the terminal shoots of the Cordia. In a domatium containing one of these larvæ I found two small white Hymenopterous pupæ but did not succeed in rearing the adult parasites. The numerous caterpillars of a sixth species are about an inch long, chocolate brown with a pale mid-dorsal streak. They have been reared by Mr. Zetek who sent me specimens and photographs (Plate 9) of the cocoon, caterpillar and its method of feeding and hiding on the Cordia leaves. The adult moth, which is silvery white with black markings, is a Pyralid and was identified by Mr. W. Schauss as *Conchylodes salamisalis* Druce. Its life history is sketched in the following note contributed by Mr. Zetek: "The larva makes a sort of silken retreat at the base of the upper surface of the leaf by binding threads crosswise, thus forming a triangular cavity in which it can lie concealed. There is only one larva to a leaf. On one small plant, about five feet tall I saw 15 such larvæ. When ready to pupate, it spins a capsule 7/8 in. long by 5/6 in. in diameter, rounded at both ends and so well sealed that it is difficult to detect the sutures. After completing its cocoon it takes the larva about 36 hours to become a chrysalis. During this time, especially if the case be disturbed, the larva moves so violently inside, as actually to make the cocoon bound up an inch. The pupal stage last 12 days. Adults emerged June 12, 1923." During 1924 I found Conchylodes caterpillars on
many young Cordias at Ancon, Red Tank and Gamboa. During June the caterpillars were mature and ready to pupate and by the middle of July there were many young caterpillars of the next brood. Probably there are several generations on the young plants during the course of the year. The adult Cordias are immune from their attack during the rainy season, because they are leafless at that time.

Diptera. Numerous flies may be observed on the leaves of the young Cordias but are probably mostly chance visitors that alight on any low vegetation. Among those captured at Ancon and on Barro Colorado I recognized 3 species of Stratiomyids, 2 Syrphids, 1 Dolichopodid, 1 Micropezid, 2 Ortalids and 3 Muscids. The Cordia leaves are often dotted with small, spherical, densely pilose galls, which contain orange-colored Cecidomyid larvae. I did not succeed in rearing the adults. More interesting is a species of Microdon, which has been described by Dr. Mann (1928) as *M. wheeleri*, since it lives with one of the ants in the domatia. March 10 I found at Red Tank, C. Z. in a Cordia swelling inhabited by *Crematogaster (Orthocrema) brevispinosa* var. *tumulifera* four bright yellow puparia, which were smooth and cylindrical and quite unlike any Microdon puparia known to me. They were carefully kept in a Petri dish till March 27, when two of the flies emerged and proved to belong to a very small species, about 7 mm. long. On emerging the hairs on the thoracic dorsum and sides and dorsum of the abdominal segments were conspicuously golden yellow and to all appearances true trichomes, but 24 hours later they had turned black. The other pair emerged March 28 and were chloroformed in the golden phase. They proved to be females whereas the first pair were males, so that I am unable to decide whether the females also blacken like the males. This is important in connection with Mann’s description of the female. Unfortunately I failed to preserve the domatium in which the Microdon puparia were found although I kept all the ants and Coccids. The latter belonged to one of the species of Cryptostigma so common in the cauline swellings, especially when they are inhabited by *Azteca longiceps*. Perhaps one of the openings in the wall of the swellings may have been large enough to admit an ovipositing Microdon, but I failed to notice such an opening and am therefore unable to throw any light on how the Microdon larvae get into or how the flies escape from the domatium. Probably the phase with the golden trichomes just after emergence is in some way connected with securing a temporary immunity of the fly from the attacks of the ants, and perhaps the latter enlarge their nest-entrances to let the flies out, but this is pure speculation and is merely
set down here for the benefit of someone who may be fortunate enough to happen on this rare and singular insect again. The problem of the food of the *M. wheeleri* larvae is also, of course, unsolved. Donisthorpe (1912, 1923) has shown that the larva of the common European *M. mutabilis* feeds on the infrabuccal pellets which the ants cast out in their nests, and no doubt our North American Microdon larvae have the same diet, but that the tropical Microdons may have very different habits is shown by Borgmeier (1923), who has recently found the larva of a Brazilian species devouring the Coccids (*Pseudococcus inquininus*) in the nests of the fire ant (*Solenopsis savissima* var. *picea*). Perhaps *M. wheeleri* feeds on the coccids in the Cordia domatia.

*Hymenoptera.* The following species of this order have very diverse relations to the Cordia and its inhabitants.

1. A single unidentified Tenthredinid taken on the foliage at Ancon.

2. *Dicrophrys* sp. (C. T. Brues det.) An Ichneumonid taken occasionally on the foliage of young Cordias at Ancon and possibly a parasite of one of the caterpillars enumerated above.

3. *Eurytoma* sp. (?) A small larva, apparently related to the one described and figured by Chodat and Vischer, was found living in the swollen stems of the flower panicles.

4. *Blepys* sp. Living as an entoparasite of *Pseudococcus* in the cauline swellings inhabited by *Azteca longiceps*. I saw only the empty puparia but they were not uncommon and are, I am inclined to believe, identical with those of *B. tachygalis* Brues, which I found in the same Coccids living with the social beetle *Coccidotrophus socialis* in the petioles of *Tachigalia paniculata* of British Guiana (see my paper of 1921).

5. A Pteromalid (Brues det.) bred from flowers at Red Tank, C. Z.

6 and 7) At Ancon I found two small mud nests attached to the twigs of Cordia and from them reared two solitary wasps. One of them proved to be *Eumenes infernalis* Sauss. (J. Bequaert det.), the other a Sceliphron. The latter was so nearly destroyed by house-ants entering the breeding cage that more precise identification was impossible.

8. March 28 at Frijoles I found a nest of a very interesting social wasp, *Polistella pictetii* var. *wheeleri* Bequaert, among the leaves of a Cordia about 15 feet high. The nest was about 6 inches long and consisted of four small, rather irregular, pale gray paper combs partly enveloped by the leaves to which they were broadly attached. The wasps made not the slightest attempt to sting but retreated into
their nest. The structure was very similar to that figured by Ducke (1910, p. 473, Fig. 2) for Polistella picteti var. bella v. Ihering. Concerning an allied species P. emortualis Sauss. of the Guianas and Brazil, he writes: "It is myrmecophilous. I have never found it alone but always in the company of ants of the genus Dolichoderus. The nests are very similar to those of the ants mentioned, built on the leaves of the same small branch of the tree whose other leaves harbor the nests of the latter. I have even seen a colony of nests of the wasp and of the ant closely associated on the same leaf. It is surprising to note that the ants are very aggressive, whereas the wasps, though furnished with stings take refuge in the interior of the nest when it is touched." That P. picteti may also be myrmecophilous is indicated by the fact that all the swellings of the Cordia on which the nest occurred were occupied by vigorous colonies of Azteca longiceps.

(9) Ceratina sp. A beautiful metallic blue species nesting in a dead Cordia branch (Red Tank, C. Z.)

(10) A bee allied to Anthidium taken on the foliage of a Cordia (Ancon, C. Z.).

(11) The only Hymenopteron taken at the Cordia flowers was a stingless bee, Melipona orbignyi var. jenningsi Ckll (T. D. A. Cockerell det.)

Coleoptera. The series of beetles found associated with the Cordia comprises a considerable number of species. The following taken during 1923 at Ancon were kindly identified by Mr. H. S. Barber:

(1) Ladoria desarmata Muls. (Coccinellid) on foliage.
(2) Spermophagus lineolatus Mots (?) (Bruchid) on foliage.
(3) Paratenetus tropicalis Mots. (Tenebrionid) bred from dried blossoms.
(4) Melanopthalma cartralis Shp. (Lathridiidi) bred from dried blossoms.
(5) Autodice nympha Bates (Cerambycid, Fisher det.) Taken by Mr. Zetek on foliage.
(6) Psalidonota leposa Boh. (Chrysomelid) on foliage.
(7) Eustylus sexguttatus Champ. (Curculionid, E. A. Schwarz det.) on foliage.
(8) Deretomus palmarum Sharp (Curculionid) on flowers. According to Mr. Barber this beetle occurs also in great numbers on the flowers of palms.

During the summer of 1924 I captured on the foliage and branches of young Cordias at Ancon 30 additional species, which are still unidented. These comprise 2 Cerambycids, 1 Telephorid, 2 Lampyrids,
1 Lathridiid, 1 Cucujid, 1 Endomychiid, 12 Chrysomelids, 6 Curculionids, 1 Anthbid and 3 Platypodids (boring in a recently felled tree).

To this list must be added a second species of Coccidotrophus, *C. cordiae* Barber (1928), an interesting social Silvanid beetle discovered by Dr. Mann in a single domatium of a Cordia (probably *allioidora*) at Huachi, on the Río Beni, Bolivia. This beetle is somewhat larger than *C. socialis* Barb. & Schwarz, which I found nesting in the petioles of *Tachigalia paniculata* in British Guiana, but evidently has very similar habits, since Dr. Mann noticed that it was living with its larvae and with Coccids (Pseudococcus sp.)

Many of the beetles taken at Ancon were probably chance visitors, but one of them, the Cassidine *Psalidonota leprosa*, passes through its entire development on *C. allioidora*, which is therefore to be regarded as its host plant. The beetle was originally described from Mexico (Boheman, 1855). According to Champion (1885–94), it is a common insect in Central America “ranging from the Mexican State of Durango right down to Panama, and probably extending into the northern parts of South America.” He cites it from several Panamanian localities. Its range therefore coincides with that of *C. allioidora* except that it occurs, according to Leng (1920), also in Texas, where it must have a different host plant. The greenish eggs were found in late July and early August in clusters on the lower surfaces of the leaves of young Cordias at Ancon and Red Tank, and the larvae were seen feeding on the same leaf-surfaces in clusters or when older more sporadically. The larva is flattish, pale green, with a blackish-brown mid-dorsal stripe that grows broader with age, especially in the thoracic region, and a fringe of blunt, branched spines along the sides of the body. The posterior end is enlarged into a peduncled sphere beset with knobs and with the protrusible anus at the base of the peduncle on the ventral side. As in other Cassidine larvae, the modified caudal end can be turned forward over the back and supports a great glutinous black mass of faces and exuviae, which is not, however, large enough to conceal the insect. The pupa is naked and attached to the underside of the leaf by its posterior end. The tortoise-like adult beetle, which is nearly a centimeter long and broad, was described by Boheman as “flavotestaceus”, and Champion figures it of this color, which suggested the unpleasant specific name *leprosa*. This is not inappropriate for the dried specimen but is unfortunate, because the living insect is a magnificent creature, resembling nothing so much as a large drop of liquid gold. It is therefore a very conspicuous object when sunning itself on the deep green leaves of the Cordia. Since I have found it on the plant
also early in the dry season, it must have several broods during the year.

Orthoptera. The following species of this order were identified by
Mr. Morgan Hebard:

1 and 2) Stagmomantis (Mantid), two species, immature, on young
foliage of C. alliodora.

3) Cryptostilum antillarum Redt. (Gryllid), living in an abandoned
domatum.

4) Gryllacris sp. (Gryllid), immature near picta Brünner, on foliage.

5) Osmilia flavolimbata De Geer (Acridiid). At Ancon both Mr.
Zetek and I repeatedly took both sexes of this grasshopper in the act of
devouring the foliage of C. alliodora.

6) Coscineuta coxalis Serv. (Acridiid). A few specimens on the
foliage of young plants.

7) Schistocerca sp. (Acridiid), immature.

8) Aidemona azteca (Saussure) (Acridii) One female and one im-
mature individual.


10) Neoconcephalus sp. (Tettigoniid), immature.

11) Anaulacomera sp. (Tettigoniid), immature.

12) Phaneroptera parona (Griffini) (Tettigoniid) immature.

13) Phlugis sp. (Tettigoniid), immature.

Thysanoptera. Two species of this order have been identified by
Dr. J. Douglas Hood: Dicerothrips armatus Bagnall and Elaphro-
thrips sp. Both are large slender species, black in the adult and bright
coral red in the younger stages, occurring in numbers in some of the
dead and abandoned domatia at Ancon and on Barro Colorado Island.
A third, unidentified species is a minute yellowish form, common on
foliage and flowers at Ancon.

Neuroptera. Two species are represented in the collection, one a
species of Chrysopa of which Mr. Zetek on several occasions found the
eggs attached to the leaves of young Cordias, the other a species of
Hemerobiid, the larvae of which I have taken on several occasions in the
same situations. Both insects probably prey on the Aphids and
Aleurodids.

Heteroptera. The following species of this order have been kindly
identified by Dr. J. G. Myers and Dr. R. F. Hussey.

1) Proxys punctulatus Pal. Beauv. (Pentatomid) Ancon (Myers
det.)

2) Edessa collaris Dall. (Pentatomid) (Myers det.) Ancon. This
bug is common in all stages on the plant (except the eggs, which were
not seen). The nymphs and adults are green in life. Undoubtedly *C. alliodora* is a normal host plant of this insect.


4. *Hyalonymus pulcher* Stal (Coreid) Las Sabanas, Panama. (Myers det.)

5. *Dysdercus ruficollis* L. (Pyrrhocorid) Ancon (Myers det.)


7. *Monanthia monotropidia* Stal. (Tingitid) Ancon and Red Tank. (Myers det.) This insect feeds in great numbers and in all stages on the under surfaces of the leaves of *C. alliodora* and damages them severely, causing them to turn black. It seems to have a wide distribution. Wolcott (1923) found the "nymphs and adults abundant on the underside of leaves of a small unidentified tree in the mountains north of Yanco", Porto Rico.

8. *Macrocephalus notatus* Westw. (Phymatid) Ancon (Myers det.)

9. *Zeus nigax* Stal. (Reduvid) Ancon (Myers det.)

10. *Ecretotarsus splendens* Distant. (Miriid). Ancon (Myers det.) *Homoptera*. The following species have been identified by Dr. Myers and Dr. W. D. Funkhauser:

1. *Monephora lepidior* Fowler (Cercopid) Ancon, feeding on young shoots (Myers det.)

2. *Micratalis baltata* Fairm. (Membracid) Ancon, feeding on young shoots. (Funkhauser det.)

3. *Micratalis dubia* Fowl. (?) (Membracid) Ancon, feeding on young shoots, (Myers det.)

4. *Ceresa bubalus* (Fabr.) (Membracid) Ancon (Myers det.)

5. *Vanduzea triguttata* Burm. (Membracid) Ancon (Funkhauser det.)

6. *Brachybelus cursalis* Stal (Membracid) Ancon (Myers det.)


8. *Cicadella sexguttata* (Fabr.) (Cicadellid) Ancon (Myers det.)

9. *Cicadella rufimargo* (Walk.) (?) (Cicadellid) Ancon (Myers det.)

10. *Gypona obscurior* (Fowler) (Gyponid) Ancon (Myers det.)

11. *Gypona postica* Walk. (Gyponid) Ancon (Myers det.)

12. *Athysanus bicolor* Van Duze. (Jassid) Gamboa (Myers det.)

13. *Deltocephalus* sp. (Jassid) Ancon (Myers det.)

14. *Protalebra* sp. (Typhlocybidae) Ancon (Myers det.)

15. *Rudia diluta* Stal. (Tropiduchid) Ancon (Myers det.)
(16) Cryptoptus suavis Stal. (Fulgorid) Ancon (Myers det.)
(17) Colopota sinauta Burm. (Issid) Ancon (Myers det.)
(18) Ormenis griseoalba Fowler. (Flatid) Gamboa (Myers det.)
(19) Psyllid indet. (nymphal exuviae) Ancon (Myers det.)
(20) Aphid sp. (A. C. Baker det.)

This species was taken in great numbers on Cordia in November 1923 by Mr. Zetek. The insects caused the leaves to crinkle and were attended by the common crazy ant, Paratrechina longicornis Latr.

(21) Aleurodicus dugesii Ckll. (?) (Aleurodid) Ancon. Also taken late in November 1923 on the leaves of C. alliodora (A. C. Baker det.)

Coccidae. The following species were recognized by Dr. H. Morrison from extensive collections made in 1923 and 1924.


(2) Coccus hesperium (Linn.) On leaves and twigs, attended by Azteca veloz. Ancon.


(6) Cycloecanium hyperbaterum Morrison. In domatia with Azteca longiceps and Pseudomyrma ita, Red Tank. and Ancon; with Camponotus bretesi, Barro Colorado Island, and Frigoles; with Azteca pittieri, Pueblo Nuevo, Panama; with Crematogaster tumulifera, Red Tank.

(7) Pseudococcus brevipes Ckll. (previously bromeliae Bouché). In domatia with Azteca longiceps. Red Tank and Las Cascades. The Coccid occurs also in the cauline cavities of Triplaris and Cecropia.

(8) Pseudococcus maritimus (Ehrh.) In a young domatium of Cordia, without ants. Red Tank.


(12) *Saissetia nigra* (Nietn.) On leaves.
(13) *Saissetia oleae* (Bern.) On leaves.
(14) *Aspidiotus perculatus* Doane & Hadden. On leaves.

*Myriopoda.* Two species of Myriopoda were found occupying old and abandoned domatia. These were identified by Dr. R. V. Chamberlin as *Orphæus brevilabiatu*s Newp., a Chilopoda, taken at Red Tank, and *Orthomorpha gracilis* Koch taken at Ancon.

*Arachnida.* The following spiders, kindly identified by Mr. Nathan Banks, were taken on the foliage of young Cordias at Ancon and on Barro Colorado Island. Many of them were living in webs spun between the leaves or twigs:

(1) *Gasteracantha kochi* Butler.
(2) *Frontinella uncata* Cb.
(3) *Chrysozo vexabilis* Keys. This small red and black spider is unusually common on the plant.
(4) *Runcinia magna* Keys. (?)
(5) *Selenops mexicanus* Keys.
(6) *Nephele clavipes* L.
(7) *Zygoballus tibialis* Cambr.
(8) *Dendrophantes momus* Cambr.
(9) *Teudis roseus* Cambr.
(10) *Physale simplicicava* Cambr. (?)
(11) *Pisaurid* gen. incert. very young.
(12–14) *Physale*, 3 species, immature.
(15) *Dictyna sp.*, immature.
(16) *Philodromus* sp., immature.
(17) Nov. gen. nov. sp. near *Simonella*.
(18) *Mites*, belonging to the group commonly called “red spiders” were found by Mr. Zetek during November 1923 on both sides of the main ribs and riblets of the leaves of young Cordias at Ancon. “They leave a patch which is almost white,—typical of red spider injury. They were very abundant and lived on the same leaves with the Aphids.”

*Isopoda.* A few small white Isopods related to *Oniscus* were found at Ancon inhabiting an abandoned domatium.

*Nematodes.* Several peculiar species taken in the latrines of the domatia have not yet been described by Dr. Cobb.

*Fungi and Bacteria.* In addition to the moulds which grow on the walls of the domatia there is a powdery mildew of the family *Erysiphaceae* which often covers the leaves of young Cordias. Specimens collected by Mr. Zetek at Ancon could not be further identified
by Prof. W. H. Weston, to whom I sent them, because the fruiting bodies were absent. The bacteriology of the domatial latrines still remains to be investigated.

Algae and Lichens. Like other tropical trees, *C. alliodora* supports a flora of lichens and algae on its bark.

If we consider only the Arthropoda noticed in the preceding pages as visiting or infesting *Cordia alliodora* we have the following numbers of forms in each of the larger groups:

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hymenoptera (including Formicidae)</td>
<td>69</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>6</td>
</tr>
<tr>
<td>Diptera</td>
<td>14</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>39</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>13</td>
</tr>
<tr>
<td>Thysanoptera</td>
<td>3</td>
</tr>
<tr>
<td>Neuroptera</td>
<td>2</td>
</tr>
<tr>
<td>Heteroptera</td>
<td>10</td>
</tr>
<tr>
<td>Homoptera (including Coccidae)</td>
<td>35</td>
</tr>
<tr>
<td>Myriopoda</td>
<td>2</td>
</tr>
<tr>
<td>Arachnida</td>
<td>18</td>
</tr>
<tr>
<td>Isopoda</td>
<td>1</td>
</tr>
</tbody>
</table>

Total 212

In all probability this total of more than 200 forms or species represents only a fragment of the biocenose centering about *C. alliodora*, because my observations were confined to a very small portion of its known geographical range. The data are nevertheless sufficiently numerous and striking to admit of certain conclusions, especially as they are supported by similar observations on other ant-plants (Tachigalis, Cecropia, Acacia, etc.) to be considered in the sequel. There can be no doubt that *C. alliodora* has many insect enemies, which destroy or deform its foliage, injure its terminal shoots and withdraw a considerable amount of sap from its tissues. The most numerous and serious of these pests are the moth *Conchylodes salamisalis*, the Cassidine beetle, *Psalidnota leprosa*, the Pentatomid bug *Edessa collaris*, the Tingitid *Monanthia monotropidia*, a red spider, the various Membracids, Cicadellids and Jassids, the Aphis, the Aleurodid *Aleurodicus dugesii* and last but not least, the fourteen species of Coccidae recognized by Morrison. No evidence was found to indicate that any of the 54 forms of Formicidae attacked any of the leaf-eating species, though it was evident that they solicitously
attended many of the Coccids to the injury of the plant. Moreover, the majority of the 212 Arthropods, excluding the Formicidae, were found on young Cordias, the domatia of which were as yet either uninhabited or occupied only by recently fecundated, colony-founding queens of Azteca longiceps and pittieri. Hence the plants can derive no protection from these insects in the very stages when the incidence of natural selection should be most effective. Yet none of the thousands of young and seedling Cordias which I examined in Panama showed the slightest signs of being killed by its insect pests. I have no hesitancy in asserting that the plant is quite as vigorous and quite as able to withstand the attacks of insects as any other common tropical tree.

Chapter 2

OBSERVATIONS ON TRIPLARIS

The dioecious Polygonaceae trees of the genus Triplaris and their ants made a more vivid impression than the Cordias on the early naturalists who visited the American tropics. That the natives and colonists had long been duly impressed is indicated by the many vernacular names they invented for the plants and their aggressive tenants. As long ago as 1849 Weddell recognized 14 species of Triplaris and in 1856 Meisner enumerated some 25; Hemsley in 1882–86 and Dammer in 1893, however, recognized only about 10. Probably the latter number is not far from the present estimate of actually existing species, but it must be admitted that there is as much confusion in the botanical literature in regard to Triplaris as to many other genera of Neotropical woody plants. The Triplarises certainly appear to be more local than the Cordias of the Gerscanthus group and are confined to the warmest portions of South and Central America, where they grow by preference in low or even swampy places along streams. One species (T. auriculata) occurs as far north as Mexico. The genus is not represented in the West Indies, though it may occur on several of the islands adjacent to Northern South America, e.g., Trinidad. Boldingh (1914) cites T. coriacea Karst. as growing in several localities on Curacao, off the coast of Venezuela.

(A.) Historical

One of the earliest accounts of Triplaris and its ants is that of P. Bernabé Cobo (1653), who in his "History of the New World" says that the tree is called "palo santo" and describes it as follows: "This
tree is hollow throughout from the trunk to the slenderest twigs and full of certain yellow and largish ants, so virulent that their sting is apt to bring on fever and is always exceedingly painful. Since these ants are concealed within the tree, they are not seen and this is the reason why those who do not know the secret, are not on their guard; but if a single leaf be touched, so many of the ants swarm forth from all parts of the tree as to excite wonder, and they assail the person who touches the tree and, if he does not withdraw in time, martyr him with their stings.” The editor adds the scientific name of the ant as *Myrmica triplarina* and its vernacular name as “*hormiga tangarana*”; the抄ist cites the name of the tree as “*Guyacum sanctum*, according to Raimondi.”

In the botanical literature Aublet (1775) seems to have been the first to notice the peculiar behavior of the ants and their relation to the tree. Writing of *T. americana*, which he described and figured (p. 910, Pl. 347), he says that the natives of French Guiana call it the “sapa-hakaapoli”, and adds: “The ants swarm abundantly throughout the interior of the trunk, the branches and twigs of this tree, in such a manner that when one fells it, one is at once completely covered and cruelly tormented by them, a misfortune which befell me. The only way to get rid of them is to throw oneself into the water.”

In the famous work on Brazil by von Spix and von Martius (1831), I find the following note on the species of Tococa and *Triplaris americana*: “A number of plants, especially those of the genus Tococa, seem to have been designed by Nature herself as domiciles for ants. These bushes bear at the upper end of the leaf-petioles a bladder-like enlargement, in which numerous communities of small red ants nest, and the hollow branches of *Triplaris americana* L., a slender littoral tree, are often inhabited by innumerable colonies of similar creatures. Woe to him who chances to break off such a branch; a scrambling mass of viciously biting enemies pours down upon him and leaves many blisters on his skin.”

Robert Schomburgk (1838) observed the same species of Triplaris in British Guiana. He says that it is called the “jacuna” by the Arawak Indians, the ant being the “jacuna sae”, but that the Warrows call the tree the “epouchari”, the Caribs the “itassi” and the colonists the “long John”. I find that this name is still applied to both *T. americana* and *T. surinamensis* by the settlers in British Guiana. The following is Robert Schomburgk’s general description of the former species: “The sandy banks of the inland rivers of Guiana are peopled with them; and when shrubs, stunted in growth by the poverty of the
soil, scarcely reach the height of five or six feet, the _Triplaris_ overtops them forty or fifty feet. The trunk is slender and grows up straight, and its erect branches form a pyramid. As already observed, it is unisexual, and the flowers of both sexes are insignificant; those of the male last only for a few days, when they dry up; this is likewise the case with the petals of the female; the segments of the calyx however continue to grow, changing in their growth from green to white and vermilion, and become so attenuated that the branched nerves are easily perceptible. In that state they are three times as large as the fruit, which is still protected by the tube of the calyx, and the whole might in appearance be resembled to a shuttle-cock. The risps are dense, and the tree presents now a most elegant appearance. One unacquainted with the contrary, would consider the tree covered with white blossoms, tinged with red, among which the dark green leaves have only occasionally room to make themselves visible. The uncautious botanist, who, allured by the deceptive appearance, should approach the tree to pluck the blossoms, would bitterly rue his attempt. The trunk and branches of the tree are hollow, like those of the trumpet-tree (_Cecropia_), and provided between space and space with partitions, which answer to the position of the leaves on the outside.

"These hollows are inhabited by a light brownish ant, about two to three-tenths of an inch long, which inflicts the most painful bites. Its antennae are placed near the middle of the anterior portion of the head; mandibles triangular; peduncle of the abdomen with two rings; the anus hairy and provided with a sting or piercer (_Myrmica_ Latr. nova species). They fall upon their prey with the greatest virulence, and insert their mandibles almost instantly, as soon as they come in contact with any soft substance, emitting a whitish fluid; their bite causes swelling and itching for several days. If they find themselves captured, they attack and kill one another like the scorpions." The ant to which Schomburgk refers is undoubtedly a species of _Pseudomyrma_ but he makes the common mistake of confusing biting and stinging; the _Pseudomyrmas_ do both, but the pain is, of course, due to the sting.

Richard Schomburgk (1848) gives an even more vivid account of _T. americana_, which he encountered on the Barama River in British Guiana and, according to his estimate, may grow to a height of 60 to 80 feet. "The peculiar internal structure of the trunk and branches make it one of the most formidable of trees. The internodes are perfectly hollow and separated from one another by horizontal partitions, so that in this respect the tree resembles _Cecropia peltata._"
He correctly describes the yellowish brown Pseudomyrmex and their stinging habits but erroneously refers them to the genus Cryptocerus. "Being unacquainted with the structure of the tree and its formidable inhabitants, and ignoring the warning gesticulations of my Waraus, I was trying to break off one of its boughs, when thousands of these insects rushed out of the small round openings in the internodes, completely covered me and in the greatest fury seized my skin with their jaws and, vomiting a white liquid, buried their terrible stings in my muscles. But not only had the ants from the severed portion of the bough fallen into our corial, but thousands more poured out of the openings in the stump and rained down into the boat since the whole colony had been aroused by the shaking of the tree. A few powerful strokes of the oars carried the boat out of the neighborhood of the tree and in the twinkling of an eye the whole crew was in the water, for only thus could we escape from the savage onslaughters of the ants. Even a few tame apes and parrots were not spared. The former with wild leaps freed themselves from their tethers and jumped into the river after us, although few animals are more averse to water. The sting of this yellow-brown ant is only less painful than that of Ponera clavata. The swelling, inflammation and pain may persist for several days... After we had cleaned the ants out of the boat with considerable labor and many excruciating stings, we continued our voyage. I must confess that thereafter a secret horror crept over me whenever we passed one of the trees."

In 1849 Weddell described eight species of Triplaris from various parts of South America and published a key for the identification of the known forms. The following account, concealed in a footnote recently detected by Dr. J. Bequaert (1921-22), shows that Weddell was well-acquainted with the trees and their tenants: "The trunk, the branches and even the small twigs of the species of this genus are fistulose and serve as habitations for a peculiar species of ant which exhales when excited a rather agreeable odor like that of the Cicindelids. If one happens to touch the trunk of a Triplaris, and especially if one imparts a shock to it, the ants sally forth by the hundreds from the interior of the tree through the small galleries which connect the medulary canal with the outside; and if one move not away very quickly, one is covered with these dangerous hosts, whose bite is more painful than the sting of any other insect with which I am acquainted. It is a singular fact that at no matter what period of their life the Triplaris be examined in their forest, these ants are always sure to be encountered. It is singular also that in Rupprechtia,
which some authors unite with Triplaris, they are never found. I do not believe that this insect has been observed under conditions other than those I have noted. Its linear form is peculiarly adapted to its mode of life. I have had occasion to examine it and even to suffer from its attacks in many parts of Brazil, Bolivia and Peru, and everywhere it seemed to me to be identical. Several travellers have already made known a portion of the facts here related and have placed the Triplaris ant in the genus Myrmica of Latreille, but I am not aware that it has been given a specific name. That of *Myrmica triplarina* might be applied to it. It is usually pale brown. Its length is 6 to 7 millimeters, its width one millimeter; the abdomen is cylindrical and somewhat attenuated at the posterior end which is hairy.” I believe that the ant here described is the same as the one now called *Pseudomyrma arborissanctae* Emery, but this species has a number of local races and varieties and the brief description renders it impossible, unless Weddell’s types should be discovered in some European museum to determine which of the described subspecies or varieties should bear the name *triplarina*. It seems best therefore to regard it merely as a somewhat doubtful synonym of some one of the forms, preferably of the typical *arboris-sancta*.

Spruce (1869, in 1908) mentions several ligneous genera of Neotropical Polygonaceae as harboring ants in their medullar cavities—Triplaris, Coccoloba, Camperdia, Symmeria and Rupprechti—the last in contradiction to Weddell’s statement quoted above.1 “Not only is every ligneous Polygonia a habitation for ants, but the whole of the medulla of every plant, from the root nearly to the growing apex of the ramuli, is scooped out by those insects. The ants make a lodgment in the young stem of the tree or shrub, and as it increases in size and puts forth branch after branch, they extend their hollow ways through all its ramifications. They appear to belong all to a single genus, and are long and slender, with a fusiform, very fine-pointed, dark-coloured, shining abdomen, and they all sting virulently. They are known in Brazil by the name of “Tachi” or “Tacyba”, and in Peru by that of “Tangaran”; and in both countries the same name is commonly applied to any tree they infest as to the ants themselves.” Spruce describes three species of Triplaris. “*Triplaris surinamensis* Camb., a Polygonaceous tree of very rapid growth, reaching at maturity a hundred or more feet in height, and conspicuous from afar when in fruit from the abundance and bright

1Apparently the only species of Rupprechtia which harbors ants in its internodes is *Jamesoni* Meisner. (Bequaert 1921–22)
red colour of its enlarged shuttle-cock-like calyces, is common all along the Amazon, both on the river banks and in marshy inland sites; and solitary trees of it are often seen standing out above the Cacao plantations. *T. Schomburgkiana* Benth., a smaller tree, grows in the same way in the Upper Orinoco and Casiquiari. These trees as well as the other arborescent Polygonææ, have slender elongated tubular branches, often geniculate at the leaf-nodes, and nearly always with perforations, like pinholes, just within the stipule of each leaf, which are the sallyports of the garrison, whose sentinels are besides always pacing up and down the main trunk, as the incautious traveller finds to his cost when, invited by the smoothness of the bark, he ventures to lean his back against a Tachi tree." The third species of *Triplaris* allied to surinamensis, was observed in the cinchona forests of Chimborazo (2000-5000 ft.) and at lower levels. Spruce says that it is called by the Guayaquilians the "arbol de frios" (malaria tree), and that its presence "is a pretty sure indication of a humid site."

Huth (1887) states that H. von Ihering called his attention to the following account of the Brazilian *Triplaris nolitangere* Wedd. by J. Sêveriano da Fonseca (1881): "The Pao de novato is the Taixy of Pará and is also called Pau formiguero, or ant-tree. It is remarkable because it harbors in its cavities a kind of ant which is called 'novato'. These ants are yellow, as large as a 'suava' and bite painfully. They live there by the million and drive the inexperienced traveller to desperation when he attempts to fell and make use of the tall, straight trunks of the 'novato'."

Schimper (1888) had no opportunity to study *Triplaris* in the field but examined several branches of *T. caracasana* Cham. and Schl. from the "tierra caliente" of Venezuela, a tree which is called the "palo Maria" by the natives. He says: "The numerous pieces of branches sent to me show nothing that can be interpreted as an adaptation to the ants. Within the branches there is a cavity about 5 to 8 mm. broad, interrupted by diaphragms and connected, with the outside by round openings which are made by the ants. Of the latter there is almost without exception only one at each internode and usually at the upper end of a groove which runs to the next leaf below. The wall of the hollow cylinder is somewhat thinner at the groove, which is caused by the pressure of the bud and occurs also in many other plants. This thin area evidently determines the point

---

1In some parts of South America (Bolivia) *Triplaris* is called the "palo santo". This and the name "palo Maria" are obviously of rather recent Christian origin. It has been claimed by some writers that the "santo" refers to Christ's blood, as symbolized by the massed crimson fruit of the tree.
of perforation, which in the great majority of cases is at the upper end of the groove and may be due to the ants selecting, when making their orifices, only those lenticels that are situated in the upper end of the internode.”

Meinert (1892) published a brief note on a species of Triplaris (probably caracasana) and its ant, which he observed at La Moca, Venezuela. The ant was referred to the genus Myrmica but was obviously a Pseudomyrma. His statement that it is not confined to the Triplaris but occurs abundantly on other plants, has little weight, because there are many Pseudomyrmas which an observer unfamiliar with the species, might mistake for the true Triplaris inhabitant in the field.

Warming (1894), who was with Meinert in Venezuela, investigated a Triplaris (presumably caracasana) at Las Trincheras, concentrating his attention on the structure of the elliptical cleft near the upper end of each internode. This structure, as we have seen, was interpreted by Schimper as due to pressure exerted by the bud at the node below or as arising from a lenticel. Warming adopted the former interpretation but studied the internodes more closely. Like Schimper he found the wall of the internode to be thinner and to have more feebly developed fibrovascular bundles in the region of the cleft elliptical area and believed that this attenuation induces the ants to select the spot for perforation. But he noticed considerable irregularity in the perforations and their absence in some or all the internodes of whole twigs. He seems to have been the first to notice the numerous white Coccids which the ants keep in the cavities. The ants are briefly described in Warming’s paper as “en lille, brun umaadeleg bidsk Art” (a little brown, intemperate, biting species) and referred to Pseudomyrma mordax Meinert. This, however, seems to be a nomen nudum. Forel (1905), who listed the ants collected by Meinert in Venezuela referred the specimens from Triplaris to Ps. arboris-sanctae subsp. symbiotica Forel, a race originally described from Colombia.

Morteo (1904) studied preserved material of Triplaris americana which had been grown under cultivation in the East Indies, where its cavities were inhabited by a common Oriental ant, Dolichoderus (Hypoclínea) bituberculatus Mayr. He devoted particular attention to the peculiar cleft area near the tip of each internode, but interpreted the fissure as caused by expansion of the pith. He also believed that the ants perforate the cleft in order to feed on the pith, which he found to contain sugar. Like Warming, he found numerous Coccids in the in-
ternodal cavities. The discovery of sugar in the pith led him to regard it as a substitute for the extrafloral nectaries of other myrmecophilous plants. His observations, if correct, might be suggestive in connection with the presence of Coccids on the walls lined with the remains of the pith, but his statements in regard to the ants devouring it are not to be taken seriously, in view of the fact that his investigations were based on herbarium material.

Forel (1904) gives the following account of a species of Triplaris (probably americana) and its ant (Ps. arboris-sanctae subsp. symbiotica) which he encountered in 1896 in the Sierra Nevada de Santa Marta, Colombia: “Having laid my hand on the trunk of a young, green tree about four meters high, I was stung and found that the aforementioned Pseudomyrma was present on the trunk and had caused the sting. Observing the aggressive behavior of these ants, I suspected that they bore a symbiotic relation to the tree, because other Pseudomyrmas, which run about on the trees, flee instead of attacking. But seeing no dry branch and no opening, I was puzzled at first. I accosted some passing Indians and induced them to fell the tree with their machetes. I then broke up its flexible and living branches and found that they had a very narrow medullary cavity. This cavity, extending from end to end of all the branches, constituted the nest which the Pseudomyrmas occupied in a file, one behind the other, with their males, larvæ and pupe, so that they were just able to pass one another, notwithstanding the slenderness of their bodies. This singular habitation baffled me considerably and I asked myself how the colony-founding queen could have penetrated into this perfectly green tree, without a dead branch and apparently without an orifice. After long and vain scrutiny of all the branches, I inspected the lower portion of the trunk and there at last detected the dried and broken remains of an early twig, about 3 mm. in diameter but provided with a medullary cavity communicating with the central cavity of the trunk itself. This it was that served as an entrance and exit for the Pseudomyrmas.” It would seem that Forel must have overlooked the small openings which were in all probability present in the tree he examined, as in all other species of Triplaris, near the ends of the internodes of the branches and twigs. The same author, after his description of Pseudomyrma dendroica, states that Prof. E. Goeldi first found this ant in the medullary cavities of young Triplaris trees three to four meters high, and that “having transported the Triplaris inhabited by this ant from the Río Purus to the botanical garden at Pará, he observed that the Pseudomyrma soon took possession of one of the Triplaris in the garden, which had not
been inhabited before. The habits of this ant are therefore the same as those of *arborissanctae*.

Ule (1907) describes *Triplaris Schomburgkiana* and *surinamensis* and gives some excellent figures of the former. The natives of the Amazon, he says, call these trees “arvore de tachí” or “tachiceiro”, and distinguish the two species as white and black, *Schomburgkiana* having a pale and *surinamensis* a dark trunk. “The two species of Triplaris accordingly harbor in their interior a pale and a dark ant.” *Schomburgkiana* is inhabited by *Pseudomyrma dendroica* var. *emarginata* Forel, which nests by preference in the twigs and the crown of the tree but retains a medullary gallery through the trunk, reaching to the ground and sending off lateral galleries at intervals. “The bite of this ant is very painful, burns as if one had come in contact with red-hot iron and sometimes produces blisters on the affected parts of the body. From the trunk the ants wander to the ground and there destroy all the growing vegetation within a radius of a few meters. The location of Triplaris trees can be detected at once by such bare spots in the forest.” *T. surinamensis* is confined more to the banks of rivers and lakes. The darker ant which inhabits its internodes is *Ps. triplaridis* Forel. It does not make a cleared area around the trunk of the host tree. According to Ule, “the Triplaris trees are of some importance in the landscape. When they are in bloom, the male flowers first become conspicuous because they resemble great feather dusters, then the panicles of the female trees stand forth, when the fruits have developed their bright red wings, being vivid purple in *Triplaris Schomburgkiana* Benth. and rose-red in *Triplaris surinamensis*, so that the inhabitants believe that the trees are in flower. When I sailed up the Upper Amazon to Iquitos in July, the shores were everywhere brilliant with the Triplaris trees which with their rose-red fruits and the fresh green of the vegetation after the floods, produced an impression of spring.”

Pittier (1908) has published a brief note on *Triplaris tomentosa* Wed., which he observed in Costa Rica, where it is generally called the “hormigo.” It is “a small tree of the tierra caliente of the Pacific slope. It is dioecious, with the inflorescences more or less red and showy; the wood, which is of no use, is hollow and always infested with ants. In Nioyó this tree is called “tabaco”. According to Pittier, the Brunka Indians call it the “turi-svan-kra.”

In 1913 I published some notes on *Triplaris americana* (under the name *Cumingiana* Fischer and Meyer) and *auriculata* Meisn. (*Macombii* Don. Smith). The former I observed in Panama, the latter in
Guatemala. My visits to Panama in 1923 and 1924 yielded much additional information in regard to *americana* and I have recently identified the ants taken in the internodes of *auriculata*. It will be advisable, therefore, to give a revised account of these plants and their tenants in the sequel.

Ule's statement that the ants inhabiting *T. Schomburgkiana* make a clearing around the base of the tree, is of interest in connection with a communication made to me by Mr. C. D. Mell. According to this student of tropical forestry, *T. americana* is very abundant in Venezuela, where the inhabitants call it "barabas" and where he has seen many specimens, each surrounded by a cleared area, "perhaps made by the ants." It is well known that two of our North American species of *Pogonomyrmex*, *barbatus* and *occidentalis*, make clearings around their nests by destroying the vegetation and that our common *Formica exsectoides* sometimes behaves similarly in our northern woodlands. There is, therefore, no reason to suppose that *Pseudomyrma dendroica* may not have developed a similar habit, though nothing of the kind has been observed in other species of the genus.

(B) *Triplaris surinamensis* Cham. & Schl.

The only species of *Triplaris* which Professor I. W. Bailey and I had an opportunity to examine in British Guiana was *surinamensis*, the "long John" of the colonists. It seems to be very common in Dutch Guiana, where, according to Pulle (1906), it is known to the settlers as the "mira-hoe-hoe", or "mierenhout" (ant-tree). We were unable to find it in the immediate vicinity of the tropical laboratory at Kartabo, but on August 4, 1920, a native guided us to a spot near Camaria, some seven miles up the Cuyuni River, where there was a small grove of young and vigorous "long Johns", about 20 to 30 feet high, growing on the low bank. The river, owing to the daily rains, was so high that the roots and bases of the trunks were under water and the dense undergrowth around them impeded our approach. We succeeded, nevertheless, in securing a number of boughs and placed them in the canoe—a very painful task, because all the foliage was swarming with a single very vicious species of *Pseudomyrma*. The native evinced great fear of the insects, insisting that they cause fever. While the canoe was being towed the ants swarmed along the painter into our launch and tortured us all the way down the river to the laboratory.

1The natives make the same statement in regard to the powerful Ponerine ant, *Paraponera clavata* Fabr. and in Southern Brazil and Bolivia concerning the even larger *Dinoponera grandis* Guér.
The twigs and branches of *Surinamensis* exhibit the same peculiarities as those of other species as described by Schimper, Warming, Spruce and Morton. Professor Bailey, who studied the morphology of the internodes and of the peculiar oval, slit-shaped, area at their upper ends in the material we collected, has contributed the following paragraphs and several photomicrographs of sections to illustrate his interpretation:

"The fistulose stems of *Triplaris surinamensis* are characterized, as are other representatives of the genus, by the presence of a slit-like opening in the distal portion of each internode. Are these openings, which serve as convenient entrances and exits, spontaneous structures or are they excavated by the ants? An examination of immature shoots reveals the fact that the slit-like orifices originate during the earlier stages of the enlargement of the internodes, and that they are due, in all probability, to asymmetrical growth and differentiation of the cortical, fibrovascular and medullary tissues. As in the myrmecophytic Cecropias, one longitudinal surface of each internode is flattened or slightly concave and is subtended by a leaf and its accompanying axillary bud. The growth and differentiation of the tissues is retarded in this side of the internode which is, in consequence, somewhat thinner and considerably weaker (Plate 10, Fig. c). This tendency toward asymmetrical development is accentuated at the distal end of the internode, below the insertion of the lateral organs of the next (higher) node, and the concomitant peripheral tension ruptures the delicate tissue in the thinner portion of the circumference of the cauline cylinder (Plate 10, Fig. a). The asymmetry is emphasized in vigorous, rapidly differentiating shoots and a sub-nodal aperture is formed in each internode. On the contrary, in stunted, slower-growing twigs, which are more nearly cylindrical, the distribution of the slit-like openings is rather sporadic. The apertures tend to become occluded by a growth of callus from the margins of the ruptured tissues (Plate 10, Fig. b) before the enlarging internodal cavities are taken possession of by the ants. Indeed, many of them are not subsequently re-opened. Those that are, are characterized by having small circular apertures gnawed through the occluding callus.

"Coccids more or less numerous are found associated with the ants in the internodal cavities of *T. surinamensis*. In Cecropia, Tachigalia, Cuviera, Plectronia and various other Neotropical and Ethiopian ant-plants, the guest ants excavate pits in the denser tissues of the cauline cylinder which enable the Coccids to feed upon the softer tissues or upon a traumatically induced, thin-walled, centripetal callus. In *T.*
surinamensis the internodal chambers are jacketed by a thick, peripheral layer of medullary tissue (Plate 10, Fig. d), which remains green and physiologically active, even in stems which have formed a thick layer of secondary wood. The Coccids are able to insert their setæ into and to feed upon this medullary tissue. In other words, there is no evidence to indicate that the ants are concerned in facilitating the feeding of the Coccids. Although there is no reliable evidence at present for assuming that the imaginal ants solicit and feed upon the sugary exudates of the Coccids, an analysis of pellets fed to the larvae indicates very clearly that the workers carve up the Coccids and feed them to the brood. (Plate 10, Fig. e.)

“The refuse of the ant-colonies, i.e. voided infrabuccal pellets, liquid feces, fragments of malaxated insects, triturated plant-tissues, etc., is deposited at intervals along the walls of the elongated chambers. These latrines or middens give rise to luxuriant growths of delicate fungus hyphæ which are fed upon by an interesting group of structurally highly specialized Nematodes. The writer's investigations of Neotropical and Ethiopian myrmecophytes indicate that fungi are not cultivated and eaten by the ants, but that the aerial hyphæ are periodically cropped to prevent them from obstructing the chambers and interfering with the brood. That the middens in *T. surinamensis* may at times be utilized in the feeding of the brood is shown by analyses of the contents of the larval food-pouches, or trophophylaces. Not infrequently the pouches are filled with mats of hyphæ (Plate 10, Fig. f) or wads of detritus containing large numbers of Nematodes. It should not be inferred from this, however, that the imaginal ants actually cultivate the fungi, as do the Attini, or that they themselves feed upon hyphæ or Nematodes.”

The fierce, aggressive ant inhabiting the *T. surinamensis* trees near Camaria, B. G. proves to be a darker and more slender race of *Pseudomyrmica triplaris* Forel, which was taken by Ule, Goeldi and Huber in the same species of Triplaris in Brazil. I have described it as subsp. *baileyi*. The many flat Coccids of all sizes found in the internodal cavities were identified by Dr. Harold Morrison (1922) as a new genus and species, *Farinococcus multispinosus* Morr. and *Akermes secretus* Morr. They are sufficiently numerous to suggest that they may furnish the ants with considerable food in the form of honey-dew, especially during the rainy season. But certain observations, both negative and positive, cast doubt on this supposition. In the first place, no one has seen Pseudomyrmicas attending Coccids or imbibing their sweet excreta. And when the twigs are broken open and the ants escape, they are
never seen to seize the Coccids and carry them away, like the species of Azteca and many other ants when similarly disturbed. These negative observations indicate rather that the Coccids may, while still very young, find their way into the internodes, either through the preformed clefts or through the openings made by the ants, and settle on the walls without being molested and perhaps without being noticed at first by the ants. But that the latter may utilize the Coccids, though not as dairy cattle, is shown by Professor Bailey's observations, which confirm our statements in regard to other species of Pseudomyrmicinae (Wheeler and Bailey, 1920; Bailey, 1922, 1923). As he has remarked, examination of the internodal cavities shows that there are in certain situations in the walls, latrines, or middens consisting of pellets ejected from the infrabuccal pockets of the ants and over-grown with luxuriant fungus mycelium inhabited by great numbers of Nematode worms. These latrines are strictly comparable with those of Azteca longiceps in the Cordia alliodora swellings described on p. 20. But unlike the Azteca, Pseudomyrma baileyi makes good use of the latrine materials, since the workers collect the hyphae, Nematodes, particles of infrabuccal pellets and pieces of Coccids and fashion them into food-pellets which they place in the trophothylaces of their larvae. Since the Coccid fragments thus employed are rather numerous we suspect that the adult ants frequently devour these insects, possibly after they attain the proper dimensions, and horribili dictu serve up merely the remains mixed with other garbage from the latrines as the most appropriate or at least as the most available food for their progeny. The Coccids are used, therefore, as Bailey (1923) says, "for beef rather than solely as immature milch cows." Since there is a continuous growth and multiplication of Coccids, fungi and Nematodes in the internodal cavities, we are able to understand how the ants can develop and maintain large colonies in a plant which, so far as known, has neither extrafloral nectaries nor food-bodies such as we find in the myrmecophytic Acacias and Cecropias. Whether the ants also eat, instead of merely excavating, the sugary pith in the young internodes, is doubtful, but if Morteo's contention is correct, the plant itself does furnish an additional and perennial food-supply. The foregoing observations afford, I believe, at least a partial solution of the enigma which has puzzled several myrmecologists who have been unable to understand how the Pseudomyrmicas not only survive but flourish in trees which normally grow in swampy places or on river banks where for several months each year they are isolated by high water.

At the time of our visit to Camaria, the ants in the surinamensis
trees were at the acme of the breeding season, the internodes of the twigs and branches being stuffed with the slender larvae and pupae in all stages, intermingled with recently emerged males, females and workers. The Coccids, too, were flourishing. Obviously the rainy season, which increases the sap in the tree, is most favorable to the development of the Pseudomyrma colonies, the Coccids, fungi, and Nematodes, and it may be confidently predicted that the Coccids will show a considerable decrease in numbers during the dry season. But then the ants can move more freely over the surrounding vegetation and secure many small, miscellaneous insects as food.

In the gardens of private residences in Georgetown, B. G., Professor Bailey and I noticed a few large *surinamensis* trees and on their trunks several different ants, but we had no opportunity for further investigations.

A few years ago Mr. H. E. Box sent me from Blairmont, Berbice, B. G. a considerable amount of material of *T. surinamensis* containing ants and Coccids. The ants proved to belong to two different subspecies of *Pseudomyrma triplaridis*, which are described in the sequel (p. 184, 186) as subsp. *bozi* and *tigrina*. They resemble *baileyi* but are reddish. There were two species of Coccids, one being the same as the *Farinococcus multispinosus* Morrison, taken at Camaria, the other *Cryptostigma quinquepori* Newstead.

So far as known, therefore, *T. surinamensis* harbors in various parts of its range eight different organisms, namely, four subspecies of *Ps. triplaridis*, two Coccids, at least one species of fungus and one Nematode. That this can be only a small fragment of the biocenose which centers about *T. surinamensis* is evident from the following account of *T. americana* of which I was able to make a more thorough study.

(C) *Triplaris americana* Linné

My first acquaintance with *T. americana* dates from December 1910 when Mr. E. D. Christophersen showed me near Empire in the Canal Zone a few of the trees growing in a swamp which is now at the bottom of Gatun Lake.¹ At that season they were not in bloom. During my

¹I had identified the plant (1913) as *T. Cummingiana* Fischer and Meyer, which is cited from the Isthmus by Seemann (1852–57) and Hemsley (1882–86). My identification was later confirmed by Professor B. L. Robinson of the Gray Herbarium. Meinsh (1856) obviously redescribed the same species as *T. colombiana*. I now find that the Panamanian plant should be known as *T. americana* L., according to Standley (1922 p. 171), who describes it as the only Central American species of *Triplaris*. He states that "in Panama the tree is sometimes known as the "palo santo" (a name given more commonly to *Erythrina glauca*), but on the panama is called "guayabo hormiguerio," while in Salvador it is called "mulato" and "palo mulato."
two more recent visits to Panama in 1923 and 1924 I was able to make a much closer acquaintance with the plant and its inhabitants. It is less abundant than Cordia alliodora and grows singly or in small clusters on low lands along the water-courses or on the lower slopes of ravines which carry a considerable amount of water during the rainy season. On my frequent trips across the Isthmus I noticed single specimens or small groups of the tree in many parts of the Zone within a mile of the railway from Frijoles to Balboa. A few scattered specimens were seen near the ruins of Old Panama in the Republic, but none was observed in the dryer savannah region somewhat further inland. Numerous accessible trees were found during 1923 in three localities: along the stream below the large, abandoned cacao plantation at Las Cascades, on the low banks of the Rio Grande between Ft. Clayton and the locks at Miraflores, and in the ravines descending from Ancon Hill behind the new administration building at Balboa. Unfortunately clearings were being made in the two localities first mentioned and a number of the trees were being felled, but at Balboa more intelligent and appreciative persons in charge of destroying the rank vegetation had carefully spared the Triplaris trees. In the ravine nearest the administration building there are a dozen beautiful specimens, which being within a short walk of Mr. Zetek’s laboratory, could be visited at frequent intervals. During 1924 I found a few trees also in the swampy land at Marajal, near Colon, on the Atlantic side of the Isthmus.

T. americana is a small tree which rarely attains a height of more than 20 to 35 feet, with slender trunk and pyramidal crown, smooth gray bark, reddish twigs and bright green, drooping, smooth, entire, lanceolate leaves, about 5 to 8 inches long, with prominent veins and midrib. The cavities in the trunk, branches and twigs are precisely like those described for other species of the genus and the cleft elliptical areas at the distal ends of the internodes of the twigs show the same peculiarities as in the forms described by Schimper, Warming, Morteo and Bailey. The small round perforations made in the clefts by the ants are also very similar. The trees were found in bloom from February 25 till March 30. The spikes of small, sweet-scented, greenish white male flowers persist for only a short time, but in the female plant they are soon replaced by peculiar, rapidly enlarging, shuttlecock-shaped, fruits, which are at first green, then whitish and finally pure crimson. When the tree reaches this stage it is a very handsome and conspicuous object which might be advantageously introduced into the gardens of Southern Florida, California and the West Indies.
The shape of the fruits, with their long wings, indicates that they may be disseminated by the wind, like the samaras of our maples. I was unable to find any seedlings, and the smallest trees observed were not less than five or six feet high.

All the specimens of *americana* I have seen had ants nesting in their cavities, but the fauna is much more diverse than I had inferred from my meager observations of 1910, when the only ant encountered near Empire was a yellowish *Pseudomyrmica* which I identified as *arboris-sancta* Emery. This ant has since been described by Forel as a distinct variety, *loeweensohni* of the Colombian subspecies *symbiotica* of Emery's species. During 1923 and 1924 I took the following 16 species in or on the Triplaris in the various localities mentioned above:

9. *Atta cephalotes* L. Balboa; cutting leaves and collecting flowers.

Four of these ants, *Atta cephalotes*, *Dolichoderus bispinosis*, *Azteca velox* and *Camponotus lindigi* merely visit the trees. The *Camponotus* and *Azteca* attend Coccids on the twigs and stems of the flower-panicles, and the *Atta* may perhaps cut and collect the fruits. The remaining 12 species were all found nesting in the fistulose twigs and
branches, but only two, *Pseudomyrma loewensohnii* and *Azteca menceps* are obligates, most if not all the others occurring also in other myrmecophytes or even in the dead twigs of various trees and shrubs. The singular fact was disclosed that *Ps. loewensohnii* was altogether absent from the trees in the Miraflores locality and present only in a certain number of those near Las Cascades, Balboa and Mirajal. Many trees were inhabited in great part or entirely by the Crematogasters and *A. menceps*, the latter being the most common. The other forms in the list were usually confined to single twigs or branches of trees tenanted also by this Azteca or one of the Crematogasters. When *Ps. loewensohnii* was present it usually had complete possession of the tree. These statements may be illustrated by the distribution of the ants recorded in my note book under the date of March 26, 1923 as occupying the 12 trees in the ravine at Balboa behind the administration building.

1. Tree about 15 ft. high; fruiting. Twigs inhabited exclusively by *A. menceps*.
2. About 30 ft. high, with two trunks; flowering. Twigs inhabited by *C. ampla* and *B. obscurior*.
3. About 30 ft. high, beginning to fruit. Twigs occupied by *C. ampla*.
4. About 9 ft. high, in flower. Twigs and branches inhabited by *Ps. loewensohnii* exclusively.
5. About 15 ft. high; beginning to fruit; leaves much eaten. Twigs tenanted by *C. ampla*.
6. About 20 ft. high; in flower. Tenanted throughout by *Ps. loewensohnii*.
7. About 20 ft. high; in flower, but with several dead branches. Twigs occupied by *A. menceps*.
8. About 35 ft. high; beautiful specimen, flower. Tenanted by *A. menceps*.
9. About 25 ft. high, in flower. Twigs inhabited by *A. menceps* and *B. balboa*.
10. About 35 ft. high, in flower. Tenants: *A. menceps* (abundant); *Ps. alliodora* (sporadic); *C. lindigi* running on trunk and foliage.
11. About 35 ft. high; mature fruit. Tenants: *B. balboa* (in several branches); *Ps. bicolor* (sporadic); *C. lindigi* running on trunk.
12. About 30 ft. high; just passed flowering. Tenants: *C. ampla* (abundant); *T. melanocephalum* (in a few internodes); *Ps. ita* (sporadic); *C. lindigi* running on trunk and branches.
My notes on these trees are very brief and may not represent an accurate census, especially of the inhabitants of the larger specimens, because, owing to their height, I was unable to make an exhaustive inventory of their twigs and branches. Moreover, the trees were being preserved for ornamental purposes and could not be mutilated. I believe, nevertheless, that few species of ants, and only those forming very small sporadic colonies in some of the internodes, were overlooked. Quite a number of twigs from most of the trees were cut off, carried to the laboratory in bags and chloroformed so that the ant colonies could be carefully examined. It will be seen that only two of the twelve trees were inhabited by *Ps. loewensohni*, whereas five contained *A. menceps* and four *C. ampla*. One of the largest harbored none of these species. In the series of more than 20 trees between Ft. Clayton and Miraflores, those nearest the former locality were inhabited exclusively by *A. menceps*, those nearest the latter by *Crematogaster ludio*, with a few sporadic colonies of *Cryptocerus minutus*. Near Las Cascades only three among a dozen trees examined, were tenanted by *Ps. loewensohni*, and one of these, a vigorous specimen about 15 ft. high, which was felled and carefully examined, also had *A. menceps* in some of its twigs. Many of its smaller branches were quite free from ants and in part inhabited by the larvae of a Thyridiid moth (*vide infra*, p. 60), which was common also in many of the trees in the other localities.

Since, apart from the sporadic *Ps. ita* and *bicolor*, the only ant listed that stings painfully is *Ps. loewensohni*, and since it occurred only in a small number of the trees and was even entirely absent in one locality, *T. americana*, unlike its various South American congeners (*Schomburgkiana, caracasana, surinamensis*, etc.), could usually be handled and examined with impunity. And while it is not improbable that in some Panamanian and Colombian localities the plant may be inhabited exclusively by *Ps. loewensohni* or the typical subsp. *symbiotica* or by vicious species other than those enumerated in my list, a study of the trees in the Canal Zone shows that specimens harboring only such small inoffensive ants as *A. menceps, C. ampla* and *ludio*, are quite as vigorous and flourishing as those inhabited by the red, stinging Pseudomyrma. At Balboa, in fact, this ant did not occur in the largest and finest trees. Besides the case above mentioned of *loewensohni* living in the same tree as *A. menceps*, the following observation shows that the Pseudomyrma is not a very aggressive protector of its tree from alien ants. On March 28 at Frijoles, I came upon a Triplaris about 14 ft. high which had just
been felled by a native. It was in full fruit and the large crimson
panicies had been invaded for some reason by a host of the belligerent
Dolichoderus bispinosus. Closer examination showed that the cavities
of the tree were occupied by a thriving colony of loewensohni, the
workers of which were running about quietly and without the slightest
signs of hostility among the Dolichoderi. The following observation
made at Balboa, March 25, indicates, perhaps, that the other ants of
T. americana are quite as indifferent to invasions of their host tree
by alien species. A few feet from the trunk of tree No. 12 at Balboa
there was a large nest of Atta cephalotes, but all the ants had withdrawn
into the depths of their galleries. That they had been working during
the preceding night was shown by the great masses of Triplaris flowers
which they had carefully collected and left in the runways leading
to their nest-craters. Of course, these wilted flowers may have been
merely picked up on the ground, but that they may have been culled
directly from the trees is by no means improbable. I may add, in this
connection, that a few of the trees near Fort Clayton, though inhabited
by flourishing colonies of A. menceps, nevertheless had their leaves
severely damaged by Atta cephalotes.

Before listing the miscellaneous organisms associated with T. ameri-
cana and with its ants, it will be advisable to insert a few remarks
on the two obligates, Azteca menceps and Pseudomyrma loewensohni.
The types of the former were taken by Christophersen in the Canal
Zone but the precise locality was not recorded. They were probably
from the very trees to which he guided me in 1910. The habits of
this ant are similar to those of A. longiceps, described above (p. 28),
and the fullest development of its colonies occurs at the same season,
coinciding with the anthesis and fruiting of the host-plant. Like the
other Triplaris ants, menceps makes small round entrances in the
elliptical cleft areas of the internodes and also destroys the partitions
between them so that their cavities become continuous. The walls
of the cavities also have gnawed pits containing Coccids, which are
rather numerous, pinkish in color and covered with white wax. There
are, moreover, definite latrines at intervals on the walls, like those of
A. longiceps in the cauline swellings of Cordia alliodora and consisting
of numerous pellets from the infrabuccal pockets of the ants, covered
with proliferating fungus hyphae and invaded by hosts of Nematodes
and bacteria. Mites are also present occasionally. The pellets them-
selves consist of spores and small pieces of insects and plant tissue.

Ps. loewensohni, though a very vicious and aggressive ant, seems
not to sting quite as severely as the Pseudomyrmas inhabiting T.
surinamensis, Tachigalia paniculata and the bull-horn Acacias. When the twigs or branches which it inhabits are split open their walls are found to be smooth and clean and of a dark brown color. To these walls the larvæ are hung by means of their hooked, curved dorsal hairs and are fed with infrabuccal pellets like the larvæ of other Pseudomyrmex. The latrines, which occur at intervals of several inches, are of much the same composition as described for A. meneceps and longiceps, but moister and more glutinous. I found few Coccids in the internodes and at rather infrequent intervals. Instead of making pits, the ants gnaw narrow grooves one to three centimeters long and in these the Coccids lie in a linear series. They resemble the species cultivated by A. meneceps but are smaller, suggesting that loewensohni, like Ps. baileyi, may occasionally devour them instead of using them as a perennial source of honey-dew. Most of my observations on these ants, however, were made at the height of the dry season and while the trees were in flower or fruit, so that the small number of Coccids may also be due in part to less favorable trophic conditions. Since the larvæ, pupæ, males and winged females of loewensohni were not very abundant, it is probable that, like Ps. baileyi, it breeds more actively during some portion of the rainy season. This was indicated during the summer of 1924 by observations in the swamp at Marajal. Here the few colonies of loewensohni which I examined contained more brood and more numerous sexual forms and Coccids.

The following miscellaneous organisms were found associated with T. americana or with its ant-inhabitants:

Lepidoptera. Among the Heterocera there are at least five species that feed on the trees. One of these is identified by Dr. W. T. M. Forbes as a Thyridiid, the greenish caterpillar of which, nearly an inch long, is very common on the twigs, devouring the pith, tunnelling through the nodal partitions and depositing masses of coarse frass at intervals. This caterpillar is so common that it must be an important agent in facilitating the occupation of the twigs by the ants. Although pupæ were obtained during the latter part of March I did not succeed in rearing the imagines.

On the trunks of some of the trees at Balboa there were communal masses of cocoons, larger than one’s fist. From these Mr. Zetek reared many specimens of both sexes of two handsome reddish brown Saturniid moths, which Mr. W. Schauss has identified as Hylesia hamata Schauss and H. darlingi Dyar.

A large empty cocoon of another Saturniid was found attached
to the trunk of one of the trees and the case of a Psychid allied to Thyridopteryx to a twig.

The following Rhopalocera, identified by Dr. Forbes, were taken at the Triplaris flowers at Balboa.

(1) Junonia lavinia zonalis Felder.
(2) Anartia jatrophae L.
(3) Anosia plexippus L.
(4) Anosia berenice Cram.
(5) Antigonus (Systasea) erosus Huebn.
(6) Hesperid (unidentified).

Diptera. The only members of this order taken were a small Trypetid which was swept from the flowers and a small Asilid occasionally resting on the trunk.

Hymenoptera. The caterpillar of the Thyridiid above mentioned is parasitized by a small Hymenopterous larva which makes its cocoon in the twig cavity inhabited by the host. I failed to rear the imago.

A single large red Ichneumonid was seen ovipositing in one of the cocoon-masses of Hylesia hamata, but escaped.

The following were taken at the flowers: two Vespidae, Polistes canadensis L. and Eumenes nana Kirsch (J. Bequaert det.) and the following eight bees, identified by Prof. T. D. A. Cockerell (1928):—

(1) Megachile pociulifera Ckll.
(2) Apis mellifica L.
(3) Apis mellifica var. ligustica Spin.
(4) Melipona fulvipes subsp. triplaridis Ckll.
(5) Melipona orbignyi subsp. phenax Ckll.
(6) Trigona cupira F. Smith.
(7) Trigona pectoralis D. T. subsp. panamensis Ckll.
(8) Nannotrigona testaceicornis Lep.

All but one of these are social bees.

Coleoptera. Three species of beetles taken at T. americana flowers at Balboa in 1923 were identified by Mr. H. S. Barber as Coscinoptera cingulata Lec. (Chrysomelid, several specimens), Hyporhagus laticinctus Thom. (Monomimid, several specimens) and Acanthoscelides sp. nov. (Bruchid, one specimen). The last has been reared by Mr. Bridwell from pigeon-peas and the description is in MS. Three other unidentified Coleoptera were observed at Balboa, namely some small larvae, possibly Cuculionids devouring the pith in young twigs, quite a number of Coccinellid larvae on the foliage and evidently preying on the Coccids and a species of termitophilous Staphylinid living in considerable numbers in one of the nests of the termite cited below.
In 1924, five more Coleoptera were taken on the bark and leaves but were not identified (One small Coccinellid; one Curculionid, one Anthribid and two small Tenebrionids).

**Isoptera.** Some of the trees at Balboa had large elliptical, ellipsoidal, black termitaria enveloping their trunks. The termites were identified by Mr. Zetek as *Nasutitermes corniger*. A dead shoot at the base of one of the trees was inhabited by a species of Leucotermes.

**Orthoptera.** Several small cockroaches determined by Mr. Hebard as *Latiblatella angustifrons* Hebard, were found hiding between the walls of the Nasutitermes termitaria and the bark to which they were attached. Small oothecae which must have belonged to some other Blattid were occasionally found in the cavities of the twigs.

**Thysanoptera.** A large black species with greatly incrassated anterior femora was occasionally found in the twigs together with nymphal individuals.

**Heteroptera.** Dr. R. F. Hussey has identified the following bugs taken from the foliage:

- *Dysdercus ruficolis* L. (Pyrrhocorid)
- *Zelus* sp. nov. near *atripes* Champ (Reduviid)
- *Hypsilonotus lineatus* Stal. var. *neglectus* Horvath (Coreid)

**Homoptera.** An unidentified Aleurodid was occasionally seen on the leaves. The following Coccids have been identified by Dr. Morrison.

1. *Akermes* sp. On twigs.
5. *Ceroplastes cirripediformis* Comst. (?) On twigs at Balboa.

**Araneina.** The only spider seen was *Eriophora edax* Bl. (N. Banks det.), which was running on the bark.

**Acarina.** The mites found in the latrines of *Azteca menceps* have not been identified.

**Nematodes.** The nema occurring in the latrines of the same ant are being studied by Dr. Cobb.

**Phaeogams.** A large mistletoe (*Struthanthus orbicularis* H. B. K.) was found growing on two of the trees at Balboa. It is common on other trees in the Canal Zone.

**Cryptogams.** Here belong the moulds and bacteria that flourish in the latrines of *A. menceps* and *Ps. loewensohni*. 
Adding the 52 Arthropods cited in the foregoing list to the 16 different Formicidae we have 68 forms associated with *T. americana* and distributed as follows:

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Count</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hymenoptera</td>
<td>28</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>11</td>
</tr>
<tr>
<td>Diptera</td>
<td>2</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>11</td>
</tr>
<tr>
<td>Isoptera</td>
<td>2</td>
</tr>
<tr>
<td>Orthoptera</td>
<td>2</td>
</tr>
<tr>
<td>Thysanoptera</td>
<td>1</td>
</tr>
<tr>
<td>Heteroptera</td>
<td>3</td>
</tr>
<tr>
<td>Homoptera</td>
<td>6</td>
</tr>
<tr>
<td>Araneina</td>
<td>1</td>
</tr>
<tr>
<td>Acari</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>68</strong></td>
</tr>
</tbody>
</table>

The trees examined were much fewer in number than those of *Cordia alliodora* and I was unable to study any very young or seedling specimens. Nevertheless the number of insects infesting *americana* seems to be sufficient to corroborate the general conclusions derived from a study of *Cordia alliodora*.

(D) **Triplaris auriculata** Meisner

According to Standley (1922), this is probably the correct name for the tree which I called *T. Macombii* Donn. Smith in my paper of 1913. He records it as occurring in Chiapas "and perhaps elsewhere in Mexico". Donnel Smith’s material was collected at Jiquilisco, Salvador. I did not at first recognize it as a Triplaris when I encountered it in January 1911 along the roadsides of Escuintla and Patulul in Western Guatemala. It is a larger tree than *T. americana*, attaining a height of at least 40 or 50 feet, with stouter trunk and more spreading branches and large, coarse, dark green, broadly ovate, short-petioled leaves. When first seen it was putting forth branches of long yellowish flower-spikes, covered with a deciduous sheath. The fruit, which I did not see, is described by L. Donnel Smith (1894) as pale yellow. He has described (1895) a variety *rufescens* from Mayatinango, Guatemala, with brick-red flowers and more pilose leaves. My specimens seem to agree best with those of the typical *Macombii* in the Gray Herbarium. The twigs and branches are coarser than those of *T. americana*. Re-examination shows that the twigs have the same structure and are perforated in the same manner by the ants at the elliptical cleft areas,
which look like hypertrophied lenticels but are very probably formed as in other species of Triplaris by local dehiscence and subsequent healing of the expanding internodes. I have not since had an opportunity to study auriculata which seems to have a rather restricted distribution.

The following ants were collected in the internodes of the tree in 1911:

*Pseudomyrma sericea* Mayr. var. *ita* Forel.
*Pseudomyrma sericea* var. *fortis* Forel.
*Monomorium carbonarium* F. Smith subsp. *ebeninum* Forel.
*Azteca prorsa* Wheeler.
*Tapinoma ramulorum* Emery subsp. *inrectum* Forel.

Of these the Pseudomyrmas and Azteca are the most abundant and characteristic, the latter being, perhaps, peculiar to the plant (obligate). The Monomorium and Tapinoma occur also in the twigs of other trees. Cutting the branches of *T. auriculata* is decidedly painful owing to the Pseudomyrmas which, though they form smaller colonies, sting quite as severely as *Ps. loewensohlri*. *A. prorsa* is closely related to *A. pittieri*, *longiceps* and *menceps* and seems to have very similar habits. It is timid and inoffensive.

In order to complete my enumeration of the ants inhabiting Triplaris, I may refer briefly to the records of those taken in undetermined species. The following have been cited in the literature merely as occurring in Triplaris or without further comment:

1. *Pseudomyrma dendroica* Forel. In hollow branches of Triplaris sp. Amazonas (E. Ule)
3. *Pseudomyrma arboris-sanctae* Emery. In Triplaris sp. Bolivia (Balzan, W. M. Mann); Peru (Staudinger); Amazonas and Matto Grosso (F. Silvestri)
Ps. dendroica and latinoda are closely related to arboris-sancta and triplaridis and undoubtedly have very similar habits. The Azteca was taken in the stems of a peculiar Triplaris which judging from Dr. Orlando White’s herbarium specimens accompanying it, is quite unlike those with which I am acquainted. The only ant recorded from T. Schomburgkiana is Ps. dendroica var. emarginata Forel, which was taken by Ule in Amazonas (see p. 164). Morteo, as we have seen (p. 47), records the occurrence of the common Oriental Dolichoderus (Hypolinea) bituberculatus as living in T. americana when growing under cultivation in the East Indies. Omitting this ant, there are some 30 different Formicidae and more than 50 other organisms known to inhabit the hollow branches and foliage of the various species of Triplaris in different parts of the American tropics.

Chapter 3. OBSERVATIONS ON TACHIGALIA

The beautiful Caesalpinaceous trees of the genus Tachigalia are confined to Amazonas, Eastern Peru, the Guianas and Venezuela, and therefore have an even more restricted distribution than the species of Triplaris. About 20 species have been described, but the “Index Kewensis” recognizes only 13 as valid, and perhaps this number may be reduced when more material is available and the range of variation in the different forms has been thoroughly studied. The type species, at least, varies considerably even during its ontogeny, the juvenile form when growing in the shade having a very different habitus from the large tree exposed to the sun-light.

The genus was established by Aublet as long ago as 1775 for a species, paniculata, which he found growing along the rivers of French Guiana. He named the plant Tachigalia from the Carib “tachigali”, “tachi” being the name employed by the Indians of the Guianas and Brazil for the stinging ants of the genus Pseudomyrma, which regularly inhabit the enlarged petioles of Tachigalia as well as the internodal cavities of Triplaris. Part of Aublet’s description of T. paniculata may be quoted: “The trunk of this tree rises to a height of fifty or sixty feet or more, with a diameter of three feet. Its bark is gray, rugose, its wood is hard and whitish. It produces at its summit a large number of stout branches which spread in all directions and are laden with twigs furnished with alternate winged leaves, with two rows of opposite leaflets, the greatest number of which is six on each side. They are firm, entire, terminating in a point, smooth and green above, grayish green beneath. Their petiole is very short,
articulated to a triangular swelling five inches long and terminating in a point, accompanied at its origin by two stipules which are soon deciduous. The largest leaflets are six inches long by two and a quarter inches broad. The flowers arise at the end of the twigs and are borne in large, long panicles, the stems of which are simple and covered with flowers throughout their length." The corolla is yellow and sweet-scented and the seeds are surrounded by a flat, elliptical wing or expansion. The tree flowers and fruits in April and November. Aublet described also a *T. trigona*, which proves, however, to be a synonym of *paniculata*.

Tulasne (1844) redescribed *paniculata* and added six other forms, only two of which are now recognized as distinct, two, *eriocalyx* and *sericea*, being synonyms of *paniculata*. *T. angustifolia* described by Miquel (1851) from Surinam also proves to be a synonym of Aublet's species.

None of these botanists deigned to leave us any notes on the relations of the Tachigalias to their ants. This was left to Spruce, who writes in his article submitted to the Linnean Society in 1869 but not published till 1908: “The Tachigalias are low-growing riparial trees, of black-water rivers, and have pinnate, often silky foliage; and small, yellow, sweet-smelling, nearly regular flowers disposed in panicles. All have trigonous petioles, which are mostly diluted at the base into a fusiform sac, tenanted by ants. *T. caripes* (*recte caripes*, later regarded by Bentham (1870–76) as a variety of *paniculata*) grows abundantly on the banks and on inundated islands, of the Uuapes. It is a spreading tree of 30 feet, and has the ramuli, petioles and leaves clad with a fine, close, silky pubescence. The sacs of the petiole are inhabited by small black ants, whose entrance is by a little hole on the underside of the sac. *T. ptychocephala* sp. n. grows in moist sandy caatingas by the same river, and has a similar sac on the petiole.”

Ule (1907), in Amazonas and Eastern Peru, observed three species of Tachigalia, which were identified by Harms (1906) as *formicarum* Harms, *paniculata* Aubl. and *spicata* Aubl. The first, from Tarapoto, Peru, proved to be a new species and is a tree 30 meters high, with yellowish flowers. Its large petiolar sacs were inhabited by *Pseudomyrma latinoda* Mayr subsp. *tachigaliæ* Forel. Ule states that “the ants live mainly in the petiolar sacs; in blooming and fruiting specimens they also settle in the axes of the large, hollow, swollen flower panicles. Only on one occasion, near Iquitos, did I observe that they had also perforated and taken possession of the twigs.”
J. Huber (1909) described a *T. macrostachya*, which was collected by Ducke on the Rio Trombetas, Amazonas, and had its hollow petioles inhabited by *Ps. latinoda* var. *endophyta* Forel.

In 1921 I gave a detailed account of *T. paniculata* and its inhabitants as observed by Professor I. W. Bailey and myself at Kartabo, British Guiana, and Professor Bailey (1923) has since published a description of the anatomical peculiarities of the plant. The reader may also be referred to my paper for an account of the ants, coccids and other organisms and especially of the very interesting social Silvanid beetles, *Coccidotrophus socialis* and *Eunausibius wheeleri*, which live in the petiolar cavities of the young trees before they are occupied by the ants.

The following list includes all the known ants which I have found in the petiolar swellings of *T. paniculata*, together with those recorded by others as occurring in other species of the genus:

1. *Neoponera crenata* Roger. (*T. paniculata*)
2. *Neoponera unidentata* Mayr. (*T. paniculata*)
3. *Pseudomyrmica damnosa* Wheeler (*T. paniculata*)
4. *Pseudomyrmica latinoda* Mayr. var. *coronata* Wheeler (*Tachigalia* sp. ?)
5. *Pseudomyrmica latinoda* var. *endophyta* Forel (*T. macrostachya*)
9. *Pseudomyrmica maligna* Wheeler (*T. paniculata*)
10. *Pseudomyrmica maligna* var. *cholerica* Wheeler (*T. paniculata*)
11. *Pseudomyrmica maligna* var. *crucians* Wheeler (*T. paniculata*)
12. *Pseudomyrmica picta* Stitz (*Tachigalia* sp.)
17. *Crematogaster* (Orthocrema) *delitescens* Wheeler (*T. paniculata*)
18. *Crematogaster* (Orthocrema) *limata* F. Sm. subsp. *palans* Forel (*T. paniculata*)
19. *Solenopsis helena* Em. subsp. *hermione* Wheeler (*T. paniculata*)
(22) *Lepto thorax* (Goniothy rax) umbr atilis Wheeler (*T. paniculata*)
(23) *Azteca foveiceps* Wheeler (*T. paniculata*)
(24) *Azteca tachigalis* Forel (*Tachigalia* sp.)
(25) *Azteca traili* Emery (*T. paniculata*)
(26) *Brachymyrmex heeri* Forel (*T. paniculata*)
(27) *Brachymyrmex heeri* var. *basalis* Wheeler (*T. paniculata*)
(28) *Camponotus* (*Myrmobrachys*) *pittieri* Forel var. *panalis* Wheeler (*T. paniculata*)
(29) *Camponotus* (*Myrmobrachys*) *zoc* Forel (*T. paniculata*)

Of these 29 forms probably the only ones that can be regarded as obligates are the various Pseudomyrmicas and Aztecas, the remainder being merely inquilines which frequently nest in the cavities of other plants. Perhaps *A. traili* should be assigned to this latter group. In my paper on *T. paniculata* I gave a list of 28 miscellaneous organisms associated with the plant, its ants or its Coccids (*Pseudococcus brevipes*). Dr. Morrison (1922) has since described a second coccid, *Ripersia petiolicola*, which occasionally lives on the petioles but was not mentioned in my paper. As known to date, therefore, the Tachigalia biocenoses embrace more than fifty different organisms. The conclusions which we reached as a result of our investigations are well summarized in the two concluding paragraphs of Professor Bailey's paper:

"The hollow foliar axes of the ant-plant *Tachigalia paniculata* are colonized by at least seven "obligatory" guest insects. The domatia of juvenile plants are taken possession of by two extraordinary social beetles, but during the subsequent development of the plants these insects are dispossessed by ants. Both the beetles and the ants avail themselves of the structural peculiarities of their host plant in a singularly efficient manner. Not only do they make use of the hollow foliar axes as convenient nesting chambers, but they feed, either directly or indirectly, upon the softer tissues in the interior of the domatia. The beetles eat the parenchyma of the wide, primary medullary rays, utilize it in the construction of their puparia, and solicit and obtain liquid carbohydrates from herds of Coccids which graze upon it. The ants also feed upon this tissue vicariously through intervention of Coccids, and utilize it in the construction of carton partitions.

"There is no evidence to indicate that the structural peculiarities of *T. paniculata* are initiated by ants or by gall forming insects, or that they originated as adaptations for attracting a defending army of ants. The relations between the host plant and the beetles and the
ants are not those of a mutually beneficial symbiosis (Belt, Schimper), but an interesting type of parasitism, in which there is a remarkable parallelism in the behavior of representatives of such widely separated groups of insects as the Hymenoptera and the Coleoptera. The nesting and feeding habits of the insects, and their relations to the coccids, are largely determined by the structure and arrangement of the various vegetative tissues during different stages in the development of the petiole and rhachis. In studying the habits of phytophagous and plant inhabiting insects, it is evident that the anatomy of the host plants deserves more careful consideration than it has received heretofore."

Chapter 4. OBSERVATIONS ON CECROPIA

The trees of the Moraceous genus Cecropia have been much more carefully investigated than any other myrmecophytes. This is in part due to the fact that they are so abundant and are so readily recognized, because they contrast markedly with the remaining vegetation and especially at low altitudes constitute a very characteristic feature of the landscape. They are usually rather small or medium-sized trees, with smooth, pale-barked, slender trunk and branches, the latter few in number and arranged like the branches of a candelabrum and bearing large, coarse, long-petioled palmate leaves, which are usually silvery-white beneath. When moved by the wind the lower surfaces give a touch of vitality to what may be a rather monotonous background of vegetation. Writing of this feature of the Cecropias and of the coppery under surfaces of the leaves of the laurels and Chrysobalanis along the Amazon, Spruce (1869, in 1908) says: "When my boat has been floating lazily in the water, under a burning and dazzling sun, with not a breath of air stirring, I have sometimes— as my eye wandered along the endless forest margin—given vent to some such exclamation as this "How tame and monotonous!" when the coming on of a squall, by simply revealing the glowing tints of the underside of the leaves, has in a moment waked up the scene into life and beauty." The Cecropias, unlike Cordia and Tachigalia, are dicocious and their inflorescence is inconspicuous, consisting in both sexes of bunches of compact green catkins, or aments. The trees are known to the natives of Brazil under the names "imbauba", "imbauva" "ambauva", "ambaiba" or "ambay", to the Peruvians as "ceticos", to the natives of Central America as "guarumo", and to those of the Antilles as "lagrums" or "yagram". The British colonists in South
America call them "shakewood", "trumpet" or "drum" trees. The West Indians in the employ of the Panama Canal Zone refer to them as "trompies".

In Brazil, according to Bequaert (Wheeler and Bequaert, 1929), "the Cecropias generally grow in dense grooves. Some of the species of the Amazonian Basin are commonly found in the second growth, in plantations, along roadsides and in waste-places. They may be observed right in the towns and sometimes grow out of the walls of old buildings. This would seem to indicate that the seeds are scattered in the excrement of birds and bats that feed on the fruit. Other species prefer the alluvial woods, or what is known in Brazil as "varzea", i.e. low-lying land that becomes water-logged when the rivers reach their highest level. Finally a few species thrive in the "igapo", or true inundated forest, and are the very first plants to colonize the shifting mud-banks in the river itself, as well as the new alluvial land. During much of the year these Cecropias stand in swiftly flowing water many feet deep, so that the ant-colonies that inhabit them must have their food-supply restricted to the food-bodies produced by the plant and the honey-dew furnished by the Coccids in their internodal cavities".

My own observations in British Guiana, Mexico, Central America, Cuba and Porto Rico agree with Bequaert’s account, except that in these countries there seem to be no forms adapted to amphibious conditions. Though the trees are sometimes found in moist places they are more frequent on the hills or mountain sides, either in small grooves or single and intermingled with the other plants of the jungle or hylæa. When man interferes with the natural conditions, the Cecropias behave as veritable tree-weeds and rapidly take possession of the newly turned soil of railroad and ditch embankments, roadsides, clearings; etc. I was able to witness the occupation of such sites on a grand scale in Panama, during the building of the canal and relocation of the transisthmian railroad. Bequaert’s suggestion that the seeds may be spread by birds and bats seems very probable.

Of all the neotropical ant-plants the Cecropias are the most widely distributed. They are common throughout tropical Mexico, Central America, the Antilles and South America except Patagonia and parts of Argentina and in some of these regions often ascend to altitudes of four or five thousand feet. Although botanists have been sufficiently interested in the genus Cecropia to describe about 100 species, they have failed to give us any adequate monograph or key to the various forms, so that their identification in the field is a matter of no little
difficulty. Moreover, as Bailey (1922, p. 371) has shown, the leaves of the same species undergo profound changes in form during ontogeny, and the specific characters are probably still further obscured by hybridization. Apparently only certain species are myrmecophilous, while others are never regularly inhabited by ants. There are also two genera, Pourouma, with about 20 species, and Coussapoa, with about 15 species, which are closely related to Cecropia and at least occasionally harbor ants, but our knowledge of these plants is very fragmentary.

The association of ants with Cecropias has long been known. It was briefly described by Marecgravius (1648), Piso (1658) and Ray (1688) in the seventeenth century, but excited no further inquiry till 1874, when Belt recorded his observations in Nicaragua. Since that time a number of papers, wholly or in part devoted to the Cecropias and their ants have been published by Fritz Müller (1876, 1880, 1883), Schimper (1888), Schumann (1889), Warming (1894), Ule (1897, 1905, 1906), Retting (1904), H. von Ihering (1907), Fiebrig (1909), Wheeler (1908, 1913), Bailey (1922) and Wheeler and Bequaert (1929). The papers of Müller, Schimper, von Ihering and Fiebrig on C. adenopous L. and of Bailey on C. angulata are specially worthy of notice.

A general description of the structure of the Cecropias is given in my ant-book (1910, p. 305–310) and is reproduced by Bequaert in his article on the myrmecophytes in my “Ants of the Belgian Congo (1922). Ule (1907) has also published a brief account which I translate: “All the Cecropias that harbor ants have essentially the same structure which Schimper has described in detail. The internodes of the branches and twigs are hollow and separated from one another by transverse partitions. Each internode possesses a leaf, and above it there is a groove which it produces by pressure of the petiole on the axial bud while it is still enclosed. In this groove there is always a pit. A similar shallow groove also occurs in other ant-plants, but the pit is peculiar to Cecropia. Now at this point the Cecropia is always perforated by the fecundated (Azteca) queen, and this is the more easily accomplished because the wall of the pit is thin and lacks fibrovascular bundles. After the queen has slipped into the cavity or chamber through the opening, the latter, as long as no workers are present, closes through the formation of callous tissue around its edges.” Later the worker progeny of the queen again open the orifice and use it permanently as the entrance or exit to the internode. “The chambers which arise in the internodes in the place of the early disappearing pith are circular in cross-section, on an average
4 to 7 cm. long and separated from one another by very thin fragile partitions, which are always perforated by the ants. In the interior of the chambers the ants build up a kind of labyrinth for their larvæ out of a brown, wax-like substance probably derived from the Cecropia tree. As a rule each chamber is at first inhabited by only a single female, whose cell is often all it contains. In addition there are always white Coccids, on the saccharine excretions of which the ants in part subsist. But the insects are also afforded another source of nourishment by the plant itself, for at the base of each leaf-petiole there is a hairy cushion (trichilium) in which proteid-containing food-bodies sprout and are eagerly sought by the ants. These pear- or egg-shaped structures, called "Müllerian bodies", resemble insect-eggs. New bodies are being formed continually in the place of those carried away by the ants. Favored by these conditions, the ants increase enormously in numbers on the Cecropia trees and pass their lives in the crown of foliage. Of certain species of Cecropia nearly all the individuals, of others only occasional trees are inhabited by ants. In their earliest youth the Cecropias are usually free from ants; they are not invaded by fecundated queens till they reach a height of some meters. The trees exposed to inundation cannot, of course, harbor ants, because they are kept away by the water."

The last remark is evidently incorrect, since the Cecropias standing in water, may be settled by Azteca queens reaching them before deaляtion. Moreover, the internodes of the trunk as well as those of the branches are inhabited by the ants, and Ule's statement in regard to the time of infestation of the young trees with the Azteca queens does not agree with my observations on many hundreds of plants. In British Guiana, Costa Rica, Guatemala and Panama I regularly found colony-founding queens in the internodes of all young trees, often in those only a foot or two feet high. Attention should also be called to the fact that Rettig has described another possible source of ant-food in the "pearl glands" on the leaves of the Cecropias. These structures are very similar to the Müllerian bodies of the trichilia and also contain proteids, oil and sugar.

It is interesting to note that the first observer to call attention to the Coccids and their nutritive value to the Cecropia ants was Thomas Belt (1874, p. 222), though he overlooked their other important source of food in the Müllerian bodies. This is clear from the following passage: "The stem of the Cecropia, or trumpet-tree, is hollow, and divided into cells by partitions that extend across the interior of the hollow trunk. The ants gain access by making a hole from the
outside, and then burrow through the partitions, thus getting the run of the whole stem. They do not obtain their food directly from the tree, but keep brown scale insects (Coccidæ) in the cells, which suck the juices from the tree, and secrete a honey-like fluid that exudes from a pore on the back, and is lapped up by the ants. In one cell eggs will be found, in another grubs, and in a third pupæ, all lying loosely. In another cell, by itself, a queen ant will be found, surrounded by walls made of a brown, waxy-looking substance, along with about a dozen Coccidæ to supply her with food. I suppose the eggs are removed as soon as laid for I never found any along with the queen ant. If the tree be shaken, the ants rush out in myriads and search about for the molester. The case is not like the last one (the bull-horn Acacia), where the tree has provided food and shelter for the ants, but rather one where the ant has taken possession of the tree, and brought with it the Coccidæ; but I believe that its presence must be beneficial. I have cut down some dozens of the Cecropia trees, and never could find one that was not tenanted by ants. I noticed three different species, all, as far as I know, confined to the Cecropie, and all farming scale-insects. As in the bull's-horn thorn, there is never more than one species of ant on the same tree."

H. von Ihering described an exceptional condition in Azteca muelleri Emery which inhabits Cecropia adenopus. In this case the ants construct a large spindle-shaped carton nest in the bole of the tree. The nest is small at first and produces no deformation of the bole, but as the ants enlarge the structure they cut away more and more of the surrounding wood to convert it into carton and the weight of the trunk and crown above the nest causes the bole to bulge at the weakened zone so that the presence of the nest is indicated from the outside. von Ihering interpreted the enlargement which is not produced by any other Cecropia-inhabiting Azteca, as a huge gall, but it is clear that it is nothing of the kind.

Both Schimper and H. von Ihering found that one of the Brazilian Cecropias, C. hololeuca, lacks the trichilia and Müllarian bodies and is not regularly inhabited by ants, and Bailey found a similar absence of these organs in C. sciadophylla var. decurrens in British Guiana, though it is occasionally inhabited by non-oblige Formicidae. On the other hand, I found (1908) that a Porto Rican Cecropia, which I referred to C. peltata L. but which is probably C. Urbaniana Snethlage, possesses trichilia and coral red food-bodies, but is not inhabited by ants. I have made similar observations on the Cecropias of Cuba. In fact, the obligate Cecropia ants, the Aztecas, are absent from all
the West Indian Islands, except a few of the Windward group. It seems that Warming (1894, p. 185, Fig. 6) had previously noticed that the Cecropias of Aguadilla, Porto Rico, though not inhabited by ants, nevertheless possessed distinct but poorly developed trichilia. If I understand his remarks, he inferred that this might represent a degenerate condition due to the absence of the customary insect stimulation. Rettig (1904, p. 16, 21) states that von Meyer (Die Secretionsorgane der Pflanzen, Berlin, 1839) described trichilia in *Porouma guianensis* Aublet and growing among the hairs small granules obviously homologous with the Müllerian bodies of Cecropia.

Bequaert (Wheeler and Bequaert, 1929) has recently compiled the following list of Cecropias definitely known to bear trichilia and to be myrmecophilous:

1. *C. adenopopus* Miquel (= *C. peltata* Vellozo, non Linne) of Brazil. Its normal ant-inhabitant, *Azteca muelleri* Emery, builds in its trunk the large carton nest and produces the swelling above described. In Paraguay, according to Fiebrig (1909), the tree is tenanted by a different species, *A. alsari* var. *mixta*, which causes no modification of thebole.


3. *C. robusta* J. Huber. Common along in the lower Amazon in woods that are frequently flooded. Stated to be myrmecophilous (J. Huber, 1910, p. 61).


9. *C. sciadophylla* Martius. This species is doubtfully myrmecophilous since it possesses no trichilia at the base of the petiole. According to E. H. Snetlage (1923, p. 358), *C. Juranyiana* Al. Richter is merely a variety of *C. sciadophylla*. Another variety, described by Snetlage as var. *decurrents*, was recorded by Ule as inhabited by *Azteca emeryi* Forel. This record may be due to an error or the ants may merely have occupied the hollow stems. Professor Bailey, who
observed the same var. *decurrents* near Kartabo, British Guiana, regards it as non-myrmecophytic. It lacks trichilia and food-bodies, although it possesses a prostoma. He occasionally found certain inquiline ants in the internodes, but no Aztecas.

(10) *C. riparia* "Warburg", Snetlage (1923, p. 363). Brazil. This species is provided with trichilia at the bases of the petioles and Ule (1906) found the internodes occupied by *Azteca alfari* Emery var. *aegilata* Forel.

(11) *C. ficifolia* "Warburg", Snetlage (1923, p. 365). Rio Acre, Brazil. The bases of the petioles bear trichilia and Ule mentions that the internodes are inhabited by *Azteca minor* Forel.

(12) *C. montana* "Warburg", Snetlage (1923, p. 368), of Peru, has trichilia and Ule found it inhabited by *Camponotus* (*Pseudocolobopsis*), *ulei* Forel.

(13) *C. mexicana* Hemsley. A number of ants were found by Ross (1909) in this species, although the bases of the petioles appear to lack trichilia.

(14) *C. leucocoma* Miquel (= *C. arenaria* Warburg). Manaos, Brazil. A true myrmecophilous species with trichilia and food bodies, as Bequaert (Wheeler and Bequaert, 1929) has shown.

(15) *C. obtusa* Trecul. Rio Negro and Rio Branco, Brazil. Like the preceding species, a true myrmecophyte. Studied by Bequaert (Wheeler and Bequaert, 1929).

Bequaert remarks that many other species of Cecropia are known to possess trichilia, *e.g.*, *C. carbonaria* Martius and Miquel, *C. cyrtostachya* Miquel, *C. Dielsiana* Snetlage, *C. Engleriana* Snetlage, *C. Francischi* Snetlage, *C. Glaziovii* Snetlage, *C. leucophaea* Pöppig and Miquel, *C. multiflora* Snetlage, *C. palmata* Willdenow (perhaps the same as *C. obtusa* Trecul), *C. saxatilis* Snetlage, *C. Ulei* Snetlage and *C. Urbaniana* Snetlage. Some botanists assume that all such species are ant-plants. It is, however, by no means certain that the presence of trichilia alone is sufficient to give them the status of myrmecophytes. This is shown by my observations on the Cecropias of Porto Rico and Cuba. A detailed field and taxonomic study of many more of these trees will have to be made before we shall be able to give a satisfactory account of the prevalence and meaning of myrmecophily in the genus.

The ants at present known to nest in the various species of Cecropia, Pourouma and Coussapoa are enumerated in the following list:

(2) *Pseudomyrma ulei* Forel. In twigs and branches of *Coussapoa* sp. Amazonas (E. Ule).


(4) *Solenopsis suavisima* F. Sm. In dry branch of *Cecropia* sp. Brazil (Luederwaldt).


(7) *Crematogaster* sp. In dead wood of *C. adenopus* with young colonies of *Aztecta muelleri*. Brazil (H. von Ihering).


(9) *Cephalotes atratus* L. In large branch of *C. sciadophylla* var. *decturrans*. British Guiana (Wheeler).

(10) *Cryptocerus pusillus* Klug. In dry branch of *Cecropia* sp. Brazil (Luederwaldt).

(11) *Cryptocerus* sp. In dead wood of *C. adenopus*. Paraguay (Fiebrig).

(12) *Aztecta alfari* Emery. In *Cecropia* sp. Costa Rica (A. Alfaro, Wheeler); Panama (Champion); Venezuela; Colombia (Forel).

(13) *Aztecta alfari* var. *aquilis* Forel. In *Cecropia* sp. Brazil (A. Goeldi); Mexiana Island (Hagmann); Colombia (Lallemand).


(19) *Aztecta alfari* var. *mixta* Forel. In *C. adenopus*. Paraguay (Fiebrig); *C. lyratiloba* Miq. Brazil (Luederwaldt); *C. leucocoma* Miq. Brazil (Bequaert).

(20) *Aztecta alfari* var. *ovaticeps* Forel. In *C. lyratiloba* Miq. Brazil (Luederwaldt); In *Cecropia* sp. Brazil (Goeldi, Bequaert).
(21) *Aztica alfari* subsp. *cecropia* Forel. In *C. lyratiloba*. Brazil (Luederwaldt); *C. obtusa* Trecul. Brazil (Bequaert); *C. "peltata"* Dutch Guiana (G. Stahel); British Guiana (H. E. Box); Cecropia sp. (Goeldi, Huber and Ule); in "swamp Cecropia" Brazil (H. v. Ihering).


(27) *Aztica coeruleipennis* Emery. In Cecropia sp. Costa Rica (Alfaro; Wheeler); Guatemala (Champion); Mexico (Schumann); *C. mexicana* Mexico (Ross).

(28) *Aztica constructor* Emery. In Cecropia sp. Costa Rica (Alfaro, Tonduz, Pittier); Guatemala (Wheeler); Panama (Christophersen, Wheeler); in *C. "peltata"*, Trinidad (Wheeler).


(30) *Aztica coussapoa* Forel. In branches of Coussapoa sp. Amazonas (E. Ule).

(31) *Aztica delpini* Emery. In Cecropia sp. (probably) Matto Grosso, Brazil (Germain).


(34) *Aztica delpini* subsp. *antillana* var. *guadeloupensis* Forel. In Cecropia sp. (probably) Guadeloupe (Forel); Roseau, Dominica (F. Lutz).


(38) *Aztecta foreli* Emery var. *eiseni* Pergande. In *Cecropia* sp. (probably *mexicana*) Colima, Mexico (Townsend).


(41) *Aztecta instabilis* F. Sm. In *Cecropia* sp. (Mexico, Colombia, French Guiana, Central America); in *C. angulata* Bailey. British Guiana (Wheeler).

(42) *Aztecta lanuginosa* Emery. In *C. hololeuca* Miq. Brazil (Luederwaldt) In *C. adenopus* Brazil (H. von Ihering); in carton nests on *Cecropia* sp. (W. Ehrhardt).


(45) *Aztecta schimperi* Emery. In carton nest on *C. leucocoma* Miq. Manaus, Brazil (Bequaert).


(49) *Aztecta ulei* Forel var. *gibbifera* Forel. In trunk of *Cecropia* sp. Brazil (Luederwaldt).


(51) *Aztecta xanthochroa* Roger. In *Cecropia* sp. Costa Rica (Alfaro, Schwarz and Barber); Guatemala (Wheeler); in *C. mexicana*. Mexico (Ross).


(53) *Aztecta xanthochroa* subsp. *australis* Wheeler. In *Cecropia* sp. (very probably), Peru (Staudinger).

(54) *Aztecta xanthochroa* subsp. *salti* Wheeler. In *Cecropia* sp. Colombia (G. Salt.)


(56) *Camponotus* (T. *mexyrmex*) *bonariensis* Mayr. In dead wood of *C. adenopus*. Paraguay (Fiebrig).

(58) *Camponotus (Myrmothrix) balzani* Emery. In dead branches of *C. adenopus*. Brazil (H. von Ihering).

(59) *Camponotus (Myrmothrix) rufipes* Fabr. subsp. *renagleri* Emery. In dead wood of *C. adenopus*. Paraguay (Fiebrig).

(60) *Camponotus (Myrmobrachys) canescens* Mayr. In trunk of *C. adenopus*. Brazil (Luederwaldt).

(61) *Camponotus (Myrmobrachys) vezenyi* Forel. Occasionally in dead wood of *C. adenopus*. Paraguay (Fiebrig).


 Probably all the ants in this list, except the Aztecas, are to be regarded as merely occasional inhabitants, or inquilines. And even among the Aztecas only certain species would seem to be really obligatory tenants of the plants—namely *A. alfari, delpini, coeruleipennis, constructor, muelleri* and *zanthochroa*. Of these *A. alfari* is the Cecropia ant par excellence. Its geographical range is almost coextensive with that of the plants. It is represented by some 14 different varieties and subspecies, ranging from Mexico to Paraguay and Argentina, and is known to inhabit at least six or seven different species of Cecropia. No doubt further collecting will add considerably to the number of recognizable forms of this highly variable insect.

While the earlier observers, Fritz Müller and Schimper, were inclined to regard the Aztecas as the protectors of the Cecropias against the attacks of the Attini, or leaf-cutting ants, all the more recent authors, including H. von Ihering, Rettig, Fiebrig, Ule, Bailey and myself, have come to see in the Attini no such menace to the life or well-being of the plants. The various arguments in support of this contention have been set forth in detail, especially in the contributions of von Ihering, Fiebrig and Bailey, and need not be repeated here. That the Cecropias are centers of important biocenoses consisting of a great number and variety of organisms, some of which are far more injurious than the Attini, was first shown by Fiebrig in his study of *C. adenopus* in Paraguay. A conspectus of the forms he recorded together with additions by von Ihering, Bailey, Zetek and others, is given in the following paragraphs:

**Mammalia.** Fiebrig mentions apes and bats (Phylostoma sp.) as eagerly feeding on the fruit of *C. adenopus*. The most important mammal, however, is the sloth, *Bradypus tridactylus* L., which accord-
ing to Bates, H. von Ihering and others regularly devours the foliage and is not molested by the Aztecas. The sloth's relation to the tree is, in fact, so constant and so well known to the natives that the name "imbauba" and its derivatives really mean "slothtree". Menegaux (1909), in his monograph of the genus Bradypus, states, on the authority of Geay, that the sloth feeds only on Cecropia leaves and cites Gmelin (1788), who says that B. tridactylus "vicitat folis teneris imprimis Cecropiae, non bibit, imbre metuit." Observations on the sloths at the Barro Colorado and Kartabo laboratories confirm this statement in regard to the feeding habits of the animal.

Aves. Fiebrig mentions doves as occupying the adenopus trees and feeding on their ripe fruit and woodpeckers as devouring the Heliotis larvæ (vide infra) which live in the twigs and branches. He also observed birds' nests among the foliage and figures one of them.

Lepidoptera. No less than six different moths and butterflies feed as larvæ on the large leaves of the Cecropias:

1. Gynaecia dirce L. The caterpillars of this beautiful Nymphalid were found feeding in great numbers on Cecropia at Ancon by Mr. Zetek. They are black with branched orange-colored spines. The pupa is gray and provided with two broad horns at the anterior end. Gundlach (Wolcott, 1923) had previously noted the same habit of the caterpillars in Porto Rico: "la oruga vive debajo de hoja de Cecropia, comiendo las nervosas gruesas."

2. Historis orion Fabr. Mr. Zetek also found the caterpillars of this Nymphalid devouring the foliage of the Cecropias at Ancon and reared the butterflies. The caterpillar is described by Wolcott (1923) as flattish, medium gray, with white saddle and states that Gundlach notes its occurrence on C. peltata in Porto Rico ("la oruga se crea en la Cecropia).

3. The Syntomid moth, Correbidia terminalis Walker, is cited by Wolcott from Porto Rico with the following note by Gundlach: "vive en la cara inferior de las hojas de Cecropia, formando luego im capullo poco primeroso."

4. The Dioptrid moth, Diops ocellata Cr., is another Cecropia pest which was observed by Fiebrig in Paraguay. "The hairy larva of Diops ocellata Cr., devours the large leaves. It is not easily detected on the white-felted undersides on account of its chalky-white, black dotted coloration. I often found this larva, which reaches a length of 4 cm., in considerable numbers on a tree."

5. Fiebrig describes another moth caterpillar (undertermined) "of respectable dimensions" as living in the cambium layer of the C.
adenopus trunk. The pupa “rests beneath the bark, which at one point is perforated by a T-shaped slit that enables the beautiful chocolate brown and sulphur-yellow moth to escape. The injury to the tree caused by this caterpillar is probably unimportant.”

(6) Heliothis sp. Fiebrig also describes in detail the habits of an undetermined boll-worm. He says: “The third caterpillar which I observed on Cecropia belongs to the moth 7584 (Heliothis sp. in litt.) and is unquestionably the most interesting. It competes with the Azteca (alfari var. mixta) and lives in the younger portions of the twigs, precisely where the Dolichoderine is encountered. Such caterpillar-infested twigs are extremely common at all seasons of the year. At certain times I found them on nearly every tree I examined and in large trees with 60-80 main and accessory twigs I have found 30-50 of them occupied by the twig-mining caterpillars.” After describing the perforation of the twigs by the woodpeckers which feed on the caterpillars, Fiebrig continues: “I was long uncertain in regard to the time and place of the caterpillar invasion till I succeeded in finding their youngest stage, scarcely more than a millimeter long, in company with the Aztecas that were just founding their colonies in the uppermost chambers! Here I detected the obviously just hatched caterpillar in the completely closed internodal cavity beside the egg-laying ant-queen with her eggs and larvae and embedded in and evidently feeding on a damp brown mass of pith which had been chewed up by the mother ant. On several occasions also I found these small caterpillars up to a length of 6 mm. in the initial chambers of both young and older trees and repeatedly in company with just-emerged Azteca workers. Later, however, when, after perforation of the disseipments, a greater portion of the twig becomes habitable by the ants, the caterpillars and ants were no longer observed in one another’s company. Often, indeed, I found them separated, the Azteca being in the outermost tip of the twig and the caterpillar below, shut off by an intact disseipment. While, therefore, at first the ant and caterpillar live peaceably side by side—a condition the more remarkable, because the small, large-headed, strongly mandibulate caterpillars differ so markedly from the white, nearly naked Azteca larvae in their darker color and habitus, and especially in possessing stiff bristles—later the “pugnacious” ants, which move upwards towards the tips of the branches, followed by the caterpillars, nevertheless leave the latter in full possession of the Cecropia twigs. Since we cannot suppose that the soft-skinned caterpillars are aggressive, we shall not be mistaken in inferring that the ants are driven out
by the masses of caterpillar frass, often spun together, which plug up the chambers and render them uninhabitable. It is also possible that the caterpillars, which are capable of emitting considerable mucus, may use their silk as a means of defense. Only after the caterpillars have completely eaten out the ambay twig, does one of their number about to pupate, gnaw a large hole in the wall of the twig at one of the former ant-entrances. This opening is used as an exit not only by the individual that made it but also by all the other moths that develop in the twig! "It would seem, therefore, that the Heliothis caterpillars in their younger stages are synecetes of the Azteca, that after hatching from eggs laid by the mother moth on the outer surface of the plant, they probably enter the internodes through the perforations made by the nest-founding queens and that later the peculiar habits of the caterpillar render any further synecetism with the ants impossible. It is probable that this same Heliothis larva was observed by Schimper (1888). At any rate, his Fig. 3, Pl. II, shows a similar caterpillar lying on a large mass of frass in a young adenopus internode just above a cavity inhabited by Azteca.

(7) Another undetermined Lepidopteron caterpillar is mentioned by H. von Ihering in Eastern Brazil.

_Hymenoptera._ The following Chalcidids, Vespids and Apids have been found associating with Cecropias or their ants:

(1) _Conoaxima affinis_ Brues (1922). This Chalcid was described from a specimen which I took in a Cecropia internode (not in an Acacia spine, as stated by Brues!) at Quirigua, Guatemala, in 1911. I have since taken both sexes of the species at Balboa, C. Z., and have seen the larvae in various stages devouring the young colony-forming queens of _Azteca alfari_ subsp. _lucidula_ var. _canalis._

(2) _Conoaxima aztecicida_ Brues. The habits of this species, which was taken in 1920 by Professor Bailey in internodes of _C. angulata_ at Kartabo, B. G., are the same as those of the preceding species. The larvae were found destroying the young nest-founding queens of _A. constructor_ and _A. alfari._ Professor Bailey's observations are recorded in the following note: "Although many of the successive internodal cavities of each young plant become inhabited, few of the queens succeed in raising a brood. When the stems are cut open, most of the chambers are found to contain dead queens. I was unable to account for this high mortality until I discovered the presence of a small scar in the callus which fills the entrance aperture. This scar within a scar indicated, of course, that some insect had emerged since the queen became sealed within her domatium. Following up this clue, I soon
found chambers—with modified callus in the apertures—which contained, in addition to the dead and frequently dismembered queen, the larva, pupa, or imago of a Hymenopterous parasite. The evidence at hand seems to indicate that the queens are parasitized before they enter their dwellings.”

(3) Conoaxima sp. A specimen of an undescribed species of Conoaxima was recently found by Dr. George Salt in the topmost internode of a young Cecropia at Vista Nieve, at an altitude of 5000 ft. in the Sierra Nevada de Santa Marta, Colombia. The internodes of the plant, which was only about 6 ft. high, were occupied either with solitary nest founding queens of a new subspecies of Azteca xanthochroa Roger, which I have called salti, or lower down with young colonies consisting of queens with brood or with brood and small workers. In the internode containing the Conoaxima was a mouldy mass, in all probability the remains of an Azteca queen that had been devoured by the parasite.

(4) H. von Ihering mentions a rather large Chalcid which he found in the midst of ants (Azteca muelleri) in C. adenopus at Alto da Serra, Brazil. In all probability the insect was one of the Eucharidæ, many species of which are known to parasitize ant-larvae.

(5) The Calverts (1917) found on one of the branches of a Cecropia in Costa Rica a large pendent paper-covered nest which was occupied by an active colony of wasps (apparently some species of Polybia) for at least four months.

(6) Tripona sp. At Kartabo, B. G. Professor Bailey discovered a colony of a very small stingless bee, which Professor Cockerell has identified as an undescribed species, near goeldiana, in the internodes of a branch of Cecropia angulata. This nest is figured in my “Social Life among the Insects” (1923). The same bee was also found nesting in a hollow liana.

Diptera. The following five Diptera seem in their larval stages to be either scavengers in decomposing portions of the Cecropias or parasites of leaf-eating species.

(1) Great numbers of a Tachinid fly were bred by Mr. Zetek from the pupæ of the Chrysomelid beetle, Cœlomera cayennensis Fabr. (vide infra), which feeds on the foliage of the Cecropias at Ancon, C. Z.

(2) H. von Ihering bred a species of Drosophila from larvæ living in matter derived from the decomposition of vegetable excrescences in an internode of C. adenopus.

(3) Prof. Bailey bred numbers of a species of Drosophila from the male aments of C. angulata at Kartabo, B. G.
(4) von Ihering mentions slender Dipteran larvae in soft, gelatinous excrescences in the upper internodes of *C. adenopus*.

(5) Fiebrig found the moist frass masses of the Heliocthis caterpillars described above to contain Dipteran larvae.

**Coleoptera.** Some six or eight different beetles have been found to attack Cecropias:

(1) A small unidentified Bostrichid, according to Fiebrig, feeds not only on the dead twigs of *C. adenopus* but often also on the green internodes inhabited by the Aztecas. The female beetles lay their eggs in the fresh cambium and the hatching larvae completely destroy this layer and also bore into the wood.

(2) Fiebrig found a Cerambycid which bores both in the dry twigs and in the wood of the trunk.

(3) *Coelomera cayennensis* Fabr. According to H. von Ihering, this Chrysomelid and a similar but smaller species lay their eggs on the leaves of *C. adenopus* and there undergo their entire development. "The larvae gnaw away the upper layers of the leaf but are never molested by the ants, notwithstanding their great injury to the foliage." Mr. Zetek has found this same beetle in all stages on the Cecropias at Ancon, C. Z. and has bred from its pupae numbers of Tachinid flies (*vide supra*). The full-grown larvae measure about 15 mm. and have the abdominal segments provided laterally with blunt-spines and the last segment developed as a large, rugulose, shovel-shaped organ. They are opaque blackish with the head, pronotum, legs and several tuberculate spots on the dorsal surface of each abdominal segment, except the last, dull orange yellow. Most of the larvae pupated January 16, the pupae being naked and attached to the leaves by their posterior ends. The imaginal beetles, which emerged February 20, have opaque black elytra, with the remainder of the body more shining and of a dirty fulvous tint, except the antennæ, tibie, tarsi and venter, which are black. The Cecropias are very probably the true host plants of this beetle, which has very nearly the same geographical distribution. It was originally described from French Guiana. In the Bowditch Collection of Chrysomelidae in the Museum of Comparative Zoölogy I have seen specimens from Peru, Colombia, Venezuela, Bolivia, Panama, Yucatan and Rio de Janeiro, Brazil.

(4) Fiebrig mentions a Chrysomelid, possibly *C. cayennensis* or an allied species, as feeding on the leaves of *C. adenopus* in Paraguay.

(5) He also mentions a very common Chrysomelid larva, evidently one of the Cassidinæ, as feeding in dense droves on the foliage. It
possesses a blackish brown, chitinous, disk-shaped process, which it
holds over its back when disturbed, like the similar processes, often
covered with faeces, seen in other members of the group.

(6) The larva of a Hispidine Chrysomelid, according to Fiebig,
often mines the lobes of the leaves in succession, surrounding each
with a gallery and eventually pupating and completing its develop-
ment in a boss-shaped gall at the base of one of the lobes.

(7) A small yellow Curculionid is said by Fiebig to visit the
catkins.

(8) Great numbers of small Curculionids, possibly allied to the
preceding species, were found by Professor Bailey in the male aments
of *C. angulata* at Kartabo, B. G.

Orthoptera. Fiebig observed Mantids and migratory locusts on the
foliage of *C. adenopus*. The latter almost completely defoliated whole
groups of the trees in the course of a few hours.

Thysanoptera. Very common, according to Fiebig, on the under
surfaces of the leaves.

Heteroptera. Fiebig records several Lygaeids, especially a pale
brown and a delicate white species, as infesting the lower surfaces
of the leaves, and a stout brown Pentatomid which guards its eggs on the
foliage. All three of these bugs are extremely common and may occur
on the same tree. They are in all probability very injurious.

Homoptera. Fiebig mentions a prettily colored Jassid as being
common in all stages on the leaves. He also found an aphid and a
pinkish Cocciid living with the ants in the internodes. Wolcott (1923)
records *Aphis gossypii* Glover as occurring on the leaves of *C. peltata*
at Lares, Porto Rico.

Acarina. A species of mite is recorded by Fiebig as occurring
among the Thysanoptera on the undersides of the leaves of *C. adenopus*.

Nematoda. A Tylenchus-like form was found by Fiebig living
among the moist detritus left by the Heliocthus larvae in the twigs.

Fungi. Moulds occur in the same situation as the Nematodes and
are often found covering the bodies of young queens that have died
in the internodes before establishing colonies.

This list comprises some forty different organisms, mostly associated
with a single species of Cecropia (*adenopus*). Fiebig states that he has
omitted a number of forms and remarks: “When I compare them with
the Hexapods occurring in Paraguay on other plants, it seems to me
that the ambay is more thoroughly infested than the great majority of
the woody plants of the region, and this the more astonishing, because
its leaves are not enticing nor juicy and because the tree might seem
to be protected from most of its enemies by the peculiar properties of its sap."

Among the organisms enumerated in the foregoing list the Coccids occupy a constant and privileged position. All those who have studied the Cecropias carefully—Belt, Fritz Müller, Schimper, Warming, H. von Ihering, and Fiebrig—have noticed these insects and all, with the exception of Fiebrig, have regarded them as an important source of food for the Aztecas. Fiebrig’s assertion that they "have no direct relations with the ants" must be attributed to faulty observation. Recently Professor Bailey has devoted special attention to the Cecropia coccids and has made some observations of interest in connection with the species occurring in other myrmecophytes. I quote from his paper (1922, p. 388) which owing to its publication in a botanical journal, may be readily overlooked by entomologists: "Having found a very close and significant relation between ants and coccids in most Ethiopian ant-plants, I devoted particular attention to the investigation of their behavior in C. angulata. I did not succeed in finding a single large, ant-inhabited specimen which did not contain numerous coccids. When a tree is split open the ants are as solicitous for the welfare of the coccids as they are for that of their eggs, larvae and pupae. They seize them in their mandibles and carry them about until some unopened portion of the plant is found where they may be deposited in safety. In artificial nests, the workers spend hours in tending and stroking the coccids, and in feeding upon their sugary exudates. In view of these facts, it cannot be doubted that the miniature milk cows are an important source of liquid carbohydrates for the ants.

"As in many of the African myrmecophytes the ants excavate pits in the walls of their domatia which enable the coccids to reach and feed upon the softer tissues of the Cecropia. Such excavations are essential, owing to the fact that the internodal, medullary cavity is entirely jacketed by a dense, horny layer of sclerenchyma. In the African ant-plants, the ants cut through to the cambium and induce the formation of a nutritive callus. In C. angulata the pits are not located in the sides of the internodal chamber, but in the nodal diaphragms. At the time when the ants begin their excavations, the nodal partition consists of five distinct layers. The soft internal layer, which is provided with strands of conducting tissue and which is fed upon by the coccids, is separated from the external layers of porous, medullary tissue by two layers of dense, thick-walled tissue. The ants remove the two external layers and cut circular pits in the underlying sheets of horny sclerenchyma. The coccids sit in these pits and thrust
their setae into the succulent tissue which is thus exposed. That the pits are not made by the coccids, as suggested by von Ihering is indicated, not only by the fact that the delicate sucking mouthparts of these insects are not adapted for excavating in dense tissues, but also by the fact that I have actually observed the ants in the process of excavating them."

The preceding account of the Cecropias shows that the general picture of their relations to the ants is very similar to those of other myrmecophytes with hollow or fistulose stems or petioles, such as the Cordias, Tachigalias and Triplarisæ, but there are two peculiarities, the preformed pit, or prostoma of the internodes and the Müllerian bodies, which have been repeatedly cited by authors as irrefutable proof of the adaptation of the trees to the Aztecas. The prostoma, however, is now generally conceded to be merely a deepening of the groove, or rill formed by pressure of the axillary bud. Prof. Bailey found that as a rule no pit is present in C. angulata, but merely a broad groove, whereas in C. sciadophylla var. decurrens, which is not inhabited by Aztecas, the thinning of the internodal wall in the groove is much greater than in angulata. "Such facts as these," he says, "suggest that the so-called prostoma of C. adenopus, and of other myrmecophytic species of Cecropia, is not an adaptation for attracting ants, but is merely a structural peculiarity, produced by the pressure of the axillary bud, which is utilized by the ants in their parasitism upon the plants."

There remain then only the Muellerian bodies and possibly the pearl glands to support the view that the Cecropias have developed specific attractions or inducements for the ants. But the botanists have recently also cast doubts on the finalistic interpretation of these structures. The matter is well summarized in the following passage from Professor Bailey's paper (1922, p. 387): "These small bead-like structures, which are packed with fat and protein, are formed in large numbers in a curious cushion or mat of hairs situated at the base of each petiole. The ripe food bodies are so assiduously collected by the ants that it is almost impossible to find one in situ, except in young uninhabited plants. Indeed, the ants frequently trim away the surrounding hairs and dig out the immature food bodies. Schimper interpreted these so-called Müllerian corpuscles, and similar structures which occur on the leaflets of certain myrmecophytic species of Acacia, as metamorphosed glands or highly specialized allurements for attracting ants. Rettig and others, however, have called attention to the fact that such glands occur on plants that
are not frequented by ants, and it is difficult for the adherents of myrmecophily to account for such occurrences without resorting to the purely gratuitous assumption that they are survivals from former symbioses. Ule is of the opinion, in addition, that the expenditure of carbohydrates and nitrogenous substances, contained in these corpuscles, is not compensated for by the protection which the ants afford to the plants."

Chapter 5. NOTES ON RUBIACEÆ AND VERBENACEÆ

Of all the families of plants the Rubiaceae comprise the greatest number of myrmecophytes, but curiously enough, nearly all of these are paleotropical. From the Neotropical Region only a few species of Duroia, Remijia and Patima are known to be associated with ants. Though the genera Randia, Uncaria, and Psychotria occur in both hemispheres, and in Africa and New Guinea comprise some noteworthy ant-plants, none of the American species, so far as known, has developed this peculiarity.

(A) Duroia and Remijia

The genus Duroia, which is confined to the Amazonian region and northern South America, includes 10 species, three of which are known to be myrmecophilous, namely D. hirsuta Pöppig and Endlicher, petiolaris J. D. Hooker and sacchifera (Martius). The last is provided with a pair of peculiar sac-shaped domatia at the bases of the leaf-blades; the other species have no such structures but instead present swollen internodes which are inhabited by ants. A fourth species, D. dioica Karsten has similar swollen internodes but these are not definitely known to be inhabited by ants. Only one of the 14 known species of Remijia, R. physophora Bentham, is myrmecophilous and like D. sacchifera possesses a pair of pouches at the leaf-bases.

Spruce (1869, in 1908, p. 396) has the following notes on Duroia sacchifera (= Amajoua or Amaiona sacchifera, incorrectly cited as "Amaiona") and Remijia physophora: "Rubias afford a few instances of sac-bearing leaves, especially in the genus Amaiona (Aubl.). In caatingas of the Rio Negro, almost throughout its extent, grows Amaiona sacchifera Mart., a small bushy tree with leaves three together, above a foot long, obovate with a minute apiculus, tapering to the base, where there are two contiguous sacs inhabited by small red
fire-ants. The fruit resembles a large plum (except that like the leaves it is harshly hairy), and when ripe is soft and edible; but long before it reaches that stage the ants crowd on it and seem to suck the juices through the pores of the cuticle. To the same order belongs Remigia physophora Bth., a remarkable tree found at the falls of the Uaupes, having the aspect of an Amaiona, but the dry capsules and other characters of Cinchona and its allies. The opposite leaves, 9 inches long, are oblong-oval, obtuse with a short apiculus, near the base abruptly panduriform and bearing a small ant sac on the midrib. All the other known species of this large genus have nonsacciferous leaves."

In 1889 Schumann also published on Duroia and Remijia. Of the former genus he studied the three species petiolaris, hirsuta and saccifera, but his account is too long for quotation. In petiolaris and hirsuta the internodes of the terminal flower-bearing branches form hollow, spindle-shaped thickenings distally and these are provided with a longitudinal cleft or sometimes with two clefts, one above the other, in which the ants make their entrances. The third species, saccifera, has, as Spruce observed, a pair of sacs at the base of the leaf on the upper side. Each sac has its own preformed entrance, which is on the upper side of the leaf blade. Neither Schumann's figure nor his description yield a very clear notion of the position of these entrances. He also gives a brief account of Remijia physophora, which has similar sacs but their openings are on the lower surface of the leaf-base.

Ule's description (1907) of D. hirsuta, which he observed in the field, is very clear. He writes: "To the family Rubiaceae belongs Duroia hirsuta K. Sch., a small dioecious tree, 3 to 5 meters high, which grows both in the inundated forest and on terra firma. The short-petioled leaves are about 18 to 24 cm. long and 7 to 10 cm. broad and ovate. Above and along their edges they bear rather long, sparse, eventually deciduous hairs; beneath the ribs especially are always coarsely hairy. The stipules are united to form an elongate conical hood, covered basally with a circket of long hairs, among which scattered glands persist. Duroia has terminal, corymbose cymes of white flowers. The terminal branches consist of an elongate internode, which is followed by a very short one and finally by the inflorescence. Now the elongate internode also develops towards its tip a bladder-like dilation which bursts open on the underside and there displays a groove the tips of which heal over. In this slit there is a perforation made by the ants. These hollow stems are always inhabited by two species of ants, Myrmelachista nigella Roger and Azteca duroiae Forel n. sp." The
formation of the internodal cleft by dehiscence, as described by Ule, is interesting in connection with the similar formation in Triplaris (see p. 49).

More recently Bequaert (Wheeler and Bequaert, 1929, p. 16) has been able to study *D. saccifera* in the type locality near Manaos, Brazil, where he found it growing in dense thickets of the second growth woods. He describes the plant and its domatia as follows: "It forms either a low bush about 6 feet high, with hard, woody twigs, or a small tree, 8 to 10 feet high, with an unbranched main stem of about 5 feet. The leaves are placed in whorls of three, more rarely opposite, especially in young plants, and near the base of the branches. They measure 15 to 30 cm. in length and 5.5 to 12 cm. in greatest width and are elongate-oval, with entire margins, ending in a short slender point. The basal half is gradually attenuate, the base itself briefly rounded off. The petiole is very short and almost wholly occupied by the lateral pouches. At the tips of the branches the leaves form an elongate bud enclosed in a large bract, which drops off after the leaves develop. The entire plant is covered with hispid, somewhat whitish hairs, which are particularly long on the stem; the midrib of the leaves and the myrmecodomatia. Neither flowers nor fruit were seen." Spruce's account of these has been quoted. "The myrmecodomatia of *D. saccifera* are two pouches at the base of the leaf on each side of the petiole. The sacs are completely separated from each other by the whole width of the petiole on the upper as well as on the under side of the leaf. They are nearly symmetrical, ovate, 10 to 14 mm. long, 6 to 7 mm. wide and 4 to 6 mm. thick, and are completely closed at the lower end and along the petiole, but open at the upper end by a narrow slit in the deep, sinuous notch that divides the base of the leaf-blade from the pouch. The pouches might be regarded as having been formed by the recurring of the decurrent bases of the blade to the upper side of the leaf, and the growing fast of the free edges of the recurved portion of the petiole. If this conception of their mode of origin is correct, the outer surface of the domatia corresponds to the underside of the blade and their inner surface to the upperside. Both the inner and outer surfaces are densely covered with long, hispid hairs. Those of the inner surface converge towards the upper slit, which they partly close. The ants found in the myrmecodomatia were *Solenopsis corticalis* Forel and *Brachymyrmex heeri* Forel var. *aphidicola* Forel. It is interesting to note that in spite of the pouches being inhabited by ants, the young leaves of this plant were badly damaged by leaf-cutting ants (Attini), while the older leaves were eaten by caterpillars. The same
species of Duroia was observed at Carmo, on the right bank of the Rio Branco, September 1. In this locality the ants found in the pouches were *Azteca ulei* Forel var. *cordax* Forel."

The various ants which have been taken in the domatia of Duroia and Remijia are enumerated in the following list:


Owing to the small size of the domatia, especially the leaf-sacs, all of these ants belong to diminutive or very small species. Moreover, most of them are timid and harmless and none of them can be of any considerable use to the plants. So far as we are able to judge from the list, the ant fauna of the Duroias varies with the locality and consists largely of forms which occur also in *Cordia nodosa* and the Melastomaceae, which have leaf-sacs (vide infra) much like *D. saccifera* and *Remijia physophora*, or in almost any convenient plant cavities.

(B) *PATIMA FORMICARIA* Johnston

Mr. H. O. Lang, while on an expedition in British Guiana during 1922, discovered another Rubiaceous myrmecophyte with fistulose stems which are regularly inhabited by ants. He kindly sent me a number of herbarium specimens of the plant together with its tenants. Dr. I. M. Johnston of the Gray Herbarium has since described it as
Patima formicaria (1924, p. 83), a species allied to P. guianensis Aublet, "but having taller tetragonal stems, larger long-acuminate leaves, larger flowers and apparently many-celled fruit." Mr. Lang has supplied the accompanying photographs (Plates 13–14) and the following field note: "The plant was growing in most cases as single stems like large-leaved shoots. Though this no doubt is its regular way, in a few instances there were as many as four or five together arising from the same root. They were about 6 to 9 feet high, with lemon-yellow flowers and spinach-green fruit. I found them growing in the tropical rain forest trees about 150 feet high and collected about 30 of these shoots from different places on the hill which is just at the mouth of the Merume Creek, facing the Mazaruni River. Although all the shoots of the plants were hollow, not all of them contained ants." The Gray Herbarium also possesses specimens of this plant collected by Hitchcock at Tumatumari on the Potaro River, B. G.

The specimens received from Mr. Lang show that the plant is very smooth, with long, lanceolate, opposite leaves and tetragonal fistulose stems about 1.5 to 2 cm. in diameter. The longer internodes measure about 5 to 10 cm. and have large medullary cavities. Some of the shorter internodes are more swollen in the middle, or fusiform. There are elliptical openings made by the ants just below the nodes, and the insects gnaw through the latter, thus making the internodal cavities continuous. No Coccids were present on the walls of the cavities. The following ants were taken by Mr. Lang in the living internodes:

1. Neoponera carinulata Roger.
2. Pseudomyrmca tenax Mayr.
3. Crematogaster (Orthocrema) limata F. Sm. var. palans Forel.
5. Camponotus (Paracolobopsis) patima Wheeler.
6. Camponotus (Paracolobopsis) patima var. dolentulus Wheeler.

The first to fourth in this list are species that occur also in dead twigs of various neotropical plants. The Camponotus may have similar habits or it may, perhaps, prove to be an obligate tenant of the Patima.

Borreria verticillata L. is yet another Rubiaceous plant in the stems of which I found a number of ants in British Guiana, but as only the dead stems are inhabited, this case had best be considered in connection with a number of other nonmyrmecophytic plants. (see p. 92).
(C) Clerodendron Siphonanthus R. Br.

No verbenaceous myrmecophytes have been recorded from the New World though there are several belonging to the genus Clerodendron and at least one belonging to the genus Vitex in the Old World tropics. Mr. Zetek and I, while examining the ornamental trees and shrubs planted many years ago on the Prado at Balboa, C. Z., came upon a specimen of the Oriental Clerodendron Siphonanthus R. Br., which must have been set out as a seedling. Having attained a height of about seven feet, it was beginning to die as a result of heavy infestation by scale insects. It had evidently flowered and fruited in preceding years, because there were growing near it a number of vigorous young plants from a few inches to about three feet high. On closer examination the old plant was seen to be tenanted by two species of ants, Pseudomyrmex gracilis var. bicolor and Azteca velox subsp. nigriventris. The former occupied only a single branch, the latter all the remaining branches and the trunk. The insects were living in the internodes, whose medullary cavities they had made continuous by gnawing through the nodes. In the smaller branches these cavities were as much as 4 to 5 mm., in the larger branches and trunk only 2.5 to 3 mm. in diameter. The ants had made no entrances in the walls, but seemed to have gained access to the medullary cavities through the broken ends of a few of the branches. At intervals on the walls of the internodal cavity there were latrines, i.e. blackened accumulations of feces and infrabuccal pellets, invaded by many Nematodes, moulds and bacteria. Dr. Cobb has studied the Nematodes. On the surfaces of the branches the ants were busily attending great numbers of Coccids, among which Mr. Zetek distinguished four species. The most abundant was identified by Dr. H. Morrison as Saissetia hæmispherica Targ. Two species of Aleurodidae and two species of spiders were taken on the foliage.

I have recorded this instance of an Oriental plant, belonging to a genus known to contain several myrmecophytes and peopled by Neotropical ants, because it is the converse of Morteo’s case of the Triplaris americana introduced into the East Indies and there acquiring one of the native ants (Dolichoderus bituberculatus) as a tenant. I am inclined to believe that the Clerodendron siphonanthus at Balboa was first attacked by the scale-insects and that these then attracted the Aztecas and induced them to settle in the cavities of the stem and branches. The two cases, that of the Triplaris and that of the Clerodendron, suggest that some interesting modifications of ant-
behavior might be obtained by introducing Old World myrmecophytes into the American tropics and vice versa.

Chapter 6. THE MYRMECOPHYTIC ACACIAS

Several shrubs and trees of the huge Mimosaceous genus Acacia, which comprises more than 600 described species, widely distributed in the tropical and subtropical regions of both hemispheres, have unusually large, paired, stipular spines which are regularly inhabited by ants. These myrmecophytes may be divided into three groups, according to their peculiar discontinuous geographical distribution, the first comprising the famous bull-horn Acacias, ranging from Northern Mexico to Colombia, with a doubtful species in Cuba, the second represented by the single species, *A. cavenia*, in Paraguay, and the third comprising some seven species in the savannas of Eastern Africa. The bull-horn Acacias present the most interesting and intricate problem and therefore require a more detailed discussion; the Paraguayan and African forms, which are perhaps not true myrmecophytes may be dismissed with briefer discussion in the concluding paragraphs of this section.

(A) The Bull-horn Acacias

The bull-horn Acacias, known to the natives of Mexico as "cuernezuelo", "cornisuelo", "palin", or "guisache corteno" and to the Panamanians as "cuernito" or "cachito", are bushes or small trees, rarely attaining a height of 20 feet, with delicate pinnately compound leaves with one or more extrafloral nectaries on the upper surface of the petiole and usually one between each pair of pinnæ on the rachis and with huge paired spines which are filled with a pulpy medullary substance till they are full-grown. The young leaflets produce small, elongate-elliptical, yellow or whitish food-bodies ("Beltian bodies") at their tips. The ants enter the mature spines by gnawing an opening just below the tip of one of the pair and then hollow both of them out, thus producing a bifurcate domatium with a single entrance. They collect, store and eat the food-bodies and visit the extra-floral nectaries. The flowers are yellow, buff or flesh-colored, small and aggregated in dense spadix-like, cylindrical spikes or globose heads. The pod-like fruits show considerable variation in structure in the different species, being indehiscent or dehiscent on one or both sides and with the seeds in some species embedded in a
sugary, pulp-like arillus. As a rule, the species prefer rather dry, open country (savannahs), but I have found one of the Panamanian forms (*A. melanoceras*) growing in swamps or moist jungle along water-courses.

Until recently it was supposed that there were less than half a dozen authentic species of bull-horn Acacias, but Safford (1910, 1914, 1915, 1923) and Schenck (1913, 1914), after studying a considerable amount of herbarium material have recognized as many as 28. These are here listed alphabetically, with their known geographical distribution:

*buclerophora* Robinson. British Honduras (Plate 15).
*bursaria* Schenck. Western Guatemala (Plates 16–17).
*campecheana* Schenck. Yucatan, Sinaloa (Plate 18).
*chiapensis* Safford. Chiapas, Mexico.
*collinsii* Safford. Chiapas, Mexico (Plates 19–22).
*corniger* Linné. (= *spadicigera* Schl. & Cham.) Vera Cruz, Mexico (Plates 25–29).
*costaricensis* Schenck. Costa Rica; Nicaragua (Plate 30).
*cubensis* Schenck. Northern Cuba.
*dolichocephala* Safford. Veracruz, Mexico (Plate 31).
*donnelliana* Safford. Honduras (Plates 32–33 a).
*furcella* Safford. Veracruz, Mexico.
*globulifera* Safford. Northern Yucatan (Plate 33 b.)
*herandezii* Safford. Central Mexico.
*interjecta* Schenck. Singapore (in cultivation).
*multiglandulosa* Schenck. Eastern Panama (Plates 37–38).
*Nelsonii* Safford. Guerrero, Southwestern Mexico (Plate 39).
*nicoysensis* Schenck. Costa Rica (Plate 40).
*panamensis* Schenck. Panama.
*penonomensis* Safford. Panama.
*rossiana* Schenck. Veracruz, Mexico.
*sinaloensis* Safford. Sinaloa, Mexico.
*sphaerocephala* Schlcht & Cham. Veracruz, Mexico (Plates 41–43).
*tepican* Safford. Tepic, Western Mexico.
*turgida* Safford. Chiapas, Mexico (Plate 45).
*veracruzensis* Schenck. Veracruz, Mexico.
*yucatanensis* Schenck. Yucatan, Honduras.

An even more recent study of these plants by Standley (1922, 1928) has led to a considerable reduction in the number of species. He re-
gards Hernandezi and furcella as synonyms of cornigera; sinaloensis and tepicana as synonyms of Hindisi; chiapensis as a synonym of globulifera; yucatanensis of Collinsii; and penonomensis of costaricensis. Probably cubensis and interjecta are merely garden forms of cornigera. Schenck's multiglandulosa is certainly a synonym of melanoceras Beurling, which was overlooked by Schenck and Safford. With these changes the number of species in the foregoing list would be reduced to 20, and this number is probably too high.\(^1\) Unfortunately Safford did not live to complete his study of the bull-horn Acacias. I have reproduced photographs of these plants which he generously gave me several years ago. Among them is a photograph of a species with remarkably swollen and divergent spines, \textit{A. turgida}, of which he seems to have published no description.

We have as yet no knowledge of the precise species of bull-horn Acacia occurring in Colombia. Jacquinus recorded "\textit{A. cornigera}" from Carthagena and Beurling (1854) long ago very briefly described an \textit{A. melanoceroides} taken by Billberg in the same locality\(^2\). Dr. George Salt informs me that a species grows at Bonda and Tacurina, and Forel described a subsp. gaigei of \textit{Pseudomyrma spinicola}, a well known bull-horn ant as taken at Fundacion by Dr. G. M. Gaige. All these localities are in the dry Cienaga region of Northern Colombia. Probably the plant is \textit{A. costaricensis}, the same species that occurs in the dryer parts of Panama and Costa Rica.

Both Schenck and Safford have recognized several groups among the species of bull-horn Acacias. Safford establishes four groups, which are subdivided into sections. A fifth group, the Hebacanthae, contains several species not cited in the foregoing list, because their thorns are peculiarly flattened and not inhabited by ants. These plants are of peculiar interest as I shall endeavor to show in the sequel.

The beginnings of our ecological knowledge of the bull-horn Acacias have been often recounted. The early botanists often referred to these plants, which were first observed and figured by Hernandez (1651) and Jacquinus (1763). Commelin figured the food-bodies as early as 1697 and Plukenet in 1720. All the other early accounts such as those of Breinius (1739) and Ph. Müller (1752, 1768) and most of the later such as those of Beccari (1884–86), Schimper (1888) and Rettig (1904) are based either on herbarium material or on specimens grown in Euro-

\(^{1}\)Such is also the opinion of Mr. I. M. Johnston, who in a letter calling my attention to the identity of \textit{A. yucatanensis} and Collinsii, remarks: "I have investigated the other reductions in this group which Standley has made and am inclined to think that he can be followed in this particular instance with safety. I think that segregation in this group of plants has become too detailed and that the total number of species is well under 20."

\(^{2}\)See footnote on p. 191, in connection with \textit{A. melanoceras}. 
pean botanical gardens. The type species, *C. cornigera*, was described by Linné in 1737 from material grown in George Clifford’s garden. Safford (1923), from whom I take this fact, says that “it was afterwards found growing in its native habitat, near Laguna Verde in the mountains of Vera Cruz, Mexico in 1820 by the botanical explorer Christian Julius William Schiede and was described 10 year later under the name *Acacia spadicigera*, which must be regarded as a synonym of Linnaeus’ *Acacia cornigera*. Hernandez’s plant which, he says, was called “Hoitmamaxalli”, or “forked thorn” by the Aztecs was recognized by Safford and described as a distinct species, *A. hernaiz*.  

F. Smith in 1862 published a note on ant-inhabited Acacia spines, which has been overlooked in the literature. He described the ant as “*Pseudomyrma modesta*”. The specimens were collected by R. W. Stretch in Panama, the Acacia being in all probability *A. costaricensis* (= *penonemis* Saff.), the ant one of the rufotestaceous forms of the species which have been more recently designated as *Ps. belti* Emery or *Ps. spinicola* Emery. The description is however too meager to admit of more precise identification.

The first naturalist to make a careful study of the Acacias and their ants in the field was Thomas Belt (1874). His observations were on some of the plants growing about a league from Matagalpa, Nicaragua, and refer almost certainly to the species now known as *Acacia costaricensis* Schenck. As the *locus classicus* of our knowledge of the interrelations of the plant and its ants and of the future hypothesis of myrmecophily, his account is worth quoting in extenso, especially as it contains certain statements that need correction or explanation: “Clambering down the rocks, we reached our horse and mule, and started off again, passing over dry weedy hills. One low tree, very characteristic of the dry savannahs, I have only incidentally mentioned before. It is a species of acacia, belonging to the section Gummiferae, with bipinnate leaves, growing to a height of fifteen or twenty feet. The branches and trunk are covered with strong curved spines, set in pairs, from which it receives the name of the bull’s-horn thorn, they having a very strong resemblance to the horns of that quadruped. These thorns are hollow, and are tenanted by ants, that make a small hole for their entrance and exit near one end of the thorn, and also burrow through the partition that separates the two thorns; so that the one entrance serves for both. Here they rear their young, and in

---

1This reference is to p. 23, where he is describing the army-ant raids: “Many of the smaller birds build on the branches of the bull’s-horn thorn, which is always thickly covered with small stinging honey-eating ants, that would not allow the Ecitons to ascend these trees”
the wet season every one of the thorns is tenanted; and hundreds of ants are to be seen running about, especially over the young leaves. If one of these be touched, or a branch shaken, the little ants (Pseudomyrmica bicolor, Guér.) swarm out from the hollow thorns, and attack the aggressor with jaws and sting. They sting severely, raising a little white lump that does not disappear in less than twenty-four hours.

"These ants form a most efficient standing army for the plant, which prevents not only the mammalia from browsing on the leaves, but delivers it from the attacks of a much more dangerous enemy—the leaf-cutting ants. For these services the ants are not only securely housed by the plant, but are provided with a bountiful supply of food, and to secure their attendance at the right time and place, the food is so arranged and distributed as to effect that object with wonderful perfection. The leaves are bipinnate. At the base of each pair of leaflets, on the mid-rib, is a crater-formed gland, which, when the leaves are young, secretes a honey-like liquid. Of this the ants are very fond; and they are constantly running about from one gland to another to sip up the honey as it is secreted. But this is not all; there is a still more wonderful provision of more solid food. At the end of each of the small divisions of the compound leaflet there is, when the leaf first unfolds, a little yellow fruit-like body united by a point at the base to the end of the pinnule. Examined through a microscope, this little appendage looks like a golden pear. When the leaf unfolds, the little pears are not quite ripe, and the ants are continually employed going from one to another, examining them. When an ant finds one sufficiently advanced, it bites the small point of attachment; then bending down the fruit-like body, it breaks it off and bears it away in triumph to the nest. All the fruit-like bodies do not ripen at once, but successively, so that the ants are kept about the young leaf for sometime after it unfolds. Thus the young leaf is always guarded by the ants; and no caterpillar or larger animal could attempt to injure them without being attacked by the little warriors. The fruit-like bodies are about one-twelfth of an inch long, and are about one-third of the size of the ants; so that an ant carrying one away is as heavily laden as a man bearing a large bunch of bananas. I think these facts show that the ants are really kept by the Acacia as a standing army, to protect its leaves from the attacks of herbivorous mammals and insects.

"The bull's-horn thorn does not grow at the mines in the forest, nor are the small ants attending on them found there. They seem specially adapted for the tree, and I have seen them nowhere else.
Besides the *Pseudomyrma*, I found another ant that lives on these acacias; it is a small black species of Crematogaster, whose habits appear to be rather different from those of *Pseudomyrma*. It makes the holes of entrance to the thorns near the center of one of each pair, and not near the end, like the *Pseudomyrma*; and it is not so active as that species. It is also rather scarce; but when it does occur, it occupies the whole tree, to the exclusion of the other. The glands on the acacia are also frequented by a small species of wasp (*Polybia occidentalis*). I sowed the seeds of the acacia in my garden, and reared some young plants. Ants of many kinds were numerous; but none of them took to the thorns for shelter, nor the glands and fruit-bodies for food; for, as I have already mentioned, the species that attend on the thorns are not found in the forest. The leaf-cutting ants attacked the young plants, and defoliated them, but I have never seen any of the trees out on the savannahs that are guarded by the *Pseudomyrma* touched by them, and have no doubt the acacia is protected from them by its little warriors. The thorns, when they are first developed, are soft, and filled with a sweetish, pulpy substance; so that the ant, when it makes an entrance into them, finds its new house full of food. It hollows this out, leaving only the hardened shell of the thorn. Strange to say, this treatment seems to favor the development of the thorn, as it increases in size, bulging out towards the base; whilst in my plants that were not touched by the ants, the thorns turned yellow and dried up into dead but persistent prickles. I am not sure, however, that this may not have been due to the habitat of the plant not suiting it.

"These ants seem at first sight to lead the happiest of existences. Protected by their stings, they fear no foe. Habitations full of food are provided for them to commence housekeeping with, and cups of nectar and luscious fruits await them every day. But there is a reverse to the picture. In the dry season of the plains, the acacias cease to grow. No young leaves are produced, and the old glands do not secrete honey. Then want and hunger overtake the ants that have revelled in luxury all the wet season; many of the thorns are depopulated, and only a few ants live through the season of scarcity. As soon, however, as the first rains set in, the trees throw out numerous vigorous shoots, and the ants multiply again with astonishing rapidity."

The ant mentioned in this description is almost certainly mis-identified. *Pseudomyrma bicolor* does occasionally nest in Acacia spines but it can hardly be described as a "small" ant, its colonies
are not very populous and it does not attack and sting unless the spines are roughly seized. Belt, I feel confident, actually observed some form of *Ps. belti* or *spinicola*.

Since the appearance of his book, several observers have published accounts on the Acacias or their ants, notably Francis Darwin (1877), Beccari (1884–86), Delpino (1886–89), Schimper (1888), Emery (1892), Wheeler (1912), Wasmann (1915), Schwarz (1917), Calvert (1917), Safford (1923), Menozzi (1927). C. F. Baker, J. Bequaert, P. P. Calvert, A. Dampf, J. Zetek and others have furnished me with valuable specimens and data collected in Costa Rica, Honduras, Panama and Mexico. My own earlier observations (1913) need not be introduced in this connection, but I shall later return to some of them. Attention may here be called to the fact that my identification of *Acacia sphaerocephala* and *corrigera* seems doubtful in the light of the more recent taxonomic revisions of Schenck, Safford and Standley. The same is true of the specific identifications of Acacias by most of the other authors cited above. Thus Menozzi figures the spines of two species of Acacia as belonging to *A. spadicigera* (that is *cornuta*), but they are clearly those of *A. costaricensis* and *Hindsii*.

During 1923 and 1924 I had an opportunity to study two of the three known Panamanian Acacias, namely *A. costaricensis* (= *penonomensis* according to Standley) and *A. melanoceras* and therefore transcribe some of my field notes which I made on the general characters of these plants. The former species I found only on the dryer Pacific side of the Isthmus, in the vicinity of Las Sabanas, near Panama City and less frequently near Red Tank in the Canal Zone. It is probably more abundant in the savannah region further eastward. It is a rather coarse, sturdy bush, rarely more than five or six feet in height and often growing along trails or roadsides through the second growth jungle or in clearings. The grayish green leaves have rather few pairs of pinnae (about 8), with a row of three nectaries on the petiole and one at the junction of each pair of pinnae on the rachis. The spines are terete and moderately long and diverging, green at first, then reddish or chocolate brown. They seem to become hollow rather early, owing to drying up of their pulp-like pith. The flowers are in elongate spikes, the fruit turgid and when ripe splitting along both sides. The young leaflets bear yellow Beltian bodies, which the ants were seen to carry into the spines, while others were feeding at the foliar nectaries. Quite a number of the plants were examined and their ant and other inhabitants noted and collected. I select the following observations as the most interesting:
April 2, 1923. Observed numerous Acacias, from a foot to five feet high, along the Tumba Muerta Road, near Las Sabanas. Nearly all of them were inhabited by *Ps. spinicola* subsp. *atroX*. The spines of two plants, however, contained only *Ps. gracilis*, except a single pair on one of them which was tenanted by a colony of *Brachymyrmex heeri* var. *obscuriOr* and a few dead spines on the other which were inhabited by *Camponotus* (*Myrmobrachyus* *brevis*). The *gracilis* colonies were very flourishing, with much brood and numerous winged sexual forms. The workers had stored quantities of Beltian bodies in the spines, and these also contained a few Coccids and several empty Microdon puparia (*vide infra*).

July 2, 1924. Near Punta Paitea. Thirty Acacias growing along the trails near the military camp varied from a foot to 6 ft. in height. The thorns of 24 of them were inhabited exclusively by *Ps. atroX*, and one had no ant-inhabitants though it was quite as flourishing as the other specimens. In two bushes, only a foot high, evidently young suckers growing from the roots of a felled bush, I found the spines inhabited by isolated dealeted females with brood, but without any workers, though pupae of the latter were sometimes present. In one case the leaves of a large bush inhabited by *atroX* were much gnawed (by Chrysolomids). Five of the bushes were tenanted by *Ps. gracilis* exclusively. Owing to its timid disposition, this ant cannot be said to afford much protection to the plants. *Ps. atroX*, however, stings severely, but it does not attack unless the foliage is roughly handled.

*A. melanoceras* Beurling (1854, p. 123) is clearly the same as the species described as *A. multiglandulosa* by Schenck (1913) and based on material in the Berlin Herbarium collected in 1825 by J. G. Billberg in the vicinity of Porto Bello, Panama. This is evidently part of the material on which Beurling founded his species. 1 Safford has figured and redescribed the species from specimens taken by Pittier at the head of the Gatun Valley, Panama. I include a brief description of

---

1 Find that Standley (1928) has reached the same conclusion in regard to the identity of this plant.

The following is a transcript of Beurling's original description. "*Acacia melanoceras* n. sp. (Acacia sphaeracepha Chamb, et Schlect. var. sec. Bentham in Herb. Reg. Acad. scient. holm.); glabra, (ex siccatione?) nigrescenta, ramis teretiusculis, verruculose; aculeis stipulatibus binis, in cornua basi cornuata divaricata recte sina nigricantia nitida demum exsocrescentibus; petiolis pinnatis, ultra 20-jugis, infra jugum infimum supra exsocia—fossulata (fovea glandulosa minutus confertis cupulisiformibus replata); foliis eircenter 20 jugis, oblongo-linearibus, sub-falcatis, 2-3 lin. longis. ½ lin. latibus, apice (sub lente) minus simile decipulato: floribus in capitula globosa congestis; capitulis pedicellatis (pedicellis 3-4-nis), in racemos elongatos laterales terminalisque sumo gynematos (unum longiorem alterum breviorum) dispositis, No. 289. *Mimoso cornigerum* (Billberg) (Porto Bello) in silvis ad viae versus Panama." In a footnote, Beurling states: "Prope Sanct. Lazaro Carthagensem a Billbergio lecta est species simillima: "No. 139. *Mimoso cornigerum* (Bill.), "vix nisi colore haus nigrescente. primarium jugis pauciobus foliolisque duplo longioribus latioribus rectis diversa. (*Acadia melanoceroides* Beul. inc. script)."
the living plant, which is much more beautiful than *A. costaricensis* or indeed than any of the other species I have seen growing in Central America and would be a more ornamental plant under cultivation than *A. corrigera* which is occasionally grown in tropical botanical gardens. I have encountered *A. melanoceeras* which, according to Standley, "is a common shrub in the swamps and forests of the Atlantic slope," on only two occasions, once near the head-waters of the Rio Agua Salud (March 6, 1923), and once at Marajal near Colon (July 26, 1924). Both of these localities are on the moist Atlantic side of the Isthmus. On the Rio Agua Salud there were only a few bushes, each about 12 ft. high, growing on the bank of the stream very near the water; at Marajal there were several fine trees, some of which were 18 or 20 feet high, with graceful, smooth, gray-barked trunks, upright and usually growing in a cluster from the same root (Plate 37 a). The leaves are large and moss-green and have many more pinnae than *penonomensis*. A count of 50 of them showed the number to vary from 12 to 25 pairs, with an average of 20 to 22. The young leaflets bear at their tips rather large, golden-yellow Beltian bodies. The upper surface of the petiole bears numerous (20–30) conical nectaries, and there is a single nectary on the rhachis between each pair of pinnae. The spines are long (2 to 2½ inches), straight and diverging, smooth and terete, gradually tapering to a short, very acute point. When young they are green, then turn to a brilliant crimson and finally become rich chestnut brown. They are inhabited by a black Pseudomyrma, *satanica*, which is larger and even more vicious than *spinicola*. I have not seen the flowers, but the trees at Marajal were bearing clusters of mature green pods, which were straight, cylindrical, with a short terminal snout and measured 3 to 4 inches in length. The pedicel measured about three-quarters of an inch. The pod contained a firm, white, sweetish and edible pulp enveloping a row of black seeds.

According to Beurling, Safford and Standley, the flowers are in globose heads. Safford describes them as 7 mm. long, 6 mm. in diameter, solitary or in pairs, borne in the axils of the bracts on long erect branchlets composed of many nodes.

Dr. J. Bequaert has recently been able to make some observations on *A. Collinsii* (= *yucatanensis* Schenck) and its ants in Honduras. Since little has been written on this Acacia I reproduce the notes which he sent me:

"The ant acacia of northern Honduras (*Acacia Collinsii* Schenck) usually forms an erect bush, 6 to 15 feet high, with a main trunk 1 to 3
inches in diameter and covered with many slender, short side branches. The size and shape of the spines vary considerably on the same bush, those of the main trunk, at the foot of the branches, being much longer and twisted in horn-fashion. Young spines are either green or bright red and both types occur on the same bush. They soon become naturally hollow, without the help of the ants, which merely cut the opening below the tip and remove the dried pith.

"These acacias are particularly abundant near the coast, a short distance (one or two miles) from the shore, beyond the lagoons and mangrove swamps. They grow in dry, sandy, slightly undulating areas which appear to be ancient, fixed sand dunes and are covered with short grass and scattering shrubs and low trees. Many specimens may be seen along the main line of the Trujillo Railroad, about 15 to 25 kilometers from Puerto Castilla (near the stops known as Los Cuartos and El Canal). Only two small specimens were seen at Puerto Castilla, on the sandy levee between the sea and the mangrove swamp. At El Canal a number of them were also found in a rather dense and more humid wooded gallery along the banks of a stream. These specimens were larger and more tree-like than usual, reaching 20 to 25 feet in height, widely branched at the top, but with the main trunk, 4 to 5 inches thick, almost free of side branches, although covered with heavy and strongly twisted spines. Further inland I only observed the plant on one occasion, namely a single, bush-like individual which grew on the high, sandy, and densely wooded bank of the Río Aguan, near Prieta, about 90 kilometers from Puerto Castilla along the railroad to Olanchita.

"The black ant (Pseudomyrma belti) I found only in two plants, which grew near the sea shore at Puerto Castilla. The brownish form (Ps. belti subsp. bequaerti) is the common inhabitant of all the acacias near Los Cuartos and El Canal, where it occurs as well in the bushy plants of the dry, open areas as in the more tree-like form of the forest gallery. The subsp. bequaerti was also found in the single bush near Prieta. I observed how these ants actively collect the Beltian bodies at the tips of the leaflets and also visit the nectary near the foot of the petiole. At the time of my observations (March), most of the plants had flower buds, but only very few were actually blooming. After much search two or three seed-pods could still be obtained. Many of the bushes had very small, young leaves, just emerged from the bud, with food-bodies still attached. These food-bodies were either yellowish white or more rarely blackish. Both forms of Pseudomyrma are very aggressive; their sting is painful, but the pain soon abates."
The following list comprises the various ants recorded as living in the spines or on the foliage of the bull-horn Acacias:

1. *Pseudomyrma belii* Emery. In spines of *Acacia* sp. (probably *costaricensis*). Costa Rica (A. Alfaro; P. P. Calvert). In thorns of *A. Collinsii*; Honduras (J. Bequaert).


4. *Pseudomyrma belii* subsp. *fulvescens* Emery. In spines of *A. Hindsii* and *Acacia* sp. Guatemala (Wheeler); *Acacia* sp. Guatemala (Schwarz and Barber); British Honduras (J. D. Johnston; C. F. Baker); Mexico (E. Palmer, D. L. Crawford, Jourdain, A. Petrunkevitch, F. Knab); In spines of *A. sphaerocephala*, Mexico (Rangel, G. N. Collins, L. G. Culvas, J. M. Cuarón); *A. Collinsii*, Mexico (G. N. Collins); *A. cornigera* Mexico (G. N. Collins); *A. Hindsii* Mexico (G. N Collins).


(15) Pseudomyrma kuenckeli Emery. In spines of Acacia sp. Costa Rica (A. Alfaro); A. “spadicigera” (probably costaricensis or Hindsii) Costa Rica (H. Schmitt).


(22) Pseudomyrma spinicola subsp. atrox Forel. In spines of A. costaricensis. Panama (E. D. Christophersen; Wheeler).

(23) Pseudomyrma spinicola subsp. modesta F. Sm. In spines of Acacia costaricensis. Panama (R. W. Stretch).

(24) Pseudomyrma spinicola subsp. convenans Forel. In spines of Acacia sp. Guatemala (Peper).

(25) Pseudomyrma spinicola subsp. gaigei Forel. In Acacia spines (very probably), Colombia (F. M. Gaige).


(34) Crematogaster (Orthocrema) brevispinosa var. minutior Forel.
Nesting in accumulations of carton around spines of *A. cornigera* in botanical garden, Port of Spain, Trinidad (Wheeler).


(40) *Cryptocerus* (Paracryptocerus) *minutus* Fabr. In spines of *A. costaricensis*. Panama (Wheeler); *A. “spadicigera” (probably costaricensis or Hind...* Costa Rica (H. Schmidt).


(42) *Cryptocerus* (Cyathocephalus) *pallens var. discocephalus* F. Smith. In spines of *Acacia* sp. Costa Rica (A. Alfaro).


(47) *Camponotus* (Myrmobrachys) *planatus* Roger var. *acacia* Emery. In spines of *A. Hindsii*. Guatemala (Wheeler); *Acacia* sp. Costa Rica (A. Alfaro); *A. “spadicigera” (probably costaricensis or Hind...* Costa Rica (H. Schmidt).


(49) *Camponotus* (Myrmobrachys) *striatus* F. Smith. In spines of *Acacia* sp. Costa Rica (A. Alfaro); *A. costaricensis*. Panama (Wheeler).


(51) *Camponotus* (Myrmocladoeus) *rectangularis* Emery. In spines of *Acacia* sp. Costa Rica (A. Alfaro).

(52) *Camponotus* (Colobopsis) sp. In spines of *Acacia* sp. Costa Rica (A. Alfaro).

Of the various ants listed only three species can be regarded as obligate or definitely associated with the bull-horn Acacias, namely Ps. belti, spinicola and satanica; all the others are species or sub-species and varieties of species which more frequently nest in dead twigs of a great number of different plants. Emery did, indeed, describe Ps. belti from specimens taken from Cordia alliodora domatia, but this must have been a very exceptional occurrence, or more probably due to an erroneous label.

Two of the forms listed, Ps. gracilis and Camponotus planatus var. acaciae, are of special interest. The former, though a very frequent tenant of dead twigs and Cordia domatia in regions where there are no Acacias, nevertheless exhibits a strong proclivity not only to inhabit the spines of these plants, wherever they are available, but also to perforate them at the same point, to visit the foliar nectaries and to collect the food-bodies. In other words, this ant has acquired all the peculiarities of behavior of the three obligate Acacia tenants, Ps. belti, spinicola and satanica. This is perhaps true also of some or all of the other Pseudomyrmicas in the list. In my previous paper (1913) I described the founding of gracilis colonies in the thorns of young Acacias at Quirigua, Guatemala. In that region I found a locality in the banana plantations where gracilis was the only ant inhabiting the Acacias. As previously stated, it is also not infrequently the sole tenant of A. costaricensis in Panama. Of course, it is quite possible that the gracilis associated with Acacias represents a distinct physiological race derived and as yet morphologically indistinguishable from the form occurring more generally in dead twigs. At any rate, the case is interesting because it shows such a perfect adaptation to the bull-horn Acacias by particular colonies of a species which as a rule exhibits no adaptations to ant plants beyond those exhibited by most other species of Pseudomyrmica.

Camponotus planatus var. acaciae, as Alfaro (Emery, 1892) and I (1913) have found, frequently inhabits the same Acacias as Ps. belti and gracilis in Costa Rica and Guatemala. I described the mutual relations of these ants as follows: "That the Camponotus does not, as Emery supposed, merely take possession of thorns excavated and abandoned by the Pseudomyrmica, was proved on one occasion when I

1 Schenck (1914) records Pseudomyrmica arboris-sancta as occurring in the spines of A. spherocephala, spadicida and serucraneras in Mexico. The validity of this identification, which was made by Reichenperger, may be seriously doubted. In all probability the specimens belonged to some reddish subspecies of Ps. belti or spinicola.
found a small group of Camponotus workers busily engaged in perforating a green thorn. It is probable, therefore, that the Camponotus queens, after their nuptial flight, seek out the acacias and enter their young thorns even when the trees are already inhabited by the Pseudomyrma, and that the Camponotus workers continue this work side by side with the Pseudomyrmicas, both species competing for and taking possession of the thorns as fast as they attain the proper size and maturity. It is certainly extraordinary that _C. planatus_, which throughout tropical America so constantly lives in hollow twigs, should be able in widely separated localities to utilize the acacia thorns as perfectly and in precisely the same manner as the regular Pseudomyrmicas. That the Camponotus is, if anything, even more adroit in its use of the extrafloral nectaries becomes apparent when one follows the ant as it moves over the leaves, for it begins with the nectary at the base of the petiole and carefully visits each in turn, whereas the foraging Pseudomyrmicas are much more desultory and less business-like. I have not seen the Camponotus collecting the Beltian bodies, but I doubt not that they make quite as good use of them as of the nectar. The behavior of the two species of ants towards each other is peculiar. They seem never to quarrel, and if not too close together, pass one another on the twigs and leaves with an air of complete indifference. But when two of them happen to meet square face to face, each starts back suddenly and, curiously enough, the Pseudomyrma always recoils more vigorously than the Camponotus. There is something ludicrous in this behaviour because both ants are of about the same bulk, and the Pseudomyrma is really the more powerful and possesses a formidable sting, whereas the Camponotus is much less pugnacious and can defend itself only with its rather feeble mandibles and formic acid battery. But it smells rather strongly of formic acid, and I believe that this produces the more decided reaction on the part of the Pseudomyrma."

I regarded the mutual relations of the Camponotus and Pseudomyrma as a case of parabiosis, but Wasmann (1915, p. 128) has objected to my use of this word, because the two species of ants do not inhabit different parts of the same nest as in the case of _Crematogaster parabiotaica_ and _Dolichoderus (Hypoclinea) parabioticus_, to which Forel first applied the term, "but different nests (spines) on the same tree or branch." I believe, however, that all the pairs of spines that are converted into domatia on an Acacia may be really regarded as so many chambers of a single nest, when the ant-colony is well-developed. It is only the incipient colony that is confined to a single pair of spines.
One might, of course, invent some other term for the relations of mutual tolerance exhibited by the Camponotus and Pseudomyrmex, but this seems hardly necessary. It remains to be seen whether the concept of parabiosis may be extended to include all the other cases in which two or more species of ants inhabit the domatia of the same plant (Acacia, Cordia, Triplaris, Cecropia, etc.)

Besides the ants enumerated above the various Acacias also harbor a considerable number of miscellaneous insects and other organisms, which are briefly noticed in the following list:

(1) *Anees*. Birds, probably of several species, not infrequently build their nests in Acacia bushes or trees inhabited by the stinging Pseudomyrmex. This was observed by Belt in Nicaragua (*A. costaricensis*) and by myself both in Guatemala (*A. Hindsii*) and Panama (*A. costaricensis*).

*Hymenoptera*. Dr. E. A. Schwarz (1917) bred several species parasitic on beetle larvae from an Acacia trunk from Tampico, Mexico, but has cited none of them by name. I have noticed most of the following forms:

(2) Chalcidids. Bred from spider's eggs attached to twigs of *A. costaricensis*. Panama (Wheeler).

(3) Braconids. Swept from foliage of *A. costaricensis*. Panama (Wheeler).

(4) *Solitary wasp*. Nest made in an old thorn of *A. costaricensis*. Panama (Wheeler).

(5) *Polybia* sp. Nests constructed on branches of *A. Hindsii* in Guatemala (Wheeler).

(6) *Polybia* sp. Nest on *A. costaricensis*, Panama (J. Zetek).

(7) *Polybia occidentalis*. Cited by Belt as visiting the foliar nectaries of *Acacia* (*costaricensis*) in Nicaragua.

(8) *Halictus* sp. A small bee visiting the flowers of *A. Hindsii* in Guatemala (Wheeler).

(9) *Trigona* sp. A black stingless bee visiting the flowers of *A. costaricensis*, Panama (Wheeler).

*Lepidoptera*. The caterpillars of several species of moths feed on various parts of the Acacias notwithstanding the presence of the stinging Pseudomyrmex:

(10) *Adelocepha1a xanthochroia* Schauss. According to Carlos Hoffmann (*testa A. Dampf*) the caterpillars of this moth feed on the pulp of the seed-pods of Acacias at Misanhtla, Vera Cruz.

(11) Small moth caterpillars, which devour the foliage and leaflets and attach their cocoons to the twigs of *A. costaricensis* at Punta
Paita, Panama. Several of them were observed on single plants inhabited by *Pseudomyrma atrox*.

(12) A second small moth caterpillar was found cocooning on the stem of *A. costaricensis*.

(13) A third was living in old spines of the same species of Acacia.

(14) A Psychid larva had its case attached to a twig of the same plant.

**Diptera.** I have observed the larvae or pupae of five species of this order, without being able to secure the adults:

(15) In some localities in Guatemala (Esquintla, Patulul) the upper surfaces of the leaflets of *A. cornigera* bore beautiful little spherical galls, 5 to 6 mm. in diameter, single or in clusters and resembling minute strawberries, as they were bright red and uniformly covered with papillae (Plate 46 a). Each of these galls contained a Dipteran ( Cecidomyid) larva and had a preformed rhabde along which it dehisces when brown and mature, and permits the adult fly to escape. *Pseudomyrma fulvescens* is very fond of visiting these galls when young and succulent, and was often seen gnawing away the covering of papillae, but not eating in far enough to injure the enclosed larva.

(16) A second gall of much larger size and woody texture was occasionally found on the flower-stems of *A. Hindisi* in Guatemala, but as I could secure only old and dried specimens, I am unable to make any statement in regard to the insect.

(17) A very peculiar compound woody gall (Plate 46 b) was frequently found on the twigs and especially between and around the spines of *A. costaricensis* near Panama City. It consists of a number of tubular structures, each with an opening at its summit and containing in its more enlarged basal portion a Cecidomyid larva which I did not succeed in rearing.

(18) Several of the thorns of *A. costaricensis* at Las Labanas, Panama and Red Tank, C. Z., inhabited by *Ps. gracilis*, contained empty, rather smooth, brown puparia (about 7 mm. long and 3 mm. broad) of a small Microdon sp. Since the openings of the thorns were only large enough to permit the slender ants to pass in or out I am unable to account for the egress of the fly after its emergence. The flies had evidently emerged normally since the anterior dorsal portion of the puparia had been broken open at the usual transverse suture. Perhaps the insects had been devoured by the ants. From the fact, however, that these puparia were encountered in more than a dozen pairs of spines on different bushes in two localities, we must infer, I believe, that the Microdon is a regular synœkete in the nests of *Ps. gracilis*. 
(19) Among some spider's eggs in a cocoon attached to the twigs of *A. costaricensis* I found a Muscid puparium, probably that of a Tachinid.

*Coleoptera.* Several beetles have been recorded from Acacias, but only one has been specifically identified:

(20) *Agrius* sp. A small bronze-green species was common on the foliage of *A. costaricensis* at Punta Paitea, Panama. Several pairs were taken in copula.

(21) *Agrius* sp. A larger bronze-green form, not uncommon on the same plant in the same locality.

(22) *Agrius* sp. Bred by Dr. E. A. Schwarz (1917) from the trunk of *Acacia* sp. from Tampico.

(23–29) Dr. Schwarz also bred seven species of Cerambycidae (one Cerambycine and six Lamids) from the same trunk.

(30–31) At Las Sabanas, Panama two unidentified species of Chrysomelidae were found on the foliage of *A. costaricensis*. The injury to the foliage, occasionally noticed, probably results from the attacks of these or allied species.

(32) Curculionid. The larva, apparently of some weevil, was found living in the spines of *A. costaricensis* near Las Labanas, Panama, and feeding on the pith.

(33) Curculionid sp. A small black species taken on the foliage of the same Acacia.

(34) *Bruchus cinerifer* Fabr. Cited by Schenck (1914) as boring into the pods and feeding on the seeds of *A. sphaerocephala* in the Mexican tierra caliente.

(35) *Bruchus* sp. Possibly the same as the preceding observed by Carlos Hoffmann (tested A. Dampf) as occurring in the seeds of *Acacia* sp. at Misanthla, Vera Cruz. Through the holes made by this beetle the caterpillars of *Adelocephala xanthochroia* enter the pods and feed on the pulp.

(36) *Bruchus* sp. Dr. Schwarz observed this species, which may be the same as *B. cinerifer*, infesting the flowers of an *Acacia* sp. at Tampico and ovipositing and developing in its pods "without being molested by the ants in any of its stages."

(37) *Bothrioderes* sp. A Colydiid bred by Dr. Schwarz from the trunk of *Acacia* sp. from Tampico.

(38) *Lathropus* sp. A Cucujid from the same trunk.

(39) *Trogosita* sp. An Ostomid from the same trunk.

(40) *Clerus* sp. Bred from the same trunk by Dr. Schwarz.

*Orthoptera* (41) *Blattid* sp. A large compressed ootheca of some
roach was taken from the cavity of a large dead spine of _A. melanoceras_ at Marajal, C. Z. (Wheeler).

_Isoptera._ (42) _Eutermes_ sp. An ellipsoidal nest of this termite was situated among the branches of an _A. melanoceras_ tree at Marajal and had galleries descending from it along the trunk. When the latter were broken open a violent battle ensued between the termites and the ants (_Ps. satanica_).

(43) _Eutermes_ sp. Abandoned tunnels of another termite were found on the trunk and branches of an _A. costaricensis_ bush inhabited by _Ps. gracilis._

_Heteroptera._ (44) The only member of this order taken was a large Pentatomid, which was crawling on the foliage of _A. costaricensis_ at Las Sabanas, Panama.

_Homoptera._ Coccide. Of this family I have found only three species associated with Acacias:

(45) _Coccus elongatus_ (Sign) (H. Morrison det.). A few specimens taken in spines of _A. costaricensis_ inhabited by _Ps. gracilis_ at Pueblo Nuevo, Panama.

(46) _Pseudococcus texensis_ Tinsley (H. Morrison det.). Numerous specimens taken in spines of _A. veracruzensis_, collected by Dr. A. Dampf at Vera Cruz, and inhabited by _Crematogaster atra_ and _corvina._

(47) _Pseudococcus_ sp. Inhabiting the cavities of flower-peduncles of _A. Hindsii_ which contained colonies of _Solenopsis_ sp. Guatemala (Wheeler).

_Myriopoda._ Two species of this class were found inhabiting old abandoned spines of _A. costaricensis_ near Panama City, namely:

(48) _Polyzenus_ sp. Forming small colonies.

(49) A Geophilus-like form, living singly.

_Araneina._ At least four species of spiders were found inhabiting webs and concealing their egg-cocoons among the leaves and branches, of _A. costaricensis_, and at least six in similar situations on _A. melanoceras_. The following four have been identified by Mr. N. Banks.

(50) _Eustala fuscovittata_ Keys. On foliage of _A. costaricensis_ at Punto Paita, Panama.

(51) _Phyale_ sp. On the same species of Acacia in the same locality.

(52) _Acrosoma obtusispina_ Keys. A large species inhabiting orb-webs among the branches of _A. melanoceras_ at Marajal.

(53) _Nephila clavipes_ L. Another large spider inhabiting similar webs on the same species of Acacia.

_Acarina._ (54) Numerous mites found attached to the workers of
*Camponotus brevis* Forel inhabiting spines of *A. costaricensis* at Corazol, C. Z. Panama.

Although the 54 different organisms, other than ants, above listed as associated with the bullhorn Acacias have been less satisfactorily studied and identified than those recorded for *Cordia alliodora* and *Triplaris*, and undoubtedly represent only a small fragment of the actual Acacia biocenoses, they are sufficient, nevertheless, to show, first, that these plants have plenty of natural enemies and are in this respect like other nonmyrmecophytic trees and shrubs in the tropics, and second, that the obligate ant-tenants, though more virulent than those of *Cordia alliodora* and the Cecropias, are nearly or quite as tolerant of alien ants and other insects on the same plants. I therefore reiterate my statement of 1913 that the relations existing between the Acacias and the obligate Pseudomyrmex are not properly those of symbiosis, in which the plants have adapted themselves to the ants, but those of host and parasite, in which the adaptations are solely on the part of the ants.

This contention, in its essential features, was rejected by Wasmann in his paper of 1915. Like other authors he has been greatly impressed by the coexistence of the capacious spines, abundant foliar nectaries and Beltian bodies in these Acacias, and though he is quite unable to account for these various structures, nevertheless regards the plants as having perfected them for the purpose of securing the protection of the ants. This is clear from the following quotation (p. 130): "If, therefore, we weigh the "pros and cons" of the so-called myrmecophily of the ant-acacias, I believe that we arrive at the same conclusion, which I had already reached in my previous paper (1915, p. 303, 315, 321), namely a position midway between the two extremes of an over-estimation and an underestimation of the myrmecophilous adaptations. The initiative that resulted in the occupation of the acacias by certain acacia ants of the genus Pseudomyrmex, had its source in the latter. They selected these trees gradually with ever increasing regularity for purposes of establishing their colonies on account of the advantages accruing to their species. This specialization of the nesting instinct is, of course, to be conceived without any such anthropomorphism as that implied in supposing the ants to be aware of these advantages through intelligent reflection. Both the favorable domiciliary conditions, which the spines of these trees afford the ants, and the favorable nutritive conditions provided by the extraloral nectaries, are therefore not a product of "natural selection" due to "adaptation" to the ants under consideration. The prerequisite physiological condi-
tions for these actual adaptations must have been developed beforehand by the laws of growth of the host-plants. But after certain species of Pseudomyrmex had adapted themselves to these preconditions and had taken up their regular abode on the respective Acacias, it was possible, through the protection thus incidentally acquired by the host plant—even supposing this protection to be by no means considerable—that the further development of the extrafloral nectaries and especially of the Beltian corpuscles was favored to a degree which the same peculiarities would not have attained without such myrmecophily. In this sense we may still speak of a true “symbiosis” between the ant-acacias and the acacia-ants, which is now more than a mere parasitism, though it arose originally from a unilateral parasitism. Somewhat similar conditions are found in the symphyl of many myrmecophilous and termitophilous Coleoptera, which is also more than mere parasitism, though it had its beginning in unilateral parasitism.”

Of course, there is no way of either confirming or refuting this piece of pure phylogenetic speculation, which is so much like others in which Wasmann has indulged from time to time in regard to tropical organisms that he has never observed in a living condition. Obviously the ants could not have settled in the Acacias till their spines had developed to their present dimensions, and it was these organs, so easily convertible into domatia, that induced the ants to take up their abode on the plants. This is clearly indicated by two species of Acacia, among the many very diverse nonmyrmecophytic forms that grow in the same general geographical region, namely the swordthorns, A. macracantha Humb. and Bonpl. of Mexico, hirtipes Safford of Guatemala, Standleyi Safford and gladiata Safford of Mexico and the spion-thorns, cochlicacantha Humb. and Bonpl. of Ecuador and cymbispina Sprague and Riley of Mexico and Central America. All these plants have large spines which are too much flattened to be used as domatia by the ants. I have not seen specimens of the various species but the following data collated from the literature indicate that food-bodies and nectaries like those of the bullhorn Acacias are present in at least some of them:

A. macracantha, according to Standley (1922) has compressed spines 2.5 to 5 mm. long, but he makes no mention of food-bodies or nectaries.

In A. Standleyi (Plate 44), according to Safford (1914), the young leaflets are tipped with food-bodies and the main leaf-rhachis bears “a conspicuous annular nectar-gland at the base of each pair of pinnae and usually one on the petiole, just below the lowest of these”. The spines are “3–3.5 cm. long, 6–8 mm. broad at the base, very widely
divergent, the pair separated by a thickened ridge (the persistent base of the petiole) adnate to the branch.”

A. *hirtipes*. Nothing is said in Safford’s description (1914) about food-bodies but the foliar nectaries are “dark purplish, circular, bowl-shaped, with a thick annular margin, one in the smaller leaves of the short branchlets, one borne at the base of each pair of pinnae and an additional one on the petiole; on the larger leaves of the longer branches similar glands borne at the base of each pair of pinnae of the upper half of the leaf, but none in the lower half except a solitary gland on the petiole.” The large stipular spines are “broadly v-shaped, cinereous, puberulent, except at the points, 3–4.2 cm. long, 10 mm. broad at the cuneate base, the latter flattened but not adnate to the branch as in A. *Standleyi.*”

A. *gladiata* is considered by Standley as possibly merely a form of *Standleyi*. The leaf-rhachis usually bears a nectary at its base and often one just below each pair of pinnae. The leaflets are “often mucronate or tipped with a waxy apical body, as in the true myrmecophilous acacias.” “Large spines very long and divergent, usually flattened and sword-like, linear-lanceolate in outline, somewhat constricted at the base, resembling certain forms of the spines of *Acacia cochliacantha* H. & B. but connate instead of separate at the base and never split or inflated, gradually narrowed toward the apex to an acute point, 35 to 52 mm. long, 5 to 8 mm. broad, glabrous, reddish or wine-colored when young, at length brown or tan-colored.”

A. *cymbispina*. This form is usually identified as *A. cochliacantha*, originally described from Ecuador, but is specifically distinct, according to Sprague and Riley. The spines are widely divergent and compressed, greatly enlarged and spoon-shaped, that is strongly convex on one side and concave on the other. This Acacia was observed by the Calverts (1917), who found it growing along the Bananita River, in Costa Rica. According to their account it resembled the bull’s horn Acacia, “but had a less woody stem or trunk and paired thorns not curved nor inclined toward each other but merely at right angles to the stem bearing them. There were no little fruit-like bodies at the tips of the young leaflets, but along the midrib of each leaf was a row of urn-shaped glands, one at the base of the twenty-seven pairs of pinnae.” There were no ants on this Acacia, “but it looked so much like bull’s horn thorn as to suggest that it might be the starting point for the development of the latter.”

These cases show that the mere presence of well-developed foliar nectaries, or of nectaries and food-bodies, does not suffice to induce the
ants to make their abode in the Acacias. The same conclusion is also reached from observation of many other plants, such as the species of Cassia, Stillingia, Populus, etc. which may attract ants or other insects to their nectaries, but cannot retain them as permanent occupants, because they possess no structures that can be converted into suitable domatia. It would be hazardous to maintain that _A. cochleacantha_ and _gladiata_ are either persisting, older, phylogenetic stages in the evolution of the bull-horn Acacias or more recent, involutionary derivatives of the same. More probably the two species and their allies represent independent developments from some stock common to that of the bull-horns; and their survival as well as that of many more delicate species of Acacia in Mexico and Central America without ant-protection, is not calculated to strengthen the contention of Wasmann and other believers in an adaptive myrmecophily on the part of the plants. Additional evidence of the absence of such adaptation is also available from the study of some of the African Acacias and of one South American species, _A. cavenia_, to which we may now turn.

**(B) Acacia cavenia** Hooker and Arnott

We possess three accounts of this Paraguayan Acacia, which really bears only a certain superficial resemblance to the bull-horns in the great enlargement of its spines and their occupation by ants.

Fiebrig (1909) describes the plant as a shrub covering considerable areas in the Chaco of Paraguay, near the Bolivian boundary, and restricted to loess-like alluvial soil which is occasionally inundated and is not inhabited by Attine ants. Though the stems are so slender as rarely to exceed a centimeter in diameter, some of their stipular spines may become very large (90 mm. long and 8 mm. broad at the base), “but only at certain seasons, apparently as a result of abundant atmospheric humidity.” Fiebrig found that their pith is devoured by a Tineid caterpillar, which before pupation gnaws an exit-hole near the tip of one of the spines of a pair. This caterpillar may hollow out not only a single spine but also its fellow and a portion of the adjacent stem. At the time of the moth’s emergence the head of the pupa is pushed out of the opening. Later the spines are invaded by ants (_Pseudomyrma fiebrigi_ Forel), which utilize the moth’s exit-hole as an entrance. The young leaves of the Acacia bear no Beltian bodies. No mention is made of the presence of extra-floral nectaries.

Previously, in 1896, Emery had described a number of ants taken by Dr. J. Bohls from the large spines of a Paraguayan Acacia, which
is almost certainly *A. cavenia*, since the specimens were collected in a locality, San Salvador, very near the Chaco in which Fiebrig made his observations. According to Emery, the species of *Pseudomyrmica* made delicate galleries in the woody substance of the spines, whereas the species of *Cryptocerus* hollowed them out completely. "The opening of the *Pseudomyrmica* nests was made near the tip of the spine, the openings of the other species were at a variable distance from the base and sometimes there were several."

More recently *A. cavenia* has been studied again by Chodat and Vischer (1920) at Trinidad, Conception, etc. in the periodically inundated country along the Rio Paraguay. Their interpretation of the enlargement of the spines differs from that of Fiebrig, as will be seen from the following quotation and an examination of their figures 324 and 325: "We have also found spines of considerable dimensions without any insect in them. One might ask, therefore, whether Fiebrig's theory is really sufficient to account for the production, or origin of these hypertrophied stipules. We suspected the existence of a morphogenetic stimulus produced by the sting of an insect in some other part of the stem, and we therefore sought for such organisms in the pith of the branches. Examination confirmed our suspicions. Below the insertion of the spines (stipules) we found the larva or pupa of a Chalcidid quite analogous to the one that produces the myrmecodomatia, or galls described for the Cordias. How does the infection occur. How does the female oviposit? The fissures indicate that the animal may penetrate the tissues either in the region of one of the buds or of its fellow of the opposite side. But this point should be observed at the time and place of its occurrence. The infection may be deep in the pith or more superficial (see Fig. 324). It will be noticed in Fig. 324 that the larva, after devouring a portion of the pith of the stem, moves towards the base of the spine, which becomes hypertrophied. Sometimes, as in the Cordias, two or several (?) larvae may be found. Moreover, the canal be means of which the larva penetrates the thorn, may be transverse and bring about a communication between the two stipules (see Fig. 325). Fiebrig had previously indicated the presence of these continuous chambers or galleries but he assigned them an inverse origin. We are confirmed in our theory by the fact that Fiebrig himself noticed that the stipules may become hypertrophied without exhibiting any localized attack in their pith or base, that is, without any internal or external indications. For us, and we have made many concordant and no discordant observations, there is always an infection of the stem before the stipules are hollowed out. We must suppose, therefore, that
the excitation starts from the stem and is transmitted either by the plant tissue or by substances secreted by the animal, or, what is even more probable and agrees with most of our observations, by the direct action of the progressing larva. It may happen also, no doubt, that the infection is caused directly at the base of the leaf, since on one occasion we found a stipular spine that contained a pupa and a kind of cocoon, without any communication existing between the spine and the gallery in the stem."

It would seem therefore, if this account be correct, that the enlarged spines of *A. cavenia* are really Hymenopterous galls and that the Tineid larva observed by Fiebrig is a secondary, or inquiline which feeds on their medullary tissue. The authors say nothing about the Tineids nor the ants which later inhabit the spines.

The following are the ants that have been collected in these organs of *A. cavenia*:

2. *Pseudomyrmca acanthobia var. fuscata* Emery (J. Bohls).
7. *Cryptocerus grandinosus* F. Smith (J. Bohls).

There is no evidence that any one of these species is an obligate tenant of *A. cavenia*. Many and probably all of them are generally found nesting in dead twigs or branches of other trees or shrubs. Even apart from this fact, there is nothing to indicate any "myrmecophilous" peculiarities in the plant.

(C) The African Acacias

Some six different species of African Acacias (*A. seyal* Delile, *depanolobium* Harms, *formicarium* Harms, *pseudofistula* Harms, *malacocephala* Harms, and *Bussei* Harms) have been found to possess
greatly swollen spines inhabited by ants. Their consideration in this place may be greatly abbreviated both because I am dealing only with the Neotropical ant plants and because Bequaert (1921–22) has so recently and so adequately reviewed what is known in regard to the African Acacias: Most observers (Schweinfurth, Ascherson, Keller, Sjöstedt, Glover Allen, Winkler, Schenck, H. Lang) of these plants in the field admit that the hypertrophy of their spines is really a gall-formation produced by Dipterous or Hymenopterous larvae. Bequaert gives the following reasons for adopting this interpretation: "They are not found on all specimens of the same species of Acacia, even in one locality; while on some plants practically all the thorns are swollen, others nearby bear hardly any galls; furthermore, their size is quite variable and their shape rather irregular. Mention may still be made of the fact that, while the species of Acacia enumerated above have a rather wide distribution in eastern Central Africa, swollen thorns have been noted in only a few localities within this range."

The list of ants inhabiting the spines, as compiled by Bequaert, comprises 16 species (13 species of Crematogaster, one of Cataulacus and two of Tetraponera), and he adds: "As would be expected from the fortuitous production of galls on plants, none of the ants mentioned in the preceding pages seems to restrict the location of its nest to galls. They are evidently all arboreal species which are in the habit of sheltering their brood in hollow branches or cavities of trees." ¹

Chapter 7

VARIOUS NON-MYRMECOPHYTIC PLANTS WITH ANT-INHABITED STEMS, ETC.

Among the vast number of Neotropical plants there are many that cannot be regarded as myrmecophytes though they furnish ants with sufficiently commodious living quarters (pseudodomatio) in their internodes or other caulinere structures. Several of these plants are so frequently or regularly inhabited as to be of special interest, at least to

¹Recent researches, which could not be considered by Professor Wheeler, throw a new light on the problem of the African ant Acacias. Paoli (1929 and 1930) studied two of the species, Acacia fistula Schweinfurth and A. Bussel Harms, in Somaliland. He found that these plants produce regularly two types of thorns. Some remain slender, while others slowly swell up at the base or over most of their length. The swelling is due to normal growth and is not induced by an insect. Eventually the pith of the swollen thorn dries up and the cavity thus produced may or may not be settled by ants. The swollen thorns are not insect galls but normal productions of the plant. The African ant Acacias are true myrmecophytes, but they lack the Belgian food-bodies of the American species. Both A. fistula and A. Bussel bear small nectaries on the petioles, but these are also found on non-myrmecophilous Acacias. Paoli and Menozzi (1930) list many ants found in the thorns of the African ant Acacias. J. Bequaert
the collector. The simplest cases are those in which the internodes become hollow by disappearance of their pith before they are occupied. In others the ants clean out the pith and in still others they occupy burrows that have been more or less extensively excavated by wood-boring beetle larvae, caterpillars, etc. The data cited in the literature often leave doubt as to which of these conditions obtains in a particular instance. The predilection of the ants for certain species of plants with inhabitable stems is probably enhanced by the regular development of extrafloral nectaries or the frequent occurrence of particular Coccids on their shoots or foliage. In the following paragraphs I have brought together a number of records on Neotropical plants that frequently have ant-inhabited stems, etc. There are, of course, several woody plants in temperate regions, like the common elder of our Northern and the white ash of our Southern states, the English walnut and blackberry in Switzerland, etc. which are similarly tenanted by a number of Formicidae, but these plants I have not included.\(^1\) I have also omitted the galls of oaks and other plants, which after serving for the development of their makers, often furnish convenient habitats for small colonies of ants, especially of the genera Leptothorax, Crematogaster and Camponotus (subgenera Myrmentoma and Colobopsis), etc. both in Europe and North America.

Gramineae and Cyperaceae

Bamboos. The hollow internodes of various bamboos are sometimes inhabited by ants, but this occurrence seems to be rather local. In the large Javanese bamboos surrounding the tropical laboratory at Kartabo, B. G. I failed to find any ants, and examinations of the smaller species in that region were equally negative. Lutz, Forel, Luederwaldt (1926) and other collectors in Brazil and H. Schmitt in Costa Rica, however, have found quite a series of bamboo-inhabiting forms. The following is a list of the recorded species:


---

\(^1\) See Stäger's interesting paper (1917) on the stem-inhabiting ants of Switzerland. He records seven different forms, belonging to the genera Leptothorax, Crematogaster, Dolichoderus (Hypoclines) and Camponotus (Colobopsis), as living in the stems of *Rubus ulmifolius*. Three of these forms occur also in walnut twigs. In all cases the ants invade cavities previously excavated by solitary wasps (mainly Crabronidae), solitary bees (Ceratina) and beetles.
(4) Neoponera crenata var. moesta Mayr. Brazil (H. Luederwaldt).


(6) Pheidole bambergarum Forel. Brazil (A. Lutz; Luederwaldt).

(7) Pheidole guilelmi-muelleri Mayr subsp. avia Forel.

(8) Pheidole lutzi Forel. Brazil (A. Lutz; Luederwaldt).

(9) Solenopsis saevissima F. Smith. Brazil (H. Luederwaldt).

(10) Solenopsis franki Forel subsp. idæ Forel. Brazil (H. Luederwaldt).


(13) Crematogaster (Orthocrema) distans Mayr. subsp. parviceps Forel. Brazil (Luederwaldt).

(14) Crematogaster (Orthocrema) lutzi Forel. Brazil (A. Lutz).

(15) Crematogaster (Orthocrema) quadriformis Mayr. In Guadua distorta. Brazil (Luederwaldt).


(19) Cryptocerus (Cyathocephalus) varians F. Smith subsp. marginatus Wheeler and Mann. Haiti (W. M. Mann).

(20) Iridomyrmex iniquus Mayr. In bamboo: Brazil (H. Luederwaldt).

(21) Iridomyrmex iniquus var. succinea Forel. Brazil (Luederwaldt).

(22) Iridomyrmex leucomelas Forel. Brazil (Luederwaldt).

(23) Tapinoma atriceps Emery. Brazil (A Lutz; Luederwaldt).

(24) Tapinoma atriceps var. breviscapa Forel. Brazil (A. Lutz; Luederwaldt).

(25) Myrmelachista (Decamera) bambergarum Forel. Brazil (Goeldi).

(26) Myrmelachista (Decamera) padereuskii Forel. Brazil (A. Lutz).

(27) Camponotus (Tangemyrmex) lutzi Forel. Brazil (A. Lutz).

(28) Camponotus (Myrmothrix) cingulatus Mayr var. bambergarum Forel. Brazil (Goeldi; Luederwaldt).


(32) *Camponotus (Hypercolobopsis) paradoxus* Mayr subsp. *janitor* Forel. Brazil (A. Lutz); in *Bambusa taguarae* Nees and allied species (Luederwaldt).

Luederwaldt also records two Coccids, *Lachnodiella taguarae* Hemp. and *Orthezia grandis* Hemp., living with *Pheidole lutzi* in the bamboo internodes.

*Uniola* and *Cladium*. In the Bahamas I frequently took colonies of the following ants in the culms of a large grass, *Uniola paniculata* L., and a sedge, *Cladium jamacense* Crantz:

2. *Pseudomyrma flavidula* F. Smith
3. *Macromischa splendens* Wheeler
4. *Crematogaster (Acrocalia) lucayana* Wheeler
5. *Crypticerus (Cyathocephalus) varians* F. Smith
7. *Camponotus (Colobopsis) culmicola* Wheeler

According to Stäger (1917), the regular occurrence of ants in the culms of grasses in the savannahs of Colombia was noticed by E. A. Goeldi as early as 1896. I have found various species of *Pseudomyrma*, especially *Ps. flavidula*, in the same situations in Panama and British Guiana.

**Scitamineæ**

*Crematogaster (Orthocrema) limata* F. Sm. subsp. *parabiotaica* Forel, which is associated with so many different plants, is also recorded as living in the inflorescences of a species of Costus in Amazonas (E. Ule).

**Orchidaceæ**

Many of the epiphytic species of this huge family undoubtedly harbor ants either about their roots, between the plants and their support, or in the pseudobulbs, but unfortunately many of the observations lack precision and the ants have rarely been identified. Bequaert (1921–22) includes only two Neotropical genera, *Diacrium* and *Schomburgkia*, among the myrmecophytes. He remarks that "*D. bicornutum* (Hooker), of Trinidad and Guiana, has a swollen spindle-shaped stem which is normally hollow and perhaps regularly inhabited by ants
(Rodway, 1911, p. 111). Schlechter claims that even under cultivation the pseudobulbs form at their base a slit through which the ants gain access into the cavity." The pseudobulbs of several species of Schomburgkia are also described as hollow and ant-inhabited. I find that only the following ants have been identified as orchid tenants:


Polygonaceae

Coccoloba uvifera (L.) Jacq.—This peculiar tree, the "seagrape", is very common along the beaches of tropical Florida and the West Indian islands. As a rule it is less than 15 ft. high, but in exceptional cases may attain a height of nearly 50 ft. with a trunk more than a yard in diameter. The peculiar, leathery, shining, orbicular or even transversely elliptical leaves make it a quaint and conspicuous object among the littoral vegetation. The foliage is a source of food for a number of miscellaneous insects and the following ants not infrequently inhabit its short, hollow internodes:

(9) *Camponotus (Myrmobrachys) planatus* Roger. Cuba (Wheeler).

The following insects have been recorded by Wolcott (1923) as infesting *C. uvifera* in Porto Rico:

(1) *Dichomeris zingarella* Walsh. Gelechiid moth reared by Busck.
(2) *Ctenodactylomyia watsonei* Felt. Cecidomyid fly reared from galls by R. H. van Zwaluwenburg.
(3) *Cryptocephalus perspicax* Weise. Chrysomelid beetle feeding on foliage.
(4) *Atelabus coccoloba* Wolcott. Curculionid beetle feeding on foliage.
(5) *Exophthalmodes roseipes* Chevr. Curculionid beetle feeding on young foliage.
(6) *Lachnopus curvipes* Fabr. Curculionid beetle on foliage.
(7) *Tangia* sp. Fulgorid.
(8) *Ormenis marginata* Brunnich. Fulgorid.
(9) *Ormenis pygmea* Fabr. Fulgorid.
(10) *Cyarda* sp. Fulgorid.

*Coccoloba rugosa* Desf. The few specimens of this plant which I saw in Porto Rico, were small trees with very slender trunk and few branches and enormous, coarse, cordate clasping leaves, (30-60 cm. broad!) among the large veins of which, on the lower side and at the base, a small yellow ant, *Iridomyrmex melleus* Wheeler builds fragile carton nests. More frequently, however, this insect inhabits the hollow twigs of a variety of plants.

In South America Spruce (1869, in 1908) observed a number of ant-inhabited Cocoloba species as well as several other Polygonaceous genera (Campderia, now included in Cocoloba, Lymmeria, Rupprechtia and Triplaris, which has been considered at length (p. 41 et. seq.) All these, he says, “grow in moist situations, and most of them on lands subject to inundations. Not only is every lignescent Polygonaea a habitation for ants, but the whole of the medulla of every plant, from the root nearly to the growing apex of the ramuli, is scooped out by these insects.” These are species of Pseudomyrma, which are
known in Brazil by the name of "Tachi" of "Tacyba" and in Peru by that of "Tangarana"; and in both countries the same name is commonly applied to any tree they infest as to the ants themselves." One of the species of Coccoloba he mentions in particular: "Some Tachi trees seem as if they were actually trying to run away from the ever encroaching ants. Coccoloba parimensis Benth., found by Schomburgk in British Guiana and by myself on the Rio Uaupes, is an arbuscle with a stem 15 feet long, that tapers upwards and arches over so as finally to touch the ground, the ants all the while hollowing it out, as it stretches away apparently in the hopeless attempt to escape their invasion. Some slender Coccolobas climb high into the adjacent trees, not by twining but by crooking their branches and thereby hoisting themselves up; others are self-standing bushy trees, but still have the same slender geniculate branches."

Bixaceae

*Bixa orellana* L. This bush or small tree, the "achiote anatto" or "anotto", reaches a height of 30 feet and is common throughout the West Indies and Central America. It is also cultivated both in these regions and in the East Indies, because the testa of its seeds yields a beautiful orange-red pigment, the famous "anatto" dye. Pittier (1908) gives a good account of the plant. "*Bixa orellana*, a tree of even elegant aspect, with rose-colored, rather conspicuous flowers and capsular fruit covered with soft spines and containing numerous seeds. The outer integument, or tests of these seeds contains a yellowish red coloring matter, which is extracted with hot water and may be decomposed, according to Chevreul, into two pigments, *buxine*, which is yellow, and *orelline*, which is red.

*Bixa orellana* seems to be indigenous through tropical America and has been cultivated like the cacao plant from the most remote times. It easily matures its fruits up to an altitude of 1200 m. The wild form, or *Achiote simarron*, with smaller leaves and less developed floral organs, is found in Costa Rica in the woods of the Pacific slope up to an altitude of about 800 m. The dye which is fast and brilliant, was used by the natives to stain their bodies and also to tint their clothes and various other objects. At the present time it is employed in coloring butter, certain kinds of cheese, sarozas and other fabrics. In the Creole Kitchen it is used to color rice.

The word *achiote*, which designates both the tree and the red, resinous paste extracted from the outer integument of the seeds, is a
corruption of the Nahoutl *achiotl*. In the Guyanas, the Indians call the tree and its product *urau*, whence the French *rocou* is derived. *Anatto* and *bijia* are other names applied to the coloring matter."

I found this plant rather common in Panama, both in the gardens at Ancon and Balboa, and wild, especially on the Atlantic side of the Isthmus near Colon, Marajal and on Barro Colorado Island. The leaves are broad and subcordate and covered with microscopic glands beneath, while the petiole bears at its junction with the blade a distinct thickening with a pair of large nectaries, which are visited by the ants. It is not surprising to find, therefore, that the short internodes are frequently inhabited by these insects. These internodes have to be hollowed out by the ants, since they contain a persistent pith. A careful study of the plant in different localities will probably yield quite a number of different ants. The following list includes those collected in Panama and two forms recorded by Forel (1906) as taken in Costa Rica:


The general insect fauna of _B. orellana_ has not been studied, but is probably quite as abundant as that of many other tropical trees. Two species of Coccids, _Howardia biclavis_ Comst. and _Inglisia vitrea_ Cockerell, are cited by Wolcott (1923) as infesting the plant in Porto Rico.

**Marcgraviaeae**

The types of _Azteca longiceps_ Emery subsp. _juruensis_ were taken by E. Ule in the twigs and branches of a species of Schwartzia (Norantea) in Amazonas.

The juvenile stages of the species of Marcgravia have the form of peculiar creepers which adhere to the trunks of trees or the surfaces of rocks. On each side of the reptant stem is a regular series of round-elliptical leaves which are also rooted to their support and leave very narrow spaces between the latter and their lower surfaces. In a plant running over rocks in the island of Dominica, W. I., I found numerous colonies of _Wasmannia auropunctata_ Roger utilizing these spaces for nesting purposes. I believe that Forel (1899–1900) must have taken the type specimens of his _Azteca hypophylla_ in such quarters under the leaves of some species of Marcgravia in Colombia, since he describes the insect as making “its nest under the round leaves of a plant which climbs on tree trunks like ivy. The ant glues the edges of each leaf to the bark of the tree with carton.”

**Combretaceae**

_Terminalia catappa_ L. This fine tree, known as the Indian or Malabar almond and in tropical America, where it is often planted for shade, as the “almandra” is easily recognized by its peculiar shining, obovate leaves, about 15 to 20 cm. long, with narrow cordate base and short petiole, clustered at the ends of the branches. The small white flowers are in slender spikes and the drupe-like, edible fruit has the shape of an almond. The internodes of its terminal twigs are often hollowed out and inhabited by ants. I have collected the following species from the trees planted along the drives at Balboa and Fort Amador, C. Z. Panama:

- (1) _Pseudomyrmza zebelli_ Forel.
- (2) _Solenopsis laeviceps_ Mayr var. _antoniensis_ Forel.
- (3) _Solenopsis zeteki_ Wheeler.
- (4) _Crematogaster (Orthocrema) brevispinosa_ Mayr var. _ampla_ Forel.
(5) Cryptocerus (Paracryptocerus) minutus Fabr.
(6) Dolichoderus (Hypoclinea) lutosus F. Smith.

Although T. catappa is not a native of the American tropics it is
nevertheless attacked by several insects, as shown by the following
data collected by Wolcott (1923) in Porto Rico:
(1) Megalopyge krugii Dewitz. Megalopygid moth, feeding on
foliage.
(2) Oeceticus kirbyiGuilding. Psychid moth cited by Gundlach as
feeding on foliage.
(3) Attelabus sexmaculatus Chevr. Curculionid beetle, feeding on
foliage.
(4) Aspidiotus destructor Sign. Coccid.
(5) Pseudococcus virgatus Ckll. Coccid.
(6) Saissetia nigra Nietn. Coccid.
(7) Saissetia oleæ Bernard. Coccid.
(8) Chrysomphos sonidum L. Coccid.

In the twigs of another Terminalia, T. (Bucida) buceras Wright, in
Porto Rico, I have taken colonies of the "hormigilla", Myrmelechista
ambigua subsp. ramulorum.

Bombacaceae

Probably the twigs of several of the large arborescent species of
this family, especially the various silk-cotton trees, are not infre-
dently inhabited by ants, but I can cite only two records in support
of this statement. J. Huber and A. Goeldi found twigs of Bombax
mungaba on the Rio Purus, Amazonas, inhabited by Pseudomyrma
sericea Mayr., and recently Prof. Jack, of the Arnold Arboretum, has
brought me from Soledad, Cuba a number of twigs of the common
Ceiba tree, Ceiba pentandra, containing colonies of Pseudomyrma
elongata Mayr var. cubensis Förel.

Euphorbiaceae

Mabea. About 30 species of this genus are known from Brazil and
the Guianas. They are shrubs with flexuous hollow branches, and
some of the species, especially M. fistulifera Mart. and angustifolia
Benth., seem to be well-supplied with calyx-glands, or glands on the
branches of the flower panicles (M. occidentalis Benth.). The latex of
M. piriri Aubl. of the Guianas yields rubber, and the stems of both
it and M. fistulifera are made into tobacco-pipes, as described in the
following quotation from Spruce: "The Mabeas are still more remark-
able than the Tachias, the long-sarmentose branches stretching away to a great length among the adjacent vegetation, although never actually twining. All Mabeas of the section Taquari have this habit, and all are infested by Tachi ants. The slender but tough twigs, hollowed and polished internally by ants, are a favorite material for tobacco-pipes with the Indians of the Amazon, who strip off the bark and paint and varnish the surface of the wood. These “Taquaris”, as they are called, are commonly sold in the shops of Para. A bundle of them which I purchased there is now in the Kew Museum. The arborescent Mabeas, however, with tall erect trunks and paniculate inflorescence, are apparently never touched by ants.

Sapium. Also a fairly large genus, comprising 25 species, and occurring in both the Old and New World tropics. The petioles have a pair of nectaries at their junction with the leaf-blade. The latex of S. biglandulosum Aubl. is medicinal and is said to yield a kind of rubber, but that of some of the Panamanian species (probably S. aucuparium Jacq.) is, according to Standley (1928 p. 240), “chewed by boys, who place it on twigs for the purpose of catching small birds.”

Azteca longiceps Emery subsp. sapii Forel was taken by Ducke in the hollow stems of S. glandulosum Morong at Ica, Amazonas, and Pseudomyrma caroli Forel var. sapii Forel was taken by E. Ule in the hollow stems of an undetermined species of Sapium at Bom Fim, Jurua, Amazonas.

Alchornea. This genus contains about 30 species of frutescent or arborescent plants which, like those of the preceding genus, occur in the tropics of both hemispheres. The leaves are described as bearing two to several nectaries at the base on the lower side. A. irucurana Casar of the subgenus Eualchornea is called “irucurana” or “arariba” by the Brazilians and yields a valuable wood. The following ants have been taken in its branches by K. Fiebrig in Paraguay:

1. Pseudomyrma sericea Mayr var. ita Forel.
2. Forelius maccooki Forel var. brasiliensis Forel.
3. Forelius maccooki subsp. fiebrigii Forel.

Leguminosae

The genera of this huge family, besides Tachigalia, which have been cited as containing species tenanted by ants in the New World are Sclerolobium, Pterocarpus and Platymischium:

Sclerolobium. According to Spruce, “the species of Sclerolobium are
not usually riparian but one species (*S. odoratissimum* sp. nov.) is eminently so, constituting a great ornament of the shores and islands of the Rio Negro towards the mouth of the Casiquiare, and perfuming the whole breadth of the river with the abundance of its pale yellow honey-scented flowers; and it is notable that this is the only species of the genus in which I have found saccolferous petioles. The sac is large, extending upwards from the knee of the petiole to the base of the second pair of leaflets, and it has a furrow along the upper surface. I presume the ants have been induced to take up their residence on these particular plants on account of the abundance and long persistence of their honied flowers." Bequaert believes that the petiolar sac described by Spruce "is merely an insect gall which, when empty, becomes settled by ants." In two other species, *S. tinctorium* Bentham and *paniculatum* Vog., Spruce observed no such domatia but merely the infestation of the flower-panicles "with little fire-ants, which, however, seemed to have their permanent habitation in the ground about or near the tree-roots, and never to perforate the leaf-stalks."

*Pterocarpus.* A genus comprising some 20 species of tropical trees with hard wood of considerable economic value and yellow flowers. Spruce alludes to *P. ancylocalyx* Bentham as "a small tree on the banks of the Solimoes, or Upper Amazon, which has the rachis of the racemes thickened in the middle, the swelling being sometimes (but not ways) tenanted by ants." Forel (1904) cites *Pseudomyrma sericea* Mayr as having been taken by E. Ule in the swollen flower-axes and twigs of *P. ulei* Harms at Jurua Miry, Amazonas.

*Platymischium.* A Neotropical genus comprising trees or shrubs with yellow flowers. In at least some of the 15 known species the stems are hollow or even dilated at the nodes and inhabited by ants. The following species have been recorded:


Perhaps some of the species of the genus Cercidium may prove to harbor several species of ants in their twigs and branches. *Cryptocerus rohweri* Wheeler, at least, has been taken from the branches of *C. torreyanum* in Arizona.
Olacaceae

Agonandra. In Paraguay Chodat and Vischer (1920) found two species of ants, Crematogaster (Orthocrema) goeldii Forel var. chodati Forel and Cryptocerus eduardi Forel, nesting in the trunks of A. brasiensis Benth. and Hook., a dicuous tree with pendent twigs, thin, elliptical, pointed leaves and small, racemose flowers. These botanists promise a fuller account of the plant and the nesting habits of the ants and merely remark (p. 193): "The material which we brought back from Paraguay for the purpose of studying the myrmecephily of the Agonandra, does not permit us to reach such precise (sic!) conclusions from this genus as those obtained from the Cordias and Acacia cavensis. In fact, in the trunks of this species, the existence of medullary galleries with rather large openings excavated perpendicularly to the wood can be observed only at certain points. It seemed to us that these galleries had been excavated by some phytophagous insect, possibly a Coleopteron." It is difficult to see how "myrmecephily" can apply to this case any more than to the excavations made by Camponotus herculeanus L. and its various races in the wood of North American and European trees which have been previously attacked by various beetles.

Loranthaceae

Phoradendron. In Arizona I found the stems of a mistletoe, Ph. flavescens Nutt. var. villosum Nutt., growing on live oaks (Quercus emoryi) to be regularly inhabited by colonies of Crematogaster (Orthocrema) arizonensis Wheeler. According to Schwarz (1901) the cavities tenanted by the ants are made by a Cucurionid beetle of the genus Otiocephalus. The plant, indeed, constitutes the center of an interesting biocenose, comprising a Coccid, Pseudococcus phoradendri Cockerell, which lives in the cavities with the ants, another Coccid, Lecanium phoradendri which, according to Schwarz, lives on the outer surface of the plant, a Coccinellid beetle, Cephaloscymnus occidentalis Horn, that feeds on this Coccid, a butterfly caterpillar, Thecla halesus, that consumes the leaves and two beetles, a Bostrichid (Amplicerus sp.) and a Scolytid (Stephanoderis sp.) that bore in the stems.

Rutaceae

Xanthoxylon. Many years ago I found that the twigs of the common prickly ash of our Southern States, X. clavis-Herculis L., in the vicinity of Austin, Texas were frequently inhabited by colonies of three species
of *Pseudomyrma* (*Ps. brunnea*, *flavidula* and *pallida*), and more recently Mr. E. D. Christophersen has found two species of ants, *Pheidole gauthieri* Forel var. *oxymora* Forel and *Camponotus* (*Hypercolobopsis*) *christopherseni* Forel, living in the large, corky spines which stud the trunk of *X. panamense* P. Wils. Although I have often examined the spines of this Central American tree and have found in many of them galleries that had been eaten out by insects, I failed to find any ant-colonies. The species taken by Christophersen may have been chance occupants of such burrows.

**Anacardiaceae**

*Schinus*. Luederwaldt (1926) records the occurrence of *Procryptocerus subpilosus* F. Smith subsp. *lepidus* Forel in dry excrescences on *Schinus terebinthifolius* Raddi in Brazil.

**Rubiaceae**

*Borreria verticillata* (L.) G. F. W. Mey. As previously stated (p. 92) the hollow, internodes of this low shrub are often inhabited by ants. I first observed it in a small clearing, covering less than an acre, behind the tropical laboratory at Kartabo, B. G., where it was very abundant. Its small, agglomerated flowers attracted many bees, especially Meliponine, and the dead stems seemed to be even more frequently occupied by ants than those of any other plants in the vicinity. According to Schumann (1897 p. 114), *B. verticillata* is common in the warmer parts of America from Florida and Mexico to Argentina, not rare in West Africa and on the Cape Verde Islands and has been recorded from Mozambique. The following is a list of the ants taken in its internodes at Kartabo:

1. *Pseudomyrma acanthobia* Emery
2. *Pseudomyrma*
3. *Pseudomyrma*
4. *Pseudomyrma*
6. *Monomorium*
7. *Solenopsis corticalis* Forel
8. *Crematogaster*
9. *Leptothorax* (*Goniothorax*) *aculeatinodis* Emery
10. *Leptothorax* (*Goniothorax*) *spininodis* Mayr
12. *Myrmelachista*
13. *Brachymyrmex*
14. *Camponotus*
Gentianaceae

Tachia. The only Neotropical genus of this family said to be associated with ants is Aublet’s Tachia (Myrmecia Schreber). In the original description of the type species, T. guianensis, Aublet states that “the trunk and branches, which are hollow, serve as a retreat for ants; it is for this reason that this shrub is called by the Galibis ‘Tachi’, which according to their report, signifies in their language “ant-nest”. According to Spruce, “the pretty Gentianaceous shrubs of the genus Tachia have long, slender, hollow branches, that either hang down or support themselves on the branches of adjoining shrubs and trees; yet although this character is (as I suppose) an undoubted inheritance of the effects of ant-agency, it is singular that Tachias are now-a-days often found entirely free from ants; while the name taken by Aublet from the Tupi language, distinctly implies that in his day they were notoriously ant-infested.” These remarks seem to indicate that the Tachias are not myrmecophytes but shrubs sometimes or perhaps only locally inhabited by ants. I have seen no record of Formicidae from these plants.

Compositae

The sole Neotropical representative of this huge family recorded as harboring ants is the Brazilian Erigeron maximus Link. H. von Ihering and Luederwaldt found its stalks inhabited by Azteca muelleri Emery var. wackettii Emery. Like the typical form of the species, this variety also makes carton nests in the trunks of Cecropia.

Chapter 8

THE EPHYTYTIC BROMELIACEAE AND THEIR FAUNA

Some years ago considerable attention was devoted to a study of the epiphytic Bromeliaceae of the Neotropical Region, but there are few references in the literature to their ant-inhabitants. Several botanists, notably Cedervall (1884), Schimper (1884, 1888, 1903), Ule (1900), Mez (1904), Wercklé (1909) and Aso (1910), investigated the anatomy and ecology of these epiphytes, and quite a number of zoologists, including Fritz Müller (1879, 1880), Ad. Lutz (1903), Calvert (1910a, 1910b, 1911a, 1911b, 1917) Scott (1912), Knab (1912, 1913a, 1913b) and Picado (1911, 1912a, 1912b, 1913) were keenly interested in the associated faunal components.
Most of the Bromeliaceae are epiphytes on living trees or shrubs, but some of them occasionally grow on inanimate supports, such as rocks, fences, telegraph-wires, etc., and although the majority of the genera and species are confined to the rain-forests, certain species, especially of the genus Tillandsia, flourish in dry, open forests or coppices or along sea-beaches. The plants lack stems and their slender roots serve merely for holding fast to the substratum. Many species, however, if they happen to be detached from their support, readily take root in the soil and continue their growth under the new conditions. The leaves grow in the form of a close rosette and are widened at their bases, which are arranged in such a manner that each can receive and retain a certain amount of water, derived from the rain, dew or mist, and both inorganic and organic detritus (windblown leaves, soil, etc.). Some large Bromeliads may thus store as much as 20 litres of water. On this account the epiphytic Bromeliaceae have been called “tank-epiphytes” (Schimper, 1903) and may be regarded as so many diminutive pools, which in the tropics replace the ponds of more temperate regions (Picado, 1913). The flowers, often showy though evanescent, are usually borne on a long leafy or scaly axis arising from the center of the leaf-rosette. The fruits are very diverse, being in some species berries, in others dehiscent pods. Peculiar appendages in the form of asymmetrical wings or crests or pappus-like tufts of silky hairs are developed from the walls of the capsule and serve to disseminate the seeds, which are usually numerous but differ considerably in shape in the various genera.

Owing to the peculiar arrangement of the leaves and their method of retaining water and detritus, the plant, according to Picado, may be divided into an aquarium, or tank, and a terrarium; the former represented by all the water-holding leaf-bases, the latter by the dry detritus which is left over around the periphery after the older outer leaves of the rosette have decayed or broken off and therefore no longer hold water. Both the tank and the terrarium furnish habitations for a large number of organisms, the tank for many aquatic and amphibious creatures (Infusoria, fly, beetle, and dragonfly larvæ, Copepods, tree-frogs, etc.), the terrarium for many cryptobiotic forms (worms, Isopods, earwigs, Myriopods, Onychophora, etc.). Ad. Lutz believes that fully one fifth of the species of Brazilian mosquitoes, including some nosophoric (malarial) forms, regularly breed in the tanks of Bromeliaceae and Knab has bred a number of Culicidae from these plants in Mexico and Panama, including the large species of Megarinus, which are so cannibalistic as larvæ that only one of them can
live in a single water-holding leaf-base. The foliage of the Bromeliads, of course, affords food for several caterpillars and leaf-eating beetles, bugs, etc., and opportunities for various spiders to construct their webs and prey on the small Diptera that oviposit in the tanks.

Ad. Lutz discovered that the water in the reservoirs is unusually pure and that no putrefaction of its organic contents takes place as long as it remains in contact with the plants' leaves. It has long been known that the latter are covered with peculiar shield-shaped scales (modified trichomes), which are always most abundant at the leaf-bases and have been carefully studied by Cedervall, Schacht, Schimper, Mez and Aso. Schimper showed that the water as well as its contained salts and organic substances are absorbed by the leaves through these scales and are essential to the growth of the plant. He states that "the spoon-shaped leaf-bases, which are closely applied to one another, nearly always contain even during the dry season considerable quantities of water, pieces of rotting leaves and twigs, dead animals and earthy materials of undeterminable origin. Experiments have shown that these substances are not only utilized by the plant but are indispensable to its existence, since the roots, under the most favorable circumstances, take up but little water to cover transpiration and besides under natural conditions usually remain quite dry on account of the umbrella-like form of the leaf-rosette."

Most epiphytic Bromeliads are strongly negatively geotropic and therefore grow in such a position that their leaves are able to acquire and retain considerable quantities of meteoric water and both mineral and organic detritus. Picado has confirmed and extended the observations of previous investigators. He has proved that the absorption of minerals from the water by the leaves is an habitual nutritive process and that these organs secrete a gummy matter (consisting of 77% bassorine and 27% arabine and diverse soluble substances), which has both an amylolytic and a proteolytic action on the organic detritus and thus renders its soluble portions assimilable by the plant. The insoluble refuse forms a kind of peat, which is free from proteids and starches and contains almost no traces of salts. Hence the purity of the water in the reservoirs and the absence of decomposition in the refuse as long as it remains in contact with the living leaves. The terrarium, which is formed by the failure of the old peripheral leaves to form acequate reservoirs, may therefore be said to consist of peat. The formation of this substance in the Bromeliads is compared by Picado with that of our northern bog-peat, which, unlike humus, is formed only under water that is constantly being renewed, "The climate, in which these
plants (the epiphytic Bromeliaceae) grow, being very mild and the water in their tanks being very pure, since all its soluble contents are slowly and constantly diminished by absorption, the decomposition of the detritus occurs under conditions closely analogous to those that lead to the formation of peat-bogs."

The Bromeliaceae of the type here discussed flourish most luxuriantly where they are fully exposed to the sun-light on the high branches of trees and where they would seem also to be most advantageously situated for securing their meteoric water and wind-blown detritus. But these conditions are rather unfavorable for ants, since as a rule they can find nesting sites only under the dry roots of the plants or in the terrarium. For this reason most of the water-bearing Bromeliads are avoided by the ants. There are certain species of Tillandsias, however, which afford them much more favorable quarters. Since Picado has very little to say about these plants, we may turn to Schimper who was led to study them closely, because he found them constituting the great bulk of the epiphytic flora in the West Indies, where he first investigated the ecology of tropical plants (1884). His earlier account is reproduced in his paper of 1888 from which I quote: "In Tillandsia flexuosa, which inhabits very dry, sunny situations, the tips of the leaves are brought together over the water-reservoir and spirally twisted around one another, so that the latter is entirely concealed from the direct sun-light but accessible to the rain and dew by means of the long slender canals. But the most complete protective arrangements are found in Tillandsia bulbosa, which also grows in sunny situations and is represented on our Plate IV. The leaves of Tillandsia bulbosa are spoon-shaped at their ensheathing bases, whereas the blade is cylindrical and either trough-like, with a narrow slit, or tubular, with the leaf-margins closely approximated or overlapping each other. The blade is always more or less strongly retroflected and twisted around its axis. The sheaths form an onion-like bulb which is nearly everywhere compactly closed and since they are strongly and convexly spoon-shaped and applied to one another only at their margins, contain large cavities continued above into the tubular leaf-blade and provided with only a very small orifice opening to the outside at the junction of the sheath and blade. The peripheral half of the tubular blade consists of chlorophyll-containing parenchyma and a very thin layer of aquiferous tissue; the inner side, on the contrary, is quite colorless and carpeted with exceedingly numerous, very large scales, which are sunk into a dense layer of aquiferous tissue. While young, the sheath, so far as it is covered by the other leaves, is devoid of
chlorophyll, thin and invested on both surfaces with scales which sur-
pass in dimensions those of most of the other species and are so densely
crowded that the epidermis is reduced to narrow strands. The plant
entirely lacks the very strong negative geotropism characteristic of the
rosettes of the epiphytic Bromeliaceae. It occurs sometimes on the
upper, sometimes on the lower side of the branches, or on perpendicular
trunks, and grows in an erect horizontal or inverted position, with-
out ever exhibiting a trace of geotropic curvature. The bulbs always
contain water in their inner cavities, besides earthy materials and
small dead insects, whereas the outermost cavities are free from such
substances and harbor ants. That the contained water does not fall
out, even in the inverted position, requires no explanation, since each
chamber, except for its small upper orifice, is tightly closed on all
sides. How the water manages to gain entrance, however, calls for
brief explanation. If drops of water are allowed to fall on the margins
of the leaf-blades, no matter whether they overlap or are merely ap-
proximated, the liquid is greedily sucked in by capillarity. The same
occurs at the margins of the sheaths and at the narrow orifice at the
base of the blade. By such means the cavities may be filled in a short
time, and this occurs in nature in the presence of rain or dew. It should
be emphasized, in case this experiment is repeated, that the first drop
is less quickly imbibed, if the plant happens to have remained un-
moistened for some time. The outer leaves are, in fact, usually not
easily wetted and take up only a small amount of water. Not only
does water enter the wetted bulbs, even when they are inverted, but
they may, in any position, as shown in our figure, imbibe water and
eventually conduct it into their reservoirs. The earthy materials, which
are always present in the water, are derived from the small amounts of
solids that are washed off by the rain from the leaves and branches of
the host tree. The plant probably secures its nitrogen also from the
cadavers of the ants, which are not content to remain in the peri-
pheral cavities, but also, as we have found, make fatal incursions into
the water-containing chambers. The narrow orifice at the base of the
leaf-blade serves the ants as an entrance.”

Schimper thus seems to have been the first to notice the regular
nidification of ants in Tillandsias. Since 1901, when I recorded the
occurrence of several species of these plants in the neighborhood of
Cuernavaca, Mexico, I have been able to observe the same association
on numerous occasions in several of the countries surrounding the
Gulf and Caribbean. The insects live only in the species of Tillandsia
that have the leaf-bases more or less spoon-shaped and compactly
overlapping. The species concerned are those designated in the literature as *T. utriculata* Linn., *fasciculata* Swarts, *balbisiana* Schultes, *Benthamiana* Klobsch, *aloifolia* Hooker and *flexuosa*. Unfortunately I failed to collect specimens of the various Tillandsias in which I found Formicide so that I am in most cases uncertain of the precise identification of the plants.

The ants enter and leave the Tillandsias either through the small preformed openings near the tips of the expanded leaf-bases, as Schimper observed, or as I have observed, through larger openings which they gnaw in the leaf-bases. Since such openings are made not only in the outermost but also in the enclosed leaves, the ants are provided with a number of convenient intercommunicating chambers. Incipient colonies of larger species and single adult colonies of minute species often confine themselves to the space between a single leaf-base and those which it covers, so that not infrequently several different species may occupy as many different chambers in the same plant and live as near neighbors, or in a kind of parœcism or parabiosis. The ants rarely enter the wet innermost portion of the plant, and I am inclined to believe that the openings which they gnaw prevent any deleterious retention of water in their chambers by serving to draw it away. More careful observations in the field, however, are required to substantiate this supposition.

Owing to the fact that Picado did not bestow special attention on the Tillandsias, the Hymenoptera in his conspectus of the known Bromeliaceous fauna, comprise only the two species of ants (*Odonomachus hastatus* and *Apterostigma calverti*) observed by Calvert in some of the genera of larger Costa Rican Bromeliads. The following list of ants shows that they really constitute a considerable portion of the Bromeliad biocenose as a whole. I include several forms recorded by Luederwaldt as occurring among or under the roots of epiphytes. Though the latter may not have been Bromeliaceæ, the ants mentioned very probably live occasionally among the roots of these plants. It is obviously impossible to draw a hard and fast line between such nesting sites and the ant-gardens.


(4) Neoponera crenata var. mæsta Mayr. In the same plants. Brazil (Luederwaldt).


(9) Odontomachus hastatus Fabr. Between leaves of Bromeliaceae and other epiphytes. Costa Rica (P. P. Calvert); Brazil (Luederwaldt).


(14) Pheidole anastasii Emery var. sospes Forel. Among roots of epiphytes. Brazil (Luederwaldt).

(15) Pheidole angusta Forel. Among roots of epiphytes with Ectatomma (Gnamptogenys) annulatum as neighbors, Brazil (Luederwaldt).


(19) Crematogaster (Orthocrema) arcuata Forel var. aruga Forel. In Tillandsia aloifolia. Panama (Wheeler).

(20) Crematogaster (Orthocrema) brevispinosa Mayr. In tufts of Bromeliaceae.


(22) Crematogaster (Orthocrema) brevispinosa var. tumulifera Forel. In Tillandsia aloifolia. Panama (Wheeler).

(34) Solenopsis corticalis Forel subsp. amazonensis Forel. In Tillandsias (Pseudocatopsis sp.). Peru (E. Ule).
(44) Dolichoderus (Hypoclinea) championi Forel subsp. trinidadensis Forel var. tæniasis Forel. In Tillandsia aifoïlia. Panama (Wheeler).
(46) Dolichoderus (Monacis) bispinosus Olivier. In Tillandsia aifoïlia. Panama (Wheeler).
(60) Camponotus (Myrmothrix) cingulatus Mayr. Among Bromeliaceae. Brazil (Luederwaldt).
(64) Camponotus (Myrmobrachys) planatus var. continentis Forel. In Tillandsias. Florida (Wheeler).

Many of the ants in this list live also in hollow twigs or in other available plant-cavities. One species, Apterostigma calverti, is of unusual interest, because it belongs to the fungus-growing Attini, which regularly nest in the ground, under stones or in and under rotten logs, and is therefore exceptional in having become arboreal and in constructing its gardens in the terraria of large Bromeliads with the excrement of the beetles or caterpillars that feed on their foliage. Cyphomyrmex auritus is another fungus-growing ant which is recorded by Luederwaldt as nesting and making its gardens among the roots of epiphytes. It may, therefore, occasionally live among Bromeliads. I am inclined to believe that yet another Attine ant, Cyphomyrmex salvini Forel, may eventually be found to have similar habits. In Panama I have taken it repeatedly under the bases of palm-petioles several feet above the ground. It might, therefore, nest about the roots of Bromeliads and other epiphytes. Its gardens consist of the collected excrement of small insects and are covered with a peculiar fungus very much like that cultivated by C. rimosus Spinola and its various subspecies (see Wheeler, 1907, p. 771, Pl. 50, Fig. 29).

The colonies of ants nesting in Tillandsias are singularly free from parasites or myrmecophiles. The only ant-guest which I have seen in these plants is a flat, broadly elliptical Microdon puparium in a colony of Pseudomyrmex gracilis subsp. mexicana, taken many years ago at Cuernavaca, Mexico. The adult larva of this insect is figured in my paper of 1901.

The following table includes a list of the number of species of bromeliadicicolous animals cited by Picado and the ants above enumerated:
WHEELER: NEOTROPICAL ANT-PLANTS AND THEIR ANTS

Rotifera .................. 1
Planarians ................. 5
Oligochaeta ................. 8
Hirudinea .................. 3
Gastropoda ................ 4
Crustacea .................. 9
Oncophora .................. 2
Myriopoda .................. 16
Arachnida .................. 29
Thysanura ................. 1
Orthoptera ................. 29

Thysanoptera ................. 1
Dermoptera ................ 28
Plecoptera ................ 1
Odonata .................... 1
Hemiptera .................. 8
Coleoptera ................ 36
Lepidoptera ................. 3
Diptera .................... 88
Hymenoptera (Formicidae) .. 66
Batrachia .................. 6

Total ....................... 342

This list represents, of course, only a small fraction of the total bromeliadicolous fauna, which has nowhere been exhaustively studied. Throughout great regions of Brazil, Eastern Peru and the Guianas no systematic search has been made for the animal tenants of the luxuriant epiphytic flora. The majority of the recorded species (261) are insects, but whole groups of animals, such as the Infusoria and Nematodes, have received no attention. If we include the Bacteria, fungi and algae which must be associated with the plants and their tenants the total Bromeliad biocenosis would probably be very extensive. Picado mentions Saprolegniaceae on the aquatic insect larvae and Werckle states that the flowers of certain Tillandsias are often greatly injured by smuts. There are, as we have seen, fungi in the gardens of Apterostigma calverti and other species no doubt invade the peaty remains of the terraria. The fauna and flora of the epiphytic vegetation may be suggested as very promising subjects for intensive investigation in some of the laboratories that have been recently established in the American tropics.1

1Professor Wheeler intended to expand the Chapter dealing with the Bromeliaceae. Among other recent papers which he wanted to review are three important contributions by Miss Skwara (1930, 1934a, 1934b) on ant plants and bromeliads of Mexico. [J. Bequaert].
REFERENCES

AFLARO, A.

ASO, K.

AUBLET, J. B.

BAILEY, I. W.

BARBER, H. S.

BECCARI, O.

BELT, T.

BENTHAM, G.

BEQUAERT, J.

BEURLING, P. J.
BOHEMAN, C. H.

BOLDINGH, H.
1914. The flora of Curaçao, Aruba and Bonaire (Leiden).

BORGMEIER, T.

BOULGER, G. S.

BREYNIUS, J.

Brès, C. T.

BUSCALIONI, L. AND HUBER, J.

CALVERT, P. P.

CALVERT, A. S. AND CALVERT, P. P.

CEDERVALL, E. V.

CHAMPION, G. C.

CHODAT, R.

CHODAT, R. AND CARISSO, L.

CHODAT, R. AND VISCHER, W.

COBO, P. BERNABE

COCKERELL, T. D. A.

COMMELYN, J.

DAMMER, U.

DARWIN, F.

DELPINO, F.

DONISTHORPE, H. S. J. K.


DUCKE, A.

EMERY, C.


FIEBRIG, K.

FOREL, A.


GÜRKE, M.

HARMS, H.

HEMSLEY, W. B.

HERNÁNDEZ, F.

HOHENDERK, L. S.

HUBER, J.

HUTH, E.
1887. Myrmecophile und myrmecophobe Pflanzen. (Berlin), 27 pp., 2 Pls.

HEERING, H. VON

JACQUIN, N. J.
1763. Selectarum stirpium americanarum historia. (Vienna), vii + 284 pp., 183 Pls.

JOHNSTON, I. M.

KNAB, F.

KOELSCH, K. A.

LENG, C. W.

LINNÉ, C. VON
1737. Hortus Cliffortianus. (Amsterdam), x + iv + 501 + 16 + 36 pp. 1 Pl.

LUEDERWALDT, H.

MANN, W. M.
Marcgravius de Liebstad, G.

Maza, M. G. de la and Roig, J. T.

Meinert, F.

Meisner, K. F.

Ménégaux, A.

Menozzi, C.

Mez, C.

Miquel, F. A. W.

Moebius, M.

Morrison, H.

Moroteo, E.

Müller, Fritz

Paoli, G.


Picado, C.


Piso, G.


Pittier, H.


Plukenet, L.

1720. Opera omnia botanica. 6 vols.

Pulle, A.

1906. An enumeration of the vascular plants known from Surinam, together with their distribution and synonymy. (Leiden).

Ray, J.


Rettig, E.


Rodway, J.

ROSS, H.

RUZI, H. AND PAVON, J.

SAFFORD, W. H.

SALDANHA DA GAMA, JOSÉ DE

SCHENCK, H.
1913. Acaciae myrmecophilae novae. Fedde’s Repertorium, 12, p. 370.

SCHIMPER, A. F. W.
1888b. Die epiphytische Vegetation Amerikas. (Jena), 162 pp., 6 Pls.

SCHUMANN, K.


SCHWARZ, E. A.


SCOTT, H.


SEEMANN, B.


SEVERIANO DA FONSECA, J.

1881. Viagem ad redor do Brazil. (Vol. 1: 325).

SKWARRA, E.


SMITH, F.

1862. Descriptions of new species of aculate Hymenoptera, collected at Panama by R. W. Stetch, Esq., with a list of described species, and the various localities where they have previously occurred. Trans. Ent. Soc. London, (3) 1, pp. 29-44.

SMITH, J. DONNEL


SNETHLAGE, E. H.


SPIX, J. VON AND MARTIUS, C. VON

Spruce, R.

Stäger, R.

Standley, P. C.

Tidestrom, I.

Tulasne, I. R.

Ule, E.

Warrburg, O.
Warming, E.

Wasmann, E.

Weddell, H. A.

Werckle, C.

Wheeler, W. M.
1921. A study of some social beetles in British Guiana and of their relations to the ant-plant Tachigalia. Zoologica, 3, pp. 35–183, 5 Pls.

Wheeler, W. M. and Bailey, I. W.

Wheeler, W. M. and Bequaert, J.

Wittmack, L.

Wolcott, G. N.
Part II. NEOTROPICAL PLANT ANTS

In the following pages I have endeavored to bring together the scattered information which has long been accumulating in our myrmecological literature concerning the Formicidae inhabiting living plants in the Neotropical Region, together with descriptions and records of the forms recently collected by Dr. W. M. Mann, Dr. J. C. Bradley, Prof. I. W. Bailey, Mr. H. O. Lang and myself. The citations of the literature are restricted to the actual records and do not cover mere taxonomic descriptions. These may be readily found by consulting the various fascicles by Professor Carlo Emery on the Formicidae in the "Genera Insectorum". In some cases, no doubt, the collected records refer to the occurrence of ants in dead twigs and do not properly belong in my list, since their authors sometimes fail to make the necessary distinction. Many species, however, which normally nest in dead twigs may occasionally inhabit cavities in living vegetable tissue. For the same reason I may have omitted a number of species which should have been included. Since, however, the list is presented merely as a convenient basis for future observations, these defects are not to be regarded too seriously. In its present form it gives a definite and suggestive picture of the known neotropical ants which have either already become exquisitely adapted and specialized for living in the various myrmecophytes that occur within their geographical range or are on the road to acquiring such an adaptation.

Subfamily PONERINAE

Genus NeoponerA Emery

NeoponerA carinulata Roger

British Guiana: Merume Mouth (H. O. Lang), nesting in the fistulose stems of Patima formicaria Johnston (Rubiaceæ).

NeoponerA crenata Roger


British Guiana: Kartabo (Wheeler); in hollow petioles of Tachigalia paniculata Aubl.

Panama: Barro Colorado Island, Gatun Lake, C. Z. (Wheeler), in cauline swelling of Cordia gerascanthus L.
Neoponera stipitum Forel

Guatemala: Quirigua (Wheeler); in internode of a young Cecropia. British Guiana: Kartabo (Wheeler), nesting in a large branch of Cecropia sciadophylla var decurrens Smetl.

Neoponera unidentata Mayr


British Guiana: Kartabo (Wheeler); in hollow petioles of Tachigalia paniculata Aubl. In the same locality I have also taken this ant on several occasions in the cauline swellings of Cordia nodosa L.

Neoponera villosa F. Smith


Mexico: Vera Cruz at the foot of Orizaba; in the pseudo-bulbs of an orchid, Schomburgkia tibicinis.

Genus Anochetus Mayr

Anochetus (Stenomyrmex) emarginatus Fabr.

Wheeler, Ecology 2, 1921, p. 96.

British Guiana: Kartabo (Wheeler); in ant-gardens about the roots of epiphytes. This ant usually nests under bark or in the cavities of dead limbs.

Genus Odontomachus Mayr

Odontomachus affinis Guérin subsp. mayri Mann.

Mann, Psyche 19, 1912, p. 39 9.

Brazil: Madeira Mamore R.R., Matto Grosso (W.M. Mann). In ant gardens, living in parabiosis with Dolichoderus (Monacis) debilis var. rufescens. O. affinis usually nests in the ground. Its habits have been studied by Borgmeier. (Deutsch. Ver. Wiss. Kunst. 7, 1920, p. 31-38).

Odontomachus hastatus Fabr.

Calvert, A Year of Costa Rican Natural History, 1917, p. 231, fig.

Costa Rica: (P. P. Calvert), frequently nesting in Bromeliads.
Subfamily PSEUDOMYRMINAE

Genus Pseudomyrmex F. Smith

Pseudomyrmex acanthobia Emery


Paraguay: San Salvador (J. Bohls); in woody thorns of Acacia (cavenia).

Var. Fuscata Emery


Paraguay: San Salvador (J. Bohls); in woody thorns of Acacia (probably cavenia).

The other varieties and subspecies of acanthobia live by preference in dead twigs or the culms of grasses.

Pseudomyrmex alliodorae sp. nov.

Plate 47, Fig. a

Worker: Length 2.5—2.8 mm.

Head subrectangular, about one and two-thirds times as long as broad, as broad in front as behind, with feebly convex sides and very slightly sinuate posterior border. Eyes very large, elongate-elliptical, flat, more than half as long as the head, somewhat nearer the anterior than the posterior corners. Ocelli well-developed. Mandibles convex at the base, more flattened distally, with five well-developed teeth. Clypeus very short, laterally depressed, its anterior border projecting in the middle as a short, narrow lobe with straight edge and sharp corners. Frontal carinae represented by a short, convex, longitudinal ridge continuous with the clypeal lobe. Frontal groove absent. Antennae short; the scapes scarcely attaining the middle of the head, rather slender, curved, about four times as long as broad; first funicular joint one and one-half times as long as broad; remaining joints, except the last, transverse, nearly twice as broad as long. Thorax rather elongate, the pro- and mesonotum together equal to the epinotum; the promesonotal and mesoepinotal sutures pronounced, the dorsal outline at the latter rather deeply and abruptly notched. Pronotum longer than broad, slightly narrowed behind, bluntly submarginate on the sides; mesonotum rather flat, broader than long, its anterior border bluntly angular, its posterior border rounded. Epinotum nar-
rowed behind, its base feebly convex, nearly twice as long as the straight sloping declivity. Petiole from above elongate-elliptical, broadest in the middle, about one and two-thirds times as long as broad; in profile without a peduncle, nearly as high as long, evenly rounded above and slightly higher just behind the middle, the sides flattened but not marginate above, the anterodorsal tooth well-developed, directed downward. Post-petiole less than twice as broad as the petiole, convex and rounded dorsally, ventrally and laterally, slightly broader than long and somewhat narrowed anteriorly. Gaster of the usual shape. Fore femora dilated and convex, somewhat more than twice as long as their median diameter.

Somewhat shining; head and thorax more subopaque. Mandibles opaque, very finely and indistinctly punctulate; head and thorax densely punctate, the punctures on the former distinctly coarser; gaster very finely and superficially punctulate.

Pilosity and pubescence white, the former short, uneven and sparse on the body, absent on the appendages; the pubescence very fine, short and uniform over the whole surface of the body and appendages, rendering them pruinose.

Dark brown; anterior portion of head, gula, sides of pronotum and posterior borders of gastric segments paler, more yellowish brown; mandibles, clypeus, anterior borders of cheeks, antennae, tarsi and tips and bases of femora and tibiae yellow.

Female. Length 3-3.2 mm.

Very similar to the worker but with the head longer, fully twice as long as broad, with larger eyes and ocelli. Thorax through the wing-insertions slightly narrower than the head through the eyes. Mesonotum subhexagonal, slightly broader than long, very feebly convex in profile. Pronotum more sharply submarginate on the sides than in the worker; epinotum decidedly shorter and more rounded in profile.

Petiole longer and more distinctly pedunculate. Sculpture, pilosity and color as in the worker, except that the punctation of the head is finer and the surface, therefore, more shining. Wings hyaline and colorless, with pale yellow veins and pterostigma.

Described from numerous workers and two females. This ant was not infrequently found nesting in the cauline swellings of *Cordia gerascanthus* at Ancon, C. Z., Panama. On one occasion I took it also in a hollow twig of *Triplaris americana* near Miraflores, C. Z. It is rather closely related to *Ps. dolichopsis* Forel, *elongata* Mayr and *subtilissima* Emery, but cannot be referred to any of these species.
Pseudomyrma belti Emery


The worker measures 5–6 mm. and is black, with the mandibles, border of mouth, antennae, articulations of legs and tarsi reddish. The body is opaque and densely punctate, the abdomen more finely than the head and thorax, the epinotum and summit of petiole also with superimposed foveolae. The pilosity is pale and sparse, the pubescence grayish, appressed and sericeous. The head is ovate, scarcely longer than broad, the eyes occupying less than half its sides, the ocelli small, the anterior border of the clypeus with a narrow, median, truncated lobe, which is not dentate at the corners. Frontal groove distinct, second funicular joint as broad as long, remaining joints, except last, broader than long. The thorax resembles that of Ps. spinicola Emery, but the mesonotum is more convex and projecting and the epinotum is shorter and with a more obtuse angle between the base and declivity. The petiolar node and its peduncle are much shorter, the latter not longer than broad, the former with a small, acute ventral tooth. The postpetiole is broader than long, nearly twice as broad as the petiole, subtriangular, narrowed in front and convex behind.

The female measures 8–10 mm. and resembles the worker in sculpture, color and pilosity, but has the head one and one half times as long as broad, with rather straight, subparallel sides and straight posterior border. Mesonotum shining, with a blackish or dark brown streak on each side. The wings are infuscated, with dark brown veins and pterostigma.

The male was not described, but its head was figured by Emery. It has larger though less convex eyes than spinicola.

The species was first taken by A. Alfaro at Alajuela, Jimenez and Siberia, Costa Rica in the thorns of an Acacia which Wasmann believes to have been Acacia spadieigera, but which was probably costaricensis. I possess a cotyope worker and numerous workers taken by Dr. P. P. Calvert from Acacia thorns at Santa Cruz, Guanacaste, Costa Rica and numerous workers and a female taken by Dr. J. Bequaert in thorns of Acacia yucatanensis Schenck at Puerto Castilla, Honduras.
Subsp. *pelloسا* subsp. nov.

*Worker*. Length 5–5.5 mm.

Differing from the typical form of the species in having the sides of the pronotum more distinctly submarginate, the petiole and especially its peduncle longer, the latter stouter and with more prominent spiracles, the node higher, more convex and more sharply truncated behind, the postpetiole broader in proportion to its length and more convex. The sculpture, especially of the thorax, is coarser, the foveolae on the epinotum and petiolar node sharp and discrete. The pubescence and pilosity is longer and more conspicuous. The color is the same, except that the thorax and petiolar peduncle are red, with the dorsal surfaces of the pro-, meso- and epinotum, except their borders, black. There is usually some infuscation of the sides of the thorax, especially of the mesopleura. The mandibles,clypeus and cheeks are brownish yellow, the antennae and legs brownish red, with the femora and tibiae, except their tips and bases, dark brown or blackish.

Described from numerous specimens taken by Prof. C. F. Baker at Granada, Nicaragua, in thorns of *Acacia costaricensis*. I have also a number of specimens taken by Mr. William Fluck in another unrecorded Nicaraguan locality and also in Acacia thorns.

Subsp. *fulvescens* Emery


*Worker*. Length 3.5–5.5 mm.

Head longer than in the preceding subspecies, fully one and one-third times as long as broad, the punctuation finer so that the surface is more shining, the pilosity and pubescence somewhat sparser. Thoracic dorsum straight in profile, mesonotum rather flat; petiole and postpetiole much like those of the typical *belti*, but the postpetiole is somewhat narrower; the petiolar node varies, being as broad as long in some specimens and somewhat longer than broad in others. Yellowish or ferruginous red, the postpetiole, gaster and legs, except their articulations, usually darker.

*Female*. Length 6.5–8 mm.

Head fully one and two-thirds times as long as broad, parallel-sided,
the eyes more than twice as long as broad, flattened. Mandibles robust, with convex surfaces and external borders. Epinotum long, its declivity rather abrupt, shorter than the base. Sculpture, pilosity and color much as in the worker; foveolation of epinotum coarser. Mandibles red, clveus, antennae and anterior third of head yellow; sides of mesonotum and sometimes the mesopleura castaneous; ocellar region infuscated. Wings grayish hyaline or slightly brownish, with brown veins and pterostigma.

**Male.** Length 6.5–8 mm.

Head, including the eyes, distinctly longer than broad, narrowed behind, with rather straight posterior border. Eyes about half as long as the sides of the head. Antennal scapes twice as long as broad; first funicular joint longer than broad. Epinotum rather long, sloping, but with distinct base and declivity. Surface of body more shining and more finely punctuate than in the worker and female. Dark brown; mandibles, clveus, scapes, first funicular joint and tarsi whitish yellow; sides of pronotum, sutures of thorax, bases and tips of femora and tibiae and the borders of the gastric segments yellowish brown. Wings like those of the female.

The types of this subspecies were found by Beccari in cauline swellings of *Cordia gerascanthus* L. from Guatemala, but the occurrence of the ant in this plant must be very exceptional, since it is the commonest and most widely distributed obligate of the various bull-thorn Acacias in Central America and Mexico. I give here a list of the localities from which I possess specimens:

Guatemala: Escaïnla, Patulul, Zacapa and Quirigua (Wheeler), in thorns of *Acacia hindsii* Benth., *Acacia* sp. *bursaria* Schenck; Trece Aguas, Alta Vera Paz (Schwarz & Barber).

British Honduras: Manatee (J. D. Johnston), in thorns of *Acacia* sp.; Belize (C. F. Baker), in thorns of *Acacia* sp.

Mexico: Tampico (Ed. Palmer, D. L. Crawford, H. Jourdain); Tonola, Chiapas and Los Cocos, Vera Cruz (A. Petrunkewitch), in thorns of *Acacia* sp.; Santa Lucrecia, Vera Cruz (F. Knab); Julapa (Rangel), in thorns of *Acacia sphaerocephala*; San Sebastian, Chiapas (G. N. Collins), in thorns of *Acacia Collinsi* Saff. Pichucalco, Chiapas (G. N. Collins), in thorns of *A. cornigera* L.; Llano Grande, Chiapas (G. N. Collins), in thorns of *A. hindsii*. San Luis Potosí, probably in thorns of *A. hernandesii* Safford.

The subspecies *fulvescens* is also recorded by Dr. Safford from the following localities in Mexico: Tanquian, San Luis Potosí (L. G. Cuevas), in thorns of *Acacia sphaerocephala*; Tampico (J. M. Cuaron)
in thorns of the same Acacia; San Sebastian, near Tuxtla (G. N. Collins) in thorns of *Acacia collinsi*.

**Subsp. saffordi** subsp. nov.

*Worker*. As large as *fulvescens* and with the head of the same proportions, but with the coarse opaque sculpture of the typical *belti*, the petiole, especially its peduncle shorter than in either of these forms, the node slightly broader than long, the postpetiole also broader than long but only one and two-thirds times as broad as the petiolar node. Mesonotum rather convex and prominent. Dark brown; anterior portion of head, borders of orbits, two longitudinal streaks on the gula, pronotum, sides of petiole, tibiae and tarsi paler, reddish brown.

Nine workers taken by Mr. G. N. Collins from thorns of *Acacia collinsi* Saff. at Chicoasen, Chiapas, Mexico, and received from Dr. Safford. Three small workers and an immature and imperfect female taken by Mr. Collins at Yerba Lanta, Chiapas in the same species of Acacia seem to belong to the same subspecies, although the workers are more uniformly dark brown. I also refer to this subspecies a series of workers from the Department of Solola, Guatemala, 3,000 feet. They have the top of the head black, but the thorax and petiole are uniformly deep brownish red.

**Subsp. venefica** subsp. nov.

*Worker*. Length 3.5–4 mm.

Decidedly smaller than the subsp. *fellosa*. Head of the same proportions. Epinotum longer, the base very convex and decidedly longer than the declivity into which it passes through a convex curve, without an angle. Thoracic sutures very deep and broad. Petiole as in *fellosa* but the node slightly longer than broad; postpetiole a little broader than long, twice as broad as the petiolar node. Sculpture and pilosity as in *fellosa*. Very dark brown, nearly black; clypeus and frontal carinae yellow; mandibles, antennae, thoracic sutures, posterior and lateral borders of pronotum, tarsi, articulations of legs and posterior borders of gastric segments pale reddish brown.

*Female*. Length 5 mm.

Head short, less than one and one half times as long as broad, broadest behind the eyes, narrower through the cheeks, which are straight and subparallel. Eyes less than twice as long as broad, feebly convex. Sculpture, pilosity and color as in the worker, but the prono-
tum, except its dorsal disc, the whole of the scutellum, the sides and posterior portion of the epinotum and the petiole, except the dorsal surface of its node, yellowish brown. Wings grayish hyaline, not infuscated; veins pale, the pterostigma dark brown.

**Male.** Length 4.4–4.5 mm.

Head as broad as long, rounded but not narrowed behind. Eyes convex, more than half as long as the sides of the head. Scapes nearly two and one half times as long as broad; first funicular joint longer than broad. Epinotum low and sloping, not very convex. Postpetiole a little longer than broad, behind nearly three times as broad as the node of the slender petiole. Sculpture, pilosity and color like those of the worker, but the head and thorax more shining and more finely punctate; the antennae and legs infuscated; the wings as in the female.

Described from numerous specimens of all the phases taken by Mr. J. H. Batty in the thorns of *Acacia sinaloensis* Saff. at Escuinapa, Sinaloa, Mexico. Another series of workers and deilated females taken by Mr. C. H. Tyler Townsend in thorns of *A. Hindsi* at Manzanillo, Colima, Mexico, may be referred to the same subspecies, though the head of the female is distinctly longer and the pale portions of the thorax and petiole are darker. Of this same subspecies, which is characterized by the small size of all the phases, I have a male, female and worker taken by Prof. C. F. Baker at Acapulco, Mexico.

**Subsp. vesana** subsp. nov.

**Worker.** Length 3.5 mm.

Characterized by its small size, pale color and the shape of the pedicel. The petiole is very short, there is almost no peduncle and the node is high, triangular when seen from above, as broad as long; the postpetiole is nearly twice as broad as long and twice as broad as the petiolar node; rather abruptly narrowed anteriorly. Base and declivity of epinotum subequal, straight, the latter sloping. Head a little longer than in the subspecies *venefica*, punctation of head and thorax somewhat finer, foveolae of epinotum and petiolar node less distinct. Yellowish red; mandibles and anterior portion of head yellow; legs slightly brownish, postpetiole and gaster dark brown.

A single specimen taken by Mr. Fred Knab at Córdoba, Mexico, probably on some species of Acacia. This form is obviously transitional to the subsp. *fulvescens* in color and sculpture, in the structure of the pedicel, but not in the shape of the head.
Subsp. bequaerti subsp. nov.

Worker. Length 3.5–4.5 mm.

Head distinctly shorter than in the other forms of the species, more rounded and elliptical. Sides of pronotum scarcely submarginate. Petiole with well-developed peduncle, the node from above triangular, as long as broad, postpetiole nearly as long as broad. Surface somewhat shining and lustrous; the foveolae on the epinotum and petiolar node more indistinct than in the other subspecies. Dark brown, sutures of thorax, petiole and postpetiole, the tarsi, antennae, greater portion of tibiae, mandibles and anterior half of head reddish; posterior half of head feebly infuscated.

Numerous workers taken by Dr. Joseph Bequaert in thorns of Acacia yucatanensis Schenck at Puerto Castilla, Honduras.

Subsp. wasmanni Wheeler


I have not been able to recognize this form among my material. Wasmann described and figured it from specimens collected by W. Brakhoven in thorns of Acacia sphaerocephala at Tampico, Mexico, and regarded it as an independent species. He did not compare it with the subsp. fulvescens, but with the typical belti and hence made much of the length of the head. The workers observed by Wasmann had the sides of the head sub-parallel, which is not true of any of the forms of belti known to me. The other characters mentioned in his description may nearly all be observed in fulvescens, which is rather variable. The measurements given are: Worker: 5.5–6.5 mm; Female: 7–8 mm.; Male: 7–8 mm. There is nothing in Wasmann’s figures to show that his specimens will not admit of the interpretation I have given.

Pseudomyrma caroli Forel

var. saphi Forel


Brazil: Bom Fim, Jurua, Amazonas (E. Ule), in the perforated stems of Sapium (Euphorbiaceae).

The typical caroli was described from Costa Rica. I have taken it at Escuintla, Guatemala and have received many specimens of it from Manatee, British Honduras (J. D. Johnston).
PSEUDOMYRMA CHODATI Forel


Paraguay: (R. Chodat), in the cauline swellings of Cordia longituba Chodat.

PSEUDOMYRMA DAMNOSA Wheeler

Wheeler, Zoologica 3, 1921, p. 139, § ♀ ♂', Fig. 13. Bailey, Bot. Gazette 75, 1923, p. 34.

British Guiana: Kartabo, Kalacoon and Penal Settlement (Wheeler); in hollow petioles of Tachigalia paniculata Aublet.

PSEUDOMYRMA DENDROICA Forel


Brazil: Rio Purus, Amazonas (A. Goeldi), in hollow branches of Triplaris.

Var. EMARGINATA Forel


Brazil: Marary Jurua, Amazonas (E. Ule), in hollow twigs of Triplaris schombrekiana Benth.

PSEUDOMYRMA ELONGATA Mayr


Florida: Cards' Point (Wheeler), nesting in Tillandsias.

Var. TANDEM Forel


Pseudomyrma fiebrigi Forel


Paraguay: San Bernardino (K. Fiebrig), in thorns of Acacia cavenia H. & A.

Pseudomyrma gebelli Forel

Panama: Las Sabanas (Wheeler), in Tillandsias growing on manzanillo trees (Hippomane mancinella L.) also in branches of almendra (Terminalia catappa), at Ancon C. Z.

Pseudomyrma gracilis Fabr.


Guatemala: Quirigua (Wheeler), nesting in thorns of Acacia.

Panama: Chivachiva Trail, near Red Tank, C. Z. (Wheeler); Tumba Muerta Road, near Las Sabanas (Wheeler), in thorns of Acacia penonemonensis Saff.

Bolivia: Riberalta (W. M. Mann), in cauline swellings of Cordia gerascanthus var.

As a rule this ant nests in dead twigs. This is also true of the following variety.

Var. bicolor Guérin

The workers are of the same stature as the typical gracilis, black, with the mandibles, clypeus, cheeks and frontal carinae yellow, the thorax and petiole dull orange, with the mesonotum, a large spot and streak on the base of the epinotum, two elongate spots on the pronotum and the ventral border of the pleura black. The legs are variable, usually black, with the tips of the femora and tibiae yellow, streaked with black on the extensor surfaces. Some of the specimens lack the black spots on the pronotum and some have merely the peduncle of the petiole and the pronotum somewhat reddish and thus form a transition to the true gracilis. The variety resembles the subsp. mexicana Roger but is more slender, with the same stature as the typical gracilis.

Panama: Chivachiva Trail, near Red Tank, C. Z. (Wheeler), in cauline swellings of Cordia gerascanthus (common). Same locality in
the hollow stems of *Triplaris americana*. Tumba Muerta Road, Las Sabanas (Wheeler); in fistulose stems of *Clerodendron siphonanthus* (introduced from the Orient.)

**Subsp. mexicana** Roger


**Pseudomyrmca kuenckeli** Emery


This ant was originally described from Alajuela, Costa Rica, and as nesting in wood. In his paper of 1892, Emery mentions that he received from A. Alfaro one specimen taken in an Acacia thorn. The further fact that I took this Pseudomyrmca in 1900 at Cuernavaca, Mexico, running in considerable numbers on the trunk and branches and living in the dry twigs of small acacias not of the bull-horn type, but probably *A. farnesiana*, shows that unlike *Ps. belti* and *spinicola*, it is only an occasional tenant of the bull-horn Acacias.

**Pseudomyrmca latinoda** Mayt


The type of this species was taken by Prof. James Trail in Northern Brazil, probably in some myrmecophyte (Triplaris or Tachigalia). Prof. Forel gave me a specimen from Sarayacu, Brazil, which he regarded as belonging to the typical form and which agrees well with Mayr’s description. Probably Forel’s *dendroica* and my *maligna* and *damnosa* may be eventually regarded as subspecies of *latinoda*, but for the present I treat them as distinct species to avoid introducing more confusion into a sufficiently intricate congeries of closely related forms.

**Var. coronata** var. nov.

*Worker*. Length 5—5.5 mm.

Larger and more robust than other forms of the species. Black, with the head reddish yellow and with the same peculiar markings on
the occiput as in var. nigrescens (vide infra), only more distinct. Mandibles red, blackish at the base. Antennæ and tarsi reddish yellow, somewhat paler than the head; legs dark brown or blackish, with the knees and posterior borders of the gastric segments reddish. Form of body, sculpture and pilosity very much as in nigrescens and with the funicular joints 2-10 very nearly as short and transverse.

**Male.** Length 6 mm.

Head and body of the usual shape; eyes half as long as the sides of the head; antennal scapes a little less than twice as long as broad; funiculi short, first joint a little longer than broad, remaining joints, except the last, not more than twice and mostly less than twice as long as broad. Epinotum rounded and sloping, without distinct base and declivity. Petiole and postpetiole much as in the worker.

Very smooth and shining, sparsely punctate; ocellar region sub-opaque, finely and densely punctate; sides of thorax indistinctly rugulose.

Pilosity like that of the worker, but somewhat less abundant and less even.

Piceous black, including the genital valves; mandibles, clypeus, anterior portion of head, antennæ, tarsi, articulations of legs, thoracic sutures, portions of pleura and borders of gastric segments, sordid or brownish yellow. Wings distinctly infuscated, with dark brown veins and pterostigma.

Described from numerous workers and four males taken by Mr. H. O. Lang at Kamakusa, British Guiana in the hollow petioles of Tachigalia paniculata Aublet.

**Var. endophyta** Forel

*Forel, Mém. Soc. Ent. Belg. 20, 1912, p. 22, §.*

Taken by A. Ducke on the Rio Ariramba, near the Rio Trombetas, Amazonas, Brazil, in the hollow leaf-petioles of Tachigalia macrostachya Huber. The worker measures 4.1-5.3 mm. and is therefore larger than the typical latinoda which measures only 4 mm., according to Mayr. *Endophyta* is entirely yellowish red, with a brownish spot in the ocellar region.

**Var. nigrescens** Forel

*Forel, Rev. Suisse Zool. 12, 1904 p. 38 §.*

The worker of this variety was taken by Prof. E. A. Goeldi at Para, Brazil, probably in some myrmecophyte (Tachigalia?). It averages
about the same size (4.4-4.8 mm.) as *endophyta*, but has the thorax, abdomen, femora and anterior surfaces of tibiae brown, with the mandibles, head, tarsi and posterior surfaces of the tibiae and sometimes also the anterior portion of the pronotum, reddish yellow. There is a brown spot covering the ocelli and connected with a transverse band of the same color on the occiput. This band sends off a longitudinal branch towards or to the posterior orbit of each eye.

**Subsp. bradleyi** subsp. nov.

*Worker*. Length 3.5—4 mm.

Differing from the subsp. *tachigalia* Forel (*vide infra*) in having the head much less deeply excised behind, with more nearly straight and parallel sides, eyes somewhat smaller, one-third as long as the sides of the head, the frontal groove much more distinct and becoming very deep and broad in front of the anterior ocellus. Mesoepinotal impression decidedly deeper, the petiolar node much thicker in front, scarcely longer than broad, subcuboidal, trapezoidal from above, its ventral surface flat and unarmed. Postpetiole from above semicircular, twice as broad as long. Fore femora slightly more dilated than in *tachigalia*.

In sculpture, pilosity and pubescence very similar to *tachigalia* but the vertex of the head somewhat more shining.

Color much darker, dark brown, with the gaster blackish; pro- and mesonotum somewhat paler; mandibles, clypeus, anterior third of head and tarsi dull whitish yellow; antennae, femora and tibiae dark brown, knees and bases of funiculi paler.

Described from nine workers taken by Prof. J. C. Bradley at Peréné, Peru, in the hollow petiole of a Tachigalia.

**Subsp. opacior** Forel

*Ps. latinoda* var. *opacior* Forel, Ann. Soc. Ent. Belg. 48, 1904 p. 170 §.

This form was described as a mere variety from Cuba (Coll. Ballion), but it evidently deserves to rank as a subspecies. The worker measures 4.3 mm. and is uniformly dull yellowish brown, with paler antennae and legs. The head is densely punctate and subopaque, the punctuation of the remainder of the body is also denser and coarser than in the other forms of the species. The petiolar node is broader than long. The head is more narrowed anteriorly and the anterior slope of the pronotum is less abrupt, the epinotum less rounded and more angular than in the typical *latinoda* and the var. *nigrescens*, the only forms with which Forel compares it.
Subsp. Tachigalle Forel


Forel described all three phases of this ant from specimens taken by E. Ule at Tarapoto, Amazonas, Peru, in the hollow petioles of Tachigalia formicarum Harms.

The worker measures 4.5-5.5 mm. and has the head longer and narrower than in the preceding forms, with the posterior border rather broadly and deeply excised. The petiolar node is lower and has two teeth on the ventral side. Funicular joints, except the first and last, very short and transverse. Body and legs only feebly shining and rather densely punctate, with dense yellowish pubescence, especially on the gaster. The color is a dirty yellowish brown, the anterior portion of the head, mandibles, antennae, tarsi, borders of gastric segments, articulations and the nodes of the pedicel in part yellowish.

The female measures 9-9.5 mm. and has a longer head than the worker, the mandibles geniculate at the base and marginate externally, with two apical and no basal teeth. The clypeus has a prominent anterior lobe and median carina. The petiolar node is one and one-half times as long as broad and scarcely broader behind than in front. The surface of the body is much more shining than in the worker, rather coarsely and densely punctate. Brownish black or blackish brown, with the cheeks, clypeus, antennal foveæ, antennæ, tibiae, tarsi, articulations and borders of the gastric segments yellowish red or yellowish. Wings tinged with blackish brown, with blackish brown veins and pterostigma.

The male measures 6.2-6.7 mm. The clypeus has a concave border but no median carina. The funicular joints are short, not twice as long as broad, the scape being of about the same length. Eyes small, shorter than their distance from the posterior corners of the head. Sculpture, pilosity and color as in the female, but the membranes of the wings are yellowish, the legs almost entirely yellow, the funiculus, except its first joint, brown.

Pseudomyrma Maligna Wheeler

Wheeler, Zoologica 3, 1921 p. 143 ♀ ♂; Bailey, Bot. Gazette 75, 1923 p. 34.

British Guiana. Kartabo (Wheeler), in hollow petioles of Tachigalia paniculata Aubl.

Var. Cholerica Wheeler

Wheeler, Zoologica 3, 1921 p. 146 ♀; Bailey, Bot. Gazette 75, 1923 p. 34.

British Guiana. Kartabo (Wheeler), in hollow petioles of Tachigalia paniculata Aubl.
WHEELER: NEOTROPICAL ANT-PLANTS AND THEIR ANTS

Vari. crucians Wheeler


British Guiana. Kartabo (Wheeler) in hollow petioles of Tachigalia paniculata Aubl.

Pseudomyrma nigrocincta Emery


Costa Rica. Alajuela and Jimenez (A. Alfaro), in thorns of Acacia (spadicigera, according to Wasmann); Guanacaste and Turrucuares (P. P. Calvert), in thorns of Acacia sp.

Pseudomyrma nigropilosa Emery


Costa Rica (A. Alfaro); in thorns of Acacia; Guanacaste, Santa Cruz (P. P. Calvert), in thorns of Acacia.

This ant more frequently nests in dead twigs.

Pseudomyrma picta Stitz

Stitz, Deutsch. Ent. Zeitschr. 1913 p. 209 & Fig. 2.

This species was described from worker specimens taken by E. Ule at Alto Acre, Brazil, in hollow petioles of Tachigalia.

It measures 5.5 mm. and resembles Ps. sericea Mayr in form but is more robust and the head is much larger, flattened, as broad as long, with convex sides and straight posterior border. It has two elongate diverging impressions on the front for the scapes, which reach a little beyond the middle of the head. The clypeus is strongly carinate and has a narrow median lobe, with straight entire border. The frontal groove is distinct and terminates in a deep longitudinal impression in front of the anterior ocellus. The eyes are large, elongate, two-thirds as long as the sides of the head. The thorax is much like that of sericea but broader, with the pronotum and base of epinotum more flattened and more sharply submarginate on the sides. The petiole and postpetiole are also similar to those of sericea, the postpetiole, according to Stitz being broader than the pronotum, with convex posterior border.
Slightly shining; surface covered rather uniformly with very short dense pubescence, which is somewhat longer on the gaster. Hairs sparse, much as in *sericea*, longest and most conspicuous on the abdomen.

Ferruginous yellow, with the anterior portion of the head paler; mandibles sordid brown, with blackish brown dental border. The body is spotted with black as follows: “Deepest portion of frontal groove with a short, black, longitudinal spot; on each side of the vertex, between the lateral ocellus and posterior inner orbit a narrow longitudinal stripe on each side; on the lower surface of the head behind the eye a broad longitudinal band reaching to the occipital border, most strongly developed under the eye; a very strong median band along the gula to the edge of the occiput. The pronotum has on the transverse ridge (separating its anterior and posterior faces) a round spot on each side, sometimes also one or two spots on its sides. The edges adjoining the mesonotal sutures are marked by a black band. The black color is more extensive on the epinotum; its basal surface is black, also the adjacent portion of the declivity. Among the spots on the epinotum the most prominent is an elongate ring-shaped spot, which runs obliquely from the middle of the lateral surface to the insertion of the petiole. The anterior surface of the petiolar node has three black longitudinal bands, the two lateral of which skirt its borders but pass over on the lateral surface and are broadest behind, where like the median band, they partially extend over onto the posterior surface. The gastric tergites and sternites have broad black borders. The coxae are usually dark. The middle and hind femora and tibiae have in the extensor surface at the distal end a longer or shorter, blackish brown stripe; the tarsal joints of these legs are brown with only their tips yellow.”

**Var. heterogyna** Wheeler and Mann, var. nov.

*Worker*. Length 4.5—5 mm.

Smaller than the type but very similar in sculpture, pilosity, color and the shape of the petiole, but the black spots are more variable, the large one in the base of the epinotum often reduced to a median longitudinal band. The postpetiole is shorter and not as broad as the pronotum and with a somewhat concave posterior border. The petiolar node is stouter and shorter, not longer than broad, its anterior surface rather flat, convex only above where it joins the abrupt posterior surface. The second funicular joint is as long as broad, the succeeding joints distinctly broader than long.

*Female* (dešálated). Length 9 mm.
Head large, distinctly longer than broad and strongly rectangular, except in front of the eyes, where it is narrowed. Eyes more than half as long as the head. Mandibles strongly convex. Antennal scapes not reaching to the middle of the head; funicular joints as long as broad. Thorax stout, with convex mesonotum, the promesonotal suture very deeply impressed. Epinotum short, subcuboidal, with distinct base and declivity. Petiolar node subcuboidal, nearly square from above, but slightly narrowed in front. Postpetiole shaped as in the typical _picta_ worker, with convex posterior border, its ventral surface very convex anteriorly. Gaster as in the worker, with pointed tip.

Black; tip of gaster, mandibles, anterior two-fifths of head, cheeks, antennæ, fore tibìæ and tarsi and terminal joints of middle and hind tarsi reddish yellow; knees and posterior borders of gastric segments reddish. The light and dark portions of the upper surface of the head are separated by a sharp, straight, transverse line. The pilosity and pubescence are much as in the worker, the punctuation more distinct, the surface somewhat more shining.

Described from eight workers and a single female taken by Dr. W. M. Mann at Cavinas, Bolivia, in the hairy cauline swelling of a species of _Platymischium_.

**Subsp. casta subsp. nov.**

*Worker.* Length 4.5—5 mm.

Uniformly opaque and ferruginous, with the extreme bases of the gastric segments blackish, a longitudinal blackish spot on the base of the epinotum and in one specimen with two black spots on the pronotum; the mandibles and anterior portion of the head yellowish, the antennal funiculi brown. Scapes reaching a little beyond the middle of the head, joints 2-4 of the funiculi as long as broad, the succeeding joints shorter. Base and declivity of epinotum subequal, the former flattened and distinctly submarginate on the sides like the pronotum. Petiolar node from above not longer than broad, stouter anteriorly than in the typical _picta_, in profile much more convex anteriorly than in both the preceding forms, the line of juncture of the antero-dorsal and posterior surfaces straight and transverse, rather sharp, the lateral surfaces flat, marginate above as in the other forms of the species. Postpetiole convex, shaped much as in _heterogyna_ and bearing the same relations in size to the petiolar node.

Described from nine specimens taken by Prof. J. C. Bradley at La Sombre, Putumayo, Peru, in the hollow petioles of _Tachigalia_.

Pseudomyrma satanica sp. nov.
(Plate 47, fig. b)

Worker. Length 5.5—6 mm.

Closely related to spinicola (vide infra) but somewhat larger. Head slightly longer than broad, somewhat depressed or flattened, broadest through the eyes, as broad through the well-developed posterior corners as at the clypeus, occipital border straight. Eyes larger and more convex than in spinicola, ocelli well-developed. Mandibles rather flat, with 6 subequal teeth, the external borders rather straight. Clypeus very short, convex in the middle, laterally depressed, the anterior border with a very short lobe which is irregularly excised in the middle and has on each side a triangular, flattened and not very acute tooth. Frontal carinae continued backward as longitudinal swellings, much as in spinicola but including a distinct frontal groove which terminates in a short, deep, longitudinal impression in front of the anterior ocellus. Antennae stout, scapes reaching nearly to a line joining the posterior orbits; second funicular joint as long as broad, remaining joints, except the last, distinctly broader than long. Thorax and pedicel much as in spinicola, but the mesonotum more convex and projecting and the epinotum higher, with subequal base and declivity, the posterior corners of the petiolar node more acute, subdentate, the postpetiole less narrowed and more convex in front; the tooth on the ventral side of the peduncle lacking.

Subopaque; abdomen more shining than the head and thorax; punctuation coarser than in spinicola and its subspecies. Mandibles rather opaque, more coarsely striato-punctate.

Pilosity yellowish, less abundant, pubescence grayish, conspicuously longer and more abundant than in spinicola, well-developed, even on the thorax.

Black; postpetiole and gaster dark brown, the posterior margins of the segments of the latter somewhat reddish; mandibles, clypeus and insertions of scapes brownish yellow; antennae, lateral borders of pronotum and legs reddish brown, the median portion of the scapes, femora and tibie darker and more blackish.

Female. Length 8—8.5 mm.

Very similar to the worker, except in the shape of the head, which is subrectangular, nearly one and three-fourths times as long as broad, with nearly parallel sides and straight posterior border. Eyes large and elongate, more than two-fifths as long as the sides of the head. Clypeal lobe more rectangular and longer than in the worker, frontal
groove distinct but not terminating behind in an impression. Mandibles robust, rather flattened at the tips, with rounded, convex external borders. Thorax shaped much as in spinicola subsp. scelerosa, but the epinotum is shorter and more rounded. Posterior corners of petiolar node large, prominent, subdentate and somewhat turned outward. Postpetiole longer than broad, nearly parallel-sided behind, rounded and narrowed in front.

Sculpture, pilosity, pubescence and color much as in the worker, but the punctuation coarser, especially on the epinotum and petiolar node and the pubescence on the head and gaster longer. Wings deeply infuscated as in spinicola subsp. scelerosa, with dark-brown veins and pterostigma.

**Male.** Length 6.5—7 mm.

Very similar to the male of spinicola subsp. scelerosa, but the head is longer and more produced behind the eyes, the latter more convex, the first funicular joint only as long as broad, the epinotum less convex and more sloping, the petiole more convex above. Wings scarcely paler than in the female.

Described from numerous specimens taken near the headwaters of the Rio Agua Salud, C. Z., Panama, and Marajal, near Colon, C. Z. They were inhabiting the large straight thorns of two superb trees about 12 feet high of Acacia multit glandulosa Schenck. The ants are extremely aggressive, fiercer even than belti and spinicola and their stings are more painful. I should have attached this form as a subspecies to spinicola were it not that its behavior is quite different. Instead of advancing to the attack like belti and spinicola, with the gaster turned forward under the thorax, it keeps its body rigid with the gaster extended as in Ps. gracilis Fabr. and turns it forward to sting only after seizing the intruder with its mandibles. Multiglandulosa is one of the most beautiful of the bull-horn acacias. Its foliage is heavy, spreading and bright green, the large leaves each with 8-15 pinnae, the pinnules when young tipped with golden yellow food-bodies. There are numerous extrafloral nectaries on the base of the petiole and one between each pair of pinnae. The handsome thorns, when young, are bright crimson.

**Pseudomyrma sericea Mayt**

(Plate 48, fig. a)

Brazil: Jurua Miry, Jurua, Amazonas (E. Ule), in the swollen flower axes and twigs of Pterocarpus ulei Harms. Bom Lugar, Rio Purus, Amazonas (J. Huber and A. Goeldi), in the hollow twigs of Bombax mungaba.

Var. acaciarium var. nov.

Worker. Length 3—3.5 mm.

Closely related to the var. ita Forel of Costa Rica, but smaller. The petiole and postpetiole are similar but the dorsal surface of the former is even less convex and distinctly margined in the sides and behind, the posterior surface sharply truncated and flat. Seen from behind the sharp angle at which these surfaces meet is straight and transverse. Postpetiole nearly twice as broad as the petiolar node. Thorax and head much like those of the var. ita.

Pubescence white, sericeous, much more abundant than in ita, so that the surface is pruinose.

Black; mandibles, clypeus, antennae, sides of pronotum, neck, fore tibiae and tarsi and tips of fore femora brownish yellow; a fuscous spot on each mandible, the extensor surface of the funiculus and a long black spot on the tip of the scape black.

Female. Length about 4.3 mm.

Head fully one and one-half times as long as broad. In other respects much like the worker. Wings whitish hyaline, with colorless veins and pale brown pterostigma.

Male. Length 4—4.5 mm.

Head longer than broad, elliptical. Eyes nearly two-thirds as long as its sides. Mandibles long, well-developed, deflected at the tip, their straight apical borders minutely denticulate. Scapes one and one-half times as long as broad, first funicular joint as long as broad. Thorax narrow, the dorsal surface in profile rather straight, sloping backwards, epinotum with subequal base and declivity. Petiole and postpetiole similar to those of the worker, the nodes lower and the surfaces more rounded.

Black; mandibles, clypeus, antennae, coxae, legs and pronotum ivory yellow, the mandibles with a large black spot in the middle; clypeus infusionated in the middle, antennae at the tips; the pronotum with a dark brown transverse streak on the dorsal surface, femora feebly infusionated in the middle. Wings colored as in female.

Several colonies of this ant were found nesting in the thorns of Acacia penonemensis Saff. along the Tumba Muerte Road, near Las Sabanas, in the Panamanian Republic.
Var. cordlæ Forel

(Plate 48, fig. b)


Peru: Tarapoto (E. Ule) in the cauline swellings of an undetermined Cordia; Eastern Peru (Spruce 3932), in cauline swellings of Cordia gerascanthus forma micrantha.

Bolivia: (Bang) in cauline swellings of Cordia sp.

A number of workers and three deálated females were taken by Dr. W. M. Mann in cauline swellings of Cordia gerascanthus var. at Ivon Beni and Huachi Beni, Bolivia.

Var. fortís Forel

(Plate 49, fig. a)


Guatemala. Patulul and Escuintla (Wheeler), in hollow twigs of Triplaris macombii D. Smith.

Var. ita Forel


Costa Rica: San Mateo (P. Biolley) in trunk and foliage of Bixa orellana.

Paraguay: San Bernardino (K. Fiebrig), in branches of Alchornea irucurana.

Guatemala: Escuintla and Patulul (Wheeler); in hollow twigs of Triplaris auriculatà.

Panama: Numerous colonies were taken in the cauline swellings of Cordia gerascanthus at Ancon, C. Z. and in twigs of Triplaris americana at Balboa.

The worker of this form differs from the typical sericea in having a smaller postpetiole and the petiole with a less convex anterodorsal surface. The latter terminates behind in a distinctly transverse border. The female (deálated) measures 5.5 to 6 mm. and is much more like the type in the shape of the petiole and postpetiole. The head is longer and its posterior border more deeply excised than in the worker.
Var. LON Gi Or Forel

Peru: Tarapoto (E. Ule), in perforated twigs of *Platymischium stipulare* Benth.

Var. RUBIGINOSA Stitz
Stitz: Deutsch. Ent. Zeitschr. 1913 p. 211 &.

Brazil: Alto Acre (E. Ule), *Triplaris* sp.

**PSEUDOMYRMA SPINICOLA Emery**


The worker of the typical form of this species measures 4-5.5 mm. and is ferruginous red or testaceous, with the gaster towards the tip and the middle portions of the femora somewhat infuscated, the mandibles, clypeus and cheeks pale yellow. Head distinctly longer than broad, the eyes rather convex and two-fifths as long as its sides; the clypeus with a short, broad median lobe which is distinctly toothed on each side; the frontal groove rather indistinct, the frontal carinae continued back as a pair of low narrow welts which subside at the middle of the head. Antennal scapes reaching to the middle of the internal orbits; second funicular joint longer than broad, joints 3-7 as long as broad. Thoracic dorsum straight in profile, except for the projecting semicircular mesonotum and the rather pronounced mesoepinotal impression. Sides of pronotum distinctly submarginate, the base of the epinotum longer than the declivity and forming a distinct angle with it. Metathoracic stigmata prominent. Petiole with well-developed peduncle, the node rather low, rounded, longer than broad, narrowed gradually in front and abruptly behind; the anteroventral tooth small and acute. Postpetiole nearly twice as broad as the petiolar node, slightly broader than long, narrowed in front, convex behind. Legs rather long and slender. The body is densely and finely punctate, slightly shining, covered with short whitish pubescence and with a few pale erect hairs on the dorsal surface. Mandibles shining, rather coarsely but not sharply striatopunctate.

In the female the head is fully one and one-half times as long as broad, the sides subparallel. The color is darker than in the worker,
the front, mesonotum and epinotum somewhat infuscated. Wings smoky, with piceous veins and pterostigma. Length 7–8.5 mm.

The male was seen by Emery and its head figured. I have seen no specimens of this sex belonging to the typical spinicola.

The types were taken by Anastasio Alfaro at Alajuela and Jimenez, Costa Rica, in the spines of an acacia (identified by Wasmann as A. spadicigera). I have specimens from Surubres, San Mateo, Costa Rica (P. Biolley).

Subsp. atrox Forel


The worker measures 4–4.7 mm. and is somewhat smaller than the typical form of the species, with subopaque mandibles, the median lobe of the clypeus less pronounced, less emarginate and more feebly dentate. Head somewhat shorter, the eyes a trifle larger, somewhat more than one-third the length of the sides of the head. Petiole decidedly shorter, its node scarcely longer than broad, the peduncle also more abbreviated, the postpetiole somewhat narrower, scarcely twice as broad as the petiolar node. Pilosity sparser and shorter, pubescence more dilute, the punctuation less pronounced and the surface therefore somewhat more shining. The color is the same as that of the typical spinicola.

The type specimens were taken by Mr. Christophersen in Panama. This is the common form of the species in the Savanna country south of the city of Panama where I have often taken it near Las Sabanas and Pueblo Nuevo. The acacia in the thorns of which it lives, is probably penonomensis Saff.

Subsp. convarians Forel


The worker of this form was taken by Peper at Patulul, Guatemala, probably on Acacia. It measures only 3.6 mm. The head is short, only one and one-fourth times as long as broad, with more convex sides and posterior border than in the typical spinicola, the scapes are shorter, scarcely reaching to the median transverse diameter of the head, the funicular joints, except the first and last, are broader than long. The petiolar node is much higher and shorter and the legs are shorter. The sculpture and pilosity as in the type, the color slightly paler.
Subsp. gaigei Forel


The worker of this subspecies was taken by Dr. F. M. Gaige at Fundacion, in the Santa Marta Mountains of Colombia. It measures 4.5–5.2 mm. The postpetiole is very broad, two and one-half times as broad as the petiole, which is gradually narrowed in front and has a shorter peduncle than the typical spinicola. The funicular joints are broader, the head more opaque, the color of a more vivid reddish, with the gaster brown.

I have received two cotypes from Dr. Gaige, who probably took them in Acacia thorns.

Subsp. infernalis subsp. nov.

**Worker.** Length 3.5–4.5 mm.

Head as in the typical spinicola, about one and one-third times as long as broad, with feebly convex sides and feebly excavated posterior border. Clypeal lobe broadly emarginate in the middle, with a rather large, blunt tooth on each side. Antennal scapes reaching a little beyond the middle of the internal orbits, funicular joints 3–10 as broad as long. Base and declivity of epinotum subequal, forming a distinct obtuse angle in profile. Petiolar node long and low, its posterior corners almost subdentate, the peduncle very short, without a tooth on its ventral surface. Postpetiole as long as broad, about one and two-thirds as broad as the petiolar node. Legs long.

Punctuation moderately strong and dense, uniform, the surface slightly shining; mandibles and clypeus somewhat more shining than the head.

Hairs and pubescence much as in the typical spinicola, the pubescence longest and most distinct on the head and gaster.

Castaneous brown; the gaster, femora and tibiae, except their tips and bases, somewhat darker; the head paler anteriorly, the mandibles, clypeus, antennae and, in some specimens, also the lateral borders of the pronotum, brownish yellow.

**Female.** Length 6.5—7 mm.

Head longer than in the typical spinicola, very nearly twice as long as broad, the sides parallel, except at the anterior corners where they are slightly dilated, the posterior border nearly straight. Eyes elongate, more flattened than in the typical spinicola, clypeal lobe longer and much narrower, its corners rounded, not dentate. Mandibles larger, parallel-sided, flattened near the tips, their external borders
straight. Thorax rather long and narrow, but through the wing-insertions as broad as the head. Pronotum concave on the sides, strongly submarginate above; mesonotum and base of epinotum straight in profile, the latter longer than the declivity and forming with it a rounded angle. Petiole and postpetiole similar to those of the worker, the former with a longer, lower and posteriorly more angular node, the latter distinctly longer than broad.

Sculpture, pilosity and color much as in the worker; mesonotum more shining; prothorax and borders of gastric segments yellowish or golden brown like the mandibles, clypeus, cheeks, antennæ and tarsi. Wings deeply infuscated, with very dark brown veins and pterostigma.

Male. Length about 5 mm.

Head, including the eyes, distinctly longer than broad, oval, narrowed and rounded behind, without posterior corners. Mandibles with well-developed though scarcely denticulate apical borders. Clypeus depressed, tuberculate in the middle, concave on the sides, its anterior border with a small, median, projecting lobe. Scape about twice as long as broad, first funicular joint nearly one and one-half times, second nearly four times as long as broad, remaining joints shorter. Mesonotum convex. Epinotum small, low, convex and rounded, without distinct base and declivity. Petiole without a distinct node, about three times as long as broad, gradually narrowed anteriorly. Postpetiole distinctly longer than broad, behind about twice as broad as the petiole. Gaster long, enlarged at the tip. Legs slender.

Sculpture finer than in the female; epinotum very smooth and shining; mandibles opaque, indistinctly punctate.

Pilosity and pubescence much as in the worker and female; clypeus and mandibles very hairy.

Color as in the worker and female but the pale portions, including the genitalia, are whitish yellow. Antennæ fuscous. Wings slightly paler than in the female.

Described from numerous specimens of all three phases found living in the thorns of *Acacia penonomensis* Saff. at Las Cascades C. Z. (type locality), along the Chivachiva Trail, near Red Tank, C. Z., at Venado, C. Z. and Pueblo Nuevo, in the Panamanian Republic. This form is readily distinguished by its dark color.

**Subsp. scelerosa** subsp. nov.

*Worker*. Length 3.5—4 mm.

Head as in the subsp. *conservans*, slightly longer than broad, with
convex sides and straight or feebly convex posterior border. Clypeal
lobe entire, transverse, with rather blunt corners. Eyes about two-
halves as long as the sides of the head. Antennal scapes reaching beyond
the middle of the head, almost to a line joining the posterior orbits;
funicular joints 2–4 a little shorter than broad, 5–10 as long as broad.
Pronotum less distinctly submarginate on the sides, epinotum more
rounded, the angle between the base and declivity less distinct than
in the typical spinicolus. Petiole and postpetiole much the same as in
the type. Legs rather long.

Punctuation finer, the surface somewhat more shining, the pilosity
and pubescence somewhat finer and less abundant. The color is paler,
more uniformly yellowish red, the mandibles, clypeus, legs and antennae yellow.

Described from a number of specimens taken by Prof. C. F. Baker
at Granada, Nicaragua, in the thorns of Acacia costaricensis Schenck.

Pseudomyrmca subtilissima Emery

Emery, Bull. Soc. Ent. Ital. 22, 1890 p. 65 $\phi$ $\phi$ Pl. 6 Fig. 7; Biol. Centralbl.
1915 p. 305.

Costa Rica: Alajuela (A. Alfaro) in thorns of an Acacia (identified
by Wasmann as spadicigera), which was inhabited also by Ps. belti.

Pseudomyrmca tenuis Mayr

(Plate 49, fig. b)

Numerous workers of the typical form of this species were taken
by Mr. H. O. Lang at Merumé-Mouth, British Guiana, in the fistulous
stems of a Patima formicaria, Johnst. This ant nests by preference,
at least in British Guiana, in dead twigs.

Pseudomyrmca triplaridis Forel

p. 231.

Worker. Length 4.4–4.8 mm.

Mandibles shining, with a few striae, more porrect than in arboris-
sanctae (triplarina Wedd.) Clypeus higher, carinate, more truncate
than in that species. Funicular joints 3–9 more than twice as broad
as long; the funiculus much thicker and shorter than in arboris-sanctae
and its race *symbiotica*. Head narrower than in *arboris-sanctae*, more as in the race *symbiotica*. Thorax less convex and broader than in *arboris-sanctae*, rather flat as in the race *symbiotica*, but broader and somewhat more sharply marginate and with much steeper epinotal declivity. First node as in *arboris-sanctae*, shorter and broader than in *symbiotica* and somewhat marginate anteriorly. Second node less narrowed in front.

Moderately shining; head feebly shining, more densely and more deeply punctate than in *arboris-sanctae* and *symbiotica*. Erect pilosity as in these two forms. The appressed pubescence, however, is longer and denser; on the gaster it forms a gray investment which partially conceals the sculpture.

Blackish brown; tarsi, tibiae, antennae and anterior part of head ferruginous; mandibles brownish red; femora brown.

Female. Length 7.5—8 mm.

Much more slender than *arboris-sanctae*. Mandibles longer, narrower, feebly bent, not at all angularly geniculate and without a transverse impression in the external border (both of these peculiarities obtain in *arboris-sanctae*, though much less strongly than in *dendroica*) with about 6 teeth on the apical and three teeth on the inner border. Head longer than broad, broader behind, with straight posterior border (feebly concave in *arboris-sanctae*). Epinotum with two sharply separated surfaces, though node as in *arboris-sanctae*, but the second much less and very feebly narrowed in front, 1¾ to 1¾ times as broad as long.

Brownish black; legs brown; mandibles, antennae and anterior portion of head ferruginous. Wings tinged with brownish black veins and pterostigma. Pilosity and sculpture as in the worker.

Male. Length about 5 mm.

Head rounded rectangular, broader behind, with distinct, nearly straight posterior border. Antennae rather short; third to last funicular joints about twice as long as broad. Thorax barely broader than the head. Like the female in sculpture, pilosity and color, but the mandibles, tarsi, scapes and first funicular joint pale yellow. Nodes lower, the first below with a small tooth which is lacking in the race *symbiotica* or *arboris-sanctae*.

Juruá Miry, Juruá, Amazonas, June 1907 (E. Ule) in the hollow twigs of *Triplaris surinamensis* Cham. (Forel) Tabatinga, Para (Goeldi and Huber), in the medullary cavities of the same tree.

Two worker cotypes of this species, given me by Prof. Forel, have been compared with the following three subspecies from British Guiana:
Subsp. boxi subsp. nov.

*Worker.* Length 4—5 mm.

Very similar to the typical *triplaridis* in the shape of the head, but the epinotum has the base and declivity straight in profile and meeting at a much more distinct angle. The peduncle of the petiole is decidedly longer, the node smaller and the hook-shaped ventral tooth larger.

The punctuation is sharper and deeper so that the surface, especially of the head, is less shining than in the typical *triplaridis*. The pilosity is distinctly less abundant, the tibiae having only a few erect hairs, the pubescence much finer and shorter on the gaster. Color paler, ferruginous brown; mandibles red, with black teeth; coxae yellow, paler than the antennae and legs; gastric segments with yellowish bases and apical borders.

*Female.* Length 6.5—7 mm.

Closely resembling the worker, but the head somewhat longer; the punctuation coarser, so that the surface, especially of the head, is subopaque. The pilosity is even sparser than in the worker, the color decidedly darker brown, but with the yellow markings of the gaster paler and more vivid. The antennae, cheeks, clypeus, tibiae and tarsi are yellowish brown, the wings distinctly infuscated, with strong blackish veins and pterostigma.

*Male.* Length 6.5 mm.

Head through the eyes as broad as long, its posterior border straight, its posterior corners rounded. Antennal scapes about 2½ times as long as broad, the first funicular joint longer than broad, the third to 12th joints a little more than twice as long as broad, the second three times as long as broad.

Surface of body a little smoother than in the worker, pilosity almost lacking, pubescence rather long but dilute. Color much as in the worker, the wings as in the female.

Described from many workers and a few females and males taken by Mr. H. E. Box on the Blairmont Plantation, at Berbice, British Guiana, in the branches of *Triplaris surinamensis*. Among the specimens is an old, deälated mother queen, measuring fully 11 mm. with the gaster enormously distended and its sclerites widely separated as in old termite queens. This condition, of which I find no mention in the literature, I have observed occasionally also in the old mother queens of some other species of *Pseudomyrma*. 
Subsp. baileyi subsp. nov.

(Plate 50)

Worker. Length 4.5—5 mm.

More elongate and more slender than the preceding form, head decidedly longer, fully one and one-third times as long as broad, suboblong, as broad in front as behind, with very feebly and evenly convex sides and straight posterior border. Eyes more elongate; clypeal lobe somewhat more transverse, the scapes reaching only to the second third of the internal orbits. Thorax, especially the epinotum, longer and narrower; sides of pronotum more sharply submarginate; base of epinotum longer in proportion to the declivity which is more sloping and forms a more rounded angle with the base. Petiole longer than broad, the node as long as broad (distinctly broader in the typical form), postpetiole also distinctly longer in proportion to its width.

Sculpture and pubescence very much as in the type but the erect pilosity on the body distinctly more abundant.

Color somewhat darker brown, especially in the dorsal surface; mandibles, anterior portion of head and antennae paler.

Female. Length 7—7.5 mm.

Head greatly elongated, fully one and three-fourth times as long as broad, more sharply rectangular than in the worker, with straight, parallel sides, sharp posterior corners and distinctly excised posterior border. Eyes elongate and very flat. Thorax very long, subdepressed above, broadened through the mesonotum where it is somewhat wider than the head. Pronotum sharply marginate and concave on the sides; mesonotum more convex in profile, the epinotum very long, its base straight, fully three times as long as the declivity, which is much more nearly vertical than in the worker. Petiole one and one-half times as long as broad; postpetiole behind scarcely broader than long. Gaster elongate.

Sculpture, pilosity and color as in the worker but with the following differences: the front and gular surface of the head, sides of pronotum, ventral surface of petiole and bases of gastric segments bright brownish yellow. Wings grayish hyaline, with resin-yellow pterostigma and pale yellow veins.

Described from numerous specimens taken at Camaria on the Cuyuni River, British Guiana, in the hollow branches of Triplaris surinamensis. This very distinct subspecies is dedicated to Prof. J. W. Bailey. It is quite as fierce and aggressive as the various forms of triplarina (vide infra), damnosa, maligna, etc. In the locality in
which it was found it was in full possession of a cluster of about a
dozen trees which grow so close to the river that their roots are sub-
merged during the rainy season.

**Subsp. Tigrina subsp. nov.**

*Worker.* Length 4—5 mm.

Resembling *baileyi* in the elongation of the head, but it is only
1 1/4 times as long as broad and appears to be more rectangular because
the sides are more nearly straight and parallel. Eyes distinctly shorter.
Epinotum a little shorter but of the same shape as in *baileyi*, the
petiole more abruptly truncated behind, the postpetiole distinctly
shorter in proportion to its width.

Surface of body, and especially of the head, much smoother and
more shining than in *baileyi*, with smaller, shallower and sparser
punctures.

Hairs less abundant, pubescence shorter and finer, though abundant
and partially concealing the surface on the gaster.

Color decidedly paler, yellowish red; mandibles red; posterior por-
tion of head and the remainder of the body brownish, with yellowish
sutures; the borders and bases of the gastric segments reddish yellow;
antennae and legs yellowish, with the middle portions of the femora
brownish.

*Male.* Length 6.5—7 mm.

Head decidedly longer than in the male *boxi*, longer than broad;
eyes much narrower. Surface of body more shining, the suberect
pilosity on the dorsal surface and even on the tibiae distinct, though
sparse. Petiolar node lower than in *boxi*. The wings are much paler
than in the other subspecies and the typical form, being grayish
hyaline, with pale yellow, weak veins and pale brown pterostigma.

Described from numerous workers and a few males taken by
Mr. H. E. Box on the Blairmont Plantation, Berbice, British Guiana,
in the branches of *Triplaris surinamensis* (not the same tree as the
one inhabited by the subsp. *boxi*).

**Pseudomyrma Triplarina** (Weddell)

Brazil. (Weddell), in *Triplaris*; Coixipo, Matto Grosso (F. Silvestri). Bolivia: (Weddell, Balzan), in *Triplaris* ("palosanto"); Huachi Beni (W. M. Mann), in *Triplaris*.

Peru. (Weddell); Collanga (Staudinger). Tarapoto, Amazonas.

Dr. Bequaert (1921–22) has recently ascertained that Weddell, as early as 1849, discovered this ant and its relations to *Triplaris* in Brazil, Bolivia and Peru. He describes the insect as follows: "Je ne crois pas que cette insecte ait été observé dans d'autres conditions que celles que j'ai notées; sa forme linéaire est particulièrement adaptée à son genre de vie. J'ai eu l'occasion de l'examiner et même de souffrir ses atteintes dans bien des parties du Brésil, en Bolivie et au Pérou; et partout il m'a paru identique. Déjà plusieurs voyageurs ont signalé une partie des faits dont il vient d'être question, et ils ont rapporté la fourmi du *Triplaris* au genre *Myrmica* de Latreille; mais je ne sache pas qu'on lui ait donné de nom spécifique; on pourrait lui appliquer celui de *Myrmica triplarina*. Elle est ordinairement d'un brun clair. Sa longueur est de 6 ou 7 millimètres, et sa large de 1 millimètre; l'abdomen est cylindrique et un peu attenué vers son extrémité postérieure qui est pollue." Since there can be no doubt of the identity of this ant with Emery's *arboris-sanctæ* described in 1894, the rules of nomenclature require the substitution of the older name. This is unfortunate, both because the insect has been so long known under the name *arboris-sanctæ* and because Forel has described another species as *Ps. triplaridis*.

The following is a translation of Emery's description of *Ps. arboris-sanctæ*:

"*Worker. Testaceous, head somewhat darker, borders of mandibles fusous, abdomen, except the pedicel, in great part brownish, abundantly pilose and delicately pubescent, shining; head and thorax anteriorly rather shining; head a little longer than broad, scarcely narrowed in front, truncated behind, its anterior portion somewhat less finely, the posterior portion very finely, microscopically punctulate; eyes moderately large, flattened; clypeus anteriorly with a truncated lobe; mandibles smooth at the base, apically punctate-striate; antennal funiculi with joints 3–10 broader than long; thorax incised in the region of the mesometanotal suture; pronotum convex, obtusely marginate on each side; mesonotum sub-semicircular, epinotum with the sides not distinctly marginate, the angle between the base and declivity obtuse, rounded; petiole with a very short peduncle in front, posteriorly with a large node, which is transverse, nearly twice as broad as long; postpetiole transverse cupuliform. Length 5–6 mm."
Female. Testaceous throughout; first gastric segment often with two brown spots at the base; vertex around the ocelli and the thorax sometimes clouded with brown; sculpture nearly as in the worker; eyes larger, nearer to the mouth; peduncle of petiole nearly straight above, not concave, the node trapezoidal, scarcely broader than long; postpetiole less distinctly transverse than in the worker. Length 8–9 mm.

Collected by Balzon in Bolivia where it lives in a tree called "palo santo" (Triplaris?). On another occasion I received the same species from Tarapotas, in Amazonas. The new species is recognizable by its color, by the mandibles, which have their apical half strongly striated or striato-punctate, by the strongly transverse petiolar node of the worker, by the antennal funiculus, the second joint of which is much smaller than the first and not broader than long, by the nearly uniform punctuation of the head and the size and distribution of the punctures. All these characters are in part found in other species (some of which are still unpublished), but all are united in this species. I do not exclude the possibility that this species may be the Tetraponera testacea of F. Smith, but his description is too indefinite to enable one to establish its identity."

Var. cordobensis Forel


Argentina: Cordoba (C. Bruch); probably from Triplaris. The worker is described as follows: "Length 6–6.5 mm. Differs from the type of the species in its larger eyes and the form of the head, the posterior border of which is narrower, less sharp and not concave. The angle between the base and declivity of the epinotum is also sharper, the former less convex and the latter higher (long). The color is reddish yellow throughout, more vivid than in the type, which has the gaster brown. In other respects identical."

Var. rurrenabaquensis Wheeler & Mann, var. nov.

Worker. Length 4–5 mm.

Smaller than the type and the preceding variety and somewhat more slender, the head narrow behind as in the latter, the antennal scapes a little shorter and broader, joints 2–10 of the funiculus more transverse, the eyes larger, the clypeal lobe shorter, more rounded at the corners and less distinct than in the typical arboris-sancta. Brownish yellow, with dark brown gaster and ocellar region; mandibles,
clypeus and antennæ yellow, paler than the legs which in most specimens are as dark as the body. The pilosity, especially on the gaster, is somewhat more abundant than in the type of the species.

Described from six specimens taken by Dr. W. M. Mann at Rurrenabaque Beni, Bolivia, in the cavities of *Triplaris*.

**Subsp. symbiotica** Forel


Colombia. Dibulla (A. Forel); in trunk and branches of *Triplaris* (probably *americana*).

Venezuela: Las Trincheras (Meinert), in *Triplaris*.

Forel describes the worker and male as follows:

"Worker. Length 4.4–4.7 mm. Reddish yellow, with the middle of the gastric segments brownish. Smaller and paler than the type. Erect pilosity much sparser, very sparse on the tibiae and scapes. Mandibles narrower, with more oblique terminal border, more feebly sculptured, shining towards the base. Thorax subopaque, much more densely punctate, as is also the head. The pubescence is also decidedly shorter and decidedly less abundant. The promesonotal suture is more deeply impressed, forming a small notch in the thoracic dorsum. Pronotum not at all submarginate, with convex sides. Sting very short. In other respects like the type."

"Male. Length 5–5.5 mm. Head rather oval, mandibles sharp, with an apical tooth. Frontal groove deep. Petiolar node as long as broad, subopaque or feebly shining, punctate. Pilosity even more scattered than in the worker, except on the abdomen. Yellowish brown. Wings subhyaline, with pale veins."

Forel has described the nesting habits of this ant in the trunk and branches of *Triplaris*. More recently Dr. George Salt has sent me workers and females of this subspecies taken by him in *Triplaris* branches at Aracataca, Colombia, which is not very far from the type locality.

**Var. loewensohni** Forel

(Plate 51, fig. a)

Panama. Frijoles (Christophersen and Wheeler); in trunk and branches of Triplaris americana; also Las Cascades and Marajal, Balboa (Wheeler).

All three phases of this variety were taken in 1911 by Mr. Christophersen and myself near Frijoles in a region which is now at the bottom of Gatun Lake. It differs but little from the subsp. symbiotica as shown in Forel's description which is here translated:

"Worker. Length 5.5–5.7 mm. Larger than the type of the subspecies and of a more yellowish brownish yellow. Head slightly more coarsely punctate and less narrowed in front. Otherwise identical.

Female. Length 8–11 mm. The same differences as in the worker. Petiolar node a little narrower than in the typical arboris-sanctae.

Male. Length 5.5–5.8 mm. Of a deeper brown color. Petiolar node lower and narrower than in the typical symbiotica."

During 1923 and 1924 I again took this variety in a different locality near Frijoles, near Las Cascades and at Balboa in the Canal Zone.

**Pseudomyrma ulei** Forel


Brazil: Jurua Miry, Jurua, Amazonas (E. Ule), in twigs and branches of Coussapoa sp. (Ule No. 5717).

**Subfamily MYRMICINÆ**

**Genus Pheidole** Westwood


Brazil: São Paulo (A. Lutz), living in large bamboos.

**Pheidole cramptoni** Wheeler

**subsp. petiolicola** Wheeler

Wheeler, Zoologica 3, 1921 p. 147 ♂ ♀.

British Guiana: Kartabo (Wheeler), in the hollow petioles of Tachigalia paniculata Aubl.
WHEELER: NEOTROPICAL ANT-PLANTS AND THEIR ANTS 191

PHEIDOLE GAUTHIERI Forel

var. OXYMORA Forel


Panama: (Christophersen), nesting in the spines of Xanthoxylon sp. (probably panamensis P. Wies) 1

PHEIDOLE LUTZI Forel


Brazil: São Paulo (A. Lutz), nesting in the cavities of bamboo.

PHEIDOLE MINUTULA Mayr


Brazil: (J. Trail), probably in the leaf-sacs of Tococa; Jurua Miry, Jurua, Amazonas (E. Ule), in the leaf-sacs of Tococa ulci Pilger.

I took numerous colonies of this ant in the primitive forest near Kalacoon, British Guiana, in the leaf-sacs of Tococa aristata Benth.

The soldier agrees more closely in the sculpture of the head with Mayr’s original description than with Forel’s account of the specimens taken by Ule. The humeral angles have a small, acute tooth, however, and the epinotal teeth are minute, slender and acute. In the worker also the humeri are dentate and the epinotal teeth are like those of the soldier though smaller.

The female (undescribed) measures 4–4.3 mm. The rugae on the head are coarser than in the soldier and extend very nearly to the posterior border and corners. The mesonotum is flat, the teeth on the epinotum very minute, short and broad at the base. Shining, mesonotum more coarsely, abdomen more finely punctate. Brown, the head darker and more blackish, especially about the ocelli, the appendages and pleura paler, the mandibles and anterior portion of the head red, the wings distinctly brownish, with brown veins and pterostigma. Pilosity much as in the soldier.

The male (undescribed) measures about 2.5 mm. Head and thorax opaque and very finely punctate, the former black behind, the mesonotum dark brown above, the remainder of the thorax, the mandibles,

1 According to Pitter (1922) “the corky prickles of the lower third of the trunk are said to be often hollow and inhabited by ants.” The type-locality of the plant is Mamei Hill, C. Z.
clypeus, abdomen and appendages sordid yellow, the wings somewhat paler than those of the female, the pilosity similar, but shorter and more appressed. The hairs on the legs are very short, bristly and oblique.

Subsp. folicola Forel

Brazil: Jurua Miry, Jurua, Amazonas (E. Ule), in the petiolar sacs of Maieta poeppigii Mart. and M. guianensis Aubl.

Pheidole (Hendecapheidole) tachigallic Wheeler
Ph. tachigallic Wheeler, Zoologica 3, 1921 p. 148 2 ♀ ♂; Ph. (Hendecapheidole) tachigallic Wheeler, Amer. Mus. Novitates No. 46, 1922 p. 3.

British Guiana: Kartabo (Wheeler), in the hollow petioles of Tachigalia paniculata Aubl.
I have also taken a single colony of this ant at Kartabo in a cauline swelling of Cordia nodosa L.

Genus Crematogaster Lund

Crematogaster corvina Mayr

Mexico: Vera Cruz (A. Dampf), nesting in thorns of Acacia vera-cruzensis Schenck.

Crematogaster sanguinea Roger
subsp. lucayana Wheeler


I found the var. torrei Wheeler in Cuba nesting in dead branches and twigs. Probably the typical form also prefers such nesting sites.

Var. etiolata Wheeler

Crematogaster (Eucrema) acuta Fabr.

Panama: Tabogilla Island (Wheeler), nesting in Tillandsias on manganillo trees (*Hippomanes mancinella*); Barro Colorado Island, Gatun Lake, C. Z. (Wheeler), in cauline swellings of *Cordia alliodora*; Tumba Muerte Road, near Las Sabanas (Wheeler), in thorns of *Acacia penonomensis*.

Large colonies of this ant nest by preference in dead branches.

Crematogaster (Orthocrema) arcuata Forel

var. aruga Forel

Panama: Otoque Island and Taboga Island (Wheeler), nesting in Tillandsias.

Crematogaster (Orthocrema) arizonensis Wheeler


Arizona: Huachuca Mountains (Wheeler); nesting in stems of mistletoe (*Phoradendron flavescens* var. *villosum*).

Crematogaster (Orthocrema) Armandi Forel


Brazil: Matto Grosso (Spencer Moore), in the pseudobulbs of an orchid (*Cattleya*?).

Crematogaster (Orthocrema) atra Mayt

Mexico: Vera Cruz (A. Dampf), nesting in thorns of *Acacia vera-cruzensis* Schenck.

This ant is apparently merely a subspecies of *brevispinosa* Mayt.

Crematogaster (Orthocrema) brasiliensis Mayt


Northern Brazil: (James Trail), probably in myrmecophytes.

British Guiana: Kamakusa (H. O. Lang), nesting among the matted roots of an undetermined epiphyte.

Bolivia: Tumupasas (W. M. Mann), nesting in the petiolar sacs of *Tococa* sp.
Var. ludio Forel


Panama: Fort Clayton and Miraflores, C. Z. (Wheeler); common in the hollow branches of *Triplaris americana*.

British Guiana: Kartabo (Wheeler), in petioles of *Tachigalia paniculata* Aubl.; Grand Batavia Island, Cuyuni River (Wheeler), in cauline swellings of *Cordia nodosa* L.; Kamakusa (H. O. Lang), in petiolar sacs of *Tococa aristata* Benth.

Bolivia: Huachi Beni (W. M. Mann), in cauline swellings of *Cordia alliodora* var.

The specimens taken by Mr. Lang include a deñalated female, which is entirely yellow. This phase of the typical *brasiliensis*, according to Forel, has a black gaster. The epinotal teeth are as long as broad at their bases and rather blunt at the tip. In the worker, as in the typical *brasiliensis*, the mesonotal carinæ are minutely dentate.

CREMATOGASTER (ORTHOCREMA) BREVISPINOSA Mayr


Costa Rica: (A. Alfaro), in *Acacia* thorns; Surubrès, near San Mateo (P. Biolley), in bromeliads.

Nicaragua: Granada (Gen. E. Chamorro), in thorns of *Acacia costaricensis*.

Paraguay: San Salvador (J. Bohls), in woody thorns of *Acacia* (probably *cavenia*).

Var. ampla Forel

Colonies, comprising all three phases of this ant, were taken near Las Cascades, C. Z. Panama, March 14, 1923, in the hollow twigs of *Triplaris americana*.

Var. minutior Forel


Mexico: Cuernavaca (Wheeler), nesting in *Tillandsia benthamiana*. 
Subsp. tumulifera Forel


Costa Rica: San José (P. Bioley), in stem of a *Clematis*.
Panama: Las Sabanas (Wheeler), in Tillandsias; Chivachiva Trail, near Red Tank, C. Z., common in cauline swellings of *Cordia alliodora*.
Guatemala: Zacapa (Wheeler), in thorns of *Acacia hindsii* and Tillandsias.

_Crematogaster (Orthocrema) curvispinosa Mayr_ var. panamana var. nov.

*Worker*. Length 1.8—2 mm.

Differing from the typical form of the species in its somewhat smaller size, somewhat more slender thorax and in having the epinotal spines more slender and tapering, though as long as in the type and curved inward in the same manner. Head very smooth and shining, as long as broad, very much rounded behind, with the eyes at the posterior third of the sides. Antennal scapes almost reaching the convex posterior border of the head. Pilosity white, long and very sparse as in the type, each epinotal spine with a long hair near the middle. Color also as in the type, piceous brown, mandibles a little paler, gaster and usually also the head black.

*Female*. Length 3.5—4 mm.

Head more rectangular than in the worker, with distinct posterior corners and nearly straight posterior border. Antennal scapes shorter than in the worker. Thorax short, somewhat more than twice as long as broad, narrower through the wing insertions than the head, epinotum sloping, the spines reduced to small, rather acute teeth. Petiole and postpetiole as in the worker, the anterior angles of the former a little less rounded. Gaster very small, not longer than the remainder of the body, broadest through the first segment, very acute at the tip. Sculpture and color as in the worker, pilosity more abundant on the dorsal surface of the head, thorax and gaster. Wings grayish hyaline, with pale yellow veins and pterostigma.

Numerous specimens found nesting in the thorns of *Acacia penonomensis* Saff. along the Tumba Muerte Road, near Las Sabanas, Panama.

_Crematogaster (Orthocrema) delitescens* Wheeler


British Guiana: Kartabo (Wheeler), in the hollow petioles of *Tachigalia paniculata* Aubl.
CREMATOGASTER (ORTHOCREMA) DISTANS MAYT
Guatemala: Zacapa (Wheeler), in Tillandsias.
Costa Rica: Alajuela (Wheeler), in Tillandsias.

CREMATOGASTER (ORTHOCREMA) GOELDII FOREL
VAR. CHODATI FOREL
Paraguay: Concepcion (Chodat and Vischer), in the trunk of Agonandra brasiliensis, inhabited also by Cryptocerus eduardulì Forel.

CREMATOGASTER (ORTHOCREMA) LAEVIS MAYT
Brazil: (James Trail), probably in myrmecophytes; Jurua Miry, Jurua, Amazonas (E. Ule), in petiolar sacs of Maieta tococoides Cogn.; Cachoeira, Jurua (E. Ule), in the petiolar sacs of Maieta juruensis Pilger.

CREMATOGASTER (ORTHOCREMA) LIMATA F. SMITH
Brazil: (James Trail), probably in myrmecophytes.
British Guiana: Kartabo (Wheeler), in the internodes of young Cecropia angulata Bailey; in large branch of Cecropia angulata Bailey; in large branch of Cecropia sciadophylla var. decurrens Snethl.

VAR. PALANS FOREL
Wheeler, Zoologica 3, 1921 p. 151 ² ².
British Guiana: Kartabo (Wheeler), in the hollow petioles of Tachigalia paniculata Aublet; Merumé-Mouth (H. O. Lang), in the fistulose stems of Patima formicaria Johnston.
The female (undescribed) is 8–9 mm. long, yellow, with blackish funiculi, black gaster and ocellar spots, three longitudinal dark brown streaks on the mesonotum and blackish wings with dark brown veins and pterostigma. Head decidedly broader than long, slightly narrower in front than behind, with straight posterior border and convex dorsal surface. Scapes reaching to the occipital corners. Epinotum with two stout acute teeth, which are distinctly longer than broad at the base. Posterior corners of petiole acute and dentate.
The *male* (undescribed) measures 4–4.5 mm. and is colored like the worker, dark brown, with the head behind the clypeus, the mandibles, antennæ and legs yellow, the femora and tibiae somewhat infuscated in the middle. The wings are as dark as in the female.

**Subsp. parabiotica** Forel


Brazil: Jurua Miry, Jurua, Amazonas (E. Ule), in Tillandsia; Alto Acre (E. Ule), in inflorescence of *Costus* sp.; Pará (W. M. Mann), in ant gardens in parabiosis with *Dolichoderus bispinosus*.

British Guiana: Kartabo (Wheeler), in “ant gardens” in parabiosis with *Camponotus femoratus*.

Panama: Las Sabanas and Tabogilla Island (Wheeler), in Tillandsias; Chivachiva Trail, near Red Tank, C. Z. (Wheeler), in cauline swellings of *Cordia alliodora*.

Bolivia: Rurrenabaque (W. M. Mann), in the leaf sacs of *Tococa* (Rusby) No. 1756.

This ant has also been taken by Forel, Christophersen and myself living in parabiosis with *Dolichoderus* (Monacis) parabioticus in dead wood in Colombia, Panama and other Central American localities.

**Crematogaster (Orthocrema) lutzi** Forel


Brazil: São Paulo (A. Lutz), nesting in cavities of bamboo.

**Crematogaster (Orthocrema) montezumia** F. Smith

var. *sulcata* Mayr


Brazil: Rio Grande do Sul, in ant garden among Tillandsias.

**Crematogaster (Orthocrema) sculpturata** Pergande


**Crematogaster (Orthocrema) sumichrasti** Mayr

A single colony found nesting in a cauline swelling of *Cordia alliodora* at Quebrada de Oro, C.Z ., Panama.
CREMATOGASTER (ORTHOCREMA) VIRGULA Forel
Costa Rica: Alajuela (Wheeler), nesting in Tillandsias.
Panama: Chivachiva Trail, near Red Tank, C. Z. (Wheeler), nesting in cauline swellings of Cordia alliodora.

Genus MONOMORIUM Mayr
MONOMORIUM CARBONARIUM F. Smith
subsp. EBENINUM Forel
Panama: Corrozoal, C. Z. (Wheeler), in Tillandsias.
Guatemala: Escuintla (Wheeler), in the hollow twigs of Triplaris auriculata.
Porto Rico and Bahamas: (Wheeler), in Tillandsias.

MONOMORIUM FLORICOLA Jordan
Spanish Honduras: Tela (Prof. Oakes Ames), nesting in the pseudobulbs of an orchid, Epidendrum imatophyllum Linde.

Genus XENOMYRMEX Emery
XENOMYRMEX STOLLI Forel subsp. FLORIEANUS Emery var.
LUCAYANUS Wheeler.

Genus ALLOMERUS Mayr
ALLOMERUS DECEMARTICULATUS Mayr
Brazil: (James Trail), probably in Tococa or Cordia; Oiapoc, (A. Ducke), in dilated peduncle of Hirtella sp.
Mayr distinguished three species of Allomerus according to the number of antennal joints in the worker as decem-, octo- and septem-
articulatus. The discovery by Dr. Mann of a form with nine joints and Forel’s observation that occasional specimens of septemarticulatus may have eight joints or one of the basal funicular joints partially divided, leads me to include all the forms in one species and to regard the number of joints in the worker as a subspecific character. In all the forms, so far as known, the female has ten antennal joints, the male thirteen.

Subsp. novemarticulatus Wheeler & Mann, subsp. nov.

Worker. Length 1.2—1.3 mm.
Closely resembling the typical octoarticulatus in structure, sculpture, pilosity and color but the antennæ 9-jointed. Scapes reaching half the distance between the posterior orbits and occipital corners of the head. Promesonotum moderately convex, mesepinotal impression moderately deep but acute. Epinotum a little longer than broad, the base in profile straight, shorter than the declivity and forming with it a distinct though rounded angle. Petiolar node laterally compressed, longer than broad; postpetiole a little broader, as broad as long and a little broader behind than in front.
Described from eight workers taken by Dr. W. M. Mann on the Rio Madid, Bolivia, in leaf-sacs of Tococa.

Subsp. octoarticulatus Mayr


Brazil: (James Trail); Para (Forel collection), in the leaf-sacs of Remijia physophora Benth; Marary, Amazonas (E. Ule), in the petiolar sacs of Tococa setifera Pilger.

Bolivia: Rio Negro, Tumupasa and Riberalta (W. M. Mann), in the cauline swellings of Cordia hispidissima.
The worker closely resembles the preceding form in the size of the eyes, length of the scapes and shape of the thorax, but the epinotum and petiolar node are as broad as long and the latter is not compressed laterally. The post-petiole is slightly broader than long and more rounded though a little broader than the petiolar node.
The female measures 6 mm. and has the head longitudinally rugulose. The body is reddish brown, the head and mesonotum above and the greater part of the abdomen brown.
The male measures 5.3 mm. and is colored like the female.
Var. exsanguis Wheeler and Mann, var. nov.

Worker. Length 1—1.3 mm.

Of the same dimensions as the typical octoarticulatus, the antennal scapes of the same length, the eyes of the same size, but of a pale, whitish or ivory yellow color, with the mesonotum more depressed above, the epinotum shorter than broad and in profile more rounded with a more sloping declivity. The petiole has a distinctly shorter petiole and a more anteroposteriorly compressed node, the postpetiole shorter in proportion to its length. The erect hairs on the head and thorax seem to be shorter and less numerous.

Female (deislated). Length nearly 6 mm.

Very similar to the female of the typical octoarticulatus. Mandibles deep red, rather subopaque, antennae, pronotum, mesonotum, scutellum and gaster behind the first segment reddish brown. The epinotum has a feeble projection or angle on each side.

Described from five workers and a single female taken by Dr. W. M. Mann at Esperanza, Bolivia, in a cauline swelling of Cordia hispidissima.

Var. demerarae var. nov.

Worker. Length 1.5—1.8 mm.

Differing from the two preceding forms of the subspecies in having the scapes somewhat longer, the eyes distinctly larger, the thorax longer, the mesonotum for the most part straight and sloping in profile, the mesoeinotal impression somewhat shallower but longer, the epinotum distinctly longer than broad, subangular in profile, but with very sloping declivity, one and one-half times as long as the base. The peduncle of the petiole is longer, the node conical in profile, seen from above as long as broad, somewhat compressed anteroposteriorly at the summit, which is transverse. Postpetiole subcircular, very nearly as long as broad and slightly broader than the petiole.

Female. Length 6—6.5 mm.

Antennal scapes reaching the posterior ocelli. Epinotum with distinct teeth, which are short and rather acute, shorter than the length of their bases. Sculpture of head finer than in the preceding forms, very indistinctly rugulose; the scutellum and epinotum smooth. The color of the body is more uniformly reddish brown, the dorsal surface of the head and thorax and the posterior portion of the gaster slightly darker in some specimens, mandibles subopaque, more shining along the borders. Wings blackish or dark brown, with dark brown veins and pterostigma.
Male. Length 5.5—6 mm.
Very similar to the male of the typical octoarticulatus. Brownish yellow, posterior portion of head, pronotum, except its borders, mesonotum, scutellum, posterior portion of epinotum, gaster and nodes of pedicel, base of scapes, apical portion of funiculi and middle portions of femora and tibiae dark brown. Wings colored as in the female.

Described from many specimens of all three phases which I took at Kartabo, Kalacoon and on Grand Batavia Island in the Cuyuni River, British Guiana, in the cauline swellings of Cordia nodosa L. Mr. H. O. Lang has also taken the same variety in the same plant at Kamakusa, in the interior of British Guiana.

According to Hohenkerk (Journ. Board. Agric. Brit. Guiana 11, 1918 p. 99) the natives call this ant “Kurabelli”. In the localities above mentioned, it inhabited most or all of the cauline swellings on every one of the numerous specimens of C. nodosa examined both by Prof. J. W. Bailey and myself.

Var. angulatus Wheeler & Mann, var. nov.

Worker. Length 1.5 mm.

More deeply colored than the preceding forms of the subspecies, reddish yellow, head a little darker, mandibles red, their bases and teeth and the border of the clypeus blackish. Eyes smaller than in the typical form and the var. exsanguis but the scapes somewhat longer. Promesonotum more convex, mesoepinotal impression short and acute, deeper than in the typical octoarticulatus. Epinotum as long as broad, the base and declivity forming a very distinct angle in profile as in the var. tuberculatus Forel, but not subdentate and with the base straight. Petiolar node rising more abruptly from the peduncle than in var. demerara, but less than in tuberculatus. Post-petiole broader than long, about one-third broader than the petiolar node, with rather straight sides.

Thirteen workers taken by Dr. W. M. Mann on the Lower Rio Madidi, Bolivia, in cauline swellings of Cordia hispidissima.

Var. tuberculatus Forel


Worker. Length 2—2.3 mm.
Somewhat larger than the preceding forms. Head more nearly square, less trapezoidal, that is less narrowed in front, with less convex sides, scarcely longer than broad, the scapes slightly shorter. Mesoe-epinotal constriction deep. Epinotum with two small tubercles or swellings at the angles. Color less uniform, sordid yellow, head reddish or brownish yellow, a brown band or cloud on the middle of the gaster.

Male. Length 5.2 mm.
Posterior portion of head behind the eyes longer and narrower, somewhat more rectangular and less rounded than in the typical octoarticulatus. Epinotum with two blunt tubercles. Color slightly paler, more yellowish brown.
This form was described from specimens taken by J. Huber at Monte Verde, on the Middle Purus, Amazon Basin, in the leaf-scapes of a Tococa. I have examined cotytes received from Prof. Forel.

Var. MELANOTICUS Wheeler & Mann, var. nov.

Worker. Length 1.6—1.8 mm.
Resembling the typical octoarticulatus in the shape of the head but the scapes somewhat longer. The promesonotum at its posterior end descends abruptly to the mesoeepinotal constriction which is very pronounced. The epinotum is as long as broad, in profile with subequal base and declivity, the former convex, the latter sloping and somewhat concave, the angles as distinctly tuberculate or subdentate as in the var. tuberculatus. Petiole nearly as high through the node as long, the node rising abruptly from the well-developed peduncle, which is as long as the node. The latter is transversely elliptical from above, the postpetiole very similar but slightly broader.

Deep castaneous brown; head, pro- and mesonotum and posterior portion of first gastric segment black; mandibles deep red; antennae and legs brown, the femora darker in the middle, the tarsi and posterior borders of the gastric segments sordid yellow.

Female. Length about 6 mm.
Head smaller, the thorax longer and narrower than in the var. demerarae, the former nearly as long as broad, the sides of the epinotum with blunt projections instead of teeth, the median surface more concave. Sculpture of head distinctly coarser, that of the mesonotum finer, so that this region is more shining. Mandibles more coarsely striate and punctate. Pubescence gray instead of golden yellow, much more dilute.

Black; mesopleura, legs and antennae dark brown, borders of
gastric segments golden brown. Wings dark, of the same shade as in the var. demerarae.

Male. Length 5.6 mm.

Head longer especially behind the eyes, than in the var. demerarae, thorax somewhat more slender. The epinotum as in that form, rounded and sloping, without angular swellings. Subopaque; pilosity and pubescence as in the female.

Dark brown; dorsal surface black, mandibles, articulations of antennae and legs, tarsi, edges of gastric segments and external genital valves sordid yellowish brown. Wings colored as in the female.

Described from numerous workers, a female and a male taken by Dr. W. M. Mann at Tumupasa (type locality) and Isiamas, Bolivia, in leaf-sacs of Tococa sp.

Subsp. septemarticulatus Mayr


Brazil: (James Trail), probably in a myrmecophyte; Amazonas (K. Schumann), in leaf sacs of *Duroia saccifera* Spruce; São Joaquim, Rio Negro, Amazonas (E. Ule), in leaf sacs of *Duroia saccifera* Spruce.

As already stated, Forel found a variation of the number of antennal joints in some workers from seven to eight joints. The female is identical with that of *octoarticulatus*, but is a little smaller and paler.

Genus Solenopsis Westwood

*Solenopsis corticalis* Forel


Subsp. amazonensis Forel


Peru: Cerro de Escaler, about 1300 m. (E. Ule), nesting in a Tillandsia (*Pseudocatopsis* n. sp.).

*Solenopsis helena* Emery subsp. *hermione* Wheeler


British Guiana: Kartabo (Wheeler), in petioles of *Tachigalia paniculata* Aubl.
Subsp. ULTRIX Wheeler


British Guiana: Kartabo (Wheeler), in petioles of Tachigalia paniculata Aubl.

Solenopsis PICEA Emery

Taken by Dr. W. M. Mann at Ixiamas, Bolivia, nesting in a cauline swelling of Cordia gerascanthus var.

Solenopsis Tenuis Mayr


Northern Brazil: (James Trail), probably in a myrmecophyte.
Bolivia: Ixiamas (W. M. Mann), in a cauline swelling of Cordia hispidissima.

Solenopsis Zeteki sp. nov.

Worker. Length 1—1.1 mm.

Head subrectangular, distinctly longer than broad, as broad in front as behind, with nearly straight sides and posterior border. Eyes very small, consisting of only four or five very minute ommatidia, situated at one fourth the distance between the anterior and posterior corners. Mandibles narrow, with oblique, 4-toothed apical borders. Clypeus moderately convex in the middle, bicarinate, but without teeth in the anterior border, which is straight, transverse and entire in the middle. Antennae slender, the scapes reaching a little more than half way between the eyes and posterior corners of the head; first funicular joint as long as the five succeeding joints together; joints 2–7 fully twice as broad as long, the two-jointed club slender, much longer than the remainder of the funiculus, the basal about one-third as long as the terminal joint. Thorax small, much narrower and slightly shorter than the head, including the mandibles, with short mesoepinotal impression, the epinotum small, similarly rounded, without distinct base and declivity. From above, the promesonotum is nearly one and one-third times as long as broad, rounded on the sides and in front, the epinotum about one and one-fourth times as long as broad. Petiole in profile as high as long, with a short peduncle, the node rising abruptly, with a conical summit, the ventral surface convex, with a distinct tooth near the anterior end; from above, the node is subcircular, as long as broad. Postpetiole slightly broader
than the petiole, a little broader than long, convex and rounded above but decidedly lower than the petiolar node. Gaster small and narrow, the first segment elongate-elliptical, narrowed in front and behind. Legs rather slender.

Very smooth and shining throughout, with very minute, scattered, piligerous punctures.

Hairs whitish, delicate, sparse and erect or suberect on the body, on the appendages reduced to very fine appressed pubescence.

Mandibular teeth and eyes black, all the rest of the body pale yellow, the head and thorax a shade darker than the abdomen and appendages.

Described from several specimens taken from a colony that was nesting in a cauline swelling of Cordia alliodora on the Chivachiva Trail, near Red Tank, C. Z. Panama.

This species which is dedicated to Mr. James Zetek, resembles sulfurea Roger of Venezuela, succinea Emery of Costa Rica and inermiceps Wheeler and Mann of Haiti in having the clypeus unarmed, but it is much smaller and the antennal scapes are much shorter than in the species mentioned.

Genus Macromischa Roger

Macromischa petiolata (Forel)


Mexico: Cuernavaca (Wheeler), in Tillandsia benthamiana.

Genus Leptothorax Mayt

Subgenus Goniothorax Emery

Leptothorax (Goniothorax) echinatinodis Forel subsp.

Aculeatinodis Emery var. Pleuriticus Wheeler

Wheeler, Zoologica 3, 1921, p. 158  ♂ ♀.

British Guiana: Kartabo (Wheeler), in hollow petioles of Tachigalia paniculata Aublet.

Subsp. cordincola subsp. nov.

Worker. Length 2—2.3 mm.

Resembling the subsp. dalmasi Forel and aculeatinodis Emery but
considerably smaller and differing in other respects. Mandibles sub-opaque, striated; clypeus smooth in the middle, without median carina and with the lateral carinae feeble. Head very shining, but finely, superficially and not very evenly striate, with longitudinal seams of coarse punctures, most numerous anteriorly, posterior corners very smooth. Thorax above rather delicately longitudinally reticulate, rugose, densely punctate on the sides, except the mesopleura, which are smoother and more shining. Epinotal spines as long as the basal surface, as in dalmasi, rather stout and erect, but curved outwards and downwards. Petiole and postpetiole with well-developed spinules, longitudinally rugose and punctate above. Gaster smooth and shining, its base very finely and obscurely striate. Hairs whitish, erect, blunt, abundant and of even length on the body, appendages with very short, appressed hairs or pubescence.

Piceous black, head and gaster, except at the base, darker; mandibles, scapes, basal half of funiculi, epinotal spines, tibiae and tarsi brownish yellow. In many specimens the pronotum is paler and more reddish than the remainder of the thorax, thus approaching the coloration of the subsp. aculeatinodis Emery.

Numerous specimens taken from the cauline swellings of Cordia alliodora along the Chivachiva Trail, near Red Tank, C. Z. Panama. A few colonies were also found nesting in the thorns of Acacia penonomensis Saff. along the Tumba Muerte Road, near Las Sabanas, Panama.

This subspecies seems to be most closely related to the subsp. aculeatinodis, described from Costa Rica, but it differs considerably in sculpture, pilosity and color. Emery fails to give the dimensions of his specimens.

Subsp. dalmasi Forel

(Plate 51, fig. b)

Costa Rica: Alajuela and San Jose (Wheeler), nesting in Tillandsias and also in dead twigs.

Subsp. spininodis Mayr


Paraguay: San Salvador (J. Bohls), in woody thorns of Acacia (probably cavenia).
LEPTOTHORAX (GONIOTHORAX) UMBRATILIS Wheeler

British Guiana: Penal Settlement, near Bartica (Wheeler), in hollow petioles of Tachigalia paniculata Aublet.

WASMANIA AUROPUNCTATA Roger

Dominica W. I.: Roseau (Wheeler) under the appressed leaves of juvenile Marcgravias growing over a large boulder.

Genus CEPHALOTES Latr.
CEPHALOTES ATRATUS L.

British Guiana: Kartabo (Wheeler), nesting in large branch of a Cecropia Sciadophylla var. decurrens Sn.

Genus CRYPTOCERUS F. Smith
CRYPTOCERUS AZTECUS Forel
Mexico: Cuernavaca (Wheeler), in Tillandsia benthamiana.

CRYPTOCERUS BOHLSI Emery
Emery, Zool. Jahrb. Abt. Syst. 9, 1896, p. 631 ♀ ♂ Fig. C.
Paraguay: San Salvador (J. Bohls), in woody thorns of Acacia (probably cavenia).

CRYPTOCERUS EDUARDULI Forel
Paraguay: Concepcion (Chodat and Vischer), in trunk of Agonandra brasiliensis.

CRYPTOCERUS GRANDINOSUS F. Smith
Paraguay: San Salvador (J. Bohls), in woody thorns of Acacia (probably cavenia).
CRYPTOCERUS PELTATUS Emery

Emery, Zool. Jahrb. Abt. Syst. 9, 1896 p. 633 2 ♂; Fig. D.

Paraguay: San Salvador (J. Bohls), in woody thorns of Acacia (probably cavenia).

CRYPTOCERUS PILOUS Emery

Emery, Zool. Jahrb. Abt. Syst. 9, 1896 p. 630 2 ♂; Fig. B.

Paraguay: San Salvador (J. Bohls), in woody thorns of Acacia (probably cavenia).

CRYPTOCERUS QUADRATUS Mayt

Emery, Zool. Jahrb. Abt. Syst. 9, 1896 p. 634 2 ♂; Fig. E.

Paraguay: San Salvador (J. Bohls), in woody thorns of Acacia (probably cavenia).

CRYPTOCERUS ROHWERI Wheeler


Arizona: Santa Catalina Mountains (Chrisman), in limbs of palo verde (Cercidium torreyanum).

CRYPTOCERUS SCUTULATUS F. Smith

Costa Rica: Alajuela (Wheeler), in Tillandsias.

CRYPTOCERUS WHEELERI Forel


Mexico: Cuernavaca (Wheeler), in Tillandsia benthamiana.

CRYPTOCRUS sp.


Paraguay: San Bernardino (K. Fiebrig), occasionally in Cecropia peltata L.
Subgenus Paracryptocerus Emery
Cryptocerus (Paracryptocerus) complanatus Guérin
subsp. Ramphilus Forel


Brazil: Bom Fim Jurua, Amazonas (E. Ule), in perforated twigs of Platymischium ullei Harms.

Cryptocerus (Paracryptocerus) cordle Stitz

Stitz, Deutsch. Ent. Zeitschr. 1913 p. 207 2 ♂ . Fig. 1.

Brazil: Alto Acre (E. Ule), in Cordia.

Cryptocerus (Paracryptocerus) minutus Fabr.


Costa Rica: (A. Alfar) in thorns of Acacia; El Hiquito, near San Mateo (P. Biolley), in trunk of Bixa orellana.

Panama: Tumba Muerte Road, near Las Sabanas (Wheeler), nesting in thorns of Acacia penonomensis; Miraflores, C. Z. (Wheeler), in twigs of Triplaris americana.

This ant is most frequently found nesting in the dead twigs and branches of various trees and bushes or even in the culms of coarse grasses.

Cryptocerus (Paracryptocerus) pusillus Klug


Paraguay: San Salvador (J. Bohls), in woody thorns of Acacia (probably cavenia).

Like C. minutus, this ant is most frequently found nesting in dead branches.

Subgenus Cyathocephalus Emery
Cryptocerus (Cyathocephalus) pallens Klug


Paraguay: San Salvador (J. Bohls), in woody thorns of Acacia (probably cavenia).
Mexico: San Sebastian, near Tuxtla (G. N. Collins), in thorns of Acacia collinsi Saff.
Var. discocephalus F. Smith


Costa Rica (A. Alfaro), in thorns of Acacia.

Var. porrasii var. nov.

(Plate 52)

Soldier. Length 4—4.5 mm.

Differing from the typical form of the species and the var. discocephalus and patellaris Mayr in having the short scale-like hairs which emerge from the foveolae on the cephalic disc and thorax, pedicel and base of gaster much coarser and more conspicuous and with a silvery luster. The concavity of the cephalic disc is distinctly shining and its foveolae are larger and not crowded.

Worker. Length 3.5—3.7 mm.

Characterized by having the same peculiarity of the squamiform hairs as the soldier and also by the thorax which is narrower, with the marginal tooth of the mesonotum more acute and the lateral margin of the epinotum represented by three distinct teeth. The lateral spines of the petiole and postpetiole are long, flat, curved and acute, those on the former longer than on the latter.

Female. Length 5—6 mm.

Only the disc of the head shows the enlarged squamiform hairs, the pilosity of the remainder of the body being as in the typical pallens. Wings heavily infuscated, not pale as in varians, with dark brown veins and pterostigma.

Male. Length 4—5 mm.

Very similar to the male of varians but the gaster is darker, as dark as the thorax, heavily shagreened and more opaque and the wings are darker, as in the female.

Dedicated to the former genial and learned president of the Panamanian Republic, Dr. Belisario Porras, and described from numerous specimens of all four phases found nesting in the cauline swellings of Cordia alliodora and in the dead twigs of various trees and shrubs at Quebrada de Oro (type locality), Red Tank, Frijoles and Ancon, C.Z.

The colonies of this ant are not very populous. Its habits are similar to those of Colobopsis. The elliptical nest-entrance is guarded by one of the soldiers, which occludes the orifice with the disk-shaped dorsal cephalic disc just as the Colobopsis soldier uses the truncated circular
anterior surface of the head for the same purpose. The cephalic disc in old soldiers and the mother queen of the colony often becomes coated with dirt and extraneous particles so that it closely resembles the bark of the plant.

**Cryptocerus (Cyathocepalus) setulifer Emery**

(Plate 53)

*Soldier.* (Undescribed) Length 3.5–3.8 mm.

Resembling the female, but the posterior border of the cephalic disc sharper. This disc is broadly oval, the narrower being the posterior end. The thorax is much like that of *pallens* in shape but the pronotal crest is much less pronounced and interrupted in the middle. The gaster is shorter and more broadly elliptical. Color, sculpture and pilosity much as in the worker, except that the spots at the anterior corners of the first gastric segment are larger, more distinct and of a paler, more ivory yellow.

*Male.* (Undescribed) Length 3.8–4 mm.

Head, including the eyes, fully twice as broad as long, with a straight, broad posterior border and small rounded angles. Eyes and ocelli very convex. Mandibles very small, with very indistinctly and bluntly denticulate apical borders. Clypeus small and short, its anterior border entire and broadly rounded. Antennæ very long, the scapes only one and one half times as long as broad, the remaining joints much longer than broad, diminishing in length to the penultimate which is about two-thirds as long as the last joint. Thorax broad and convex, decidedly narrower than the head; humeri of pronotum rectangular; mesonotum as long as broad, subtriangular, with well-developed Mayrian furrows dividing it into three subequal convex areas. Epinotum small and short, with subequal base and declivity, meeting at a rounded right angle. Petiole and postpetiole from above subrectangular, about as long as broad, the latter at its anterior corners with short broad teeth representing those on the corresponding segment of the other phases. Gaster slender, the first segment as long as all the remaining segments together. Legs moderately long.

Head, including the mandibles, thorax, petiole and postpetiole opaque, densely and finely punctate-rugulose; gaster and legs slightly shining and merely densely punctate.

Hairs long, abundant, dull yellowish, erect, confined to the dorsal surface of the head and thorax, the tip of the gaster and flexor surfaces of the femora.
Black; antennae dark brown; tibiae and terminal tarsal joints reddish brown; genitalia and posterior borders of gastric segments golden brown or brownish yellow; wings colorless, hyaline, with pale brown pterostigma and yellowish veins.

Several colonies of this species were found nesting in the cauline swellings of Cordia gerananchus trees just back of the laboratory at Ancon, C.Z. The soldier has the same habits as C. pallens and many of the individuals have the cephalic disc incrusted with foreign matter from exposure to the elements during guard duty at the oval nest entrance.

CRYPTOCERUS (CYATHOCEPHALUS) VARIANS F. Smith
(Plate 54)


Florida: Card’s Point (Wheeler), in Tillandsias; Cocoanut Grove (Miss Nancy Fairchild), in twigs of Coccoloba uvifera.

Subsp. MARGINATUS Wheeler and Mann

Haiti: (W. M. Mann), nesting in bamboos.

Genus APTEROSTIGMA Mayr.

APTEROSTIGMA CALVERTI Wheeler
Wheeler, Psyche 18, 1911 p. 207 ♀; Calvert, a Year of Costa Rican Natural History 1917 p. 241 Fig.

Costa Rica: Juan Viñas (P. P. Calvert), nesting in Bromeliads.

Subfamily DOLICHODERINAE

Genus DOLICHODERUS Lund

DOLICHODERUS (HYPOCLINEA) BITUBERCULATUS Mayr
Morteo, Malpighia 18, 1904 p. 509 ♀.

Ceylon and Buitenzorg; inhabiting twigs of Triplaris americana Vahl. The ant is a common East Indian species.
Dolichoderus (Hypoclinea) championi Forel
Subsp. trinidadensis Forel var. taeniatus Forel

Panama: Chivachiva Trail near Red Tank, C. Z. (Wheeler), nesting in the cauline swellings of Cordia alliodora; Las Sabanas (Wheeler), in Tillandsias.

The colonies in Cordia were very sporadic and small, those in the Tillandsias much more populous. This ant more frequently nests in dead branches.

Dolichoderus (Hypoclinea) lutosus Mayr

Panama: Las Sabanas and Tabogilla Island (Wheeler), nesting in Tillandsias.

Costa Rica: Alajuela (Wheeler), in Tillandsias.

Guatemala: Escuintla (Wheeler), nesting in thorns of Acacia bursaria Schenck.

Dolichoderus (Monacis) bispinosus Olivier

Brazil: Pará (W. M. Mann), in ant gardens in parabiosis with Crematogaster limata subsp. parabiotica.

Panama: Las Sabanas (Wheeler) in Tillandsias; Chivachiva Trail, near Red Tank, C. Z., in cauline swellings of Cordia alliodora.

Fully developed colonies of this ant are very populous and live in dead branches and abandoned aerial termitaria. The colonies found in Cordia and Tillandsias were small and incipient and usually contained only a single mother queen. That pleometrosis, or the founding of a colony by a number of recently fecundated females, not infrequently occurs is indicated by my finding several associations of more than 60 deëlated females all living together in single large Tillandsias.

Dolichoderus (Monacis) debilis Emery var. Rufescens Mann

Mann, Psyche 19, 1912 p. 40 & $\varphi$ $\sigma$.

Brazil: Madeira—Mamore R.R., Matto Grosso (W. M. Mann), in ant-gardens in parabiosis with Odontomachus affinis subsp. mayri.

Genus Iridomyrmex Mayr
Iridomyrmex iniquus Mayr
var. nigellus Emery

Costa Rica: San José, Alajuela and Cartago (Wheeler), nesting in Tillandsias.

Guatemala: Zacapa (Wheeler), in Tillandsias.
Iridomyrmex ferdicensis sp. nov.

Worker. Length 1.3—1.5 mm.

Head slightly longer than broad, somewhat broader behind than in front, with evenly rounded sides and straight posterior border. Eyes small, flattened, in front of the middle of the head. Mandibles with long apical margin, furnished with two acute apical teeth, the remainder finely and indistinctly denticulate. Clypeus strongly convex in the middle, its anterior border entire and nearly straight. Frontal area rather distinct, large, triangular; frontal groove obsolete; frontal carinae short, as far apart as their distance from the lateral borders of the head. Antennae rather slender, scapes extending only about twice their greatest diameter beyond the occipital corners, funicular joints distinctly longer than broad. Thorax small and compact, the pro- and mesonotum broadly and evenly convex in outline, the mesepimotal impression short and acute, the epinotum small and short, very convex, its base rising rather abruptly from the impression, as long as the declivity with which it forms a rounded right angle, the metasternal angles produced backwards. Seen from above the pronotum is broader than long, transversely elliptical; the mesonotum narrow and rectangular, slightly longer than broad; the epinotum scarcely broader than the mesonotum and fully as broad as long. Petiole short, the scale well-developed, rather high, inclined forward, strongly compressed anteroposteriorly, rather narrow, with parallel sides and rounded, sharp and entire superior border. Gaster small, broadly elliptical, its first segment not covering the petiole.

Moderately shining; surface of body very finely sharpened.

Pilosity very delicate, whitish, represented by a few scattered hairs on the clypeus, thorax and gaster. Pubescence pale, very fine, uniformly distributed on the body and appendages, a little longer and oblique on the scapes. It is so dilute as not to obscure the shining.

Pale, sordid yellow; head slightly darker; mandibular teeth reddish.

Described from fourteen workers belonging to a single colony which I found nesting in a Tillandsia near San José, Costa Rica.

This species is quite distinct from any of the described Neotropical Iridomyrmex in its small size and the structure of the thorax.
Genus Forelius Emery

Forelius Maccooki Forel

var. Brasiliensis Forel


Paraguay: San Bernardino (K. Fiebrig), in branches of Alchornea urucurana.

Subsp. Fiebrigi Forel

Forel, Mém. Soc. Ent. Belg. 20, 1912 p. 44 ♀.

Paraguay: San Bernardino (K. Fiebrig), in branches of Alchornea urucurana.

Genus Azteca Forel

Azteca alfari Emery

Boll. Mus. Zool. Anat. Torino 11, 1896, p. 3, 4 ♀, Fig. IV; Forel, Biol.

Of this species, which is one of the most abundant ants in the Cecropias of the Neotropical Region, Forel has described ten subspecies and varieties and I have added two varieties. I here compile the various scattered descriptions as an aid in identifying the forms. Undoubtedly many additional subspecies and varieties will be discovered in Central and South America. Emery describes the worker and female of the typical alfari as follows:

"Worker. Testaceous, scarcely shining; head slightly darker, reddish; gaster infuscated posteriorly. Subopaque, pubescent and with long hairs; scape and legs without erect hairs. Stature only slightly variable, head rather elongate, narrowed in front; eyes in front of the middle of its length; mandibles shining, nearly smooth, with nearly straight dental margin, about 8-toothed; scape scarcely reaching the posterior margin of the head in the worker minor, thorax robust, convex, mesometanotal suture deeply impressed; scale cuneiform, with rounded dorsal angle. Length 2½–3 mm; head of worker 1 x 0.9 mm, scape 0.8 mm."

"The female of this species is black, with the anterior portion of the head, the mandibles, antennæ, articulations of the legs, tibæ and tarsi more or less reddish. Sculpture, pubescence and hairs as in the worker. The head is elongate rectangular, with slightly curved sides, the posterior margin entire. The posterior boundary of the eyes is
slightly in front of the posterior half of the head; the tip of the scape surpasses half the space which separates the eye from the occipital margin. The scale is higher than in the worker, with more acute border. The feebly smoky wings have reddish veins and a dark brown stigma.”

The worker types were taken by A. Alfaro at Jimenez, Costa Rica, in the internodes of Cecropia, and I have taken it at Zent, Costa Rica, in the same hosts. Emery records the species also from Venezuela where it was taken in Cecropia peltata and Forel took specimens at Santa Marta, Colombia, in an unidentified Cecropia. He also cites the species from Bugaba, Panama (Champion).

In a more recent paper (1912) Forel says: “The forms which I called alfari r. lucida and r. lucidula should be regarded as distinct species. The former is much more dimorphic and has a large female, the head very large and elongate. The latter, on the contrary, is smaller and more monomorphic, with smaller and posteriorly more excavated head.” In this paper I have retained the two forms as subspecies, since I am not certain that the differences mentioned by Forel are of specific value and since it seems wiser to keep all the forms together till the species can be more carefully studied on the basis of a much larger amount of material than either Forel or I have seen.

**Var. aequalis Forel**


“Worker. Length 2.1–3.1 mm.

Much less dimorphic and smaller than the var. aequilata Forel, near the var. ovaticeps, but the sides of the head are less convex and the scapes are shorter; their tips distant from the occipital angles by about one-fourth their length in the large worker. The head is less excised posteriorly than in ovaticeps. The epinotum is even more cuboidal than in ovaticeps, the basal surface nearly flat and the stigmata protrude as tubercles towards its extremity. Scale rounded, thick. Color reddish yellow, a shade deeper than in ovaticeps. Opaque or feebly subopaque, like ovaticeps.”

“Female. Length 7.5 mm.

Like the female of mixta, but the head narrower, longer. More reddish brown or brownish red, with brown spots. Gaster brown posteriorly.”
"Male. Length 3 mm.
Tip of funiculus easily collapsing, shrivelled in all the specimens. Head trapezoidal posteriorly, scale somewhat thicker than in mixta. Color more dark brown."

Brazil: Obidos near Pará (Goeldi), in a Cecropia; Mexicana Island, Amazon Delta (Dr. Hagmann); Forel also cites this variety from Dibulla, Colombia (Lallemand).

Var. aequilata Forel

"Worker. Length 2.6—4 mm.
Distinguished from the typical alfari by the form of the head. It is scarcely or only slightly broader behind than in front, otherwise as in the type, about one-fifth or one-sixth longer than broad. It is larger and more rectangular, with less convex sides than in the var. ovaticeps Forel from Pará. Color and sculpture as in the specific type and not as in the subsp. lucida Forel and lucidula Forel. In other respects like the specific type."

"Female. Length 7—7.4 mm.
Head more rectangular than in the var. ovaticeps, with less convex sides; otherwise the same in all particulars. Wings iridescent, suffused with yellowish brown, with brown stigma and brownish yellow veins."

"Male. Length 3.4 mm.
The head is more narrowed behind the eyes, with more distinct posterior border than in the male of the subsp. lucidula, in which it is more rounded. The color is yellow, feebly shining, but the specimens seem to be somewhat immature. Otherwise like lucidula, the male of which, however, is black and shining."

Brazil: Jurua Miry, Jurua, Amazonas (E. Ule), in internodes of Cecropia (Ule No. 5587); Rio Purus (A. Goeldi and J. Huber), in Cecropia.

Var. curtiscapa Forel

"Worker.
Scape slightly shorter. Mesonotum more projecting, forming a boss more distinct from the pronotum than in the type of the species. The basal surface of the epinotum is also a little more elevated and more convex, so that a narrow and very distinct notch is formed in the constriction of the thorax between the mesonotum and said basal surface. In other respects like the typical alfari."
"Female. Length 7.2 mm.
Testaceous yellow, with the thorax and abdomen partly brown. In other respects like the worker.
"Panama (Christophersen), in the trunk of a Cecropia." I have taken this form at Corozal, C. Z. (Wheeler), in young Cecropia.

Var. Fumaticeps Forel


"Worker. Length 2.5—3 mm.
Head shaped as in the typical alfari, decidedly narrowed anteriorly, but somewhat smaller in the major worker and less deeply excised posteriorly. In the major worker the scape does not reach the occiput, in the minor worker it surpasses it only slightly. Thorax, gaster and legs as in the typical alfari; the scale is somewhat more rounded above. Brownish yellow; head, antennae and mandibles dark brown, smoky.

Buenaaventura, Mexico, collected by Dr. Ross in Cecropia mexicana. Ross cites this variety also from Zacuaparu, Mexico, in the same plant.
I have frequently taken what is evidently this same form in young Cecropias at Puerto Barrios and Quirigua, Guatemala. There is considerable variation in the coloring of the workers in the same colony. Usually only the larger individuals have the head dark brown and often the mesopleura are of the same color, while the smaller workers may be uniformly pale or brownish yellow.

The female (undescribed) measures 7.5—8 mm. and is also rather variable in color, the thorax and abdomen being dark reddish brown or blackish brown, the head red, with the front and vertex darker, the clypeus paler, the mandibles red with black borders, the scapes and legs dark brown, the funiculi brownish yellow, the gastric segments with rather broad and sharply delimited brownish yellow borders. The wings are lacking in all my specimens, which were found living in the Cecropia internodes, either singly or with their small colonies of workers.

Var. langi var. nov.

Worker. Length 2.3—3.5 mm.
Close to the var. aequilata Forel, but smaller, with the same color, sculpture and pubescence but much less pilosity; the mesonotum dis-
tinctly less convex in the major worker, the mesoepinotal constriction much shorter and more acute, the epinotum shorter and lower, the petiolar scale more compressed anteroposteriorly. The head is of the same shape in all the workers, similar to that of *aequilata*, but distinctly broader behind than in front and the sides are less convex, the scapes in the largest workers somewhat shorter, but even the penultimate funicular joints are as long as broad, as in *aequilata*.

*Female.* Length 6 mm.

Smaller than the female of *aequilata*. Black; with red mandibles, brown scapes and basitarsi and the sides of the clypeus, funiculi and remaining tarsal joints brownish yellow. Wings whitish, not suffused with yellowish brown as in *aequilata*, with pale yellow veins and dark brown pterostigma.

*Male.* Length 2.3—3 mm.

Also smaller than the male of *aequilata*. Head only moderately narrowed behind, with rounded posterior corners. Dark brown, thorax and top of head black; antennae and tarsi pale brown. Wings whitish, with colorless veins and pale brown pterostigma.

Described from a number of specimens of all three phases taken by Mr. H. O. Lang at Kamakusa, British Guiana, in the internodes of *Cecropia*.

**Var. mixta** Forel


*Worker.* Length 2.4—3.6 mm.

Not so opaque as the type of the species, but less shining than the subsp. *lucida* Forel. Head more strongly narrowed in front than in the typical *alfari*, but less excised behind, somewhat broader. The scape is conspicuously short, like that of the var *aequalis* Forel, scarcely surpassing the posterior fourth of the head. Scale blunt above. Basal surface of epinotum quadrangular, somewhat broader than long, in front almost as broad as behind (in the var. *aequalis* the head is scarcely broader behind than in front and the basal surface of the epinotum is much narrower in front than behind, as long as its posterior width). Darker than *aequalis*; gaster brown, vertex brownish red, otherwise yellowish red.

"*Female.* Length 6.8 mm.

Blackish brown; funiculi, anterior border of head and tips of tarsi reddish. Head somewhat broader than in the var. *aequalis*. The scape
does not reach the posterior fourth of the head. Wings rather pale, with a brownish yellow tinge, brown stigma and brownish yellow veins. A single cubital cell as in other species."

"Male. Length 2.4—2.9 mm.

Head rectangular behind the eyes, not narrowed posteriorly (in the var. aequalis and the typical form of the species trapezoidal, narrowed posteriorly). Antennæ as in the var. aequalis and in the specific type; scape and first funicular joint broader than long; second joint very large, one and three-fourths times as long as broad, much broader than the first. The succeeding joints increasingly shorter and narrower, but nearly all longer than broad; the terminal joints somewhat longer (not thicker). Scale thin above and rather pointed. Black with brown appendages. Wings paler than in the female.

San Bernardino, Paraguay (Fiebrig); São Paulo, Brazil (von Ihering)
In Cecropia peltata L.

Var. ovaticeps Forel

Forel, Rev. Suisse Zool. 12, 1904. p. 44 ♀ ♂.

"Worker. Length 2.4—3.5 mm.

A little less polymorphic than the typical alfari. Head slightly narrower, with more convex sides, as narrow behind as in front. The small differ little from the large workers. Color vivid yellow (the typical alfari is brownish yellow). The sculpture is that of the typical alfari but the stature is smaller than that of the subsp. lucida Forel, and larger than that of the subsp. lucidula Forel, which is even less polymorphic."

"Female. Length 7—7.5 mm.

Very similar to the female of the subsp. lucidula Forel, but the scale is higher, thinner and more acuminate and the first segment of the gaster more elongate and more attenuate anteriorly. Deep brown, with the anterior portion of the head, the legs, the antennæ and the mandibles yellowish red. Posterior borders of the gastric segments reddish. The form of the head is precisely as in lucidula, but the mandibles are shorter and thicker. The thorax, on the contrary, is a little narrower, the two surfaces of the epinotum less distinct from one another, forming together a more feeble convexity. The wings are lacking.

Pará (E. Goeldi)."

No doubt this, like the preceding varieties, inhabits Cecropias.
Subsp. cecropiæ Forel


"Worker. Length 2.5—3 mm.
Color brown, varying from blackish brown to uniform reddish brown, with the mandibles and base of the scapes reddish. Moreover, the head is more trapezoidal, more enlarged posteriorly than in the other subspecies, a little longer than broad, but not much. Finally, joints 3–10 of the funiculus are a little thicker than in the typical alfari, rather distinctly broader than long. Apart from these characters I find none that would suffice for the establishment of a species.

Manaos, Brazil (A. Goeldi and Dr. Huber), in a Cecropia."

To the characterization of the worker Forel later added the following remarks and a description of the sexual phases: "Between the mesonotum and basal surface of the epinotum there is a sharp, slit-like incision, which descends abruptly from the basal surface and bears on its anterior (mesonotal) wall the two very prominent stigmata. This conformation is indicated also in other varieties (especially mixta) but only feebly."

"Female. Length 6—6.6 mm.
Color as in mixta and scarcely distinguishable from that form. The head is merely somewhat shorter and somewhat broader behind. Distinguishable from the specific type only by the shorter scape."

"Male. Length 2.8—3 mm.
Precisely like the var. mixta, but the antennæ thicker and stouter; the funicular joints 4–10 broader than long or at least as broad as long.

Campo Besso, near São Paulo (H. von Ihering), in a swamp Cecropia."

Forel records this subspecies also from Panama (Christophersen), "nesting in the cavities of a Cecropia trunk"; and Stitz saw specimens taken by E. Ule in Brazil. I received a fine series of workers together with branches of the Cecropia peltata in which they were living from Dr. G. Stahel, Director of the Agricultural Experiment Station at Paramaribo, Dutch Guiana, and all three phases taken by Mr. H. E. Box in Cecropia peltata at Blairmont Plantation, Berbice, British Guiana.
Subsp. lucidula Forel

A. alfari race lucidula Forel, Biol. Centr. Amer. Hymen. 3, 1899-1900 p. 113
8 ♀ 9 ♀, Wheeler, Amer. Mus. Novitates No. 45, 1922 p. 14 8 9;

"Worker. Length 2.6–2.9 mm.

Much more shining, more feebly sculptured than the type. Thoracic
impression broad and deep; mesonotum and epinotum slightly convex.
Head narrower, slightly more elongate. Stature a little more slender.
The funicular joints broader than long, especially towards the tip."

"Female. Length 7.5 mm.

Densely punctate, scarcely shining. Very similar to the female of
A. bicolor and of the same black color (see Emery’s figure), but the
sides of the head are more convex; the head is also as broad in front
as behind. Scale lower and thicker than in A. bicolor. Thorax a little
broader. The wings are almost hyaline, with the stigma brown and
the veins yellowish brown (in A. bicolor the wings are tinged with
brownish yellow).

"Male. Length 2.5–2.9 mm.

Mandibles very short, pointed, not meeting in the middle. Head
rounded rectangular, longer than broad. Scape broader than long,
as is also the first funicular joint. Funicular joints 6–10 nearly as
broad as long. Petiolar scale thin. Dorsal appendage of the median
genital valvules surpassing the external valvules, which are acuminate.
Wings rather long, subhyaline; in other respects as in the female.

"Hab. Guatemala, Retahuleu (Stoll); Trinidad (Urich)."

I have seen specimens of this ant from the following localities:
British Guiana: Kartabo and Kalacoon (Wheeler), nesting in the
internodes of Cecropia angulata Bailey.

Trinidad: Caroni and Botanical Garden, Port of Spain (Wheeler),
in internodes of Cecropia peltata.

Var. zonalis var. nov.

Worker. Length 2—2 mm.

Very close to the typical lucidula and with the same sculpture, but
smaller. Feebly polymorphic, the antennal scapes shorter, in the
worker minor reaching to the occipital corners of the head, in the
worker major about two-thirds the distance between the eyes and
occipital corners. Pubescence distinctly more abundant on the head
and thorax than in lucidula. Color varying from brownish yellow to
yellowish brown, the head usually somewhat darker. Mandibles usually not much darker than the head, clypeus paler.

_Female._ Length scarcely more than 6 mm.

Also smaller than the female of _lucidula_, of the same color and sculpture but the wings are distinctly darker and the posterior borders of the gastric segments less distinctly brownish. The head is less concave behind, with more rounded occipital corners.

All the numerous specimens which I have taken in young Cecropias in the Canal Zone and the Republic of Panama belong to this variety. I have specimens from the following places: Corrozal (type-locality), Ancon, Gatun, Monte Lirio, Colon, Rio Agua Salud, Red Tank and Otoque Island.

**Subsp. lucida Forel**

_A. alfari race lucida_ Forel, Biol. Centr. Amer. Hymen. 3, 1899–1900 p. 113 2;  

"Worker minor."

Identical with the worker of the preceding race (_lucidula_), but the thorax is more arcuate (more like that of the type), the color duller and the funiculi, excepting the first joint brown."

"Worker major._ Length 4.2 mm.

Head 1.6 mm. long and 1.25 mm. broad, very similar to Emery's figure of the major worker of _A. bicolor_, but narrower in front and a little more elongate. The scapes fail to reach the occipital angles by half their length. Funicular joints, except the penultimate, a little longer than broad. Head deeply excavated behind with feebly convex sides. Borders of gastric segments yellowish. Reddish yellow; head reddish brown, except anteriorly where it is reddish. Gaster and funiculi, except the first joint, brownish. Gastric segments brownish posteriorly. Head feebly pubescent, very shining, very feebly punctate, the punctures numerous but superficial.

_Hab. Guatemala, Pantaleon 1700._ (Champion) Found in the cavities of a Cecropia trunk."

I have taken what I regard as this subspecies in young Cecropias at Patulul and Escuintla, Guatemala. The workers agree well with Forel's description, except that in the major the head is rather broad, with convex sides. In none of the workers do the scapes surpass the occipital border. Two winged females from Patulul are very pale in color and are, perhaps, immature. They are yellowish brown, with the dorsal surface of the thorax and the bases of the
gastric segments darker, the head, antennæ and legs brownish yellow, the mandibles deep red. The scapes reach less than half the distance between the eyes and occipital corners. The surface is much less shining than in the worker, though the pubescence is poorly developed. The wings are tinged with yellow, the veins resin-yellow, the stigma brown. The size is unusually small, scarcely 6 mm., but the gaster is much contracted in both specimens.

Subsp. tuberosa Forel


"Worker. Length 2.5—3.9 mm.
Form of the head as in aequilata, but a little longer and only feebly excised behind. The eyes are larger than in the varieties of the typical subspecies. The mesoepinotal impression is strong; basal surface of epinotum convex, enlarged posteriorly and bearing at its extremity two large obtuse tubercles formed by the stigmata. The scale is cuneiform as in the typical alfari and its varieties (sharper than in the subsp. lucida). The penultimate joints of the funiculi are as long as broad (thicker than in the typical alfari and its varieties).

Sculpture and pilosity of the typical alfari. Brownish yellow; upper surface of head in great part, mandibles, tarsi and tibie brown. Sometimes the brown color extends to a part of the thorax or even of the abdomen as well as the femora.

"Female. Length 9 mm.
Blackish brown; anterior portion of head and antennæ reddish. Very similar to the female of the var. aequilata, but larger, with broader and shorter head. Scale elevated and acuminate. Wings lacking.

Ceara, Brazil (Diaz da Rocha)."

Azteca angusticeps Emery


Costa Rica: (type locality); Alajuela (Wheeler) nesting in Tillandsias.

Trinidad: Botanical Garden, Port of Spain (Wheeler), running on the trunks of Cecropia peltata L.
AZTECA BICOLOR. Emery var?

What seems to be a variety of this species is represented by a single deilated female and her incipient brood of three small black workers, taken from a Cordia alliodora domatium at Ancon, C. Z. I hesitate to introduce a new name because the large workers are unknown and the female possesses no striking characters.

AZTECA BREVICORNIS Mayt


Brazil: Amazonas (James Trail), probably in some myrmecophyte.

Var. BOLIVIANA Wheeler & Mann, var. nov.

Worker. Length 2—2.2 mm.

Agreeing very closely with the descriptions of Mayr and Emery of the typical brevicornis, except in color, which is dark brown, the gaster and posterior portion of the head being black, the mandibles red, the corners of the clypeus, the antennal scapes, first funicular joint and legs sordid yellowish, the femora fuscous in the middle, the posterior borders of the gastric segments pale brown.

Six specimens taken by Dr. W. M. Mann at Huachi Beni, Bolivia, in the hollow stems of a species of Triplaris (White, No. 958).

AZTECA COERULEIPENNIS Emery


Mexico: Atoyac in Vera Cruz (Schumann); Zacuapam (H. Ross), in Cecropia mexicana.

Guatemala: Cerro Zunil, 4,000–5,000 (Champion).

AZTECA CONSTRUCTOR Emery

Costa Rica: Atlantic and Pacific Slopes (A. Alfaro, Pittier, Tonduz), in Cecropias.

Guatemala: Quirigua (Wheeler), in young Cecropias.

Panama: (Christophersen); Ancon (Wheeler), in young Cecropias.

Trinidad: Port of Spain (Wheeler), in internodes of Cecropia peltata.

According to Alfaro, as quoted by Emery, A. constructor is "the fiercest and most aggressive of the Costa Rican species," a statement to be accepted "cum grano salis." The opening of the nest in the cavity of the Cecropia "is a fissure of 15 mm. In the cavity of the plant it constructs a nest of brown carton."

Vari. guianæ var. nov.


Worker. Length 2–3 mm.

Smaller, head distinctly longer and somewhat more rectangular than the typical constructor, distinctly longer than broad, the posterior border less deeply excised; the epinotum distinctly angular in profile, the petiolar scale somewhat sharper and even more inclined forward. The color is somewhat darker, more blackish brown, the pilosity on the body somewhat less abundant and more uneven.

Female (deiálated). Length 7 mm.

Also smaller than the typical constructor, which measures 7.5–8 mm. Head larger and broader. Surface distinctly less shining. Dark brown, not black, like the typical form; pilosity similar but pubescence grayish and much more abundant and conspicuous, especially on the head and gaster.

Described from nine workers and a single female taken at Kartabo, British Guiana, in an internode of Cecropia angulata Bailey.

Azteca coussaœæ Forel


Brazil: Jurua Miry, Jurua, Amazonas (E. Ule), in twigs and branches of Coussaœæ sp. (Ule No. 5717).

Azteca delpini Emery


This species was originally described from Matto Grosso, Brazil (Germain). Mr. H. O. Lang has sent me workers of the typical form
of the species which he took at Kamakusa, British Guiana, in large leaf-sacs of *Tococa guianensis* Aubl. A set of larger and darker workers was taken by me at Kartabo, British Guiana in a cauline swelling of *Cordia nodosa* L.

**Var. trinidadensis** Forel


Trinidad: Caroni (Wheeler), nesting in internodes of *Cecropia peltata* L.

**Azteca depilis** Emery


Brazil: Amazonas (K. Schumann), from stems of *Duroia hirsuta* Schum. and leaf-sacs of *Tococa coronata* Benth.

**Azteca duckei** Forel

Forel, Ann. Soc. Ent. Belg. 50, 1906 p. 243 ♀ ♂ Fig. 2.

Brazil: Barcellos, Rio Negro, Amazonas (Ducke), in cauline swellings of *Cordia nodosa* L.

**Azteca durole** Forel


Brazil: Jaburu, Upper Jurua, Amazonas (E. Ule), in swellings of twigs of *Duroia hirsuta* Sch.; Jurua (E. Ule), in the branches of *Porouma* sp.; Porto Alegre, Rio Purus, Amazonas (A. Goeldi and J. Huber), in the hollow stems of *Duroia hirsuta*.

**Azteca emeryi** Forel


Brazil: Cachoeira, Jurua, Amazonas (E. Ule), in the hollow internodes of *Cecropia sciadophylla* Mast.

**Azteca fasciata** Emery

subsp. *lactea* subsp. nov.

*Female. (deïlated) Length nearly 8 mm.*

Differing from the typical *fasciata* of Bolivia in the shape of the head and petiole. The former is one and one-half times as long as
broad, and regularly oblong, except for the feebly and angularly excised posterior border, the sides being straight and parallel, not feebly convex as in the typical form of the species. The petiolar node is not acuminate above as in that form, but blunt and rounded, though narrower above than below.

Yellow; head faintly reddish, with black ocellar spot; mandibles deep red. Posterior border of scutellum and a few clouds on the pleura fuscous. Each gastric segment dorsally with a transverse castaneous band and ventrally with a pair of brown spots. Last tarsal joint of all the legs blackish; middle and hind tibiae and hind femora dark brown.

Described from a single specimen taken July 9, 1924 from a domatium of *Cordia alliodora* on Barro Colorado I., C. Z.

**AZTECA FORELI Emery**


The types of this species were collected by A. Alfaro at Bagaces, on the western slope of Costa Rica. I have taken it at Zent, on the Atlantic Slope of the same republic and at Patulul, Guatemala, in both places in Cecropias.

**Var. XYSTICOLA Forel**


Populous colonies of this vigorous and aggressive ant, originally described from Colombia, were found nesting in the trunks of old *Cordia alliodora* trees near the laboratory at Ancon, C. Z., Panama.

**Subsp. CHAMPIONI Forel var. BREVISCAPA Forel**


Costa Rica: (Tonduz), in *Cecropia*.

**Subsp. URSINA Forel**


Forel described this subspecies from specimens taken by Urich in Trinidad. I found it in the Botanical Garden at Port of Spain, running on the trunks of large Cecropias and probably nesting in their cavities.
AZTECA FOVEICEPS Wheeler

Wheeler, Zoologica 3, 1921 p. 163 ♂ ♀ Fig. 16; Bailey, Bot. Gazette 75, 1923 p. 34.

British Guiana: Kartabo (Wheeler), in hollow petioles of Tachigalia paniculata Aubl.

AZTECA GOELDIG Forel


Brazil: Porto Alegre, Upper Rio Purus, Amazonas (J. Huber), in hollow branches of a tree (Laurineae?), smelling strongly of onions.

AZTECA HUBERI Forel


Brazil. Téffé, near Para (J. Huber), in branches of Platymischium sp.

AZTECA HYPOPHYLLA Forel


Colombia: San Diego (A. Forel). "Makes its nest under the round leaves of a climbing plant which from the description is very probably the juvenile stage of a species of Maregravia."

AZTECA INSTABILIS (F. Smith)


British Guiana: Kartabo (Wheeler), nesting in internodes of Cercopia angulata.

This species is known from Mexico, Central America, Colombia and French Guiana. Most of the citations of instabilis, however, refer to muelleri Emery of Brazil.

AZTECA LANUGINOSA Emery


Brazil: Santa Catharina (type-locality); São Paulo, etc. (H. v. Ihering), on Cercopia adenopus Mart.; Jaragua Distr., Prov. Santa Catharina (W. Ehrhardt), carton nest on Cercopia.
AZTECA LONGICEPS Emery
(Plate 55, fig. a)


Worker major. Length 3—3.5 mm.

Head suboblong, one and one-third times as long as broad, narrowed in front of the eyes, the sides in the middle parallel and nearly straight, the posterior border distinctly but not very deeply excised. Eyes small, flat, near the anterior third of the sides of the head; ocelli absent. Clypeus swollen and somewhat advanced at the sides, longitudinally flattened in the middle, with nearly straight, entire anterior border, the posterior suture indistinct. Frontal area and groove obsolete. Mandibles rather small and convex, with 7–8 teeth. Antennal scapes reaching to half the distance between the eyes and the posterior corners of the head; funiculi but very slightly thickened towards their tips; first joint about one and one-half times as long as broad; second joint longer than broad, remaining joints, except the last, subequal, broader than long. Thorax stout and thickset, about as long as the head including the mandibles. Mesonotum convex and rounded, but not gibbous; mesoepinotal constriction pronounced; epinotum small and low, as long as broad, its base in profile rather straight, longer than the sloping declivity. Petiolar node strongly inclined forward, rather high, its summit thin but not acute, seen from behind narrowed and rounded above, its ventral surface convex behind in profile. Gaster broadly elliptical, not much longer than broad. Legs short, with the femora distinctly compressed.

Shining; mandibles finely shagreened and with a few coarse punctures along their apical borders; remainder of the body finely and superficially punctulate.

Hairs yellowish, moderately long, erect, most abundant on the upper surface of the body, sparse on the scapes and tibiae. Pubescence fine, grayish, most conspicuous on the head, gaster and appendages.

Dark reddish brown or blackish, thorax usually somewhat paler than the head and gaster; cheeks, anterior border of clypeus and tarsi, except the terminal joint, and borders of gastric segments pale brown.

Worker minor. Length 2—2.5 mm.

Head only one and one-fourth times as long as broad and more distinctly narrowed in front, its sides more rounded, its posterior border less excised. Eyes just in front of the middle of the head.
Antennal scapes reaching to two-thirds the distance separating the eyes from the posterior corners of the head; funiculi slender, joints 3–10 proportionally shorter than in the worker major.

_Female._ Length 5.5—6 mm.

Head one and three-fourths times as long as broad, regularly oblong, with straight, parallel sides, scarcely narrowed in front of the eyes and nearly straight posterior border. Ocelli rather small; eyes moderately large, feebly convex, as long as their distance from the corners of the clypeus, their posterior orbits well in front of the middle of the head. Mandibles large, convex at the base, flattened and deflected at the tip, with 8 subequal teeth. Clypeus as in the worker major. Thorax elliptical, through the wing-insertions a little broader than the head. Epinotum sloping, with feebly developed base and declivity, the latter short. Petiolar scale much as in the worker but higher, its upper border more produced, seen from behind trapezoidal and narrowed above. Gaster elongate, suboblong. Legs long; femora, especially the fore pair, strongly compressed.

Sculpture and color as in the worker; pilosity less abundant, but the flexor surfaces of the scapes and tibiae with a few erect hairs. Mandibles entirely black, corners of clypeus and tarsal joints, except the last, red. Wings grayish hyaline, with brown pterostigma and pale yellow veins.

_Male._ Length 2.5 mm.

Head, excluding the eyes, longer than broad, rounded behind. Eyes half as long as the sides of the head, moderately convex; ocelli small. Mandibles very small, not meeting, with only the terminal tooth, which is acute and acuminate. Antennæ short; scapes not longer than broad; first funicular joint broader than long; second joint longer than broad, succeeding joints, except the last, as broad as long. Thorax large, much broader than the head; epinotum small and short, very convex, without distinct base and declivity. Petiolar scale erect, anteroposteriorly compressed, with blunt, broadly rounded summit. Legs slender.

Smooth and shining. Hairs almost, pubescence quite lacking, except on the funiculi where it is very dense and erect.

Black; mandibles, antennæ, legs and genitalia piceous. Wings colored as in the female, but the pterostigma paler.

Described from numerous specimens taken in the cauline swellings of _Cordia alliodora_ in the following localities in the Canal Zone: Frijoles, Ancon, Red Tank and Las Cascades. This is by far the most abundant ant in the Cordias, sometimes occupying all or most
of the cauline swellings. It is rather timid and, though sometimes inclined to bite, is not very offensive.

I have redescribed all four phases of the species, because it has been known hitherto only from Emery's figures and brief description of the deëlated female taken at Alajuela, Costa Rica, by A. Alfaro. That my identification is correct is shown by the perfect agreement of the head and petiole of the female with Emery's drawings, and the fact that I possess two precisely similar females taken by Messrs. E. A. Schwarz and Barber at Livingston and Trece Aguas, Alta Vera Paz, Guatemala. Forel has seen a female from Mexico. He has also described from various parts of tropical America the following four forms of longiceps which I treat as subspecies:

Subsp. cordincola Forel

This form was originally described from specimens taken by Bang at Cochabamba, Bolivia, in the cauline swellings of a Cordia (probably alliodora). Dr. W. M. Mann has given me five workers and a deëlated female which he found in cauline swellings of C. alliodora var. at Ivon, Beni, and Huachi Beni, Bolivia.

In the worker major, which measures about 2.5 mm., the head is long, rather deeply excavated behind and somewhat narrowed anteriorly. The scapes extend somewhat more than two-thirds the distance between the eyes and posterior corners of the head, the penultimate funicular joints are as long as broad. The base of the epinotum passes abruptly into the short declivity. The body is reddish brown, the thorax somewhat paler than the head and gaster, the mandibles red, with dark bases. The pilosity is very sparse, absent in the scapes and legs.

The worker minor measures only 2 mm. and is very similar to the major except that the head is shorter and more narrowed anteriorly and the scapes reach further towards the posterior corners of the head.

The female (undescribed) measures nearly 6 mm. and is black, with dark red cheeks and clypeal border; the tarsi, except the last joint, testaceous. The head is fully twice as long as broad and deeply emarginate posteriorly. The mandibles are 8-toothed. Antennal scapes extending half the distance between the eyes and posterior corners of the head, the median joints of the funiculi distinctly broader than long. The epinotum is rounded and sloping, the petiolar scale seen
from behind with a bluntly pointed summit. The erect pilosity is sparse as in the worker and absent on the appendages.

Subsp. juruensis Forel


All the phases of this form were taken by E. Ule at Jurua Miry, Jurua, Amazonas, in the twigs and branches of a Leguminose plant, _Schwartzia_. Dr. Mann has given me three major workers which he collected in cauline swellings of _Cordia alliodora_ var. _boliviana_ at Ivon Beni, Bolivia. I also possess a worker minor cotype given me by Prof. Forel.

The head of the major worker is one and one-half times as long as broad, distinctly emarginate behind. The antennal scapes reach somewhat more than half the distance between the eyes and the posterior corners of the head. The epinotum is subcuboidal, slightly longer than broad, the base longer than the abrupt declivity. The pilosity is somewhat more abundant than in the subsp. _cordincola_ and there may be a few hairs on the scapes, but none on the legs. Reddish brown, head and gaster darker than the thorax. Mandibles red, darker at the base. Length 3.4 mm.

The worker minor measures 2–2.5 mm, and has a shorter, anteriorly more narrowed and posteriorly less deeply excised head, with the scapes reaching the posterior fourth of the head.

The female is somewhat smaller than the typical _longiceps_ and the subsp. _cordincola_, measuring only 5–5.2 mm. The head is twice as long as broad. Color as in the typical form, but the pilosity feebler than in the worker. Wings brownish.

The male measures 2.9 mm. The head is somewhat longer than broad, the scape scarcely longer than the first funicular joint. Black, with the antennae, mandibles and legs pale sordid yellow.

Subsp. patruelis Forel


Forel described all the phases of this subspecies from specimens which I sent him and which were taken by Mr. C. H. Tyler Townsend near Colima, Mexico, in the cauline swellings of _Cordia alliodora_ var. I insert a translation of the original description.

"Length of worker 2.2—3 mm."
Worker major. Distinguished as follows from the subsp. juruensis Forel: Head somewhat broader, one and two-fifths times as long as broad, not broader behind than in front, with somewhat more convex sides. Eyes at the anterior third. The antennal scape reaches the posterior fourth of the head. Promesonotum gibbous, much more protuberant and higher than in juruensis, where it is moderately convex and hardly higher than the base of the epinotum. The latter rather low and almost flat. Constriction not deep. Petiole as in juruensis, but sharper above, angular in profile. Sculpture and pilosity as in juruensis but with more bristly hairs on the legs. Brownish, yellowish red, mandibles darker reddish, gaster brown, with yellowish borders to the segments. Legs as in juruensis, short, rather stout, with feebly compressed femora. Otherwise precisely as in juruensis.

Worker Minor. Head one and one-fourth times as long as broad. The antennal scapes reach nearly to the posterior sixth of the head. Eyes somewhat in front of the middle of the sides. In other respects like the worker major.

Female. Length 6 mm. Larger than juruensis and like the typical form of the species. Head 1.7 mm long and 1 mm broad, posteriorly a little broader than anteriorly. The scapes reach nearly to the posterior third of the head; funicular joints somewhat less transverse than in the typical longiceps. Petiole slightly thicker and above somewhat blunter.

Sculpture somewhat denser than in juruensis and the typical longiceps and therefore less shining. Pubescence somewhat denser, otherwise with the same pilosity. Color as in juruensis, but somewhat paler dark brown (in the typical longiceps darker, almost black). Posterior borders of gastric segments more broadly yellow. The whole clypeus and the cheeks reddish; mandibles and antennæ reddish brown. Wings slightly more brownish."

An examination of the cauline swellings of Cordia that contained the types of this subspecies shows that they were inhabited by the same large black Coccids as those found with the typical longiceps in Panama.

Subsp. saapi Forel


Forel described the worker and female of this subspecies from specimens taken by Ducke at San Antonio de Ica, Amazonas, Brazil, in the hollow stems of Sapium glandulosum. Their occurrence in this plant is not mentioned by Forel but is indicated on the label of a
female and three worker co-types which he gave me. I translate his description:

"Worker. Length 1.7—2.8 mm.

Mandibles shining, punctate, very feebly and finely reticulate, slightly curved, armed with about 7 teeth. Anterior border of clypeus slightly concave and bisinuate. Head subdepressed, 0.9 mm. long and 0.7 mm. broad in the worker major, 0.65 mm. long and 0.47 mm. broad in the worker minor, of the same shape in both, rectangular, slightly broadened behind, with feebly convex sides and scarcely concave posterior border. Eyes scarcely behind the anterior third. The scape slightly surpasses the posterior fifth of the head in the minor and is almost as short as in the major worker. Second funicular joint at least as broad as long; joints 5–10 much broader than long (about one and one-half times; the last joint at least twice). Thorax large and robust; pronotum one and one-half times as broad as long, but without humeri; mesonotum large, rounded, subdepressed; the promesonotum moderately convex. Thoracic constriction feeble and narrow; basal surface of epinotum square, subdepressed, scarcely longer than the declivity. Petiole short and thick, about as in stolli and polymorpha, but its very short anterior surface is more convex. Femora quite as dilated as in hypophylla, but proportionally shorter; fore tibiae dilated and also compressed.

Shining; very finely punctate; punctuation very sparse. Pubescence rather long and rather dense. Erect pilosity short, scattered over the body, very sparse on the appendages, also on the tibiae and scapes.

Body and appendages uniform reddish brown. Gaster brown, with the borders of the segments sordid yellow.

Female. Length 5.2—5.4 mm.

Head absolutely rectangular, depressed, 1.2 mm. long and 0.6 mm. broad, with straight posterior border and much rounded posterior corners. Eyes at the anterior fourth. The scape reaches the third fifth of the head from the front. Thorax compressed, long, scarcely broader than the head, feebly convex anteroposteriorly. Petiolar scale cuneiform, higher than in the worker.

Brownish black; appendages, mandibles and anterior portion of head reddish. Wings feebly but very distinctly tinged with brown.

AZTECA LUEDERWALDTII Forel


Paraguay: San Bernardino (K. Fiebrig), in branches of Alchornea irucurana.
AZTECA MINOR Forel


Brazil: Jurua Miry, Jurua, Amazonas (E. Ule), in the hollow internodes of Cecropia ficifolia Warb.

AZTECA MUELLERI Emery


Brazil: Santa Catharina (F. Müller, Hetschko), in Cecropia adenopus Mart.; Rio Grande do Sul, São Paulo, etc. (H. v. Ihering) in Cecropia (probably adenopus); Rio de Janeiro, in Cecropia adenopus; Alto Boa Vista, Rio (J. C. Bradley) in Cecropia; Alto Acre (E. Ule), in one of the Bombacæ.

VAR. WACKETI Emery


AZTECA OLITRIX Forel


Brazil: Jurua Miry, Jurua, Amazonas (E. Ule), in ant-gardens among Gesneriaceæ with galls; Para (J. Huber), in cauline swellings of Cordia sp.
AZTECA PITTIERI Forel

(Plate 55, fig. b)

Forel, Biol. Centr. Amer. Hymen 3, 1899–1900 p. 120 & Fig. 16.

Female (undescribed). Length 5—5.5 mm.

Head oblong, one and two-thirds times as long as broad, slightly narrower in front than behind the eyes where the sides are nearly straight and parallel, posterior border feebly excised. Eyes small and rather flat, as long as their distance from the anterior corners of the head, the posterior orbits in front of its middle. Ocelli small. Mandibles rather large, convex, elongate, with 8 teeth. Clypeus with a longitudinal flattening in the middle, somewhat swollen and advanced at the sides, the anterior border entire, nearly straight, the posterior suture indistinct. Antennal scapes reaching to two-thirds the distance between the posterior orbits and the posterior corners of the head; funiculus scarcely enlarged at the tip, first joint a little longer than broad, second as long as broad, remaining joints, except the last, subequal, distinctly broader than long. Thorax elongate-elliptical, through the wing-insertions as broad as the head; epinotum rounded and sloping, without distinct base and declivity; petiolar scale erect, acuminate but not very acute. Legs long, scarcely compressed.

Sculpture, much as in the worker; gaster and legs more shining and more finely punctate than the head and thorax; mandibles shining, sparsely punctate.

Hairs white, fine, not very long, but moderately abundant, erect on the body and appendages, sparser on the latter. Pubescence grayish and very fine, covering the body and appendages, most distinct on the head.

Black; anterior border of clypeus, apical borders of mandibles, except the teeth, tarsi and insertions of antennae, red; posterior borders of gastric segments brownish. Wings grayish hyaline, with yellow veins and dark brown pterostigma.

Small colonies of this species, originally described from Buenos Aires, Costa Rica (Pittier), were found nesting in the cauline swellings of Cordia alliodora along the Tumba Muerte Road near Las Sabanas, in the Panamanian Republic and along the Chivachiva Trail, near Red Tank in the Canal Zone. The species seems to be rare compared with A. longiceps. Its relation to this species is so close that it hardly deserves more than subspecific rank. The largest workers in my collection have the head somewhat more elongate and somewhat less narrowed in front than in Forel's figure.
Var. emarginatisquamus Forel


This variety, described from workers taken by Pittier in Costa Rica, in the cauline swellings of Cordia geracanthus, is distinguished from the type by having the petiolar scale emarginate at the summit, the eyes somewhat smaller, the legs a little more compressed and the head somewhat larger and broader behind in the major worker, with more convex sides.

Azteca prorsa sp. nov.

(Plate 56, fig. a)

Worker major. Length 2.5—3 mm.

Head somewhat depressed and flattened above and on the gular surface, one and one-half times as long as broad, narrower in front of the eyes, but behind them with straight, parallel sides, the posterior border rather deeply excised. Eyes small, flat, in front of the median transverse diameter of the head; ocelli absent. Mandibles rather small, convex, with 7-8 teeth. Clypeus convex in the middle and on the sides, its anterior border very feebly bisinuate, its posterior suture distinct. Frontal area and groove obsolete. Antennal scapes reaching to nearly two-thirds the distance between the eyes and the posterior corners of the head; funicular joints, except the first and last, somewhat broader than long. Thorax rather long, the mesonotum moderately convex, as long as broad; mesoepinotal constriction moderately deep, short, not very abrupt; epinotum as long as broad, its base and declivity sub-equal, the latter sloping but forming a distinct though rounded angle with the former. Petiole small, its scale inclined forward, narrow, elongate, elliptical, with blunt, rounded superior border. Gaster elongate-elliptical, the first segment short, truncated anteriorly. Legs rather long, feebly compressed, the fore femora somewhat dilated.

Mandibles shining, sparsely punctate; body and appendages densely and finely punctulate, shining, the legs somewhat less so than the body.

Hairs whitish, very delicate, erect, not very abundant on the upper surface of the body, shorter but distinct on the tibiae and especially on the scapes. Pubescence pale, fine and dilute, distinct on all parts of the body but only slightly dimming the shining surface.

Reddish brown; thorax, legs, anterior part of head, scapes, first
funicular joint and borders of gastric segments, paler; mandibles deep red, with black teeth; cheeks, anterior border of clypeus, and tarsi, except the terminal joint, yellowish.

Worker minor. Length 1.5—2.5 mm.

Head smaller than in the worker major, but with much the same proportions, slightly more narrowed anteriorly, the sides a little more rounded, the occipital border less deeply excised. The funicular joints are shorter and more transverse. Mesonotum more depressed, flatter and less projecting; mesoepipodal constriction less pronounced; petiolar scale proportionately thicker and more obtuse.

Sculpture, pilosity and color as in the worker major, but the mandibles have a large dark brown spot externally at the base.

Described from numerous specimens which I took during December 1911, at Escuintla, Guatemala, in the hollow twigs of Triplaris auriculata.

This form is closely allied to A. longiceps but is smaller, the head is longer, more deeply excised behind and with straight sides, the scapes shorter, the epinotum more sloping and less cuboidal, the hairs finer and less abundant.

Azteca sericea (Mayr)

Iridomyrmex sericeus Mayr, Sitzb. Akad. Wiss Wien 53, 1866 p. 498, fig. 8;

Mexico: (Heller), in pseudobulbs of the orchid Schomburgkia tibicinis. Also recorded from Guatemala (Stoll) and Cayenne (Forel).

I have taken workers and deïlated females of this species at Zent, Costa Rica, and at Patulul and Escuintla, Guatemala, in the internodes of young Cecropias.

The female resembles that of coeruleipennis Emery, but the head is more rectangular, although of the same proportions, the sides are more nearly straight, the posterior and anterior corners sharper, the posterior border more broadly and less deeply excised, the eyes less convex, the antennal scapes somewhat longer, the petiolar scale less acute above in profile, the femora broader. The surface is shining as in coeruleipennis, the mandibles subopaque, shagreened and sparsely punctate. The pale erect hairs are abundant but not very long, the pubescence very indistinct. Dark reddish brown, legs and antennæ paler; mandibles red; clypeus, bases of scapes and tarsi more yellowish red.
AZTECA SCHUMANNI Emery

Venezuela: Guainia River, an affluent of the Cassiquiare, in the leaf-sacs of *Hirtella guainiae* Hook fil.

AZTECA STANLEYULA Forel

Brazil: Para (J. Huber), in cauline swellings of *Cordia nodosa* L.

AZTECA TACHIGALLAE Forel

Peru: Cerro de Escaler, 1000 m. (E. Ule), in the hollow pетioles of an undetermined *Tachigalia*.

AZTECA THERESLAE Forel


This peculiar species was described and figured from three workers taken by Princess Theresa of Bavaria on the firewood of the steamer, while she was travelling on the Lower Magdalena River in Colombia. They were probably nesting in some myrmecophyte (*Triplanis*?). As all the specimens were of the same stature Forel was at first unable to decide whether they were major or minor workers. They evidently belonged to the former caste. In 1912 Forel described the following variety from workers taken by Christophersen on *Triplanis americana* in Panama. As it is one of the commonest ants on this tree I describe all four of its phases:

Var. MENCEPS Forel

(Plate 56, fig. b)


*Worker major.* Length 3——3.5 mm.
Head large, distinctly flattened, nearly one and one fourth times as long as broad, a little narrower in front than behind, with rounded sides, deeply and angularly excised posterior border and prominent, narrow and somewhat approximated posterior corners. Eyes small, flat, their posterior orbits just in front of the median transverse diam-
ETER of the head. Ocelli absent. Mandibles stout, convex, with 7-8 teeth, the two apical large, the others small, subequal. Clypeus convex in the middle and on the sides, its anterior border feebly bisinuate, its posterior suture feeble but perceptible. Frontal area obsolescent; frontal groove absent. Antennal scapes reaching to or a little beyond half the distance between the eyes and the posterior corners of the head; funicular joints 2-10 distinctly broader than long. Thorax stout, the mesonotum convex and projecting but not gibbous, subcircular; meso-epinotal constriction pronounced but short and abrupt; epinotum small and low, rounded and sloping, the base a little longer than the declivity into which it passes without a distinct angle. Petiolar scale small and thick, its upper margin narrowed, rounded and blunt. Gaster elliptical, less than twice as long as broad, the first segment short, truncated anteriorly. Legs, especially the femora, somewhat compressed and dilated.

Shining; mandibles sparsely, remainder of body more densely and more finely punctate, the punctures superficial and indistinct.

Pilosity yellowish, erect, not abundant, absent on the front and vertex, on the gaster confined to the posterior borders of the segments and the anterior truncated surface; shorter and finer on the head than on the thorax, absent on the appendages. Pubescence pale, very short and fine, covering the whole body like a delicate bloom but scarcely obscuring the shining surface.

Dark piceous brown; thorax often somewhat paler; mandibles deep red; clypeus anteriorly and laterally paler red; legs, funiculi and posterior borders of gastric segments brown, the tibiae and especially the tarsi paler and more testaceous.

*Worker minor.* Length 1.8—3 mm.

Proportions of the head very much as in the worker major, but smaller and somewhat more narrowed anteriorly, the basal joints of the funiculi much shorter and more transverse, the mesonotum much less convex and the petiolar scale somewhat blunter.

Sculpture, pilosity and color very similar, but the head and mandibles smoother and more shining; the pubescence less distinct.

*Female.* Length 4.8—5 mm.

Head resembling that of the worker major but nearly one and one-half times as long as broad, with less convex sides and much less deeply excised posterior border, narrower in front of than behind the eyes, the latter longer than their distance from the clypeus. Ocelli small. Antennæ much as in the worker major. Mandibles large and convex. Thorax through the wing-insertions as broad as the head; mesonotum
subhexagonal, narrowed in front. Petiolar scale strongly inclined forward, its very flat posterior surface elongate-elliptical, the superior border much less blunt than in the worker. Gaster elongate, paralleled.

Sculpture, pilosity and color as in the worker major, but the erect hairs on the thorax are decidedly less abundant, the pilosity is somewhat longer and the mandibles are black. Wings grayish hyaline, with dark brown veins and pterostigma.

*Male.* Length 2.8 mm.

Head, including the eyes, as broad as long, the eyes prominent, longer than half the sides, the ocelli prominent. Mandibles very small, but meeting with their acute tips. Clypeus convex. Antennal scapes as long as broad; first funicular joint twice as long as broad, remaining joints shorter. Thorax through the wing-insertions broader than the head; mesonotum large and protuberant, as broad as long; base and declivity of epinotum more distinct than in the worker and female. Petiole similar to that of the female but the scale is lower and erect.

Smooth and shining. Pilosity and pubescence very feebly developed. Piceous black; antennae and tarsi yellow; femora, tibiae and genitalia sordid or brownish yellow; wings grayish hyaline, with pale brown veins and pterostigma.

Described from many specimens taken at Ancon, Balboa, Fort Clayton, Miraflores and Las Cascades, C. Z., in the hollow twigs and branches of *Triplaris americana*.

I have referred my specimens to Forel’s var. *menceps*, described from the aforementioned workers taken by Christophersen, but they may belong to the typical form of the species. The differences mentioned by Forel are slight and their value somewhat dubious, owing to the small number of workers on which he based the species. I surmise that Mr. Christophersen may have taken his specimens either at Empire, where he lived (near Las Cascades), or while he was collecting with me in 1911 at the old town of Frijoles, which is now submerged.

**Azteca traili** Emery


Brazil: Amazonas (James Trail), probably in a myrmecophyte; Manaos, Amazonas (E. Ule), in leaf-sacs of *Tococa bullifera* Mart. &
Schr. Bom Fim, Jurua, Amazonas and São Joachim, Rio Negro (E. Ule), in ant gardens among Gesneriaceae.

British Guiana: Kartabo (Wheeler), in hollow petioles of Tachigalia paniculata Aubl.; Merumé Mouth (H. O. Lang) in the fistulose Patina formicaria Johnston (Rubiaceae). The specimens collected by Mr. Lang comprise several very small workers and a deëlated female. The former are very dark in color but this may be due to their belonging to an incipient colony. This seems to be the condition in several other species of Azteca (xanthochroa, muelleri, etc.), the workers growing paler as they increase in size in older colonies.

The female, taken by Mr. Lang, measures 7 mm. The head is scarcely longer than broad, broader behind than in front, with feebly rounded sides and slightly excised posterior border. The scapes reach nearly to the posterior corners of the head. The border of the petiolar scale is much compressed, produced upward and distinctly emarginate. The color is black, with the clypeus, cheeks, gula, antennae and tarsi brownish yellow, the mandibles red, the knees reddish. The surface is smooth and shining, but less so than in the worker, because the very fine pubescence is denser; the pilosity is like that of the worker, the scapes and legs with delicate erect hairs.

Forel described with some misgivings what he took to be the female of this species from Amazonas, but the head of his specimen was like that of alfari and this is certainly not like the head in my specimen or in the female of the following variety:

**Var. tillandsiarum var. nov.**

**Worker.** Length 2—3.4 mm.

Very feebly polymorphic. Differing from the typical *trailli* in having the head distinctly longer than broad in all the forms, the posterior border moderately and angularly excised, the antennal scapes extending even in the largest individuals one-fourth their length beyond the posterior border of the head. Eyes small, near the middle of its sides. Thorax with nearly straight dorsal outline, the mesoöpinotai impression very feeble, the mesonotum scarcely projecting even in large workers. Petiolar scale low, scarcely inclined forward, with acute upper border, the ventral surface much more convex than in the typical *trailli*.

Sculpture and pilosity as in the type. Pale reddish brown, thorax, petiole and posteronodal portion of gaster somewhat darker.

**Female.** Length 8.5—9.5 mm.
Head slightly longer than broad, gradually narrowed in front, broadest through the posterior corners which are rectangular, the posterior border slightly sinuate. Eyes small, as long as their distance from the anterior border of the head, their posterior orbits at its median transverse diameter. Mandibles convex, 8-toothed; clypeus with straight anterior border. Frontal area and groove obsolete. Antennal scapes not reaching the posterior border of the head, all the funicular joints distinctly longer than broad. Thorax rather robust, through the wing-insertions as broad as the head; epinotum sloping, evenly rounded, without distinct base and declivity. Petiolar scale higher than in the worker, its summit sharp, narrowed, compressed and produced upward. Gaster elongate-elliptical. Legs slender, feebly compressed.

Shining; finely punctate; mandibles very finely shagreened and coarsely and sparsely punctate.

Erect hairs delicate, abundant, rather short, uniform over the head, thorax and abdomen, shorter and somewhat less numerous on the scapes and legs. Pubescence dilute, longest and most distinct on the gaster.

Black; mandibles red, with black teeth; clypeus, cheeks, gula, antennal foveae, antennae, tarsi, tips of tibiae, knees, posterior borders of gastric segments and their ventral sclerites, except at the base, brownish yellow. Wings yellowish, with brown veins and dark brown pterostigma.

Described from numerous specimens which were nesting in flourishing and very aggressive colonies in large clusters of Tillandsias growing on mangroves along the Cuyuni River, near the Tropical Laboratory of the New York Zoological Society at Kartabo, British Guiana.

**Subsp. tococe Forel**


Brazil: Jurua Miry, Jurua, Amazonas (E. Ule), in the leaf-sacs of *Tococa guianensis* Aubl.

Bolivia: Tumupasas (W. M. Mann), in leaf-sacs of *Tococa* sp.

**Var. elatior Forel**

Forel, Ann. Soc. Ent. Belg. 50, 1906 p. 239 § ♂️

Brazil: Bom Lugar, Rio Purus (J. Huber), in the petiolar sacs of a *Tococa*.

Peru: Iquitos and Putumayo (J. C. Bradley), in the leaf-sacs of a *Tococa*. 
AZTECA TRIGONA Emery
A colony of this ant was found near Las Cascades, C. Z. inhabiting all the cauline swellings of a young Cordia alliodora and attending numerous coccids on the stems and petioles, about which fragile carton shelters had been built. The species usually makes large pendent carton nests on the branches of various trees.

AZTECA TONDUII Forel
Costa Rica: (Tonduz) in the pseudobulbs of an orchid.

Subsp. MATHILDEAE Forel var SPURIA Forel
British Guiana: Kartabo and Kalakoon (Wheeler), inhabiting the internodes of Cecropia.

Subsp. MEDIOPS Forel
British Guiana: Kartabo (Wheeler), in Cecropia angulata Bailey.

AZTECA ULEI Forel
Brazil: Jurua Miry, Jurua, Amazonas (E. Ule), in “ant gardens” among Gesneriaceae.

Var. CORDIAE Forel
Brazil: Marary, Jurua, Amazonas (E. Ule), in the cauline swellings of Cordia nodosa L.
British Guiana: Kartabo and Kalacoon (Wheeler), in cauline swellings of Cordia nodosa L.
Bolivia: Rio Negro and Tumupasas (W. M. Mann), in cauline swellings of Cordia hispidissima.
The series from British Guiana comprise many workers and three
deñulated females. The latter (undescribed) measure 7-8 mm. and have
the head if anything slightly broader than long, with straight, sub-
parallel sides behind the eyes and also with parallel sides in front of
the eyes, though the head is here much narrower; the posterior border
being angularly excised. Eyes rather large, convex, broadly elliptical,
about one-half their length from the anterior corners of the cheeks.
Lateral borders of clypeus swollen. Antennæ stout, scapes not reaching
to the posterior border of the head; first and second funicular joints
longer than broad, remaining joints, except the last, as broad as long.
Thorax robust, somewhat more than twice as long as broad, epinotum
rounded and sloping, more abruptly at its posterior end. Petiolar scale
convex in front, concave behind, with rather sharp superior border, the
ventral portion protuberant and somewhat compressed. Gaster ellipti-
tical, about twice as long as broad, the first segment narrowed an-
teriorly. Legs long and stout.

Shining; mandibles sparsely and sharply punctate; punctuation of
the body very fine, dense and superficial.

Pilosity yellow, short, rather abundant; oblique hairs numerous on
tibiae, few on scapes. Pubescence distinct only on the clypeus.

Black; mandibles deep red, with black teeth; corners of clypeus,
funiculi, bases of scapes, tarsi, except at the base, brownish yellow.
Wing-insertions pale sordid yellow.

Var. gagatina Wheeler and Mann var. nov.

Worker minor. Length 2.3 mm.

Differing from the other forms of ulei in sculpture and color, being
smooth and shining and jet-black, with the apical borders of the man-
dibles, except the teeth, the lateral corners of the clypeus, the inser-
tions of the antennæ, the antennal foveæ and terminal tarsal joints
reddish yellow. The petiolar scale is low, with rather blunt summit,
the mesonotum moderately convex.

Three specimens taken by Dr. W. M. Mann at Rurrenabaque,
Bolivia, in a cauline swelling of Cordia hispidissima.

Var. gibbifera Forel


Originally described from São Paulo, Brazil (H. v. Ihering). A num-
ber of workers, taken by Dr. W. M. Mann at Tumupasas, Bolivia in
the cauline swellings of Cordia hispidissima, are referable to this
variety.
Subsp. nigricornis Forel


Brazil: Cachoeira, Jurua, Amazonas (E. Ule), in cauline swellings of *Cordia nodosa* L.

Subsp. rossi Forel

Forel, Deutsch. Ent. Zeitschr. 1909 p. 251 §.

Mexico: (Ross), in ant-gardens among the roots of orchids.

_Azteca velox_ Forel


Panama: Ancon, C. Z. (Wheeler), attending coccids on young *Cordia gerascanthus* trees; Las Cascades (Wheeler), living in twigs and branches of *Triplaris cumingiana*.

Guatemala: Patulul (Wheeler), nesting in trunk of *Acacia hindsii* Benth.

Costa Rica: Alajuela (Wheeler), nesting in Tillandsias.

Subsp. nigriventris Forel


Brazil: Bom Lugar, Rio Purus (A. Goeldi and J. Huber), in cauline swellings of *Cordia nodosa* L.


Panama: Balboa (Wheeler), nesting in the fistulose stems of *Clerodendron siphananthus* (introduced from the Orient).

_Azteca virens_ Forel


Brazil: Parà, Amazonas (A. Goeldi), living in the green stems of a plant (undetermined).

_Azteca xanthochroa_ (Roger)

(Plate 57, fig. a)

Mexico: (type locality); Teapa in Tabasco (H. H. Smith); Zacualpan (H. Ross), in Cecropia mexicana Hemsl.; Palomares (A. Petrunkewitch).

Honduras: Puerto Castilla (J. Bequaert), in Cecropia sp.

Guatemala: Las Mercedes 3000 ft. (Champion); Quirigua, Escuintla and Puerto Barrios (Wheeler), in internodes of young Cecropias; Trece Aguas, Alta Vera Paz (Schwarz and Barber).

Costa Rica: (A. Alfaro), in Cecropias.

The singular yellow female of this species was described by Roger from Mexico in 1863. Mayr in 1886 described what he took to be the conspecific worker, but which Emery claims was A. instabilis Sm. var. mexicana Emery. I find that I have also misidentified the worker of xanthochroa, for my record from Coroni, Trinidad (Amer. Mus. Novitates 45, 1922 p. 15), as I find from rereexamination of the specimens, refers instead to A. delpini subsp. trinidadensis Forel. In 1896 Emery assigned workers taken by Alfaro in Costa Rica to xanthochroa, but a study of materials which I collected in Guatemala in 1911 shows that although his specific allocation is correct, these workers must belong to a distinct variety. I have frequently taken dilated queens of the typical xanthochroa accompanied by young colonies of workers in the internodes of Cecropias at Quirigua and Puerto Barrios, Guatemala, and these workers are different in several significant particulars from those described by Emery. Though the largest individuals approach the pale flavotestaceous color which he describes, the medieæe and minimææ are all much darker, being dark brown. The color shows a gradual gradation from the smallest to the largest individuals. The head of the major is broader, as broad as long, distinctly narrower in front than behind and the scapes reach to the posterior corners of the head and in the minor workers further beyond these corners than in Emery's figure. Since there is no doubt that the Guatemalan workers belong to the true xanthochroa I believe one must regard Emery's workers as representing a distinct variety. I suggest that it be called var. costaricensis var. nov.

Concerning this variety Emery states on the authority of Alfaro that it differs from the other Cecropia Aztecas. It habitually runs with its gaster elevated. The opening of the nest is a longitudinal fissure in the Cecropia internode. It constructs carton septa across the internodal cavities. It is less aggressive than the other species and does not bite the hands of the collector.

I find in my collection specimens of three additional subspecies of xanthochroa, which are here described.
Subsp. australis subsp. nov.

Female. Length 10.5—11 mm; wings 10 mm.

Slightly larger than the female of the typical *xanthochroa* and differing in the following characters: Head much more narrowed behind, where it is scarcely broader than in front, the mandibles more flattened and more deflected at the tips, more shining and more coarsely punctate and without striae. Surface of body and especially the head, more shining. Color yellow, resembling that of the typical *xanthochroa* but the brown spot on the head is more extensive, there are usually three longitudinal brown streaks on the mesonotum, the bases of the gastric segments are brown, the antennal scapes blackish, the funiculi yellow, the mandibles deep red, with blackish borders, the anterior border of the clypeus infuscated, the legs reddish, the tibiae darker, the fore tibiae and all the basi tarsi blackish; the wings as in the type, brownish yellow, with resin yellow veins and dark brown pterostigma. I can detect no significant differences in pilosity and pubescence.

Described from three specimens from Songo, Bolivia (type locality), and two from Callanga, Peru, purchased from Staudinger and Bang-Haas.

Subsp. isthmica subsp. nov.

Worker. Length 2—4 mm.

Very similar to the minor worker of the typical form of the species and of the same dark brown color, but the mandibles and anterior portion of the head are more yellowish. The antennae are distinctly shorter, the scapes surpassing the posterior corners of the head to a noticeably less extent and the funicular joints broader in proportion to their length. The terminal funicular joints are blackish, the petiolar scale a little higher and more compressed anteroposteriorly, the pubescence, especially on the head, more abundant and more conspicuous.

Female. (deêlated) Length 6.5 mm.

Much smaller than the female of the typical *xanthochroa* which measures 9-10 mm. Head decidedly shorter, with more convex eyes and shorter antennae; sides behind the eyes are more convex, the excavation of the posterior border less pronounced. Joints 3-10 of the funiculi distinctly broader than long, the first and second joints distinctly shorter in proportion to their length than in the typical *xanthochroa*. The petiolar scale is lower and less pointed above. Body smoother and somewhat more shining; mandibles, however, subopaque
and more sharply striate. The color is the same but the body is a shade paler, there is no brown spot on the head and the scapes and first funicular joint are yellow. The hairs on the body are blackish.

Described from a dozen workers and a single female, constituting an incipient colony which I found nesting in an internode of a young *Cecropia* near the source of the Rio Agua Salud, C. Z., Panama. To the same subspecies belong a number of workers which I took in young Cecropias at Culebra and Monte Sirio, C. Z., during November 1913, and a number of females taken on Barro Colorado Island, C. Z., in 1924.

**AZTECA XANTHOCHROA subsp. SALTI subsp. nov.**

*Worker minor.* Length 2.5 mm.

Smotherer and more shining than the typical *xanthochroa* or the subsp. *ishmica*, the thorax, gaster, antennæ and legs being deep castaneous brown, the head black, the mandibles and corners of the clypeus red. Pilosity shorter and less abundant, especially on the head. Antennal scapes extending a distance more than their greatest diameter beyond the posterior corners of the head.

*Female:* (deálated). Length 10-12 mm.

Head even longer and narrower than in the subsp. *australis*, especially behind, with nearly straight sides, more flattened eyes and deeper occipital excision. Surface much smoother and more shining than in either the typical form or the other subspecies. Thorax and gaster somewhat darker, more reddish yellow; head, antennæ and femora red, the clypeus and mandibles deep red; tubæ and metatarsi blackish red. Hairs on the body and tubæ blackish, longer and more abundant than in *australis*, appressed pubescence on the gaster long and yellowish.

Described from five workers and nine females taken by Dr. George Salt from the internodes of young Cecropias at Vista Nieve, Sierra Madre de Santa Marta, Colombia, at an altitude of 5,000 feet.

**Genus TAPINOMA Foerster**

**TAPINOMA ATRICEPS Emery**


Brazil: São Paulo (A. Lutz), nesting in bamboos.

**Var. BREVISCAPA Forel**


Brazil: São Paulo (A. Lutz), nesting in bamboos.
Tapinoma canalis sp. nov.

Worker. Length 1—1.2 mm.

Head subrectangular, longer than broad, as broad in front as behind, with very feebly convex sides, straight posterior border and rounded posterior corners. Eyes small, flat, placed about one and one-half times their length from the anterior corners of the head. Mandibles narrow, with oblique apical borders, armed with six teeth, the first, second and fourth from the tip larger, the others minute. Frontal carinae short, parallel, further apart than their distance from the sides of the head. Clypeus convex and rounded in the middle, the anterior border straight and entire. Frontal area and groove absent. Antennal scapes not reaching the posterior corners of the head by a distance equal to their greatest diameter; first funicular joint nearly one and one-half times as long as broad, second joint short and small, broader than long, remaining joints, except the last, all broader than long, but increasing in length and breadth distally. Thorax small, feebly but distinctly impressed at the mesoöpinotal suture, the dorsal outline otherwise slightly convex, the base of the epinotum straight, forming a distinct obtuse angle with the declivity, which is decidedly longer than the base. Seen from above the pronotum is nearly twice as broad as long, the mesonotum subcircular and about as long as broad, the epinotum slightly longer than broad and laterally compressed. Petiole very small and flat, longer than broad, its scale represented by a low, semicircular swelling at its anterior end, completely concealed under the large first gastric segment. Gaster elliptical. Legs of the usual shape.

Shining, very finely and indistinctly punctate.

Hairs and pubescence pale yellow, the former very sparse, distinct only on the clypeus, mandibles and gastric segments; the pubescence rather dense, somewhat obscuring the shining surface, rather long and oblique on the scapes.

Pale brownish yellow; legs scarcely paler; mandibular teeth reddish.

Female. (deïlated) Length 1.8 mm.

Head much as in the worker but the posterior corners less rounded and the posterior border very feebly excised, the eyes larger and more convex, only about half their length from the anterior corners. Scapes shorter, extending about two-thirds the distance between the eyes and posterior corners of the head. Thorax slightly narrower than the head, elongate subelliptical, depressed above; pronotum very short and transverse; mesonotum as long as broad, rounded in front; epinotum short, with very short base, passing gradually into the long sloping
declivity. Petiole as in the worker. Gaster elongate, more than three times as long as broad, parallel-sided, first segment covering the petiole and provided with a very distinct impression for its accommodation. Subopaque and more densely punctate than the worker. Pilosity and pubescence very similar; head and thorax pale yellowish brown; gaster dark brown; mandibles, antennae, legs and broad margins of the gastric segments brownish yellow.

Male. Length about 8 mm.

Head subrectangular, longer than broad, somewhat narrowed behind. Eyes flattened about half as long as the sides of the head. Mandibles well-developed, overlapping with their very minutely denticulate apical borders. Clypeus with straight, transverse anterior border. Antennal scapes reaching to the posterior corners of the head; basal funicular joints slightly, terminal joints considerably longer than broad. Thorax as broad as the head. Petiole very much as in the worker. Gaster short.

Sculpture and pilosity like those of the worker. Color pale sordid yellow. Wings grayish pubescent, rather opaque, with pale brownish veins.

Described from the members of a single colony inhabiting a cauline swelling of Cordia alliodora on Barro Colorado Island in Gatun Lake, C. Z., Panama.

This very small species seems to be quite distinct from any of the indigenous neotropical species of Tapinoma, such as atriceps Emery, heyeri Forel, littorale Wheeler and ramularum Emery.

**Tapinoma melanocephalum** Fabr.

Colonies of this widely distributed tropicopolitan ant were found nesting in the twigs of Triplaris americana at Balboa, C. Z. Panama.

**Tapinoma ramularum** Emery

subsp. *inrectum* Forel

Guatemala: Escuintla (Wheeler), nesting in twigs of *Triplaris auriculata*.

**Tapinoma littorale** Wheeler


Florida: Card's Point (Wheeler), nesting in Tillandsias.

Var. cubænsis Wheeler


Cuba: (Wheeler), nesting in Tillandsias.

Subfamily FORMICINAE

Genus PRENOLEPIS Mayt

Prenolepis (Paratrechina) longicornis Latr.

Panama: Ancon, C. Z. (J. Zetek), attending aphids on foliage of Cordia alliodora.

Prenolepis (Nylanderia) fulva Mayt


Brazil: San Joãquim, Rio Negro, Amazonas (E. Ule), nesting in Tillandsia paraënsis Metz.

Genus Brachymyrmex Mayt

Brachymyrmex heeri Forel

Wheeler, Zoologica 3, 1921 p. 166 𐀣 𐀣.

British Guiana: Kartabo (Wheeler), in hollow petioles of Tachigalia paniculata Aubl., in cauline swellings of Cordia nodosa.

Var. basalis Wheeler


British Guiana: Kartabo (Wheeler), in hollow petioles of Tachigalia paniculata Aubl.

Var. obscurior Forel

Panama: Ancon, C. Z. (Wheeler), attending coccids on the foliage of seedling Cordia alliodora; Balboa C. Z., (Wheeler), nesting in the twigs and running on the trunks of Triplaris americana; Tumba Muerte Road, near Las Sabanas (Wheeler), nesting in the thorns of Acacia penonomensis Saff.

Brachymyrmex pictus Mayt

subsp. balboæ subsp. nov.

Worker. Length 1—1.2 mm.
Smaller than the typical form from Brazil, the scapes shorter, ex-
tending scarcely one-fourth their length beyond the posterior corners of the head. Honey yellow, the antennae and legs whitish yellow; the gaster black on the dorsal side, with a broad pale yellow area embracing the posteromedian portion of the first segment and the median portion of each of the succeeding segments.

Female. Length 2.5 mm.
Smaller than the typical form of the species. Ocellar triangle black; a brown spot on the posterior portion of the mesonotum and the gaster dark brown above, with the posterior borders of the segments yellow. Wings long, colorless, with colorless veins and pterostigma.

Male. Length 0.8—1 mm.
Scapes reaching to the posterior ocelli. Head with the eyes slightly broader than long, rounded rectangular. Eyes elongate, about-two-thirds as long as the sides of the head, not very convex. Mandibles very slender. Whitish yellow; top of head and gaster, except its last segments, brown; antennal funiculi slightly infuscated at the tip. Wings as in the female.

Several colonies of this pretty form were found nesting in hollow twigs of Triplaris americana at Balboa, C. Z. Panama.

Genus Myrmelachista Roger

Myrmelachista ambiguа Forel
subsp. ramulorum Wheeler


Porto Rico and Culebra Island (Wheeler), in twigs of seagrape (Coccoloba uvifera) and "torchuelo" (Bucida buceros)
Costa Rica: Alajuela (Wheeler), in Tillandsias.

Myrmelachista (Decamera) bambusarum Forel


Brazil: Corcorado, Prov. Rio Janeiro (Goeldi), in small branches of bamboo.

Myrmelachista (Decamera) nigella Roger


Brazil: Bocca do Tejo, Jurua, Amazonas (E. Ule), in the twig swellings of Duroia hirsuta H. Sch.
MYRMELACHISTA (Decamera) nodigera Mayr

var. flavicornis Emery


Paraguay: San Salvador (J. Bohls), in woody thorns of Acacia (probably cavenia).

MYRMELACHISTA (Decamera) paderewskii Forel


Brazil: São Paulo (E. Lutz), nesting in bamboo.

MYRMELACHISTA (Decamera) schumannii Emery


Colombia: (K. Schumann), in cavities of Duroia hirsuta.

Var. cordincola Wheeler & Mann, var. nov.

Worker. Length 1.5—3 mm.

Averaging somewhat larger than the typical form of the species and differing in color. Brownish yellow, with the head and gaster brown, the latter usually darker than the former, the bases of the gastric segments paler than their posterior borders which are edged with black. Mandibles and anterior portion of head paler and more yellowish than the posterior portion. Antennae and legs yellow, the clubs of the former and in some specimens also the middle portions of the femora feebly infuscated. Summit of petiolar node entire, its anterior surface distinctly convex, its posterior surface nearly flat.

Described from numerous specimens taken by Dr. W. M. Mann at Osunto, Bolivia, in the cauline swellings of Cordia hispidissima.

MYRMELACHISTA (Decamera) ulei Forel


Peru: Cerro de Escaler, 1200 m. (E. Ule), in the swellings of the flower stems of a melastomaceous plant.
MYRMELACHISTA (Decamera) zeledoni Emery
Costa Rica: San Jose and Cartago (Wheeler), in Tillandsias. This species was also found nesting in dead twigs in the same localities. Recorded also from Colombia (Forel).

Genus Camponotus Mayt
Camponotus (Tanaemyrmex) bonariensis Mayt
Paraguay: San Bernardino (K. Fiebrig in litteris), occasionally nesting in Cecropia peltata L.

Camponotus (Myrmoturba) melanoticus Emery var.
Hagmanni Forel
British Guiana: Kartabo (Wheeler), nesting in large branches of Cecropia sciadophylla var decurrans Sn.
Costa Rica: Alajuela (Wheeler), nesting in Tillandsias.

Camponotus (Myrmoturba) ulei Forel
Peru: Cerro de Escaler, 1300 m. (E. Ule), in the hollow internodes of Cecropia montana Warb. (Ule No. 6845)

Camponotus (Myrmothrix) abdominalis Fabr.
Var. costaricensis Forel
Costa Rica: Alajuela (Wheeler), nesting in Tillandsias.

Var. between subsp. esuriens and var.
Mediopallidus Forel
Mexico: Cuernavaca (Wheeler), nesting in Tillandsia benthamiana.

Camponotus (Myrmothrix) femoratus Fabr.
Brazil: Manaos (E. Ule), in ant gardens among *Streptocalyx* and *Codonanthe*.

British Guiana: Kartabo (Wheeler), in ant gardens in parabiosis with *Crematogaster limata* Sm. subsp. *parabiota* Forel.

**Camponotus (Myrmothrix) Lutzi** Forel


Brazil: São Paulo (E. Lutz), nesting in bamboos.

**Camponotus (Myrmothrix) Rufipes** Fabr.

Subsp. *ringgeri* Emery

Paraguay: San Bernardino (K. Fiebrig *in litteris*), occasionally nesting in *Cecropia peliata* L.

**Camponotus (Neomyrmampley) Novogrenadensis** Mayr

A small colony of this ant was taken at Quebrada de Oro, C. Z., Panama, from the cavity of a cauline swelling of *Cordia alliodora*. The cavity also contained the remains of small narrow puparia of a species of *Microdon*. This ant nests much more frequently under bark and especially in the abandoned galleries of termitaria. In the latter situations, I have frequently found considerable numbers of the same *Microdon*.

**Camponotus (Myrmobrachys) Brettesi** Forel

Taken on several occasions in the cauline swellings of *Cordia alliodora* near the laboratory at Ancon, C. Z. It is more frequently found nesting in dead twigs, as Forel observed in Colombia.

**Camponotus (Myrmobrachys) Brevis** Forel

Not uncommon at Frijoles, Red Tank and Las Cascades, C. Z., in the cauline swellings of *Cordia alliodora*. Along the Tumba Muerte Road, near Las Sabanas, Panama, I found several colonies nesting in the thorns of *Acacia penonomensis* Saff. In 1911 I found this ant nesting in Tillandsias on Otouque and Tabogilla Island, Panama. The female measures 6—6.5 mm. and resembles the worker major. The wings are grayish hyaline, with resin-yellow veins and pterostigma. The male measures 3.5—3.8 mm. and is black, moderately shining,
with yellow tips to the mandibles. The wings are yellowish hyaline, with the veins and pterostigma paler than in the female. As Forel observed in Colombia, *C. brevis* is most abundant in dead twigs.

**Camponotus (Myrmobrachys) canescens Mayr**

A few small colonies were found nesting in cauline swellings of *Cordia alliodora* on Barro Colorado Island, in Gatun Lake, C. Z.

**Camponotus (Myrmobrachys) lindigi Mayr**

Running up and down the trunks and attending coccids on the foliage of *Triplaris americana* at Balboa, C. Z. and of *Cordia alliodora* near the laboratory at Ancon, and nesting in the ground about the roots of these same trees.

**Camponotus (Myrmobrachys) planatus Roger**


Vari. *continentis* Forel


Florida: Card’s Point (Wheeler), nesting in Tillandsias.

Costa Rica: Alajuela, etc. (A. Alfar): living in *Acacia* thorns abandoned by *Pseudomyrmex*; Alajuela (Wheeler) nesting in Tillandsias.

Guatemala: Zacapa, Quirigua, Escuintla and Patulul (Wheeler), living in thorns of *Acacia hindsii*.

Both this variety and the typical *planatus* also live under bark and in dead twigs.

**Camponotus (Myrmobrachys) pittieri Forel**

var. *poenalis* Wheeler


British Guiana: Kartabo (Wheeler), in hollow petioles of *Tachigalia paniculata* Aubl.

**Camponotus (Myrmobrachys) vezenyi Forel**

Paraguay: San Bernardino (K. Fiebrig *in litteris*), occasionally in *Cecropia peltata* L.
Camponotus (Myrmobrachys) zoc Forel

Wheeler, Zoologica 3, 1921 p. 167 #.

British Guiana: Kartabo (Wheeler), in hollow petioles of Tachigalia paniculata Aubl.

Camponotus (Myrmocladoecus) bidens Mayt

A single colony found nesting in a cauline swelling of Cordia alliodora on the Chivachiva Trail, near Red Tank, C. Z., Panama. This species and its allies more frequently nest in dead twigs.

Camponotus (Myrmocladoecus) mucronatus Emery

Costa Rica: Alajuela (Wheeler), nesting in Tillandsias.

Camponotus (Myrmocladoecus) striatus F. Smith

Subsp. alfaroi Emery

Several colonies of this subspecies were found nesting in thorns of Acacia penonomensis Saff. along the Tumba Muerte Road, near Las Sabanas, Panama. The female measures 4—4.5 mm. and has the thorax subopaque and coarsely shagreened above and finely striated on the sides. The petiolar scale is broader and thicker than in the worker. The wings are yellowish hyaline, with yellow veins and dark brown pterostigma. The male is very small, measuring only 3—3.2 mm., and is shining black throughout, except the wings, which are whitish, with paler veins and pterostigma than in the female.

This ant more frequently nests in dead twigs, as Forel observed in Colombia.

Camponotus (Myrmocladoecus) rectangularis Eméry


Costa Rica: (A. Alfaro), in thorns of Acacia.

Var. rubroniger Forel


Mexico: Cuernavaca (Wheeler), nesting in Tillandsia benthamiana.
Camponotus (Paracolobopsis) patimae sp. nov.

(Plate 57, fig. b)

Worker major. Length 6—7 mm.

Allied to salwini Forel and especially rudigenis Emery. Head large, thick, convex, subrectangular, about one and one-fifth times as long as broad, about as broad in front as behind, with nearly straight sides and broadly but not deeply excised posterior border, the cheeks swollen and projecting anteriorly beyond the clypeus, which is longer than broad, nearly parallel-sided, convex in the middle and narrowly carinate anteriorly. Frontal area very small, triangular. Frontal groove distinct; frontal carinæ approximated in front, sigmoidal in the middle, straight and parallel behind. Eyes rather small and flat, at the posterior third of the head. Mandibles short, very convex, with four large subequal teeth. Antennal scapes slender, compressed, curved, somewhat thickened at the tips which reach to the posterior corners of the head. Thorax broad through the pronotum, which is flattened above, submarginate on the sides, rapidly narrowing posteriorly to the epinotum, which is compressed and tectiform. The promesonotal suture is very distinct, the mesoepinotal suture nearly obsolete. In profile the whole thoracic dorsum is very evenly arcuate, though the outline of the epinotum really consists of three subequal, nearly straight lines. Petiolar scale rather thick, oval, broader above than below, beveled at the summit, with flat posterior surface, the superior border rounded, entire and rather blunt. Gaster elongate, elliptical. Legs long and stout, the fore femora somewhat enlarged.

Opaque; only the mandibles and posterior corners of the head somewhat shining. Mandibles finely punctate; head more coarsely and densely, the cheeks and clypeus also covered with shallow piligerous foveolæ. Remainder of body and the appendages very finely and densely punctulate.

Hairs golden yellow, erect or suberect, moderately long and abundant on the front, thorax, petiolar border and gaster, on the cheeks and clypeus short, stout and blunt. Legs with short, appressed hairs, scapes finely pubescent. Thorax and gaster with long, hair-like pubescence, not sufficiently dense to conceal the surface or forming a pelt as in salwini.

Ferruginous red; vertex of head, pleura, rarely the dorsal surface of the epinotum, dorsal border of petiole, more rarely the whole scale, and gaster, except the bases of the segments, black. The posterior borders of the gastric segments are dull yellowish. Fore coxae and all
the femora more yellowish ferruginous, their bases, the knees, tibiae, tarsi and antennae dark brown.

*Worker minor.* Length about 4.5 mm.

Head longer than in *rudigenis*, distinctly longer than broad, with straight, subparallel sides and somewhat larger and more prominent eyes, but the latter connected with the posterior corners of the head by distinct ridges and the posterolateral surfaces of the head concave as in that species. Antennal scapes longer, very thin, extending about half their length beyond the posterior corners of the head. Thorax and petiole resembling those of the worker major, but the head is not more coarsely punctate than the remainder of the body. The whole surface is a little more shining or lustrous.

Pilosity much as in the worker major.

Black; mandibles yellow; sides of head below the eyes, a spot on each side of the pronotum, a streak on each side of the epinotum, the ventral portion of the petiole, and base of first gastric segment, ferruginous. Appendages colored as in the worker major.

*Male.* Length 4.5—5 mm.

Head with a trace of the worker's postocular carina on each side. Eyes very prominent. Mandibles rather well developed, with four small teeth. Antennae long and slender. Thorax robust, much broader than the head, the mesonotum from above nearly as broad as long. Petiolar scale low, its upper border transverse, blunt, broadly excised in the middle.

Sculpture like that of the worker minor, subopaque, but the gaster more shining.

Pilosity and pubescence also similar but white and of more uneven length.

Black; mandibles, anterior border of clypeus and insertions of antennae ferruginous yellow; thorax of the same color, but pleura and epinotum spotted with dark brown and mesonotum with three broad dark brown streaks, the median abbreviated behind. Genital appendages yellow. Legs yellowish brown, tibiae, tarsi and a streak along the extensor surface of each femur dark brown. Wings yellowish hyaline, with resin-yellow veins and pterostigma.

Described from four major workers, one minor worker and four males taken by Mr. H. O. Lang on Merumé Creek, British Guiana, in the fistulose stems of *Patima formicaria* Johnston (Rubiaceae).

This species is, perhaps, only a subspecies of Emery's *rudigenis* from Venezuela, Peru and Brazil, but his description is very brief and I have seen no specimens. The head of the worker minor compared
with his figure certainly shows important differences. The color is very different, but in this respect the following variety agrees more closely with Emery’s species. Moreover, there is considerable color variation in both the series of specimens.

**Var. doleentulus var. nov.**

*Worker major.* Length 5—5.5 mm.

Very similar to the preceding form but smaller and differing in the following particulars: The posterior corners of the head are more extensively shining, the color is black, with the mandibles, gula and borders of the head deep ferruginous red; the legs are brownish yellow, with the extensor surfaces of the femora and tibiae and the bases of the femora black, the tarsi dark brown. The posterior borders of the gastric segments are more sordid yellow. The hairs are white and the pubescence is conspicuously shorter on the thorax and gaster and the surface of these regions is somewhat less opaque and more lustrous.

*Worker minor.* Length 3.5—3.8 mm.

Also smaller than the worker minor of the typical form, of the same color as the worker major, but with the sides of the pronotum, a spot at the base of the first gastric segment and in some specimens a streak on each side of the epinotum reddish.

Described from six major and six minor workers taken by Mr. Lang in the same locality and in the same species of Rubiaceae as the preceding form.

**Camponotus (Hypercolobopsis) christophersenii** Forel


Panama. Mamei (Christophersen), nesting in the spines of *Xanthoxylon* (panamensis P. Wilson).

**Camponotus (Hypercolobopsis) paradoxus** Mayr

subsp. *Janitor* Forel


Brazil: São Paulo (E. Lutz), nesting in bamboo.
EXPLANATIONS OF PLATES
PLATE 1
PLATE 1

PLATE 2


PLATE 3


WHEELER — Neotropical Ant-Plants and their Ants.

PLATE 4


PLATE 5

PLATE 6


b. *Cordia alliodora* R. and P. Ancon, C.Z., Panama. Section of very old swelling, showing large black coccids. Photograph by J. Zetek.
PLATE 7


WHEELER. ANIMAL PLANTS AND THEIR ANTS. PLATE 7
PLATE 8

PLATE 9

Larva and cocoons of Conchylodes salamisalis Druce, and leaves of Cordia alliodora R. and P. attacked by this pyralid. Ancon, C.Z., Panama. Photograph by J. Zetek.
PLATE 10


e. Pellet fed by the ants of *Triplaris surinamensis* to the larvae, showing pieces of coccids. Photomicrograph by I. W. Bailey.

f. Hyphae growing on the inner walls of the pouches of *Triplaris surinamensis*. Photomicrograph by I. W. Bailey.
PLATE 12


PLATE 13


WHEELER — Neotropical Ant-Plants and their Ants.

PLATE 14

PLATE 15

*Acacia bucerophora* Robinson. Photograph of type in Gray Herbarium by W. E. Safford.
PLATE 16

Acacia bursaria Schenck. Tucuman, Guatemala. Photograph by W. E. Safford.
PLATE 18

*Acacia cochliacantha* Humb. and Bonpl. (*=*campecheana* Schenck). Rosario Sinaloa, Mexico. Photograph by W. E. Safford.
PLATE 19

PLATE 20

Acacia Collinsii Safford (=yucatanensis Schenck). San Sebastian, Chiapas, Mexico. Photograph by W. E. Safford.
PLATE 21

*Acacia Collinsii* Safford (= *yucatanensis* Schenck). Chiapas, Mexico. Photograph by W. E. Safford.
WHEELER — Neotropical Ant-Plants and their Ants.

PLATE 22

PLATE 23

*Acacia Cookii* Safford. Alta Vera Paz, Guatemala. Photograph by W. E. Safford.
PLATE 24

*Acacia Cookii* Safford. Alta Vera Paz, Guatemala. Photograph by W. E. Safford.
PLATE 25


PLATE 26

PLATE 27

PLATE 28

Acacia cornigera L. Green house plant grown from seed, Washington, D. C. Photograph by W. E. Safford.
PLATE 29


b. *Acacia cornigera* L. Photograph of type of *Acacia spadicigera* Schl. and Cham., in Halle Herbarium.
PLATE 30


WHEELER — Neotropical Ant-Plants and their Ants.

PLATE 31

*Acacia dolichocephala* Safford. North of city of Vera Cruz, Mexico. Photograph by W. E. Safford.
PLATE 32

PLATE 33


PLATE 34

Acacia Hindsii Bentham. Acapulco, Guerrero, Mexico. Photograph by W. E. Safford.
WHEELER — Neotropical Ant-Plants and their Ants.

PLATE 35

Acacia Hindsii Bentham. Manzanillo, Colima, Mexico. Photograph by W. E. Safford.
PLATE 36

*Acacia Hindsii* Bentham (=*tepicana* Safford). Type of *tepicana*, from Tepic, Mexico. Photograph by W. E. Safford.
PLATE 37

a. *Acacia melanoceras* Beurling (=*multiglandulosa* Schenck). Marajal near Colon, Panama. Photograph by D. Fairchild.

b. *Acacia melanoceras* Beurling (=*multiglandulosa* Schenck). Marajal near Colon, Panama. Photograph by J. Zetek.
PLATE 38

a. *Acacia melanoceras* Beurling (=*multiglandulosa* Schenck). Marajal near Colon, Panama. Photograph by J. Zetek.

b. *Acacia melanoceras* Beurling (=*multiglandulosa* Schenck). Marajal near Colon, Panama. Photograph by D. Fairchild.
PLATE 39

Acacia Nelsonii Safford. Acapulco, Guerrero, Mexico. Photograph by W. E. Safford.
PLATE 40

PLATE 41

Acacia sphaerocephala Schlecht. and Cham. (=veracruzensis Schenck).
Photograph of type of sphaerocephala in Berlin Herbarium. Actopan, State
Vera Cruz, Mexico.
PLATE 42

*Acacia sphaerocephala* Schlecht. and Cham. (=*veracruzensis* Schenck). From a plant grown in Darmstadt from seeds collected in sand dunes south of the city of Vera Cruz, Mexico. Photograph by W. E. Safford.
PLATE 43

Acacia sphaerocephala Schlecht. and Cham. (=veracruzensis Schenck).
Dunes of Vera Cruz, Mexico. Photograph by A. Dampf.
PLATE 44

*Acacia Standleyi* Safford. Mexico. Photograph of type by W. E. Safford.
PLATE 45

Acacia turgida Safford (apparently not published). Herba Santa, Chiapas, Mexico. Photograph by W. E. Safford.
PLATE 46

a. Dipterous galls on leaflets of *Acacia* "cornigera". Escuintla, Patulul, Guatemala.

b. Dipterous galls on twigs of *Acacia costaricensis*, near Panama City.
PLATE 47


PLATE 48


PLATE 49


PLATE 50


Wheeler — Neotropical Ant-Plants and their Ants.

Plate 52

Cryptocerus (Cyathocephalus) pallens Klug var. porrasii Wheeler. a, soldier; b, head of same, dorsal view; c, worker.
WHEELER — Neotropical Ant-Plants and their Ants.

PLATE 53

Cryptocerus (Cyathocephalus) setulifer Emery. a, soldier; b, head of same, dorsal view; c, worker.
WHEELER — Neotropical Ant-Plants and their Ants.

PLATE 54

*Cryptocerus* (*Cyathocepalus*) *varian* F. Smith. Soldier and head of same; worker.
PLATE 55

a. *Azteca longiceps* Emery. Head of female, workers and male; thorax and petiolar node of worker.

b. *Azteca pittieri* Emery. Head of female and worker; thorax and petiolar node of worker.
WHEELER. ANT PLANTS AND THEIR ANTS. PLATE 55
WHEELEI - Neotropical Ant-Plants and their Ants.

Plate 56


WHEELER — Neotropical Ant-Plants and their Ants.

PLATE 57

a. *Azteca xanthochroa* (Roger). Head of female and workers; thorax and petiolar node of worker.
