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THE COMPOUND AND MIXED NESTS OF AMERICAN ANTS.

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PART II. THE KNOWN CASES OF SOCIAL SYMBIOSIS AMONG AMERICAN ANTS.

SOCIAL symbiosis among ants occurs in what are called "compound" and "mixed" nests. These terms are used in the sense of Forel's "fourmilières doubles" and "fourmilières mixtes." The former are defined ('**74**, p. 52) as "nests inhabited simultaneously by two or more ant colonies belonging to two or several hostile species." The latter term was adopted by Forel from Pierre Huber ('**10**). It includes the nests which are amicably inhabited in common by ant colonies belonging to different species. Both categories were later accepted by Wasmann ('**91**) with slight changes, and, somewhat more accurately, designated as "zusammengesetzte Nester und gemischte Kolonien" (compound nests and mixed colonies). Wasmann included all the various forms of compound and mixed nests known in 1891 in the following table ('**91**, pp. 176–178):

"*A.* Compound Nests (*zusammengesetzte Nester*). The consociating ants maintain independent households, or *ménages; i.e.*, constitute separate colonies. This form of symbiosis occurs between ants belonging either to the same or to different subfamilies.

I. Accidental (*i.e.*, Occasional) Forms:

1. Nests established in close proximity to each other by ants which have certain predatory proclivities. Examples: *Tetramorium cæspitum* with *Formica sanguinea; Dorymyrmex pyramicus* with *Pogonomyrmex barbatus.*
2. Nests established in close proximity to each other, with the subsidiary object of securing comfortable, warm, and secure quarters. Examples: *Formica fusca* and *Myrmica ruginodis* with *F. rufa* and *pratensis; Leptothorax muscorum* under the bark of pine trunks surrounded by *rufa* nests; *Myrmecina latreillei* Latr. with *F. rufa* and *exsecta.*

II. Regular Forms:

1. Thief ants: *Solenopsis fugax* and *Solenopsis orbula* with ants of much greater size.
2. Guest ants: *Formicoxenus nitidulus* with *Formica rufa* and *pratensis; Xenomyrmex stollii* with *Camponotus abscisus.*

B. Mixed Colonies (*gemischte Kolonien*). The different consociating ants carry on a single household, thus constituting a single colony. This form of symbiosis occurs only between ants belonging to the same subfamily.

I. Normal (*i.e.*, Regular) Forms:

1. The dominant species has its own workers, with toothed mandibles. Colonies clearly of predatory origin. *Formica sanguinea* ♂ ♀ ☿ and their developmental forms ⏜[1] workers and worker pupæ of *F. fusca* or *rufibarbis* or both, or of *F. schaufussi* or *fusca* (in North America).
2. The dominant species has its own peculiar workers without toothed mandibles.
   a. The dominant species is represented by ♂ ♀ ☿ and their developmental stages, the auxiliaries only by the workers and their pupæ. Predatory colonies:
      α. Colonies clearly predatory in origin: *Polyergus rufescens* ⏜ *F. fusca* or *rufibarbis* (or very rarely both), *Polyergus lucidus* ⏜ *F. schaufussi.*
      β. Colonies probably of predatory origin: *Strongylognathus huberi* ⏜ *Tetramorium cæspitum.*

[1] The sign ⏜ is used to express the union of two species to form a single colony. The name of the auxiliary (slave) species is always placed after the sign.

b. The dominant species is represented by ♂ ♀ ☿ and their developmental stages, the auxiliaries by the workers and their developmental stages and by fertilized females. Colonies arising by affiliation (*Bundescolonien*): *Strongylognathus testaceus* ⌓ *Tetramorium cæspitum*.

c. The dominant species appears to be represented only by the ☿ and its developmental stages, the auxiliaries by ♂ ♀ ☿ and their developmental forms.[1] Probably predatory colonies, which, however, do not arise like the above through the robbing of the pupæ of strange nests, but by the dominant species driving out the latter and taking possession both of their nest and brood. *Tomognathus sublævis* ⌓ *Leptothorax acervorum* or *muscorum*.

3. The dominant species has no worker form : *Anergates atratulus* ♂ ♀ and their developmental stages ⌓ *Tetramorium cæspitum* (workers only). Perhaps these colonies might be more conveniently designated as guest colonies.

II. Accidental (Abnormal) Forms :

1. Artificial mixed colonies arising through affiliation. Examples : *Formica sanguinea* ⌓ *pratensis*; *F. rufa* ⌓ *pratensis*; *Polyergus rufescens* ⌓ *rufa*.

2. Artificial mixed colonies of predatory origin :

a. Produced in confinement : *F. sanguinea* ⌓ workers of *fusca* or *rufibarbis* (normal auxiliaries) ; *rufa*, *pratensis*, *cinerea*, *exsecta*, *pressilabris* (abnormal auxiliaries).

b. Occurring in a state of nature : *F. sanguinea* ⌓ workers of *fusca* and *pratensis* or *rufibarbis* and *pratensis*.

3. Natural, abnormal, mixed colonies :

a. Unusual auxiliaries, with the usual dominant species. Predatory colonies :

Form. sanguinea ⌓ workers of *pratensis*.
" " " " " *rufa*.
" " " " " *rufa* and *fusca*.

b. Usual auxiliaries, with an unusual dominant species. Colonies probably arising by affiliation : *F. pratensis* ⌓ *fusca*, *truncicola* ⌓ *fusca*, *exsecta* ⌓ *fusca*.

c. Neither species living, as a rule, with other ants, either as auxiliaries or as dominant species : *Tapinoma erraticum* ⌓ *Bothriomyrmex meridionalis*.

[1] This assertion now requires modification, since Adlerz has published his later observations ('96).

C. Various combinations of the regular and irregular types of compound nests and mixed colonies. Examples: *Solenopsis fugax* with *Formica sanguinea* = *fusca*; *Tomognathus* = *Leptothorax* with *F. rufa*."

While this table leaves little to be desired in point of logical construction, it is scarcely an adequate expression of the facts at the present time. Nor could this be expected, as a decade has elapsed since its publication. It seems worth while to replace it by a number of coördinated categories, for two reasons. First, the case of *Leptothorax emersoni*, described in the first part of this paper, is in certain respects clearly transitional between Forel's and Wasmann's leading categories of compound and mixed nests, so that the dignity of these main groups is thereby considerably impaired. Second, the various cases of compound and mixed nests obviously represent several independent and more or less divergent lines of phylogenetic development, as Wasmann has shown ('91, p. 239). Hence it seems advisable to attempt a natural grouping of the cases, even at the expense of multiplying categories. I have, therefore, adopted the following headings, which may be cited with their equivalents in Wasmann's table:

I. *Plesiobiosis.* Double nests (in Forel's sense); Wasmann's accidental forms of compound nests. (*A* I, 1 and 2.)

II. *Parabiosis.* (Forel '99) Not included in Wasmann's table.

III. *Cleptobiosis.* Wasmann's "Diebsameisen"; first regular form of compound nest. (*A* II, 1.)

IV. *Xenobiosis.* Inquilines, or guest ants; Wasmann's "Gastameisen"; second regular form of compound nest. (*A* II, 2.)

V. *Dulosis.* Slavery. ("Esclavagisme," Forel.) Wasmann's normal forms of mixed colonies. (*B* I, 1 and 2.)

VI. *Colacobiosis.* Social parasitism (Forel); Wasmann's third case of normal mixed colonies. (*B* I, 3.)

VII. *Synclerobiosis.* Mixed nests of uncertain origin and meaning. Wasmann's last case (*B* II, 3 *c*) of accidental (abnormal) mixed colonies.

Although of considerable interest, the artificial mixed colonies (Wasmann's *B* II, 1 and 2) are omitted in this scheme, because they are mere beginnings in a field of experiment that has been little cultivated in Europe and is still untouched in America. It might be possible to include them with the cases of synclerobiosis. The natural abnormally mixed nests (Wasmann's *B* II, 3 *a*) are best treated in connection with the normal cases of dulosis. Combinations of regular and irregular mixed and double nests (Wasmann's category *C*) are rather rare and exceptional, and may be placed as compounds of the simpler relations under some one of the seven headings above enumerated.

I. Plesiobiosis.

As restricted in the present paper, plesiobiotic, or double nests comprise only those cases in which two, or rarely more, colonies of ants of different species excavate their galleries in close contact with one another. They are usually established under stones or logs, but a peculiar group of such nests is formed by several species that live within the precincts of the huge, exposed, mound-like nests of the agricultural ants (species of Pogonomyrmex). The colonies inhabiting double nests are usually inimical, or at best indifferent to one another. Hence, when living under stones or in old logs, they very carefully wall up the intervening space, so that the galleries belonging to the two households cannot inosculate.

Two classes of double nests may be distinguished. One of these embraces a vast series of merely accidental associations of two (or, more rarely, more) species. The associations of the other class are claimed to occur with a certain regularity and frequency, as if one or both of the species concerned were settling into definite and constant symbiotic relations. The cases of the former class are of comparatively little interest, except in so far as they represent what must have been the very first step in the development of the more specialized unions (xenobiosis, dulosis, colacobiosis, etc.). Any attempt at cataloguing these various associations would be unprofitable, if not impossible. As an illustration of such cases, it may suffice to

mention, in passing, one very beautiful example. On March 9 of the current year I found two double nests under large stones on opposite sides of a road near Austin, Texas. The ants were in both cases the huge black Ponerine *Pachycondyla harpax* and the fine honey-yellow *Camponotus fumidus*, var. *festinatus* (=*Formica festinata* Buckl.). In each case the latter species had excavated its nicely finished galleries and chambers under the middle of the stone, while the former had extended its few broad and irregular burrows along the surface so as nearly to encircle the Camponotus nest. The contrast between the color of these large ants, the one belonging to the most primitive, the other to the most specialized subfamily of the Formicidæ, was scarcely greater than that exhibited by their architecture. As soon as the nests were uncovered the Camponoti sniffed the presence of their black neighbors and hastily retreated into their galleries; while the Ponerinæ seemed as oblivious of their fellow-tenants as the occupants of a Chicago apartment building. Similar nests of *P. harpax* and *C. maculatus*, subsp. *sansabeanus*, are not infrequent in the neighborhood of Austin, but these, too, are merely accidental associations, as all three of the species mentioned are nearly always found occupying single nests.

The second class of plesiobiotic colonies, *viz.*, those which have been considered by some authors as incipiently symbiotic, really represent very little advance on cases like those above described. I am convinced that the supposed regularity of these associations may be largely the result of hasty or inadequate observation. In several instances the two species of ants are quite as often, or even more frequently, found in single nests. Usually one of the species is of diminutive size, and this has led observers to suppose that they were dealing with a small and feeble ant living under the wing of a formidable neighbor. It is, however, quite as probable that the two species occur together, because both affect the same natural conditions, such as soil, moisture, presence or absence of vegetation, etc. This is noticeably the case with Pogonomyrmex and its various satellites.

1. **Myrmecina graminicola** Förster.

Myrmecina graminicola (*M. latreillei* Curt.) is a small, rather rare ant, occurring both in Europe and North America. On our continent it is represented by two subspecies — *americanus* Emery, with its variety *brevispinosus* Emery, and a second undescribed subspecies recently discovered in Texas.

The habits of the European Myrmecina have been observed by Forel ('**74**, pp. 352–353). He found it living in small colonies under stones. It is rather sluggish and cowardly. When disturbed, instead of defending itself or running away like most other ants, it relies on the protection afforded by its very hard integument, rolls itself up in a ball and "feigns death." Forel found that it would not attack *Tetramorium cæspitum* or *Strongylognathus huberi*, even when these ants invaded its nest. The European Myrmecina is described as having a *penchant* for forming double nests with other ants. One of the two colonies found by Forel was near a nest of *Formica rufa*, the other near a nest of *Ponera coarctata*. Wasmann ('**91**, p. 176, footnote) also found a Myrmecina colony in a nest of *Formica exsecta*.

So far as I have been able to observe, our American subspecies appear to have the same habits as the European form. A few specimens of the new subspecies found at Austin were under a stone which covered besides a small colony of *Formica subsericeo-neorufibarbis* Emery (= *F. gnava* Buckl.). Two nests of the subspecies *americanus*, variety *brevispinosus*, found at Colebrook, Conn., during the past summer, were associated with *Stenamma fulvum*, subsp. *aquia* Buckl., and *Ponera coarctata*, subsp. *pennsylvanica* Buckl.

2. **Leptothorax muscorum** Nylander.

According to Emery ('**95**, p. 318), *Leptothorax muscorum*, like Myrmecina, occurs in the United States as well as in Europe, but nothing is known concerning its habits in the former locality. In Sweden, according to Adlerz ('**86**, p. 210), it has a decided proclivity for living within the confines of *Formica rufa* nests. Both Adlerz and Wasmann ('**91**, p. 225) lay stress

on this peculiarity as representing a decided step towards the conditions exhibited by the guest ant, *Formicoxenus nitidulus* (*q.v.*). It is of even greater interest in connection with the habits of its congener, *L. emersoni*.

3. **Monomorium minutum** Mayr., var. **minimum** Buckley.

This widely distributed ant forms small but very populous nests, containing from one to a dozen or more deälated queens and hundreds or even thousands of workers. It is very common under stones in the open cedar brakes in many places about Austin, Texas. Usually its nests are solitary, but it frequently forms double nests with the larger ants of the vicinity. I have often found it with *Camponotus maculatus*, subsp. *sansabeanus*; *C. fumidus*, var. *festinatus*; *Formica subsericeo-neorufibarbis*; *Pachycondyla harpax*; and under small stones on the summits of the nest-cones of *Pogonomyrmex barbatus*, var. *molifaciens* Buckl. The large ants are assailed with fury when the nests are disturbed and they accidentally stumble into the galleries of the Monomorium. These minute black ants, however, are not altogether averse to the society of other ants, as is shown by their forming mixed nests with two interesting species to be considered below, *viz.*, *Leptothorax* (*Dichothorax*) *pergandei* Emery and *Epœcus pergandei* Emery.

4. **Forelius fœtidus** Buckley (= **Forelius mccooki** Forel).

Attention was first directed to this small, dull yellowish dolichoderine ant by McCook, who found it living amicably within the nest boundaries of the Texan agricultural ant (*Pogonomyrmex barbatus*, var. *molifaciens*). The substance of his observations is contained in the following remarks ('79, p. 202): "Numbers of these ants were frequently seen traveling in long lines across or near to the nest of Barbatus (Pl. XXIV, Fig. 118). Usually their route was established upon blades of grass growing on those nests which were covered with the Aristida, or along the low tufts of grass on the margin of the disk. They seemed to prefer this elevated transit to moving directly upon the surface, which they touched only

when a break in the herbage compelled them to descend. They traveled in single, or 'Indian' file, one behind another. . . . The specimens which I preserved were taken from a small colony found within the bounds of a large Barbatus formicary which was being excavated. The agriculturals took no notice of their tiny neighbors, at least never interfered with them, and the two species seemed to be upon the most friendly terms with each other."

McCook's observations are, in the main, correct, so far as they go, but they are so incomplete as to give a wrong conception of the habits of Forelius. This ant is extremely common at Austin, where McCook made the above-quoted observations. It really prefers dry soil, nearly or quite destitute of vegetation. It throws up its little crater-shaped mounds of earth in great numbers along the paths and roads, and on warm sunny days travels in straggling files over all the barren lands. Sometimes, however, it nests under stones on the dry hill-slopes, and it is in such situations that one often finds the largest and most flourishing colonies, containing many deälated queens and thousands of workers, larvæ and pupæ. The fact that it often builds within the confines of the Pogonomyrmex formicaries is easily explained, for, though the agricultural ant naturally prefers grassy regions, nevertheless, through its singular habit of clearing away the vegetation over a large circular area, it establishes the very conditions that are preferred by the Forelius. The "friendly relations" with Pogonomyrmex are perhaps to be explained by the very small size and active movements of Forelius, which thus escapes the attention of its huge neighbors. In this respect the dolichoderines seem to be in the same position as the small white podurans (Cyphodeira), which run about unheeded in the galleries and chambers of the Pogonomyrmex nests.

5. **Dorymyrmex pyramicus** Roger.

In connection with some rather fanciful passages from the manuscript of Lincecum, McCook ('79, p. 197 *et seq.*) records several observations of his own on the relations of *Dorymyrmex*

pyramicus to *Pogonomyrmex barbatus*. Though the former ant, which ranges from Colorado and North Carolina to the Argentine Republic, is not uncommon at Austin, I have not often observed it in this locality. But I have found its small earthen mounds in very great numbers about Aguas Calientes in Mexico. Here it occurs quite as frequently outside as within the formicary boundaries, both of the typical *P. barbatus* and its variety, *molifaciens*. Like Forelius, Dorymyrmex is an ant of the barren soil, and its occurrence within the formicary precincts of the agriculturals is probably open to the same explanation. It is, however, far more pugnacious than Forelius, and, though tolerated by Pogonomyrmex, it resents any intrusion on the part of its larger neighbors. Both Forelius and Dorymyrmex, like many other dolichoderines, emit a rank secretion, which is in all probability protective.

6. **Dorymyrmex pyramicus** Roger, var. **flavus** McCook.

According to McCook ('82, pp. 155–158), this variety occurs with *Pogonomyrmex occidentalis* Cresson in Colorado. "There was scarcely a formicary which came under observation, from first to last, that had not upon the clearing one or more colonies of the erratic ant, *Dorymyrmex insanus* Buckley, or a new species of variety, *D. flavus* McCook. Usually there are two or three nests, sometimes four, located upon different parts of the pavement. These are small moundlets of fine soil, surrounding a central opening which leads into an irregular series of galleries and chambers. The same insects are parasitic upon the disks of the agricultural ants of Texas, and exhibit there characteristics similar to those in the Garden of the Gods. They are small, very active, irritable, intensely pugnacious, and courageous to the last degree. The manner in which these little fellows bullied and badgered their occident hosts was amusing, and indeed amazing." Nests of *Dorymyrmex pyramicus*, var. *flavus*, are rather common at Austin, but as yet I have failed to find them within the Pogonomyrmex formicaries, although I have no doubt that they occasionally occur in such situations.

7. **Pheidole carbonaria** Pergande, subsp. **calens** Forel.

At Aguas Calientes, Mexico, I observed several nests of this small, timid Pheidole on the slopes or about the bases of the beautiful gravel cones of the typical *Pogonomyrmex barbatus*, and its variety, *molifaciens*. The Pheidole was not found elsewhere in the vicinity, but my stay was too brief to enable me to assert that this ant really exhibits a more definite association with Pogonomyrmex than that of Forelius and Dorymyrmex. From the appearance of its soldiers, *Pheidole carbonaria* would seem to be a seed-storing species like our Texan *Pheidole kingi* André, var. *instabilis* Emery, and the Northern *Pheidole pilifera* Roger (= *pennsylvanica* Roger). If this is true, the Mexican insect may be a thief-ant feeding on the seed stored by the agriculturals in their large chambers, which are often sufficiently near the surface of the mounds to be invaded by small ants.

8. **Formica sanguinea** Latr.

McCook ('82, p. 152) found colonies of *Formica sanguinea*, with their slaves, within the clearings of three different nests of *Pogonomyrmex occidentalis* in Colorado. These and several other ants appeared to be tolerated in this situation by the occident ants. Such observations show that the association of ants with the Pogonomyrmex cannot be in all cases prompted by a desire for greater protection, since *F. sanguinea* is a bold, predaceous species, quite capable of making its way independently. It also shows that the formicary precincts of the agricultural ants may be open to some intruders of considerable size. Experience has taught me that it is not an easy matter to determine the attitude of these ants towards other animals. This is evident from the following jottings from my notebook: *Pogonomyrmex barbatus* sometimes permits the leaf-cutting ants (*Atta fervens*) to wear a groove-like path diagonally across its disk. It will also allow large tenebrionid beetles (*Eleodes tricostatus*), often to the number of six or eight, to stalk about for hours unmolested on its nest, and to feed on the refuse vegetable matter accumulated within the confines of

the pavement or even on the gravel cone.[1] On the other hand, I have counted on a single pavement no less than ten of the balls of dung abandoned by the Canthons (*C. lævis*) which had been driven away from their precious charges by the ants. Malodorous beetles like *Chauliognathus scutellaris* when placed on the nests are seized by the ants, at once carried to the edge of the pavement, and dumped over the boundary. Man and the larger domestic animals are soon attacked when they stand within the disk, and the horned toad, which seems to feed very largely on these ants, is treated in the same manner. (See Edwards, '96.)

II. PARABIOSIS.

Forel ('99) introduced the term "parabiosis" to designate a peculiar form of compound nest with inosculating galleries, in which different species of ants have their households strangely intermingled but not actually blended. Only one typical case of this description is known, but some remarkable nests in tillandsias recently observed by me in Mexico are in certain respects similar to the case described by Forel, so that they may be included, at least provisionally, in the same category.

9. Dolichoderus and Cremastogaster.

The interesting observations made by Forel ('99, pp. 380, 381) in the United States of Colombia during the spring of 1896 are here translated in full:

"I frequently observed, originally in the neighborhood of Santa Martha, two species of ants belonging to different genera and even subfamilies, a Dolichoderus and a Cremastogaster, both shining black, the former very large, noticeably larger than the latter, usually running in the very same files, both over the ground and on the trees and undergrowth, in the most perfect amity. The files were very long and dense, so that the ants met and elbowed one another continually. The two species went foraging on the trees, the Cremastogaster searching mainly for plant lice and Coccidæ, the Dolichoderus

[1] Several years ago I observed another species of Eleodes similarly engaged on the nests of *P. occidentalis* in Wyoming.

for the sap of the plants. For this reason the files bifurcated towards their ends, each species going to its own destination. I finally discovered in the trunk of a mango a large termite nest which had been appropriated by the two species of ant under discussion, and served them as a common dwelling in a manner hitherto unknown. The time was decidedly propitious, as each species had its winged sexes and its pupæ in the nest. The nest was inhabited as it had been left by the termites without additions or alterations. In no portion of the nest was there a blending of the two species of ants. Some of its corners were still tenanted by the termites. But the chambers and galleries throughout nearly their whole extent were occupied either by the Cremastogaster with their females, males, and pupæ, or by the Dolichoderus with the corresponding sexes and developmental stages. Each species had its own household, in contradistinction to the mixed formicaries of our Polyergus and Formica, which have but a single household in common. But all the chambers and galleries inhabited by one of the two species communicated freely with the cells tenanted by the other, and, as if intentionally, the apartments of one were interlaced with those of the other. Instead of one species taking possession of one-half of the nest, and the other of the remainder, they interdigitated throughout, so that there was not a piece of the nest as large as an egg which did not contain both species. The whole nest was about four or five decimeters in diameter. Thus the case is altogether different from that of the double or compound nests in Europe, where two or several inimical species may have their galleries interlacing to some extent but not inosculating. In this case we are concerned with an amicable association for lodging and for the files, which go foraging together, but without actually blending, so that the two species lead an independent life side by side. Hence the term 'parabiosis' which I have thought best to apply to this kind of association. It should be remarked, however, that the parabiotic association of these two species is not constant, though very frequent. I have also found the nest of each species by itself." [1]

[1] In conclusion Forel calls attention to the fact that some birds exhibit a similar parabiosis, *e.g.*, the joint flocks of *Corvus cornix* and *C. corone* in Europe.

10. *Nests in Tillandsias.*

On December 27 of the past year, while collecting ants in a small grove at the head of one of the *barrancas* near Cuernavaca, Mexico, I happened on some peculiar nests, concerning which I can find no account in the literature. After collecting a number of species under the stones, I turned my attention to the limbs and foliage of the acacia and guava trees overhead. On accidentally pulling to pieces one of the large bud-like epiphytic tillandsias (probably *Tillandsia benthamiana* Klotzsch), very common both in this and other localities about Cuernavaca, I was surprised to find it containing whole nests of ants, with their larvæ and pupæ snugly packed away like so many anchovies in the spaces between the moist overlapping leaves. A closer inspection showed that the ants had gnawed little holes through the leaves to serve as entrances to their chambers. These holes occasionally perforated a single leaf, but quite as often they threaded several leaves and extended to the very core of the bud. Sometimes a single colony of ants was divided up into companies, each occupying the space under a single leaf. But the most remarkable fact concerning these nests was the frequent occurrence of two or even three flourishing colonies belonging to different species in a single tillandsia, the whole habitable basal portion of which was rarely more than 2–3 inches long by 1½ inches in diameter. Often these colonies were curiously intermingled in such a manner that though there was no actual blending and the space under a single leaf was always occupied by ants of the same species, still, whole colonies or portions of a single colony were often completely surrounded by leaf spaces occupied by another colony. During the few hours which I could devote to collecting, the following seven species — three of them new to science, as Professor Forel informs me — were taken from the tillandsias:

1. *Cremastogaster brevispinosa* Mayr., var. *minutior* Forel.
2. *Camponotus abdominalis* Sm., subsp. or var. between *esuriens* Sm. and *mediopallidus* Forel.
3. *Camponotus rectangularis* Em., var. *rubroniger* Forel.

4. *Cryptocerus aztecus* Forel.
5. *Cryptocerus wheeleri* Forel.
6. *Leptothorax petiolatus* Forel.
7. *Pseudomyrma gracilis* Fabr., var. *mexicana* Em.

Of these species, which are here enumerated in the order of decreasing frequency, — the first being far and away the most abundant, — I noticed the following combinations occurring in single buds: Nos. 1 + 2; Nos. 1 + 2 + 4; Nos. 1 + 3 + 4; Nos. 1 + 5 + 6; Nos. 1 + 7.

While I am not certain that the nests of the different species could communicate with one another, I am confident, nevertheless, that these ants must be very tolerant of one another, for their entrances were situated on such a small surface as to be of necessity very close together. This is the more astonishing on account of the great diversity of behavior exhibited by the different species. When I was tearing the leaves asunder the little Cremastogasters attacked me vigorously, but their lilliputian stings and mandibles could scarcely perforate my epidermis. The huge *Camponotus abdominalis*, however, rushed out in a body, and the powerful mandibles of the soldiers, reinforced by the copious formic acid batteries of the whole company, often compelled me to drop the tillandsia and forego further exploration of its leaves. The two species belonging to the grotesque genus Cryptocerus were as gentle as lambs, preferring to rest quietly on my hands and clothing. The timid little Leptothorax took to their legs, while the superb wasp-like Pseudomyrmas made dashes at me from among their glistening larvæ and pupæ, but returned with precipitation as if afraid to abandon their offspring.

As the tillandsias appeared to suffer no injury from their tenants, and were even preparing to send forth their long spikes of reddish flowers, I was at first inclined to see in this association of plants and ants another case of symbiosis (*sensu stricto*). But apart from v. Ihering's contention ('94 p. 365 *et seq.*) that the number of "Ameisenpflanzen" in tropical America has already been considerably exaggerated, the above view also loses in probability from the fact that at least four of the seven

species which I have enumerated occur also under other conditions in the neighborhood of Cuernavaca. Nos. 1, 2, 3, and 7 were found nesting in the dead trunks and branches. No. 2 also nests under stones, and it is probable that 4, 5, and 6, at least occasionally, nest in dead wood, like many other species of the same genera in other regions. The little Cremastogaster uses a black, paper-like substance for constructing perforated partitions within the spaces which it inhabits and for closing up the openings left at the tops of the chambers by the slightly divaricating leaves of the tillandsia. A colony of this species was also found inhabiting the cup-like cavity of one of the peculiar flower-like excrescences on the branches of the guava trees — the "flores de guavera" of the inhabitants of Cuernavaca. The ants had closed the wide orifice of the cup with a layer of the black papery substance and had left a small opening near its center to serve as an entrance. The relations of the ants to the tillandsia would seem, therefore, to be very similar to those often formed by several other species with empty galls and hollow thorns, both in Mexico and other countries. These relations are of great interest as one of many expressions of the remarkable plasticity of instinct in these insects.

Living colonies of *Cremastogaster brevispinosa* and *Cryptocerus aztecus* were brought back to Austin and confined together in a Fielde nest.[1] Although the two colonies took up their habitation in different parts of the same chamber, they were never seen to quarrel with each other. On one occasion some of the Cremastogasters even ventured to lick the red, saucer-shaped heads of the Cryptocerus soldiers!

III. CLEPTOBIOSIS.

Those ants which live in or near the nests of other species and prey on the larvæ or pupæ, or surreptitiously consume

[1] This artificial nest invented by Miss Adele M. Fielde ('00) is superior to any other that I have used. It requires closer attention than the Janet nest in order that the requisite amount of moisture may be maintained, but this slight disadvantage is outweighed by numerous advantages. The ventilation of the chambers is excellent, the closest inspection of the ants is possible, and the nests are easily handled, transported, and cleaned.

certain substances in the nests of their hosts, may be grouped together as clebtobiotic species. Owing to the present incompleteness of our knowledge, this category is not very clearly circumscribed, so that further researches may greatly extend its meaning or lead to its division into several categories.

All the known cleptobiotic ants are of minute size and of subterranean habits. They are pale colored and seem to have a predilection for living with rather large ants. The minute species of Solenopsis (*S. fugax* Latr., *orbula* Emery, *latro* Forel, *molesta* Say), and according to Forel ('**94**, pp. 23, 24) certain species of Monomorium (*M. andrei* Saunders), and the species of the oriental genera Oligomyrmex, Melissotarsus, Carebara, Tranopelta, and Aëromyrma, belong to this category. *Monomorium termitobium* Forel enters into cleptobiotic relations with termites in Madagascar. Forel notes the following significant facts concerning these different species: "It is more than probable that the extremely minute size and subterranean life of the worker of these species are the results of natural selection. The workers are very small, yellow, and blind, or nearly so, whereas the large females and males, of a brown or black color, with wings and large eyes, are witnesses to the fact that the minute size, etc., of the worker is due to an extraordinary regressive development. The female of *Carebara lignita* West. is 20 mm. long and 4–6 mm. in diameter, while its worker, which I owe to the kindness of M. Emery, is only 2 mm. long! It is obvious that the minute size of the worker is its safeguard. For owing to its minuteness it succeeds in insinuating itself into the young brood of large ants or termites without being seen by the defenders. It assassinates the young in their swaddling-clothes, incapable of defending themselves. As it lives very near its hosts, it requires neither size nor strength for seeking its food at a distance, and it is therefore in a position to nourish its enormous females and males with facility. Thus it is easy to see how this form of parasitism should lead to a diminution in the size of the worker, in depriving it of its eyes, and in giving it a pale color, while the females and males which mate in the air retain their size, visual organs, and coloration."

The only cleptobiotic ant which has been at all carefully studied is the European *Solenopsis fugax*, a species with minute yellow workers and black males and queens. We owe

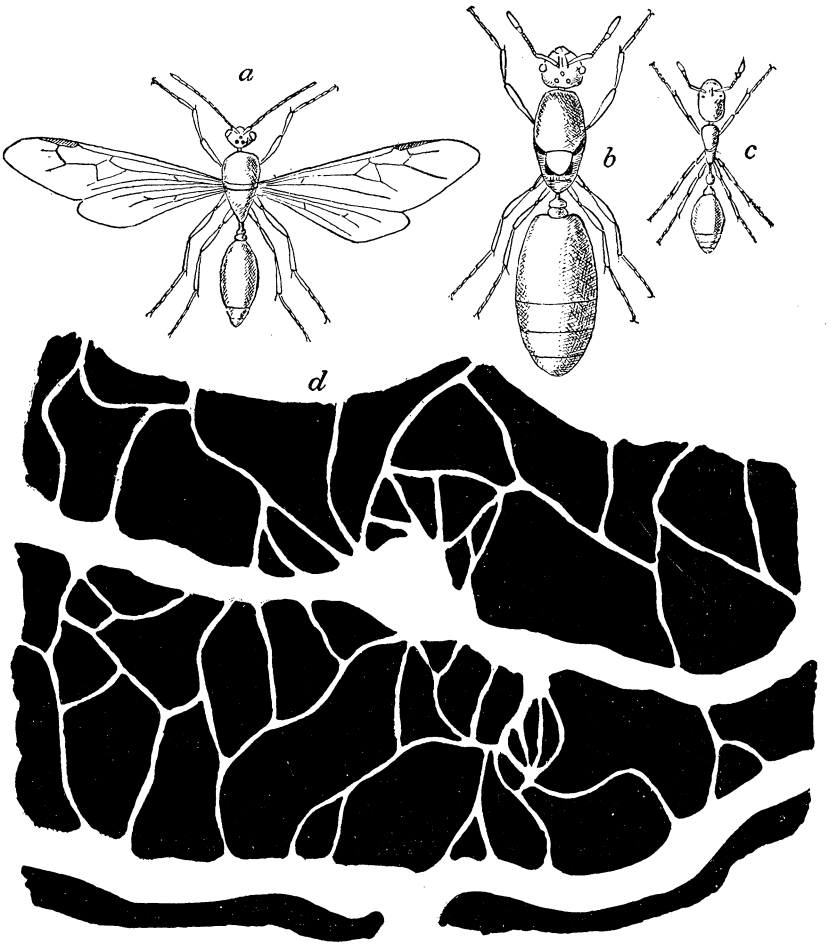

FIG. 10. — *Solenopsis fugax* Lat. (after Wasmann). *a*, male; *b*, deälated female; *c*, worker; *d*, portion of nest, showing tenuous galleries of Solenopsis entering the large galleries of the host-ant.

our knowledge of the behavior of this species to the labors of Forel ('69, '74), Wasmann ('91), and Janet ('97). I insert Wasmann's figure (slightly modified) of this insect and its nest, together with a translation of Janet's *résumé* ('97, pp. 58–60),

as both are of considerable interest in connection with our closely allied American species, *Solenopsis molesta:*

"The Solenopsis may establish itself near almost any other ants of our country. It is found especially with *Formica fusca*, *F. rufibarbis*, *Polyergus rufescens*, *F. rufa*, *F. pratensis*, *F. sanguinea*, *F. cinerea*, *Tetramorium cæspitum*, and *Myrmica scabrinodis*. Frequently it is possible to observe that the two nests are in close contact with each other. The Solenopsis nest may partially surround that of its neighbors, or it may even be excavated in part in the masses of the earth separating the galleries of the latter. That the two nests so near each other are not merely two contiguous nests, but deserve a special name such as the term 'double nest' employed by Forel, is proved by the fact that fine connecting galleries enable the Solenopsis to make incursions into the nests of their neighbors, where, as we shall see, they find an abundance of food. Wasmann ('**91**, p. 21) mentions an extremely populous nest provided with some twenty queens and extending in a semicircle around the subterranean portion of a *Formica pratensis* nest, with which it communicated by means of fine pillaging galleries. Forel and Wasmann, however, have also met with isolated nests.[1] At Beauvais I was able to ascertain, by following carefully during several hours the spading of a piece of land which was exposed to the south and had been left untouched for several years and was almost devoid of stones, that the nests of Solenopsis may often be isolated, or at least noticeably distant from the nests of any other species. Nevertheless, this distance does not at all exclude the possibility of a communication by means of long galleries with the ant nests of the neighborhood, *e.g.*, with those of the Tetramorium, which were not rare in the same piece of ground. It is probable that the Solenopsis, when necessary, manages to go a considerable distance in search of the ant pupæ that appear to constitute its principal food, but there is, nevertheless, a propensity to settle near the nests which furnish this food, and this approach is favored by the presence of stones, under which ants have such a pronounced tendency to shelter themselves. . . . In the sandy

[1] Emery ('**95**) also records the occurrence of such nests near Bologna, Italy.

soil of the piece of land above mentioned I obtained some fine and very clear vertical sections of the nests of the Solenopsis. They consisted of small chambers of a circular form measuring 8–20 mm. in diameter and only 6–8 mm. in height. Most of these chambers were at least several centimeters apart. Their floors were remarkably clean, smooth, and even hardened. They were connected by tenuous galleries, often less than 2 mm. in diameter, entering the chambers at their ceiling, at their lateral walls, or at their floors, and uniting with their surfaces by means of a perceptible infundibular orifice. Forel ('**74**, p. 385) saw several Solenopsis leave the earth and steal in among a stack of cocoons which had been heaped up by some *Formica pratensis* that had been dumped on the ground. The Solenopsis set to work perforating the cocoons and cutting the pupæ to pieces, thus destroying a great number of them. Forel is correct in his inference that the Solenopsis behave in the same manner in double nests. At this writing I repeat this observation daily on an artificial double nest of *S. fugax* and *F. rufibarbis*. Every day I give the Solenopsis about ten cocoons of Lasius queens, placing them near the entrance of the nest. It is not long before the Solenopsis make their appearance. From ten to thirty of them climb up onto each cocoon and cover it with little perforations, which, finally becoming confluent, enable them to reach its contents. If it contains a pupa, the legs and antennæ fall an easy prey to the mandibles of the Solenopsis. In this case the victim is cut into, sucked, and torn into very small pieces, which the ants hasten to carry away into the interior of the nest. The operation is much more difficult if the contents is a larva which has just spun its cocoon, or a pseudonymph. I have seen the Solenopsis drag a larva of this kind into the interior of the nest and keep working at it for twenty-four hours. At the expiration of this period the larva began to look flaccid and was covered with little black dots, which were sometimes double, corresponding with the little wounds made by the mandibles. Numbers of the Solenopsis were busy lapping up the liquid which exuded from the wounds, but it was not until thirty-six hours had elapsed that the larva was entirely devoured. Large

species of ants are unable to enter the nests of their neighbors, as the galleries of the latter are too narrow; and when the two species happen to meet one is inclined to believe, with Forel ('74, p. 246), that the small size of the Solenopsis renders them invisible to the larger ants. Then, too, in case of a conflict, the Solenopsis are numerous enough and sufficiently well armed with stings to kill even *Formica sanguinea*. In my double artificial nests I often saw one of the latter killed by a group of five or six Solenopsis, but on such occasions I also found a considerable number of Solenopsis cadavers on the refuse-heaps."

11. **Solenopsis molesta** Say.

The European *S. fugax* is represented in North America by a very closely allied species, — *S. molesta* Say. (= *S. debilis* Mayr.), — a minute yellow ant with yellow queens and dark brown males. The species has a very wide geographical range. It has long been known from the Eastern and Northern States and appears to be equally common in Texas. Although not mentioned in Forel's monograph ('99), it extends through Mexico, where I have taken it as far south as Cuernavaca in Morelos. Emery has described a variety *validiuscula* from California.

The habits of *S. molesta*, so far as I have been able to observe them, are the same as those of *S. fugax*. Although like its European congener it sometimes occurs in isolated nests, and even in houses, it has, nevertheless, a decided predilection for forming compound nests, essentially like those of *S. fugax*, with larger ants. In the Northern States it often consorts with the different species of Formica, Lasius, Stenamma, and Myrmica. In Texas it is of almost regular occurrence in the large nests of *Pachycondyla harpax* and *Odontomachus clarus*, and often occurs with the different earth-inhabiting species of Camponotus (*C. fumidus*, var. *festinatus* Buckley; *C. maculatus*, subsp. *sansabeanus*). In Mexico I have taken it with a variety of *Odontomachus clarus*. In one nest of *S. molesta*, discovered near Austin, I found the workers feeding on a dead cricket lying in the galleries of *Pachycondyla harpax*. As

S. molesta sometimes occurs far from the nests of other species, it would seem that it must often feed on other substances than the larvæ and pupæ of ants. Under these circumstances its diet may be similar to that of the European species which Emery ('95, p. 277, footnote) found near Bologna feeding on the bones and dead bodies of small animals.

12. **Pheidole lamia** n.sp. (Fig. 11 *a–c*).

This aberrant Pheidole, which I have recently taken near Austin, Texas, is, I believe, to be included among the cleptobiotic ants. It is, unfortunately, of very rare occurrence, so that up to the present time I have found only two of the nests — both under stones in rather moist, shady places. One of these nests contained a small number of workers which were feeding on a partially decomposed caterpillar. The other, containing a greater number of workers (about twenty-five), was on a refuse heap consisting of several dead ants, in the midst of a nest of *Camponotus maculatus*, subsp. *sansabeanus*. The honey-yellow workers were only 1.5 mm. long, and to the unaided eye so closely resembled the very common workers of *Solenopsis molesta* as to convince me that I must

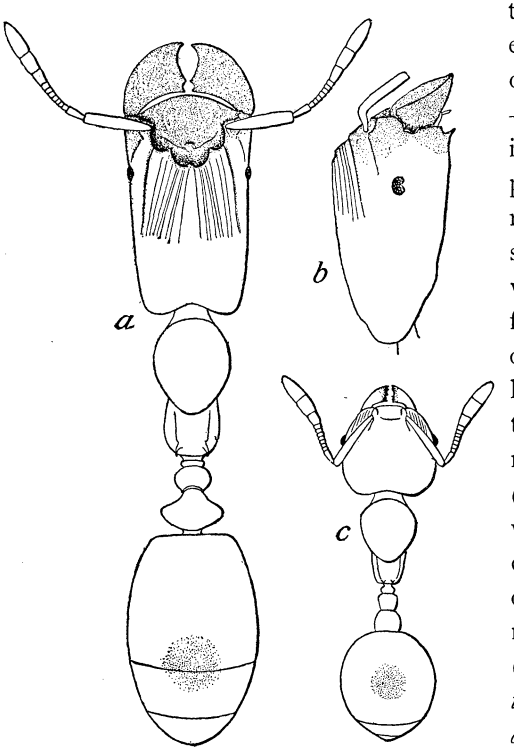

FIG. 11. — *Pheidole lamia* n.sp. *a*, soldier; *b*, head of same in profile; *c*, worker.

have overlooked these ants on several former occasions. They had evidently been feeding on the dead Camponotus and were moving in and out of their tenuous galleries excavated below the refuse heap in the compact black soil. On digging I discovered the singular soldier (2.5 mm. long, Fig. 11 *a*), which is unlike the soldier of any other Pheidole known to me except *Ph. absurda* Forel from tropical America. Forel's species, however, is larger and exhibits several other differences. The soldier of *Ph. lamia* is smooth and of the same honey-yellow color as the worker, except for the rough, brownish, Colobopsis-like anterior portion of its head. The abdomen of both soldier and worker has in its center a large dark spot, which is produced by the black contents of the stomach seen through the thin integument. The visual organs in both castes have undergone the usual reduction noticeable in hypogæic ants — there being scarcely more than a dozen facets in each of the small, emarginate eyes of the soldier.[1]

IV. Xenobiosis.

The inquilines, or guest ants (*Gastameisen*), constitute a group of considerable interest, since it is not improbable that these insects may ultimately give us some clue to the conditions that have led to the development of mixed nests from those of the double or compound variety. Unfortunately we know very little of the habits of some of the species that have been recorded as guest ants. So far as known the inquilines maintain their independent households, although they consort freely with their hosts and live with them on terms of mutual toleration, or even friendship. The best-known guest ant is the

[1] It is probable that several of our North-American species of Strumigenys are cleptobiotic. In a former paper ('00 *a*, p. 31) I recorded the occurrence of *S. louisianæ* in the nest of *Pachycondyla harpax*. While this paper is going to the press Rev. P. J. Schmitt writes me that "*S. pergandei* Emery, more than any other species of this genus, is almost always, at all events more frequently than not, to be taken in the nests of *Formica subsericea*, *F. exsectoides* or the slaveholders *F. rubicunda* and *subintegra* in the ground, and with *Lasius aphidicola* in rotten wood. There — after the fashion of *Solenopsis molesta* — it occupies a small chamber of its own, which connects with the galleries of the larger ants. These peacefully tolerate and scarcely notice their tiny neighbors."

European *Formicoxenus nitidulus*, which has been carefully studied by Adlerz ('84), Forel ('74, '86), Wasmann ('91), and Janet ('97). It is a singular fact that, notwithstanding all these valuable observations, the feeding habits of the Formicoxenus have never been observed. As this ant, in certain particulars, strikingly resembles *Leptothorax emersoni*, Janet's *résumé* ('97, pp. 54–56) of what is known concerning its behavior may be quoted before recording the little that is known concerning our American guest ants.

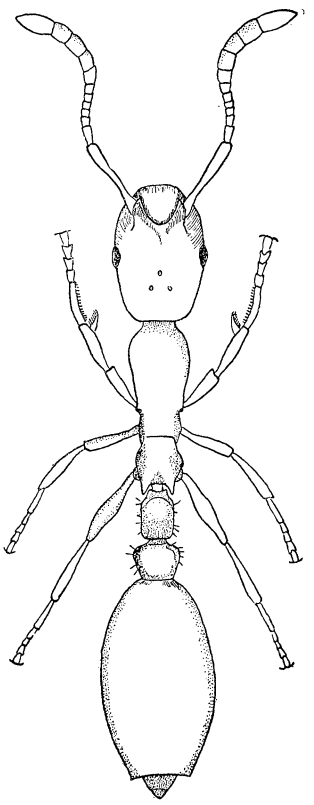

FIG. 12. — *Formicoxenus nitidulus* Nyl. Male (after Adlerz).

"*Formicoxenus nitidulus* is a pretty little species of very timid character. Forel found it to be a rare insect in Switzerland. I have several times taken small colonies of it at Beauvais. Wasmann mentions it as very common in Holland. Adlerz found it abundant in southern Sweden. It is, therefore, a north European species. The worker scarcely reaches a length of 3 mm., and the queen is but little larger. The male (Fig. 12), discovered by Adlerz ('84), is apterous like that of *Anergates atratulus* and like one of the male forms of *Ponera punctatissima*. Its shape, color, and the absence of wings make it difficult to distinguish from the worker. It may, nevertheless, be recognized from other external male characters. Its antennæ are more strongly recurved at their tips and are 12-jointed; *i.e.*, they have one more joint than the female phases (either queen or worker). In the abdomen five segments (the 7th to 11th) are visible from the exterior instead of four (segments 7 to 10) as in the females. The mandibles are smaller; the ocelli are well developed. The relations of *Formicoxenus nitidulus* to its host have been especially studied

by Adlerz ('84). Its colonies, usually consisting of a small number of individuals, may, however, be very populous at times. It establishes its nest in the very interior of the nest of *Formica rufa* or of *F. pratensis*. The small chambers which it there constructs and inhabits, together with its progeny, communicate by means of large openings with the galleries of the Formica nest. Wasmann ('91, p. 35) found a colony of Formicoxenus consisting of workers, males, queens, and young, inhabiting the cavity of an old cocoon of *Cetonia floricola*, a beetle which lives during its larval stages in the bottom of the nest of *Formica rufa*. *Formicoxenus nitidulus* often moves about among its hosts. The observations of Adlerz, Forel, Wasmann, and myself prove that these myrmecophiles are never met with outside of the nests of the *Formica rufa* and *F. pratensis*. They live in peace with their hosts, but they are not cared for by them, nor do they render them any service. Observers who have studied the behavior of this species have on exceptional occasions observed acts of a slightly hostile nature on the part of the two species, but these acts were without serious consequences. On one occasion, in one of my artificial nests, in which the ants had previously lived on good terms with one another, I saw a Formica touching a Formicoxenus with her antennæ and menacing her with her mandibles ; but she departed without even attempting to seize the inquiline. In the same nest I found a Formicoxenus which had seized the leg of a Formica in its mandibles and had died in this position. The Formicoxenus (Forel, '86, p. 134) are able, either by themselves or by carrying one another, to follow the files of their hosts when the latter move into a new nest. They also carry their progeny to the new nest. In the nests of their hosts they find shelter, warmth, and efficient protection from other ants, against which they would be unable to defend themselves. There they also find sustenance, but it has been impossible up to the present time to determine its nature."[1]

[1] In Emery's *Beiträge* ('95, pp. 271, 272), *F. nitidulus* is cited as occurring in North America. The specimens to which Emery refers were labeled "Rocky Mountains." But Emery (*in litteris*) has expressed grave doubts concerning the

13. **Xenomyrmex stollii** Forel (Fig. 13).

X. stollii is a small, smooth, dark brown ant, allied to the species of Monomorium. It is a native of Guatemala and was found, together with its larvæ and pupæ, living in a huge oak gall in company with a much larger ant, *Camponotus abscisus* Rog. More recently a subspecies, *floridanus*, of this same species was discovered at Lake Worth, Fla., by Mr. Pergande. (See Emery, '95, pp. 275, 276.) On this occasion the ants were living, unaccompanied by another species, in a hollow twig of *Xyderoxylon masticodendron*. Wasmann ('94, p. 163) expresses some doubt as to whether the Guatemala form really forms a mixed colony with the Camponotus, since the ants are members of different subfamilies; but he nevertheless regards this case as in a sense transitional to the mixed nest, since Xenomyrmex appears to build no nest of its own. From an inspection of our Texan oak galls, which are frequently inhabited by ants, I feel sure that nests of very small size on the plan

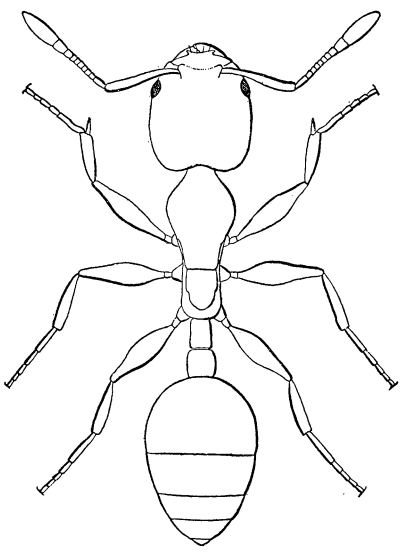

FIG. 13. — *Xenomyrmex stollii* Forel. Worker.

occurrence of Formicoxenus in this country. My own reference to this form as occurring at Colebrook, Conn. ('00, p. 48, footnote), is based on a wrong identification. The species there recorded is really *Leptothorax emersoni*, which in size, color, and superficial appearance resembles *Formicoxenus nitidulus*.

Two additional species of Formicoxenus have been recently discovered in Europe, and both have been described from female specimens only. *F. ravouxi* André ('96) was captured in a normal nest of *Leptothorax tuberum* Fabr., subsp. *unifasciatus* Latr., provided with fertile queens. The host of the other species, *F. corsicus*, described by Emery ('95 *a*, p. 12), is unknown.

Emery also describes (*ibid.*, p. 11) another ant, *Phacota noualhieri*, from a single specimen taken in a nest of *Monomorium salomonis*, var. *subnitidum*. Emery regards the new species as being in all probability parasitic or inquiline in its habits.

of the double nests of the *Formica rufa* and Formicoxenus could be formed even within one of these circumscribed vegetable growths. The guest ant could inhabit the central capsule (in which the gall fly passes its pupal stage), while the host ant might occupy the chambers dug in the ligneous substance of the gall. I am led to this supposition by finding that a new species of Leptothorax, which regularly nests in the *Holcaspis cinerosus* galls formed on the live oaks about Austin, prefers the small central capsule as a nursery. Here the single queen lives wedged in between the eggs, larvæ, pupæ, and a few workers, while the chambers of the gall are commonly tenanted by the bulk of the workers.

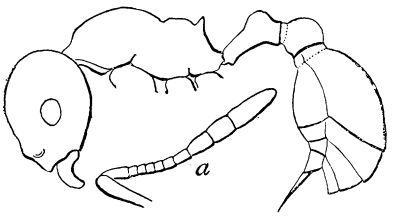

FIG. 14. — *Leptothorax (Dichothorax) pergandei* Emery (after Emery). *a*, antenna of same.

14. **Leptothorax (Dichothorax) pergandei** Emery (Fig. 14).

Our knowledge of this species, too, is extremely meager. It was described by Emery ('**95**, pp. 323, 324) from specimens taken as guests in a nest of *Monomorium minutum*, var. *minimum*, at Washington, D. C., by Mr. Pergande.

15. **Leptothorax emersoni** n.sp.

The Leptothorax described in detail in the first part of this paper may be included among the guest ants, although it certainly resembles in many respects the cases of dulosis and social parasitism.

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(*To be continued.*)