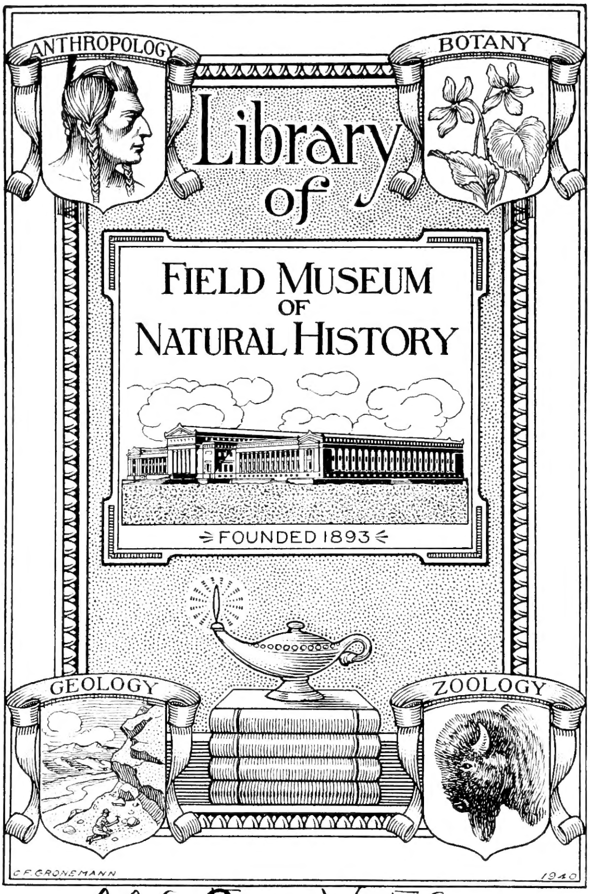

COLLECTED PAPERS ON ANTS

by

William Morton Wheeler

New Species of Formica.

By William Morton Wheeler.

AUTHOR'S EDITION, extracted from BULLETIN
OF THE
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Article XV.—NEW SPECIES OF FORMICA.

By William Morton Wheeler.

1. **Formica munda** sp. nov.

Worker. — Length, 5–7 mm.

Allied to *F. pergandei* Emery. Mandibles 8-toothed. Head, excluding mandibles, usually somewhat longer than broad, with straight posterior border and long cheeks converging anteriorly and slightly convex or flattened, but not concave as in *pergandei*. Clypeus carinate, with a rather deep median notch in its anterior border. Antennæ like those of *pergandei*. Thorax rather narrow and low, pro- and mesonotum not very convex, mesoëpinotal constriction shallow, epinotum long and low, its basal surface rather flat and somewhat longer than the very sloping declivity into which it passes through a rounded angle. Petiole thick and low, convex in front, flattened behind, with very obtuse upper border. Seen from behind the border is transverse, broadly rounded but passing rather abruptly into the straight sides which converge below Gaster small; legs slender.

Head and thorax subopaque, very finely shagreened. Mandibles, anterior portion of the head, and especially the frontal area and sides of the clypeus more shining. Mandibles sharply striatopunctate.

Pubescence grayish, very sparse, except on the gaster where, it is long and dense and conceals the shining surface except at the segmental incisures. Hairs on the body white, sparse, suberect and rather long, conspicuous on the upper and lower surfaces of the head, thorax, and gaster. On the gaster they are robust, obtuse, and very regularly distributed. The edge of the petiole is also fringed with hairs, and there is a row of oblique tapering hairs on the flexor surface of each tibia.

Head, thorax, and antennæ red; petiole and gaster black, the former with a reddish tinge. Mandibular teeth black. Lower pleuræ, and in many specimens also the vertex of the head, infuscated. Legs red, coxæ, femora, and tibiæ more or less blackened except at the articulations.

Female (deälated). — Length, 7.5–8 mm.

Resembling the worker except in the following characters: The hairs are of a yellowish cast, and on the gaster tapering and of the same thickness as on the head and thorax, although they are long and in certain lights conspicuous, especially toward the tip of the body. Pleuræ clouded with fuscous; posterior portion of head, posterior edge of pronotum and anteromedian and parapsidal blotches on mesonotum, fuscous. Metanotum and all except the anterior border of the scutellum, black. Petiole varying from dark red to blackish, of the same shape as in the worker except that in profile the superior border is much more acute in some specimens.

Described from seven females and numerous workers collected in the following localities: Cañon City, Breckenridge, and West Cliff, Colo., by the late P. J. Schmitt, O. S. B.; at Broadmoor and Roswell near Colorado Springs, Colo., by myself, and at Glorieta and Old Pecos Pueblo, New Mexico, by Professor T. D. A. Cockerell. This seems to be the form designated by Professor Emery as a variety of *F. pergandei* from Colorado (Zool. Jahrb. Abth. f. Syst. VII, 1893, p. 647). It is closely allied to this species but may be readily distinguished by the dense gray pubescence and obtuse white hairs on the gaster of the worker, and the less elongated head and more convex cheeks, especially in larger specimens. According to Emery's description of *pergandei*, it would differ also in having erect hairs on the lower surface of the head, but two cotypes of Emery's species in my collection—one received from Professor Emery and the other from Mr. Pergande — each have a few such hairs.

While collecting in the vicinity of Colorado Springs, during the summer of 1903, I found many colonies of *F. munda*. They were always in grassy places and most abundant in the irrigated plains about Broadmoor and in the pastures near the racing stables at Roswell. The species did not occur in the higher mountainous regions about Cheyenne Cañon and Manitou. The colonies were rather small, comprising only a few hundred workers, and made rather obscure mound-nests much like those of *F. schaufussi* and its varieties. I never found these colonies nesting under stones and in no case did they contain slaves, although a single colony of the allied *pergandei*, found in the very same locality (Broadmoor), contained workers of *F. subpolita*. It would seem, therefore, that although *F. munda* has a notched clypeus, it does not have the dulotic instincts of the allied *F. pergandei* and *sanguinea*.

2. **Formica dryas** sp. nov.

Worker. — Length, 5–7 mm.

With the habitus of *F. rufa*. Mandibles 8-toothed. Head, excluding mandibles, as broad as long, posterior border straight, sides rather flat, converging anteriorly. Clypeus sharply carinate, not produced in front, with nearly straight anterior border. Thorax rather robust, epinotal declivity much flattened, distinctly longer than the slightly convex basal surface. Petiole somewhat convex in front and very flat behind, with sharp superior border; seen from behind it is broad above in large workers and much produced in the middle, with straight sides rapidly converging below. Gaster and legs of the usual shape.

Head, thorax, petiole and appendages subopaque, finely but distinctly shagreened. Mandibles densely striatopunctate; clypeus and especially the frontal area smooth and shining. Gaster shining, very finely and transversely shagreened, with the appearance of "watered" silk.

Body clothed with short, erect or suberect, subobtuse, yellowish hairs, which are very conspicuous on the upper, lateral, and lower surfaces of the head, upper surface of thorax, and on the edge of the petiole; sparse and inconspicuous on the gaster, especially on its upper surface, and almost entirely absent on the antennal scapes. Eyes distinctly hairy. Pubescence yellowish, almost absent, except on the antennæ.

Head, thorax, petiole, and appendages red; gaster black or very dark brown, with red anal region. Small workers usually have darker legs and in some specimens the upper surface of the thorax is more or less infuscated.

Female (deälated). — Length, 7.5–8 mm.

Resembling the worker in coloration and sculpture, with the following differences. The red coloration of the head, thorax, petiole and appendages is somewhat duller, the posterior border of the pronotum, a large median mesonotal and two lateral parapsidal blotches, the greater portion of the scutellum and metanotum, dark brown. The gaster is smoother and more shining than in the worker. Hairs longer, tapering; somewhat flexuous on the head, thorax, and legs, conspicuous and erect on the antennal scapes and median portions of the eyes. Pubescence of head and thorax more distinct. Petiole very high with a sharp compressed edge.

Described from three females and numerous workers.

I have taken this species on three different occasions in the vicinity of Milwaukee, Wisconsin, and Rockford, Illinois. In a piece of woodland at Cudahy, south of Milwaukee, I found a flourishing colony, comprising three small mound-nests, strung along a well-worn path that had been made by the ants. This path was nearly an inch broad and in some places had been roofed over with dead grass and leaves for distances varying from several inches to two or three feet. Another colony was found at White Fish Bay, north of Milwaukee. It inhabited a single large mound-nest, possibly a natural hummock that had been enlarged by the ants, in shady woods. This colony, which seemed to be moribund or evanescent, comprised a few hundred workers and seven old deälated females. A third colony found near Rockford, Ill., was very similar but yielded no female specimens.

F. dryas is certainly very closely related to *F. rufa* and its various subspecies and varieties. This is especially true of the female *dryas* which has a highly glabrous gaster like that of the pure European type of *rufa*. The worker *dryas*, however, differs from the workers of all the American and European forms of *rufa* and resembles such species as *F. dakotensis*, *montigena*, *exsectoides*, and the next species to be described, in the peculiar shining "watered" silk surface of the gaster.

Var. **gymnomma** var. nov.

To this variety I would assign some workers that I have taken at Cold Spring Harbor, Long Island, N. Y., and in two localities near

Rockford, Ill. They differ from the typical form in having naked eyes and less hairy bodies. Some of the larger workers from the latter locality are almost as naked as *F. rufa* subsp. *integra.* The smallest workers from one of the Rockford colonies have the head and thorax very deeply infuscated.

3. **Formica nepticula** sp. nov.

Worker. — Length, 4–6 mm.

With the habitus of a small *F. rufa.* Mandibles 8-toothed. Palpi rather long. Head, excluding mandibles, a little longer than broad, cheeks slightly flattened, somewhat converging in front; posterior border straight, posterior angles rounded. Clypeus strongly carinate, its anterior border angularly produced in the middle. Antennæ of the *rufa* type. Thorax in profile with deep mesoëpinotal constriction; pro- and mesonotum rounded, hemispherical; epinotum evenly rounded, without any angle. Petiole large, as high as the epinotum, convex in front, more flattened behind, border rather sharp; seen from behind the upper border is transverse in the middle and obliquely truncated on either side, the lateral surfaces are straight and converge below. Gaster and legs as usual.

Head, thorax, and petiole subopaque, very finely shagreened; mandibles, clypeus, and frontal portion of head, but especially the frontal area, more shining. Mandibles densely striated and coarsely punctate. Legs and gaster shining, the latter finely and transversely shagreened, with the lustre of "watered" silk.

Hairs golden yellow, obtuse, suberect, and very sparse, on the upper and lower surfaces of the head, upper surface of thorax, and on the gaster. There are also a few scattered hairs on the flexor surfaces of the coxæ, femora, and tibiæ. Eyes naked. Pubescence whitish, very short and sparse, but visible on the antennæ, sides of the thorax, and on the gaster where it fails to conceal the shining surface.

Mandibular teeth and gaster black; remainder of the body and appendages deep red; antennal funiculi, legs, especially the tibiæ, mandibles, and antero-lateral corners of the head, darker and more brownish. Ocellar region and mesonotum slightly infuscated even in larger workers, but there is no increased tendency to infuscation in the smaller workers.

Female. — Length, 4–5 mm.

Mandibles and clypeus like those of the worker, except that the latter is more convex and less prominently keeled. Head slender, excluding the mandibles distinctly longer than broad, with long, anteriorly converging cheeks. Thorax distinctly narrower than the head. Petiole similar to that of the worker but with sharper superior border, often slightly notched in the middle. Gaster small. Legs slender. Wings somewhat longer than the body (5.3 mm.).

Body smooth and shining, very finely shagreened, back of head and mesonotum more opaque; gaster very glabrous, being much more delicately shagreened than in the worker.

Hairs golden yellow, suberect, slender and obtuse, much longer than in the worker and more abundant, especially on the upper surface of the head and thorax and on all parts of the legs. There are a few conspicuous erect hairs along the anterior or flexor surfaces of the antennal scapes, on the lower surface of the head, and on the border of the petiole. On the gaster the long hairs are sparse and arranged in three regular rows on the first and second, in two rows on the succeeding segments.

Mandibular teeth and gaster black, remainder of body dull yellowish red. Antennæ, legs, posterior portion of head, mesonotum, scutellum, and metanotum decidedly darker. The anteromedian and parapsidal blotches are faintly indicated on the mesonotum. Wings rather opaque, grayish hyaline, with fuscous veins and black stigma.

Male. — Length, 6.5–7 mm.

Mandibles pointed, edentulous. Head short, broadest through the eyes; posterior corners broadly rounded; cheeks short, flattened, converging in front. Clypeus carinate in front, depressed behind. Thorax just in front of the wings hardly broader than the head through the eyes. There is a median longitudinal depression on the base of the epinotum, and the metanotum is concave. Petiole very thick and blunt above, anterior and posterior surfaces both convex, border with a faint median notch.

Head, thorax, legs, and antennæ subopaque, finely shagreened; mandibles, clypeus, vertex, and scutellum shining as are also the petiole and especially the gaster.

Hairs and pubescence grayish, the former short and erect on the clypeus, thorax, gaster, and legs; the latter sparse and indistinct except on the antennæ and legs. Eyes almost imperceptibly hairy.

Black; mouth-parts, legs, and genitalia fuscous. Wings like those of the female but of a slightly darker tint.

Described from numerous workers and females and two males from a single colony found near the summit of Mt. Pisgah (altitude about 1400 feet), at Colebrook, Litchfield County, Conn., and several workers taken at Black Hawk Spring, near Rockford, Ill.

F. nepticula is very closely related to the form I have called *F. microgyna* var. *nevadensis* (*vide infra*) and known only from a single female specimen from Ormsby County, Nevada. The female *nepticula* differs, however, in having much fewer erect hairs on the antennal scapes and body and, owing to the nearly complete absence of grayish pubescence, a more shining head and thorax. Moreover, the head, thorax and appendages are decidedly darker and less red than in *nevadensis*. The worker *nepticula* resembles that of *F. dryas* in coloration and the peculiar lustre of the gaster, but its average size is less, it has erect hairs on the antennal scapes, the border of the clypeus projects in the form of an angle instead of being transverse, and the epinotum is much rounder and without a flattened declivity.

The Colebrook colony of *nepticula* was first seen during August, 1904, and was mistaken for a colony of *F. dryas*, as only workers were found in the nest. They were under a large flat stone, the edges of which they had banked with vegetable débris after the manner of *F. difficilis* and its var. *consocians*. During the past summer (June 30, 1905), on again visiting the colony, I found it to contain several of the minute females (mostly callow), and was thus able to satisfy myself that it represented a distinct and undescribed species. Numerous workers, together with many cocoons, were kept for several weeks in an artificial nest. Dozens of the tiny females but only two males hatched during the first week in July. No workers hatched till July 9, when they appeared in great numbers. The small size of the female seems, therefore, to be correlated with more precocious development than in our common species of *Formica*. The movements of the workers are extremely active and petulant, contrasting with the movements of such forms as *F. integra*, *consocians*, etc., and resembling those of *F. sanguinea*. The females are more phlegmatic except when greatly excited. The approximate date of the nuptial flight is July 11. At any rate, during the early morning hours of that day most of the females managed to escape and ascended to the ceiling of the room in which I had placed their artificial nest. The diminutive size of the females strongly indicates reduced or belated fertility, so that this species, like *F. difficilis* and its var. *consocians*, *F. microgyna*, *nevadensis*, and *montigena*, very probably establishes its colony with the aid of workers belonging to some other species of *Formica*. I suspect that *F. subpolita* var. *neogagates* is the ant used for this purpose, as its workers so closely resemble the female *nepticula* both in size and coloration. I find, moreover, that a small colony of *neogagates* workers can be induced to adopt a deälated female *nepticula*.

4. **Formica nevadensis** Wheeler.

F. microgyna var. *nevadensis* WHEELER, Bull. Am. Mus. Nat. Hist., Vol. XX, Oct. 11, 1904, p. 373. ♀.

Since both the worker and female of *F. nepticula* are known, it is no longer probable that *nevadensis* should be attached as a variety to *microgyna*. The female *nevadensis* has a very smooth and shining gaster and this is probably also the case in the unknown worker, which would thus differ decidedly from the opaque-bodied worker of *microgyna*. I believe, therefore, that we are justified in raising *nevadensis* to specific rank. The discovery of the worker of this form will enable us to decide whether *nepticula* is to be regarded as an independent species or merely as an eastern subspecies of *nevadensis*.

5. **Formica impexa** sp. nov.

Worker. — Length, 3.3–6 mm.

With the habitus of *F. rufa.* Mandibles 8-toothed. Clypeus broadly rounded in front, not produced in the middle, carinate its entire length. Head, excluding the mandibles, distinctly longer than broad, even in the largest workers. Cheeks rather long, straight, subparallel. Posterior border of head straight, posterior corners rounded. Joints 1–4 of antennal funiculus decidedly longer and more slender than the remaining joints. Thorax of the *rufa* type but with the epinotum very low and rounded. Petiole rather thick anteroposteriorly, its anterior surface convex in profile, its posterior flattened, its edge, especially in smaller workers, very blunt; seen from behind it is produced upwards in the middle and of rather variable outline, being notched in the middle in some specimens, but oftener more or less rounded.

Mandibles lustrous, finely and sharply striated. Surface of clypeus uneven. Frontal area shining. Remainder of body opaque, distinctly but finely shagreened.

Whole body and all the appendages clothed with very minute white pubescence which is rather sparse on the head and thorax, but dense and concealing the ground surface on the gaster. Body, antennal scapes, and legs covered with coarse, obtuse, erect or suberect, whitish or yellowish hairs. On the gaster these are uniformly distributed and in certain lights very conspicuous. They are also very numerous and prominent on the upper surface of the thorax, clypeus, front, vertex, posterior corners, and lower surface of head, but absent or very sparse on the cheeks, pleuræ, and coxæ. On the legs they are prominent both on the flexor and extensor surfaces.

Head and thorax red. Gaster black. Even in the largest specimens, the mandibles, anterior border of clypeus, and apical half of funiculi are dark reddish brown; ocellar triangle, upper surface of pro- and mesonotum, much of the upper surface of the petiole, legs and coxæ, except their articulations, more or less blackened. Fore coxæ largely red. Anal region yellowish. In the smallest workers the infuscation is more extensive, involving the whole of the posterior portion of the head and the epinotum.

Described from twelve workers taken August 12, 1902, by Mr. O. McCreary from a colony nesting under a stone on the Porcupine Mountains in northern Michigan. Types in the American Museum of Natural History, cotypes in the University Museum, Ann Arbor, Michigan.

F. impexa is allied to *F. oreas* Wheeler and *F. microgyna* Wheeler, with both of which it agrees in having erect hairs on the antennal scapes. It differs from *oreas* in the much coarser and less abundant, erect and obtuse hairs on the head and thorax, the prominent hairs on the gaster, the longer head, more opaque surface of the head and thorax, etc. In most of these characters it also differs from the typical *microgyna.* The erect hairs on the gaster of *impexa* are much more robust and obtuse than in the latter species. The new species also resembles *F. difficilis* Emery and notably its var. *consocians* Wheeler except in pilosity.

It is probable that the female of *F. impexa* is peculiar either in being very diminutive, like the females of *F. difficilis*, *microgyna*, *nepticula*, etc., or in having an unusual color like the female of *F. oreas*. Until this sex of *impexa* is discovered there may be some doubt as to whether the form should be regarded as a species distinct from *rufa*. It certainly differs very markedly in pilosity from all the subspecies and varieties of *rufa* hitherto described.

The North American Ants of the Genus Dolichoderus.

By William Morton Wheeler.

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Article XIX. — THE NORTH AMERICAN ANTS OF THE GENUS DOLICHODERUS.

By William Morton Wheeler.

Plates XII and XIII.

Four species of the mainly tropicopolitan genus *Dolichoderus* have been recorded from America north of Mexico and the West Indies, namely: *D. mariæ* Forel, *taschenbergi* Mayr, *plagiatus* Mayr, and *pustulatus* Mayr. When in 1886 the latter author published a comparative description of all of these forms, he called attention to their close affinity with the single European and Siberian species, *D. quadripunctatus* L., and to their still closer relationship with one another.[1] Mayr even maintained that the four forms might be regarded as varieties of a single species, but owing to the absence of annectent variations he preferred to let them stand as separate species. They were based on worker specimens, though he briefly described the females of *mariæ* and *pustulatus*.

That during the past twenty years our meagre knowledge of these interesting ants has remained *in statu quo*, must be largely, if not exclusively, due to their scarcity or extremely local distribution. Having recently found two of the species, *D. mariæ* and a variety of *taschenbergi*, rather common in the pine-barrens about Lakehurst, New Jersey, I decided to study the peculiarly North American *Dolichoderi* in my collection and to publish a revision of the species, together with some notes on their hitherto unknown habits. As a result of this study, I cannot say that I am prepared to merge all four so-called species into one, but nevertheless I feel certain that *pustulatus* is merely a subspecies of *plagiatus*. The only differences I can detect between these two forms are in size, sculpture, and coloration. Among my specimens there are individuals representing a distinct variety or subspecies of each of the four Mayrian species, and showing that these, like most of our North American ants, are decidedly variable. I am able to add descriptions of the male of *mariæ* and of the male and female of the typical *plagiatus*.

It is a singular fact that the *Dolichoderi* of America north of Mexico and the West Indies are all confined to the humid eastern portion of the continent At any rate none of the species is known to inhabit

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[1] Die Formiciden der Vereinigten Staaten von Nordamerika. Verhandl. k. k. zool. bot. Gesell. Wien, XXXVI, 1886, p. 434.

the arid Southwestern and Pacific States. I have searched diligently but in vain for these ants in Texas, New Mexico, Arizona, and Colorado. In these regions *Dolichoderus* is represented taxonomically as well as ethologically by another genus of the same subfamily, *Liometopum*. *D. plagiatus* is almost subboreal in its distribution. It is found as far north as Canada (*teste* Abbé Provancher) and when occurring further south prefers sunny glades on hills or mountains. *D. mariæ* is known to occur as far north as Connecticut (Emery), but both this species and *taschenbergi* are properly members of the Carolinian zone.

DESCRIPTIONS OF NORTH AMERICAN DOLICHODERI.

The workers of our different *Dolichoderi* may be identified with the aid of the following table:

1\. Head and thorax with shallow foveolæ, shining........................ 2
Head and thorax coarsely and deeply foveolate, subopaque............ 4
2\. Epinotal concavity with a strong median longitudinal ridge; head, thorax, and petiole yellowish red............................... 3
Epinotal concavity without such a ridge; at least the head black...... 5
3\. Body hairless above..................................*D. mariæ* Forel
At least the upper surface of head and thorax with erect hairs......*mariæ davisi* subsp. nov.
4\. Base of gaster with reddish-yellow spots..................*plagiatus* Mayr
Gaster entirely black..................*plagiatus* var. *inornatus* var. nov.
5\. Without erect hairs on the upper surface; body and legs deep black or very dark brown.. 6
With erect hairs on the upper surface; thorax reddish brown............7
6\. Body black or brown-black, legs dark brown............*taschenbergi* Mayr
Body and appendages deep black.......*taschenbergi* var. *gagates* var. nov.
7\. Base of gaster with reddish yellow spots.........*plagiatus pustulatus* Mayr
Gaster entirely black..............*pustulatus* var. *beutenmuelleri* Wheeler

Dolichoderus mariæ *Forel.*

Dolichoderus mariæ Forel, Bull. Soc. Vaud. Sc. Nat., XX, pp. 34, 35. ☿
Dolichoderus mariæ Mayr, Verhandl. k. k. zool. bot. Gesell. Wien, XXXVI, 1886, pp. 436, 437. ☿ ♀
Dolichoderus mariæ Dalla Torre, Catalog. Hymenop., VII, 1893, p. 159.
Dolichoderus mariæ Emery, Zool. Jahrb. Abth. f. System., VIII, 1894, p. 330.
Dolichoderus mariæ Emery, 27th Ann. Rep. State Board Agr. New Jersey (1899), 1900, p. 540.
Dolichoderus mariæ Wheeler, Bull. Am. Mus. Nat. Hist., XX, 1904, p. 304.

Worker (Fig. A).—Length 3.5–4.5 mm.

Head subelliptical, sides evenly rounded; occipital border rather straight; eyes placed a little in front of the middle. Clypeus flat, its anterior border distinctly emarginate and impressed in the middle. Antennal scape curved at the base, its tip extending a distance equal to its own diameter beyond the posterior corner of the head. Funicular joints all distinctly longer than broad; two basal longer than the succeeding joints; first joint nearly 1½ times as long as the second; terminal joint somewhat longer than the two preceding joints taken together. Thorax in profile with rounded promesonotal surfaces, the former somewhat flattened behind; mesoëpinotal constriction deep. Epinotum with convex basal surface, slightly flattened in the middle, nearly as long as the mesonotum and suddenly passing by a sharp edge into the very concave declivity. Seen from above the prothorax is robust; the meso- and epinotum much narrower and laterally compressed. The sharp margin between the two epinotal surfaces is broadly rounded when seen from above and extends downward on either side to the metasternal region. There is a distinct median keel on the epinotal concavity. Petiole robust, as broad as the epinotum, but not as high as the margin between the two epinotal surfaces, with shorter and more convex anterior, and longer and flatter posterior surface; dorsal margin of node blunt and, when seen from behind, straight and transverse. Gaster broad, somewhat flattened above, first segment with a straight anterior border; constriction between the first and second segments somewhat deeper than between the succeeding segments.

Whole body smooth and shining. Mandibles with a few widely scattered, coarse punctures. Clypeus with very fine longitudinal striæ. Head, thorax, and petiole finely reticulate, with shallow foveolæ, most distinct on the posterior portion of the head and on the meso- and epinotum, but especially on the last. Epinotal concavity shining, longitudinally striated. Gaster and legs very finely reticulate, more glabrous than the other portions of the body except the mandibles.

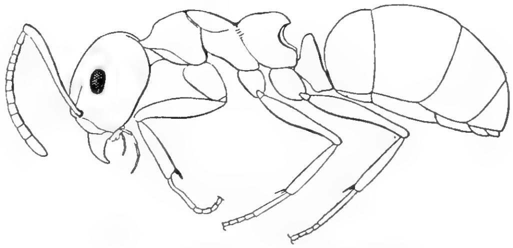


Fig. A. *Dolichoderus mariæ* Forel. Worker.

Body naked, except for a few yellowish hairs on the clypeus, mandibles, lower surface and tip of gaster, coxæ, and flexor surfaces of the femora. Pubescence pale, very sparse and indistinct except on the gaster, cheeks, and antennal funiculi.

Yellowish blood-red, terminal half of antennal funiculi black. Gaster black, with the anterior half of the first and a rather square blotch on either side of the second segment near its anterior border, yellow.

Female.—Length 4–4.5 mm.

Differs from the worker in the following characters: Clypeus convex, with a very distinct median notch. Eyes larger, ocelli present. Epinotum with convex, evenly rounded basal surface, passing into the concave surface through a rounded angle; both surfaces of equal length. Head, thorax, and petiole much smoother, quite as glabrous as the gaster. Epinotum above with shallow foveolæ, finely rugulose on the sides. Pilosity like that of the worker except that the hairs are longer on the venter. Color like that of the worker except that the head, thorax, and petiole, and the spots on the gaster are more yellow even in fully mature specimens. Each ocellus with a small brown spot. Mesonotum and posterior edge of scutellum dark brown. Wings colorless, with colorless veins and very pale yellow stigma.

Male.—Length 5–5.5 mm.

Head, including the eyes, broader than long; posterior portion evenly rounded, cheeks short, converging in front. Mandibles well developed, with denticulate blades, overlapping each other. Clypeus somewhat flattened, its anterior border without a median notch. Eyes and ocelli large and prominent. Antennæ long, all the joints longer than broad; scape rather short, as long as the first and second funicular joints together; first about half as long as the succeeding joints, which are cylindrical and subequal. Thorax robust, through the wing insertions as broad as the head through the eyes. Epinotum convex, its basal surface passing into the declivity through a broadly rounded angle. Petiole erect, low, very thick and blunt above; in profile with flat and sloping anterior and convex posterior surface. Seen from behind the upper border is straight or slightly impressed in the middle. Gaster like that of the worker but more slender and without the distinct constriction between the first and second segments. Genitalia small and embedded. Legs slender.

Mandibles smooth and shining, very sparsely and coarsely punctate. Clypeus concentrically striated, smooth in the middle. Head subopaque, densely reticulate-punctate. Thorax more shining and finely reticulate and gaster glabrous and still more delicately reticulate. Sides of scutellum sharply striated.

Pilosity and pubescence similar to those of the worker.

Deep black; tarsi and mouth-parts brown; mandibles, outer corners of clypeus, first funicular joint, wing-insertions, trochanters, and inner genital valves, honey yellow. Wings like those of the female.

The types of this beautiful species are from Vineland, New Jersey. They are in the collection of Professor A. Forel. I have seen workers from the District of Columbia, Black Mountains, North Carolina, and Manumuskin and Clementon, New Jersey, and all three phases from Lakehurst in the same State. The species has been recorded also from Virginia (Mayr) and Connecticut (Emery).

Dolichoderus mariæ davisi subsp. nov.

Worker.—Differs from the worker of the typical *mariæ* in its somewhat smaller size (2.75–3.5 mm.) and in the following characters: The basal surface of the epinotum has its greatest convexity behind the middle instead of at or very near the middle as in the typical *mariæ*. The antero-median surface of the petiole is more impressed and the edge is sharper. The sculpture of the head and thorax is more pronounced, so that these parts appear to be subopaque. The red portions of the body are duller and somewhat brownish. The most striking character, however, is the abundant pilosity. The whole surface of the body and legs, except the epinotum and dorsalmost portion of the gaster, is covered with erect or suberect whitish hairs. These hairs are most numerous on the upper and lower surfaces of the head, and on the pro- and mesonotum. On the antennal scapes they are rather long but not erect. The pubescence is hardly more abundant than in the typical form. Only the base of the first gastric segment is yellow and the lateral spots on the second segment are barely indicated.

Described from seven workers collected July 2, 1905, at Jamesburg, New Jersey, by Mr. Wm. T. Davis, to whom I take pleasure in dedicating this interesting subspecies. A dozen workers labeled "New Jersey" and received some years ago from the late P. J. Schmitt, O.S.B., are indistinguishable from the preceding. *D. davisi* exhibits such a blending of the characters of the typical *mariæ* and *plagiatus* that one is tempted to regard it as a hybrid form. More probably, however, it represents a persisting phylogenetic stage in the development of the typical *mariæ* from a *plagiatus*-like ancestor.

Dolichoderus taschenbergi *Mayr.*

Hypoclinea taschenbergi MAYR, Sitz. B. k. Akad Wiss. Wien, LIII, 1866, p. 498. ☿.

Hypoclinea taschenbergi MAYR, Verhandl. k. k. zool. bot. Gesell. Wien, XX, 1870, p. 958. ☿.

Dolichoderus taschenbergi MAYR, Verhandl. k. k. zool. bot. Gesell. Wien, XXXVI, 1886, pp. 436, 437. ☿.

Dolichoderus taschenbergi DALLA TORRE, Catalog. Hymenopt., VII, 1893, pp. 161, 162.

Dolichoderus taschenbergi EMERY, Zool. Jahrb. Abth. f. System., VIII, 1894, p. 330.

Dolchoderus taschenbergi WHEELER, Bull. Am. Mus. Nat. Hist., XX, 1904, p. 304.

Worker (Fig. B).—Length 3.5–4.3 mm.

Head a little longer than broad, elliptical; eyes in the middle of its sides. Clypeus flattened in front, convex behind, with a straight, entire anterior border, slightly impressed in the middle. Antennal scape curved at the base, its tip extending a distance equal to its own diameter beyond the posterior corner of the head. Funicular joints all longer than broad; first $1\frac{1}{2}$ times as long as the second joint, second $1\frac{1}{2}$ times as long as the third; terminal joint a little longer than the two penultimate joints together. Pro- and mesonotum evenly rounded, somewhat depressed, mesoëpinotal impression pronounced; basal epinotal surface rather faintly convex, somewhat flattened in the middle, passing over abruptly by means of a very sharp margin into the concave declivity. The margin is slightly convex when seen from above and passes down on either side to the metasternum. Petiole low and thick, not as high as the sharp epinotal margin, with a shorter and more convex anterior, and a longer, flatter posterior surface. Border rather sharp in profile; seen from behind it is straight and transverse or slightly impressed in the middle. Gaster broad, somewhat flattened above, with straight anterior border and a somewhat deeper constriction between the first and second than between the succeeding segments.

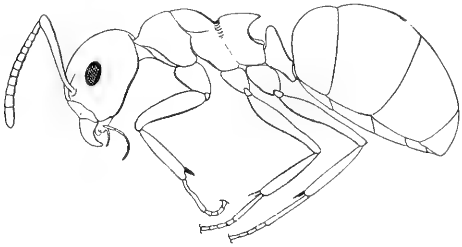


Fig. B. *Dolichoderus taschenbergi* Mayr. Worker.

Sculpture like that of *D. mariæ*, except that the foveolæ on the meso- and epinotum are somewhat more pronounced. In the mesoëpinotal constriction there are a number of regular longitudinal ridges separated by shining depressions. Epinotal concavity without a pronounced median carina, although the surface is longitudinally striated. Meso- and epinotum opaque or subopaque, pronotum and head shining, gaster very glabrous.

Pilosity and pubescence as in the typical *mariæ*.

Brownish black, antennæ, edges of mandibles, and legs dark brown.

Types from Louisiana. The species occurs also in Missouri as Emery has shown. The above description is drawn from a single specimen from the latter State in my collection.

Dolichoderus taschenbergi *Mayr* var. **gagates** var. nov.

Worker. — Differs from the typical form in being deep jet black throughout, with the exception of the edges of the mandibles and the strigils of the fore tibiæ, which are yellowish, and the neck of the pronotum which is brownish. The sculpturing of the head and pronotum seems to be less pronounced than in the typical form, so that these parts are smoother and more shining. The gaster is very glabrous.

Described from numerous workers collected at Lakehurst, New Jersey. The same form occurs at Iona (Erich Daecke), Clementon (H. L. Viereck), and Jamesburg (Wm. T. Davis) in the same State.

Dolichoderus plagiatus *Mayr.*

Hypoclinea plagiata Mayr, Verhandl. k. k. zool. bot. Gesell. Wien, XX, 1870, p. 960. ☿

Dolichoderus plagiatus Mayr, Verhandl. k. k. zool. bot. Gesell. Wien, XXXVI, 1886, p. 436. ☿

Dolichoderus borealis Provancher, Natural. Canad., V, 18, 1888, p. 408. ☿

Dolichoderus plagiatus Dalla Torre, Catalog. Hymenopt., VII, 1893, p. 160.

Dolichoderus plagiatus Emery, Zool. Jahrb. Abth. f. Syst. VIII, 1894, p. 330.

Dolichoderus plagiatus Ashmead, 27th Rep. State Board of Agr. New Jersey (1899), 1900, p. 540.

Worker (Fig. C). — Length, 3–3.5 mm.

Head elliptical; eyes rather large, in front of its middle. Clypeus convex, its anterior border notched and impressed in the middle. Antennal scape curved at the base; tip extending to a distance equal to its diameter beyond the posterior corner of the head. First funicular joint equal to the two succeeding subequal joints together; joints 4–10 nearly as broad as long; terminal a little longer than the two preceding joints taken together. Pro- and mesonotum flattened above, but slightly rounded; mesoëpinotal constriction pronounced; basal surface of epinotum in profile higher than the mesonotum, higher behind, somewhat flattened or even impressed near the middle, terminating behind in a sharp margin, below which lies the concave declivity. Seen from above the margin is broadly rounded and passes down on either side to the metasternum. The declivity in profile is not an arc of a circle, as in *mariæ* and *taschenbergi*, but has a straight or even convex outline above. Petiole thick, with a shorter and more convex anterior, and a longer, somewhat flattened posterior surface; dorsal border in profile rather sharp, seen from behind, straight and transverse. Gaster rather small, flattened, oval when seen from above, with rounded anterior border. There is a very faint constriction between the first and second segments.

Mandibles glossy, with fine longitudinal striæ and coarse punctures. Head and thorax subopaque. Clypeus and front covered with rather sharp longitudinal rugæ. Remainder of head and thorax densely punctate-foveolate, the foveolæ being so close together on the meso- and epinotum that their surfaces may be described as coarsely reticulate-rugose. Epinotal concavity, petiole, gaster, and legs smooth and shining, very finely shagreened; summit of petiole somewhat opaque and rugose.

Hairs whitish, erect, rather sparse but conspicuous on the mandibles, antennal scapes, upper surface of head and thorax, but less abundant on the gaster and very short and inconspicuous on the legs. Pubescence very sparse and barely visible, except on the gaster and antennæ.

Mandibles black, with reddish internal edges. Head, palpi, and antennæ black; scape and first funicular joint reddish yellow. Thorax and petiole dark red; meso- and epinotum and border of petiole sometimes black. Gaster black, with much of the base of the first segment and a large spot on either side of the second segment reddish yellow. In specimens from some colonies the first and second segments are reddish yellow throughout, or with only a dark median cloud on the second segment. Legs reddish yellow.

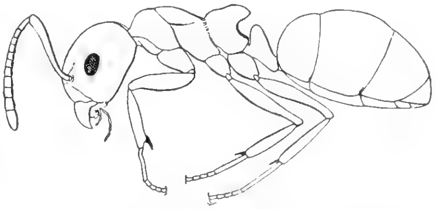


Fig. C. *Dolichoderus plagiatus* Mayr. Worker.

Female (deälated). — Length, 4–4.25 mm.

Head very similar to that of the worker. Thorax nearly as broad as the head, with the epinotum shaped like that of the worker, except that the convex basal surface is not so high as the mesonotum and does not slope upward from before backward. Seen from above the sharp margin between the basal surface and concavity is straight and very feebly excised or sinuate in the middle. The foveolæ on the head and thorax are pronounced; they are smaller and somewhat more scattered on the pro- and mesonotum and still more so on the scutellum, and somewhat elongated on the mesonotum; but much larger and almost confluent on the basal surface of the epinotum. Pro- and metapleuræ longitudinally rugose, mesopleuræ very finely punctate-rugulose. Posterior petiolar surface finely and transversely rugose. In one specimen the two basal segments of the gaster are yellow throughout, with a faint fuscous cloud in the middle of the second segment; in another specimen the gastric markings are like those of the worker. Pilosity like that of the worker.

Male. — Length, 4 mm.

Head, including the eyes, broader than long, broadly rounded behind, with prominent ocelli; cheeks short, converging anteriorly. Mandibles well developed. Clypeus with straight anterior border, entire in the middle. Antennæ rather long; scape hardly as long as the two first funicular joints, first joint about half as long as the second, which is distinctly longer than the succeeding joints; joints 3–11 subequal, cylindrical; terminal a little longer than the penultimate joint. Thorax barely as broad as the head through the eyes. Epinotum in profile with somewhat flattened basal and declivous surfaces meeting at a rounded obtuse angle. Petiole decidedly longer than wide or high, blunt above, with a short convex anterior and a long, flat, posterior surface; seen from behind, the upper border is rounded. Gaster elongate-elliptical, more slender than in the worker. External genitalia rounded and lappet-like. Legs long and robust.

Head and thorax subopaque, finely reticulate. Mandibles finely striated. Clypeus and front rather indistinctly punctate-rugulose; posterior portion of head, pro- and mesothorax sparsely foveolate. Pleuræ, scutellum, and epinotum granular. Petiole, gaster, and legs smooth and shining.

Pilosity like that of the worker. Pubescence finer and denser on the gaster and legs.

Head and thorax black, mandibles, antennæ, legs, petiole, and gaster dark brown. Wings whitish hyaline, with yellow veins and stigma, the latter with a dark brown posterior border.

The types of this species are from "Illinois" and are preserved in the Museum of Stockholm.

The above description is drawn from a number of workers collected near Rockford, Illinois, two females, one taken on Staten Island by Mr. Wm. T. Davis and the other at Lakehurst, New Jersey, by myself, and a single male taken at Newport, Rhode Island, by Joseph Leidy (Collection of American Entomological Society). There are workers in my collection from the following localities: Arlington, Virginia; Lakehurst, New Jersey; Iona, New Jersey (Erich Daecke), and Jamesburg, New Jersey (Wm. T. Davis); summit of Torne Mountain, Ramapo, New York (Wm. T. Davis), Lehigh Gap, Pennsylvania (H. L. Viereck), and Colebrook, Connecticut. The species has also been taken in Canada by Provancher and in the District of Columbia by Pergande.

Dolichoderus plagiatus *Mayr* var. **inornatus** var. nov.

Worker. — Differs from the typical form in having the gaster entirely black, without any indications of the reddish yellow spots of the typical form.

Eight workers from Rockford, Illinois, and a single worker from Lakehurst, New Jersey.

Dolichoderus plagiatus pustulatus *Mayr.*

Dolichoderus pustulatus Mayr, Verhandl. k. k. zool. bot. Gesell. Wien, XXXVI, 1886, pp. 435, 436. ☿ ♀

Dolichoderus pustulatus Dalla Torre, Catalog. Hymenopt., VII, 1893, p. 160.

Dolichoderus pustulatus Emery, Zool. Jahrb. Abth. f. Syst., VIII, 1894, p. 330.

Dolichoderus pustulatus Ashmead, 27th Rep. State Board of Agr. New Jersey (1899), 1900, p. 540.

Worker. — Length, 3–3.8 mm.

Differs from the typical *plagiatus* in its smaller size, less pronounced sculpture and more uniform coloration. Head and thorax shining, with smaller and more scattered foveolæ, except the epinotum, which is coarsely foveolate. Thorax and petiole darker, often nearly black; the spots on the gaster are smaller. There are no erect hairs on the antennal scapes.

Female. — "Length, 4.4 mm.

"Coloration like that of the worker, but the mesonotum, scutellum, and mesopleuræ are blackish brown. Pilosity and sculpture as in the worker, but mesonotum with finer, coriaceous rugosity, and shallower, more scattered foveolæ. The convex basal epinotal surface is separated from the strongly concave declivity by a very prominent transverse ridge, which is feebly emarginate in the middle." (Mayr.)

Recorded by Mayr from New Jersey, District of Columbia, and Virginia. Three workers from Dacosta, New Jersey, from the collection of the American Entomological Society, belong to this subspecies. Mayr included the following variety in his description, as is evident from his mentioning specimens without spots on the gaster.

Dolichoderus plagiatus pustulatus *Mayr* var. **beutenmuelleri** *Wheeler.*

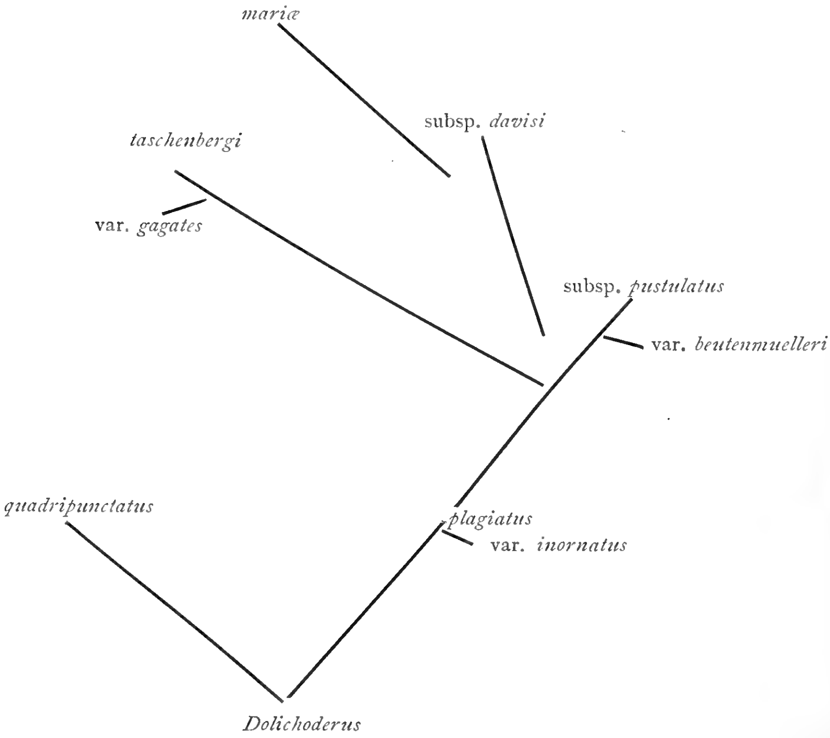
Dolichoderus plagiatus Mayr var. *beutenmuelleri* Wheeler, Bull. Am. Mus. Nat. Hist., XX, 1904, p. 304. ☿

Through a *lapsus calami* in my paper on the ants of North Carolina, this variety was attached to *plagiatus* proper instead of to its subspecies *pustulatus*. From this form it differs merely in the absence of any reddish-yellow markings on the gaster and hence in exactly the same way as the var. *inornatus* differs from the typical *plagiatus*. The antennal scapes have a few conspicuous erect hairs, especially on their flexor surfaces.

The types are from the Black Mountains of North Carolina (Wm. Beutenmüller). I have also taken several workers in various localities in the pine-barrens about Lakehurst, New Jersey. I have received from Mr. H. L. Viereck a single female belonging either to this variety or to the preceding subspecies. It was collected at Pablo Beach, Florida, April 8, by Mr. P. Laurent. As the gaster is lacking, the specimen cannot be more accurately identified.

THE RELATIONSHIPS AND HABITS OF THE NORTH AMERICAN DOLICHODERI.

A comparison of the foregoing *Dolichoderi* with one another and with the palæarctic *D. quadripunctatus* suggests a common ancestral form for both the Old and New World species. *D. plagiatus*, especially, seems to be very closely related to *quadripunctatus;* the males of the two species being, in fact, almost indistinguishable. Among the American species we can pass, on the one hand, from the highly foveolate *plagiatus* through successively smoother subspecies like *pustulatus* and *davisi* to the very smooth and brightly colored *mariæ*. The typical *taschenbergi*, on the other hand, with its extremely melanistic variety *gagates*, may also be derived from some smoother form of *plagiatus*, like *pustulatus*. These hypothetical derivations are indicated in the following diagram:



The habits of the palæarctic *D. quadripunctatus* have been studied by Latreille and Forel. Latreille's observations were embodied in a remark that the species is frequently found on old tree-trunks and that its societies are very small ("très-peu nombreuse").[1]

Forel has given a much more satisfactory account of this ant.[2] He finds that it is one of the components of a walnut-tree ant-fauna, which comprises also *Colobopsis truncata* and *Leptothorax affinis*. It nests in the wood or bark of dead branches in colonies which are rather small though much larger than the colonies of *Colobopsis*. As soon as the morning has grown sufficiently warm the workers descend the trees in files and distribute themselves over the surrounding plants where they lap up the sweet exudations from flowers, leaves, and twigs. Forel did not see them attending aphides. When disturbed they timidly crouch in the crevices of the bark. He is inclined to believe that the close superficial resemblance between the minor workers of *Colobopsis truncata* and the workers of *D. quadripunctatus* is due to mimicry. Not only are these two ants, belonging to very different genera and even subfamilies, the only European species with spotted gasters, but they closely resemble each other also in gait, stature, and behavior. Forel found as many as nine different nests of *D. quadripunctatus* in the dead branches of a single walnut tree. When workers from seven of these were placed in the same box, there were no hostilities. He concludes, therefore, that all of these nests belonged to the same colony. In other words, the colonies of this species are polydomous, but each colony contains several deälated females.

While Forel's statements go to show that the European *Dolichoderus*, like many of the tropical species, is strictly arboreal, the observations I have been able to make on our American species reveal some interesting and important differences. These observations show very clearly that our *Dolichoderi* represent at least three separate species, which are ethologically as well as taxonomically quite distinct from the palæarctic form.

The workers of *D. plagiatus* and its subspecies and varieties are occasionally found in small companies, running over the leaves of bushes and young trees in the sunny clearings of our northern woods. They lick the surfaces of the leaves wherever they are covered with honey-dew, *i. e.*, the excrement of aphides, and undoubtedly also

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[1] Histoire Naturelle des Fourmis, Paris, 1802, p. 181.

[2] Fourmis de la Suisse, 1874, pp. 286–288, and Variétés Myrmécologiques, Ann. Soc. Ent. Belg., Tome XLV, 1901, pp. 380–382.

collect the sweet substance directly from these little insects. On only one occasion have I been able to find a nest of *plagiatus*. While walking on the summit of one of the Litchfield hills near Colebrook, Conn., my attention was arrested by an unusually large number of workers (about forty) of this species clustered about some aphides on the lower surface of the leaves of a very young chestnut tree. I carefully followed the ants as they left the aphides in a straggling file and descended the tree trunk. They ran over the twigs and dead leaves and finally disappeared in a little depression in the ground about eighteen inches from the base of the tree. This depression was so well concealed under the dead leaves and twigs, that it would never have been seen without following the foraging ants. It contained between sixty and seventy workers, a number of worker larvæ and pupæ and a few callows. Many of the ants, together with the green leaves covered with aphides, were confined for a few days in an artificial nest where they could be readily seen imbibing the drops of sweet liquid from the anal openings of the plant-lice. When disturbed the ants behaved like *D. quadripunctatus;* that is, they crouched with folded antennæ in the depressions on the under sides of the leaves. Careful search failed to reveal any other colony of *D. plagiatus* in the neighborhood, and as I have never seen larger companies of these ants whenever I have found them in other localities, I feel certain that they never form large colonies. In this respect *plagiatus* resembles the European species, but though our American species still retains the ancestral habit of seeking its food on trees and bushes, it no longer nests in dead wood but in the soil.

These habits are much more strikingly displayed by *D. mariæ* and *taschenbergi* var. *gagates*. As these ants are among the most beautiful and conspicuous inhabitants of that botanical and entomological paradise, the New Jersey pine-barrens, it is surprising that none of the collectors who annually visit that region has taken the pains to observe and publish an account of these insects. Both *mariæ* and *gagates* are about equally abundant and, except in a few particulars, have identical habits. The colonies are very large, comprising thousands of individuals, and strictly monodomous—that is, restricted to a single nest. The nest is excavated in the pure sand, nearly always about the roots of the broom beard-grass (*Andropogon scoparius*) (Plates XII and XIII) or of the liliaceous "turkey-beard" (*Xerophyllum setifolium*), so characteristic of the pine-barrens; more rarely about the roots of small bushes or in remnants of pine stumps. The workers remove nearly every particle of sand from the roots and dig a pot-shaped cavity from 12–18 inches in depth and 3–5 inches in diameter. (Plate XIII, Fig. 2.) The spaces between the root-fibres serve as galleries and in them the larvæ and pupæ are kept. The withdrawal of so much sand from the roots of the grass often destroys the vigor of the plant and prevents it from flowering. Bits of dead leaves, pine-needles, etc., are heaped over the surface between the grass-blades sometimes in sufficient quantity to form a flat mound, but quite as often the top of the nest is concave owing to the withdrawal of the sand and its being only partially replaced by vegetable débris. One large nest of *gagates* about ten inches in diameter was seen in the open woods surmounted by a flat mound consisting exclusively of flakes of charred pine bark which the ants had collected and placed not only on the top of the nest but between the root-fibres to a depth of a foot. On warm, sunny days, the workers bring their brood so near the surface that the maturer pupæ may be exposed to the light, while the ants themselves bask in the sun in a great mass among the bases of the grass-stems. At such times a *gagates* colony sparkles like a mass of jet beads and a colony of *mariæ* is even more beautiful, as it reflects the sunlight from thousands of bright-red and blue-black bodies.

The nests are most easily located by first finding the ants on the foliage of some one of the numerous oaks (*Quercus nana*, *obtusiloba*, *marylandica*, *prinoides*, etc.) or pines (*Pinus rigida* and *inops*) so characteristic of the barrens. A few hundred *gagates* or *mariæ* may be seen attending aphides or coccids (*Chermes*) on a branch of one of these trees and thence traced in an uninterrupted file descending the trunk and moving over the white sand, dead leaves, and pine-needles sometimes a distance of 30–50 feet to the nest. Often several files go out from the same nest in different directions to as many different trees. From the large *gagates* nest above described six files were seen radiating and traversing the barren ground for distances varying from 20 to 40 feet before they reached their respective trees.

Although these ants subsist very largely on the excrement of plant-lice and coccids, they are also very fond of insect food. A caterpillar or dead insect dropped near one of their files is soon completely covered with ants and devoured *in situ*. It is probable that the aphides and coccids within a radius that can be conveniently patrolled by a single colony are far from being sufficient to supply its thousands of workers with food. Hence the colonies must from time to time move to new localities and excavate fresh nests. That this is not infrequently done is shown by the following observations: First, several large nests which I located during September, 1904, were found to have been deserted when I revisited them during August, 1905. Second, in a particular locality the number of abandoned is much greater than the number of inhabited nests. Third, on September 16, 1905, I actually saw a large colony of *mariæ* in the act of excavating a new nest in a bunch of grass. Such changes of domicile can be readily effected on account of the simple architecture of the nest and the ease and rapidity with which the sand is excavated. Both *mariæ* and *gagates* resemble the species of *Eciton* not only in their habit of moving everywhere in files and their probably not infrequent changes of domicile, but also in the singular habit when in their nests of hanging to one another by means of their claws till they form bunches sometimes nearly as large as one's fist.

These ants resent any disturbance of their nests with all the power of their mandibles and anal glands. The secretion from the latter seems to be very volatile and does not have the rancid butter or "Tapinoma odor" of many Dolichoderinæ, like the species of *Tapinoma*, *Forelius*, *Iridomyrmex*, *Dorymyrmex*, *Liometopum*, and some of the tropical species of *Dolichoderus*, but a peculiar smoky or pungent odor, fainter in *mariæ* and stronger and of a somewhat different character in *gagates*.

It is difficult to keep these ants in artificial nests of the Fielde or Janet patterns, as they seem to be very restless and so indifferent to the sunlight that the chambers cannot be readily opened or cleaned. The original Lubbock nest, with its contrivance for permitting the ants to seek their food on an open platform, would probably be better adapted to both of the species.

The sexual phases of *mariæ* and *gagates* make their appearance at different times. I infer this from the fact that on August 19 and 20, 1905, I found the nests of *mariæ* containing male and female pupæ, many mature males, and quite a number of callow females. Single deälated and winged females were also seen running over the sand, so that August 20 is approximately the date of the nuptial flight of this species. On September 16 and 17 I again opened several nests but in only one did I find sexual forms. These were all mature, apparently belated females, and there were only worker pupæ. The nests of *gagates*, however, were searched in vain on all of these dates for males and females and their pupæ. It is certain, therefore, that the colonies of this variety throw off their winged phases earlier in the summer, probably during July and early August. In my collection there is a male *Dolichoderus* taken June 29, 1905, at Lakehurst, New

Jersey, by Mr. Wm. T. Davis. It may be the male of *gagates*, but it differs so little from the male of *mariæ* that I have refrained from describing it. I hope to obtain the males and females of *gagates* by a more timely visit to the pine-barrens during the summer of 1906.

EXPLANATION OF PLATES XII AND XIII.

PLATE XII.

FIG. 1.—Nest of *Dolichoderus taschenbergi* var. *gagates* concealed in a tuft of grass (*Andropogon scoparius*).

FIG. 2.—A similar nest of the same ant showing the accumulation of vegetable débris between the grass-blades. About ¼ natural size.

PLATE XIII.

FIG. 1.—Nest of *Dolichoderus mariæ*. About ⅓ natural size.

FIG. 2.—Nest of the same species partially opened and showing the débris accumulated in the middle and the denuded condition of the grass-roots to make room for the ants and their brood.

FIG. 1.

FIG. 2.

FIG. 1.

FIG. 2.

The North American Ants of the Genus Liometopum.

By William Morton Wheeler.

AUTHOR'S EDITION, extracted from the BULLETIN
OF THE
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Vol. XXI, Article XX, pp. 321–333.
New York, November 14, 1905.

The Knickerbocker Press, New York

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Article XX.—THE NORTH AMERICAN ANTS OF THE GENUS LIOMETOPUM.

By William Morton Wheeler.

The soft, velvety ants of the remarkable Dolichoderine genus *Liometopum* Mayr appear to be confined to the south temperate portions of the northern hemisphere. So far as known, Europe, Asia, and North America each has a characteristic species. The large male of the European form, *L. microcephalum*, was described more than a century ago by Panzer [1] although the corresponding worker form was not discovered till more than fifty years later by Mayr.[2] This author was also the first to publish a brief description of the worker of our American species, *L. apiculatum*, from specimens collected in Mexico by Professor Bilimek.[3]

In 1894 Emery [4] described some Californian specimens as a new variety (*occidentale*) of the European *microcephalum*, but, as I shall endeavor to show, this form had best be regarded as a variety of *apiculatum*. More recently Forel has described a third species from Assam as *L. lindgreeni*.[5]

In addition to these three living species four fossil forms have been recorded from the Tertiary of Europe and North America: *L. antiquum* Mayr, *imhoffi* Heer, and *L. schmidti* Heer from Radoboj,[6] and *L. pingue* Scudder from White River, Utah, and Green River, Wyoming.[7] These species, however, were all described from imperfectly preserved male and female specimens more or less dubiously referable to the genus *Liometopum*.

During my myrmecological excursions into the southwestern States and Territories I have frequently met with our American *Liometopum* and have been able to learn something of its habits. Specimens of these ants from a number of localities have been accumulating in my collection till it seems to me to be possible to form a better conception of the geographical distribution of the species.

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[1] Fauna Insect. German., V, 1798, P. 54, T. 2.

[2] Beschreibung einiger neuer Ameisen. Verhand. zool. bot. Ver. Wien, Bd. II, 1852, p. 144.

[3] Neue Formiciden. Verhand. zool. bot. Gesell. Wien, XX, 1870, p. 961.

[4] Beiträge zur Kenntniss der nordamerikanischen Ameisenfauna. Zool. Jahrb. Abth. f. Syst., VIII, pp. 330, 331.

[5] Variétés Myrmécologiques. Ann. Soc. Ent. Belgique, Tome XLVI, 1902, p. 293.

[6] Vorläufige Studien uber die Radoboj-Formiciden. Jahrb. k. k. geolog. Reichsanst., 1867, XVII, pp. 57-61, Taf. I.

[7] On the First Discovered Traces of Fossil Insects in the American Tertiaries. Bull. U. S. Geol. Surv. Terr., III, 1877, p. 742; The Tertiary Insects of North America. U. S. Geol. Surv. Terr., 1890, p. 617.

Emery was under the impression that there were two species of *Liometopum* in North America, *L. apiculatum* Mayr, originally described from Mexico, and *L. microcephalum* Panz. var. *occidentale* Emery from California. Both of these forms are very closely related to the typical European species and he was undoubtedly right in considering the relationship especially close in the case of *occidentale*, since this form has the color and sometimes also the more rounded petiolar node of *microcephalum*. But an examination of a great number of workers from many colonies shows that all our American *Liometopa* agree in having a more or less pointed petiole and a very different arrangement of the dense pubescence on the gaster. Emery first called attention to the fact that this pubescence in *occidentale* is parted at the median dorsal line and diverges on either side instead of converging towards the median line, as in *microcephalum*. (Conf. Fig. 1 *a* and *d*.) The same is equally true of the typical *apiculatum*, and as both this character and the usually very pointed petiole are common to all our American forms, including a new subspecies to be described below, I do not hesitate to refer them all to Mayr's original Mexican species.

DESCRIPTIONS OF AMERICAN LIOMETOPA.

Liometopum apiculatum *Mayr*.

Liometopum apiculatum MAYR, Verhandl. k. k. zool. bot. Ges. Wien, XX, 1870, p. 961. ☿.

Liometopum apiculatum DALLA TORRE, Catalog. Hymenopt., VII, 1893, p. 163.

Liometopum apiculatum EMERY, Zool. Jahrb. Abth. f. Syst., VIII, 1894, p. 331. ♀.

Liometopum apiculatum FOREL, Biol. Centrali Amer. Insect. Hymenopt., III, 1899–1900, p. 104.

Liometopum apiculatum VIERECK, Trans. Am. Ent. Soc., XXIX, 1903, p. 71. ♀.

Worker (Fig. 1, *a* and *b*).—Length 2.5–6 mm.

Mandibles with about ten teeth on the apical and four or five very small ones on the basal border. Head cordate, as broad as long, in large workers sometimes broader than long, with broadly excised posterior border and rounded sides. Clypeus somewhat bulging at the lateral corners, with a straight anterior border. Frontal area very indistinct. Frontal groove lacking. Eyes in front of the middle of the head. Ocelli, even in the largest workers, very small and indistinct. Antennal scape curved at the base, its tip reaching to the posterior corner of the head. Funiculus but slightly thickened towards the tip; all the joints longer than broad, first and last joints longest, intermediate ones growing shorter distally. Thorax conspicuously narrower than the head, laterally compressed in the meso- and metathoracic regions;, in profile rather flat above, with very distinct promesonotal and mesoëpinotal sutures; seen from above the proand epinotum are of about the same length, the mesonotum somewhat shorter. Petiole produced upward into a sharp point which in some specimens may be prolonged into a soft spine; in profile inclined forward and more or less flattened or even concave both on the anterior and posterior surfaces. Gaster large, elongate elliptical, its anterior segment more or less completely concealing the petiole. Legs rather slender.

Mandibles shining, coarsely punctate towards their tips, finely and densely punctate towards their bases. Body subopaque; clypeus, head, and often also the thorax shining; finely but distinctly reticulate or coriaceous, as are also the appendages.

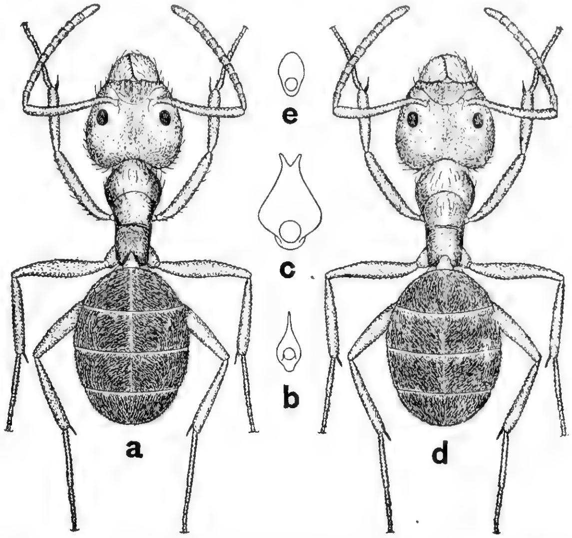

Fig. 1. *a*, *Liometopum apiculatum* Mayr. Worker; *b*, petiole of same seen from behind; *c*, petiole of female; *d*, *L. microcephalum* Panzer, Worker; *e*, petiole of same.

Body and appendages clothed with gray pubescence, so long and dense on the gaster as to hide the smooth ground surface. On the first, second, and third segments it is parted at or diverges on either side of the mid-dorsal line in such a manner as to give the gaster a shifting silky lustre somewhat like that seen on the abdomens of certain Diptera (*Sarcophaga* e. g.). Hairs gray, long, and sub-erect, especially on the head, upper surfaces of the thorax and gaster, and on the legs; short and inconspicuous on the antennal scapes.

Body dark brown or black, with the mandibles, sides of the clypeus, cheeks, and more or less of the thorax, legs, and antennæ reddish yellow or light brown; the amount and distribution of the light color varying considerably even in workers of the same colony. Mandibular teeth black.

Female (Fig. 1, *c*).—Length 12–13 mm.

Apart from the much larger size and the usual sexual characters, the female differs from the worker in being black in color, in having darker mandibles, clypeal corners, legs, and antennæ, and in the arrangement of the gastric pubescence which is not parted and divergent but straight and uniform. The erect hairs are proportionally shorter, but denser and more abundant than in the worker. Wings long (18 mm.), brownish hyaline, with brown veins and black stigma. Petiole high and lyrate when seen from behind, with a deep notch in the summit, so that it appears to be prolonged at the apex into two slightly diverging points.

Male.—Length 9 mm.

Head very small, barely half as broad as the thorax, rounded behind, with short, flat cheeks, prominent eyes and ocelli. Mandibles and clypeus like those of the worker; antennæ long; scape but little thicker than the uniformly cylindrical funiculus; as long as the first and second funicular joints together; first funicular joint more than half as long as the second; third to last joints subequal, a little shorter than the second. Thorax very robust, broadly elliptical from above; mesonotum in profile high and arched. Petiole low and rather thick, its edge broadly rounded and notched in the middle. Gaster very short, convex above. Genital valves very large; outer pair broadly rounded above, with a short, rounded inferior lobe; median pair produced behind into a short, triangular, pointed process which has its dorsal margin broadly excised at the base and the apical margin coarsely dentate. Legs slender. Wings long (14 mm.).

Body more opaque than in the worker and female, owing to the sharper reticulation of the head and thorax.

Hairs and pubescence tawny or golden, distributed as in the female; except that the antennal scapes bristle with numerous erect hairs.

Body and appendages black, mouth-parts and inner genital valves yellowish. Wings of the same color as in the female.

Types from "Mexico," in the collection of Dr. Gustav Mayr of Vienna.

The above description is drawn from numerous workers collected by Mr. C. H. Tyler Townsend on the volcano of Colima, Mexico (7500 ft.), a deälated female from Mexico, received from Dr. Mayr, and a winged female and a single male from Arizona (Am. Mus. Nat. Hist. Coll.). Forel records the species from Pinos Altos, Chihuahua, and Ciudad in Durango, Mexico (8100 ft.). I have seen numerous workers from the following localities: Cañon City (5329 ft.) and Cotopaxi (6371 ft.), Colorado (P. J. Schmitt, O. S. B.); Manitou (6309 ft.), Garden of the Gods, and Cheyenne Cañon (7000 ft.), Colorado; Paisano Pass (5079 ft.) and Ft. Davis (5400 ft.), Texas; Las Vegas (6398 ft.) (W. M. Wheeler), Las Vegas Hot Springs (6726 ft.), and Romeroville (6303 ft.), New Mexico (T. D. A. Cockerell); High Rolls (6550 ft.), Alamogordo (4320 ft.) and Beulah (8000 ft.), New Mexico (H. Viereck). Two deälated females were taken at Manitou and one at Ft. Davis. The workers from Colorado often have the thorax rather pale, so that they approach very closely to the var. *occidentale* Emery (*vide infra*), but I believe that this name should be restricted to the Californian form.

Liometopum apiculatum *Mayr* var. **occidentale** *Emery.*

Liometopum microcephalum Panzer var. *occidentale* Emery, Zool. Jahrb. Abth. f. Syst., VIII, 1894, pp. 330, 331. ☿, ♂.

Worker.—Differs from the typical *apiculatum* in having the thorax and petiole of a clearer and more yellowish red color, although in many specimens the pro- and mesonotum are spotted with black or fuscous. In some individuals the node of the petiole when seen from behind is somewhat rounder and more like that of the European *microcephalum*. On the antennal scapes there are erect hairs, which are lacking in all my specimens of the typical *apiculatum*. This character will serve to distinguish *occidentale* from the similarly colored workers of *apiculatum* often seen in Colorado.

The types are from San Jacinto (1533 ft.) and Mariposa (1962 ft.), California (Collection of Professor Emery at Bologna).

My specimens were taken near Baldy Peak, San Gabriel Mountains, California (6500 ft.), by Messrs. Brewster, Joos, and Crawford, and near Claremont, California (1141 ft.), by Professor C. F. Baker.

Liometopum apiculatum luctuosum subsp. nov.

Worker.—Length 2.5–4.5 mm.

Apart from its somewhat smaller size, the worker of this subspecies differs from the typical *apiculatum* in sculpture, pilosity, and color. The body is much smoother and more shining. The pubescence is shorter even on the gaster so that the smooth surface is more apparent, and there are only a few rather short, erect hairs on the upper surface of the body and none on the legs or antennal scapes. All the specimens are black or very dark brown, with the mandibles, lateral corners of the clypeus, the mouth, and in some specimens also the funiculi or even the scapes of the antennæ dark red or yellowish red. Insertions of antennæ and articulations of legs yellowish.

The types of this well-marked form are from Cheyenne Cañon (7000 ft.) near Colorado Springs, Colorado. I have also taken it at Prescott, Arizona (5320 ft.), in the Coconino forest on the rim of the Grand Cañon of the Colorado (6865–7050 ft.), and down the Bright Angel Trail to an altitude of about 4000 feet. A number of workers were also collected by Messrs. Brewster, Joos, and Crawford near Baldy Peak in the San Gabriel Mountains, California (6500 ft.).

THE HABITS OF LIOMETOPUM.

L. apiculatum is structurally so closely related to the European *microcephalum* that we should expect to find a similar close resemblance in habits. Generally speaking, this proves to be the case. There are, however, a number of rather important ethological differences, which leave no doubt that the American is sufficiently distinct from the European form to be regarded as a "good" species.

The habits of *L. microcephalum*, which seems to be common in Asia Minor and southern Europe (excepting France and Spain[1]),

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[1] According to Er. André, Species des Hyménoptères d'Europe et d'Algerie, 1882, p. 220.

have been studied by the leading myrmecologists, Mayr, Emery, and Forel. Mayr's account,[1] which is the earliest, may be quoted in full:

"This beautiful species probably establishes its colonies in hollow trees, since I have been unable hitherto, notwithstanding many attempts, to find its nests. It wanders about in processions ascending trees, where it could go only for the purpose of attending plant-lice. During the past three years I have repeatedly visited a couple of silver poplars standing close together and have always found this ant moving in a procession from one tree to the other, but I have been unable to discover either the nests or the winged sexes. The processions are often very long and are permanently maintained throughout the whole summer, since the workers go back and forth. Such a procession is to be seen, for example, in the Prater in Vienna, extending between four trees and measuring 180 feet in length. This procession also sends out to one side another which measures 72 feet in length and leads to two other trees."

Emery gives a more extensive account of this ant which he found to be common in Italy where it is associated almost exclusively with oak trees.[2] Between these it forms processions or files sometimes 240 feet in length. "This ant seems neither to build nor to excavate its nests, but uses the cavities and galleries dug in the wood or under the bark by the larvæ of stag-beetles (*Lucanus*), longicorns (*Cerambyx*), or other large wood-eating beetles. No other tree presents such commodious and convenient cavities of this description as the oak. . . . This ant's mode of life is largely external. It patrols great surfaces; nearly every crevice in the bark of the trees which it inhabits being used by a file of ascending and descending workers. During the hottest hours of the summer days they withdraw into their cavities, but at other times nearly all the individuals keep running about outside of the nest." Emery maintains that they do not attend aphides in order to collect their sweet ejecta, but carry these insects away as food. "*Liometopum* is preëminently a predatory ant and lives almost exclusively on animal food. . . . It runs about on the bark of the trees awaiting the coming of other insects, which it seizes. It institutes veritable *battues* for larger game. . . . While on these hunting expeditions the *Liometopum* workers always rely on the same method of quickly overwhelming their prey from all sides and holding it fast. They also behave in the same manner in their conflicts with other ants." Besides the files, which connect the various

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[1] Formicina Austriaca. Verhandl. k. k. zool. bot. Gesell. Wien, V, 1855, p. 319.

[2] Zur Biologie der Ameisen. Biol. Centralblatt, 1891, pp. 165–180.

nests of a *Liometopum* colony with one another, there are other very long files which radiate out in different directions. These Emery calls "predatory or hunting files." He describes the huge males and females preparing for their nuptial flight on a July evening. The wings of the females are very easily detached. These insects were never seen to take flight voluntarily and when precipitated into the air from the tip of the finger, they flew horizontally like termites and permitted themselves to drift with the wind. He believes that mating must take place on the trees during the twilight hours and that the lumbering females take flight from the highest twigs. He is also of the opinion that *Liometopum* is an ant of which the female is gradually losing the power of flight.

Forel had occasion to study *L. microcephalum* in Bulgaria[1] and was able to confirm many of Mayr's and Emery's observations: "*Liometopum*, as a rule, forms enormous colonies which often extend over several trees connected by files of ants going back and forth. In an old oak forest near Aëtos (comprising the largest and most beautiful oaks I have ever seen) I found a *Liometopum* colony which covered twelve huge nests. In order to ascertain whether the *Liometopum* on some more distant oaks were also members of this same colony, I brought workers from the two places together. Those from the more distant oaks were attacked and pulled about, not very seriously, but with sufficient vehemence to prove that they belonged to another colony. I found *Liometopum* colonies on oaks, poplars, willows, apricot trees (which are often very large in eastern Rumelia), and elms.

"The nest entrances are often found in spots on the tree-trunks where the bark is defective, or in dead branches, but also quite as frequently in very hard wood, so that it is very difficult to obtain a piece of the nest. In Sliven, nevertheless, I succeeded in sawing off and carrying home a dead branch inhabited by *Liometopum*. It certainly looks as if only the borings of beetles had been used; but the cavities are in all probability enlarged by the ants.

"*Liometopum* is a fiercely pugnacious ant and angrily attacks and bites the intruder. At the same time it emits (evidently from its anal glands) a secretion which Emery has described as intensely aromatic and very similar to that of *Tapinoma erraticum*. As soon, however, as the first odor has evaporated, another penetrating and more disagreeable odor, which recalls that of *Lasius emarginatus*,

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[1] Die Ameisenfauna Bulgariens. Verhandl. k. k. zool. bot. Gesell. Wien, 1892, pp. 305–318, Taf. V.

becomes perceptible. Emery has called attention to this mixture of odors. The secretion makes the fingers sticky, which proves that there is a resinous residue as in the case of *Tapinoma.*

"Alien ants are fiercely persecuted by *Liometopum.* With the exception of *Polyergus rufescens* and *Solenopsis geminata* I have never seen a more powerful or pugnacious ant. In Tatar-Bagardjik I witnessed a spontaneous battle between a small and apparently very young *Liometopum* colony and a colony of *Lasius niger.* The former was up on the trunk of an elm, the latter down at the base and had evidently been in the habit of visiting plant-lice on the tree. The *Liometopum* colony, which had probably only recently taken up its abode in the elm, attacked the *Lasius* in serried columns, and with a show of determination, sure and rapid movements, and coöperation, succeeded in putting them to flight. The *Lasius* rallied but could not manœuvre and intercommunicate so readily. The rapidity with which the *Liometopum* communicate with one another and assemble in force for the purpose of overwhelming an enemy is truly wonderful. On such occasions a faint crackling sound is heard. Hardly any other animal dares venture up onto trees inhabited by *Liometopum.* Only long-legged ants that can get over the ground very rapidly endeavor to run the gauntlet in order to reach the plant-lice, which are heartily despised by the *Liometopum.*"

There appeared as a postscript to Forel's paper on the ants of Bulgaria a brief note by Mayr. In this he describes, and on an adjoining plate figures, a nest of *L. microcephalum* found in a hollow oak in southern Hungary: "The material used was finely comminuted, decayed wood which undoubtedly had been compacted by means of some glandular secretion to form a brown substance like papier-maché. This substance was built up into short curved trabeculæ which branched and anastomosed like the meshes of a net, or in the form of small pasteboard-like plates, variously bent and perforated with numerous openings as large as pin-holes or larger. The paper nests of *Lasius fuliginosus* differ from those of *Liometopum* mainly in that they consist exclusively of pasteboard-like plates." In commenting on this observation at the end of the paper, Forel admits that he and Emery probably saw only the peripheral portions or outskirts of the *Liometopum* nest and that the paper portions are probably situated in the very heart of the tree-trunk. In other words, it is probable that the beetle-borings described by Emery and Forel are not a part of the true nest of *L. microcephalum,* but are merely used as runways or forecourts to the true penetralia in which the ants keep and raise their brood. This casts some doubt on the statements of Emery and Forel implying that a single colony of *microcephalum* has more than one nest.

It is evident that the American *L. apiculatum* has two peculiarities not observed in the European form. First, it is more highly variable than its Old World cousin, as is shown by the existence of at least one subspecies and one variety; and second, the altitudes recorded in connection with the localities in which it has been taken, show that it is confined to mountainous regions. The typical *apiculatum* and its subspecies *luctuosum* are, in fact, known to occur only at altitudes between 4000 and 8000 feet. They seem to be most abundant at 5000–6000 feet. It is true that most of the altitudes recorded for the variety *occidentale* are much lower, but it must be remembered that these are somewhat problematical. San Jacinto, Mariposa, and Claremont, which appear on the labels of the Californian specimens, are near the San Jacinto and San Gabriel ranges and the ants may have been actually taken at higher altitudes but attributed to the nearest towns. This dependence on rather high altitudes readily accounts for the fact that *L. apiculatum* does not occur in eastern North America. In that region, as I have shown in a former paper,[1] the genus *Liometopum* is represented, both taxonomically and ethologically, by the genus *Dolichoderus*.

I have observed many colonies of the typical *apiculatum* in the Paisano Pass and at Ft. Davis, Texas, at Las Vegas, New Mexico, and in the mountains about Manitou and the Garden of the Gods. These ants, like the European species, are continually moving back and forth in files,[2] often 100–200 feet long, over and under the loose rocks, ascending and descending the trees and bushes. They run with a soft, bounding gait, which, with their velvety bodies and warm gray tints, makes them resemble a host of Lilliputian mice. When disturbed they quickly turn their gasters up or to one side, towards the intruder, and emit a secretion which has a rank rancid-butter, or "Tapinoma" odor.

In their choice of nesting sites they differ from the European form precisely as the North American *Dolichoderi* differ from their European congeners: they nest in the ground, often some distance from the trees or plants on which they seek their food. I have seen nothing to prove that a single colony of *L. apiculatum* occupies more than one

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[1] The North American Ants of the Genus Dolichoderus. Bull. Am. Mus. Nat. Hist., XXI, 1905, pp. 305–319.

[2] In the Paisano Pass even on cold but sunny days in the latter part of December.

nest. June 10, 1902, I happened on a huge nest of this species on the "Crouching Lion" at Ft. Davis. It was fully two feet long and a foot and a half wide, and was situated in the ground under a large flat stone. A year or two previously the stone must have rolled down a slope onto some coarse grass and twigs and the ants had built up the earth in the interstices between these vegetable remains and compacted it with some glandular secretion till it formed a huge mass of trabeculæ, much coarser and with larger openings but otherwise similar to that figured by Mayr for the European species. The nest contained thousands of workers and fully a quart of glistening white worker larvæ and pupæ. The ants attacked me with great fury and nearly suffocated me with their intense butyric acid odor. This nest was situated in an open stony region at least 200 feet from the nearest trees. Another smaller nest of similar construction was found under a stone in the Paisano Pass, near Alpine, Texas. The specimens of *apiculatum* collected by Mr. C. H. Tyler Townsend on the volcano of Colima are also from a "large nest in the ground and dead leaves under a log." That these insects habitually build in the soil is also shown by the fact that on four different occasions, twice at Ft. Davis and twice near Manitou, I came upon isolated females in the act of establishing their colonies in small cavities excavated in the soil under stones in rather open places. One of these insects had a packet of eggs, another a packet of larvæ, and a third, that had recently died, probably from hunger or exhaustion, was being devoured by a colony of a small species of *Solenopsis* allied to *S. validiuscula* Emery. These huge females, with the exception of the females of *Atta fervens* and our larger *Camponoti*, the largest and most obese of their sex among North American ants, are thus seen to establish their colonies in the same manner as the vast majority of Formicidæ.

While collecting in Colorado during the summer of 1903, I made repeated attempts to get at the nests of *Liometopum*, which was very common in the Garden of the Gods, where it prefers the red volcanic rocks and soil just as it does in the Paisano Pass and at Ft. Davis. The files of ants were often seen disappearing under rocks, but when these were lifted in the hope of finding their nests, it was found that only a runway or perhaps a succursal nest had been uncovered. In vain rocks were removed over large surfaces, only to find the burrow at last disappearing into the ground under the roots of some great tree, immovable boulder or cliff. The fact that in these runways the ants often congregate in numbers, together with the myrmecophilous beetles mentioned below, is apt to lead the observer to believe that he has found the nest, but these cavities contain no larvæ, males, or females, and careful inspection shows that they lead off into a continuation of the runway. The cavities are, in fact, mere temporary resting places for the out- and home-bound companies of workers.

It is, perhaps, easy to account for the difference in the nesting-sites of the European and American species of *Liometopum* when we consider the great climatic differences between southern Europe and the mountainous regions of southwestern North America. The protracted periods of drought in the latter regions make the decayed wood of tree-trunks extremely undesirable abodes for moisture-loving insects like the ants. They are therefore compelled to nest in the soil and naturally seek places under stones where the moisture is longest retained.

If the observations of Emery and Forel can be accepted as final, there is also another great ethological difference between the American and European species of *Liometopum*, a difference relating to the feeding habits. Mayr was of the opinion that *L. microcephalum* could be climbing about on the trees only for the purpose of attending aphides, but Emery claims that the ants merely devour these insects and Forel speaks of their despising the plant-lice. Our American species, however, is eminently aphidicolous and coccidicolous, although, like *microcephalum*, it is always ready to feast on any caterpillars, beetles, etc., that may fall in its path. In the Paisano Pass the files of *apiculatum* were frequently seen attending the aphides on the leaves of two species of mountain oak (*Quercus emoryi* Torr. and *Q. undulata* Torr.). At Ft. Davis I found thousands of these ants in attendance on a lot of aphides that covered the flower spikes of some large yuccas. Another colony was similarly engaged on the leaves of willows and cedars. At Manitou similar observations were made. Here they were also attending snow-white Coccidæ on roots that extended across their dark runways. These ants love to collect the nectar of flowers. In the Paisano Pass a colony was busy plundering the blossoms of the cat's claw (*Acacia wrightii* Benth.). At Ft. Davis I saw unmistakable evidence of their pronounced carnivorous instincts. A file was dragging caterpillars to its nest and a mass of ants were trying to get at the soft parts of a dead specimen of one of our largest longicorn beetles (*Derobrachus geminatus* Lec.), measuring 6.5 cm. in length. These diverse observations show the close resemblance in habits between the species of *Liometopum* in the western and the species of *Dolichoderus* in the eastern states of the Union.

My observations on the dark-colored *luctuosum* are much less complete than those on the typical *apiculatum*, owing to the fact that I saw only two colonies of the subspecies in Colorado and one at Prescott, and was unable to devote much time to observing the more numerous colonies found on the rim of the Grand Cañon. *L. luctuosum* seems always to be associated with pine trees. At any rate, the colonies in Cheyenne Cañon, Colorado, and at Prescott were ascending the trunks and had their nests under the large roots of pines. *L. luctuosum*, moreover, was the only form of the species seen in the Coconino pine forest on the rim of the Grand Cañon.

Notwithstanding its restless activity and highly carnivorous instincts, *L. apiculatum* seems to tolerate quite a number of myrmecophiles. In the runways of this ant in the Paisano Pass two different Tenebrionid beetles (*Ologlyptus anastomosis* Say and *Argoporis* sp.) and a Thysanuran (*Atelura* sp.) were frequently met with. These are probably merely synœketes, or indifferently tolerated guests. Two truly myrmecophilous beetles, however, belonging to the Aleocharine Staphylinidæ, namely, *Apteronina schmitti* and *Dinardilla liometopi*, both described some years ago by Wasmann,[1] are known to occur only with *L. apiculatum*. They were discovered by the late Rev. P. J. Schmitt, O. S. B., at Cotopaxi, Colorado, not in the "nest of *Liometopum*," as Wasmann states, but in the runways of these ants, as Father Schmitt once informed me. These beetles were sought in vain in the Paisano Pass and at Ft. Davis, but I had no difficulty in finding them in the Garden of the Gods and in Cheyenne Cañon near Colorado Springs. There were sometimes as many as four or five of each species under a single stone covering one of the runways. They seem to lie in wait and take toll in the form of honey-dew from the ants that are traversing the burrow on their way to the nest. According to Wasmann, "the structure of the tongue of *Apteronina* indicates that this insect is fed from the mouth of its hosts, like *Atemeles*,

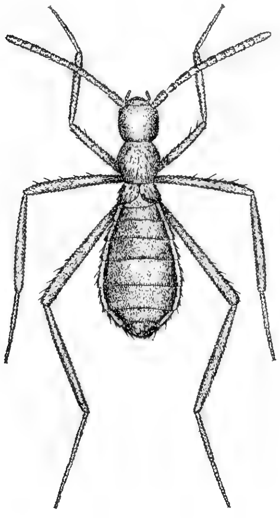

Fig. 2. *Apteronina schmitti* Wasmann.

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[1] Zwei neue *Liometopum*-Gäste aus Colorado. Wien Entomol. Zeitung, 20. Jahrg., 7. Heft 30 Sept., 1901, pp. 145–147.

Lomechusa, etc." These beetles are of more than usual interest because they are both tactual mimics, that is, they probably deceive the ants through a resemblance in form or surface texture to the *Liometopum* workers. While both beetles are highly pubescent, like these workers, they differ greatly in form; *Apteronina* being decidedly ant-like, whereas *Dinardilla* has the form of beetles which ants have considerable difficulty in seizing or holding in their mandibles. According to Wasmann, *Dinardilla* is allied to *Dinarda*, a genus comprising several interesting European myrmecophiles. *Apteronina*, according to the same authority, resembles *Apteronillus* and even more closely several *Eciton* guests of the mimetic type. Probably both of the *Liometopum* guests are in the habit of accompanying their hosts as they move along in files. In this respect the relationship of *Apteronina* with *Apteronillus* and its allies is very suggestive, since the *Eciton* guests are actually known to accompany the files of their nomadic hosts.

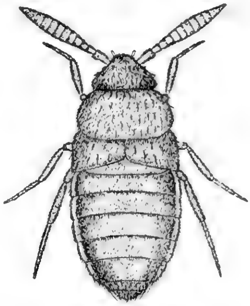
Fig. 3. *Dinardilla liometopi* Wasmann.

A study of the behavior of *Dinardilla* and *Apteronina* in artificial nests would undoubtedly yield interesting results. While I was in Colorado there were so many matters of myrmecological interest to occupy my time and attention, that I unfortunately neglected to observe these beetles under suitable conditions. I include a couple of sketches (Figs. 2 and 3) that may aid some future observer in identifying these singular creatures.

An Annotated List of the Ants of New Jersey.

By William Morton Wheeler.

AUTHOR'S EDITION, extracted from BULLETIN

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Article XXIII. — AN ANNOTATED LIST OF THE ANTS OF NEW JERSEY.

By William Morton Wheeler.

No State in the Union has been so thoroughly ransacked by collectors of insects as New Jersey. Owing to its geographical position and the diversity of its physical conditions, it has been for years the natural collecting ground for the members of flourishing entomological societies in New York, Brooklyn, Newark, and Philadelphia. And while local collectors, since the time of Rev. G. K. Morris and Mrs. Mary Treat, seem to have given little serious study to the ants, they have nevertheless collected specimens in a more or less desultory manner. Frequently when other more attractive insects are not to be taken, the entomologist, rather than return home empty-handed, will capture a few of the ants which are always to be had in abundance. These specimens accumulate in collections and, when sufficiently numerous and provided with accurate locality labels, eventually come to be of great service in faunistic studies like the one here attempted. I have examined such collections in the possession of Messrs. E. Daecke, Wm. T. Davis, H. L. Viereck, and Prof. John B. Smith, and I wish to express my obligations both to these gentlemen and to Dr. Henry Skinner, through whose kindness I have been able to study specimens in the collections of the Philadelphia Academy of Natural Sciences. All of this material, together with such specimens as I have myself been able to collect on several excursions during the past two years, enables me to record a considerable number of different forms from New Jersey.

This is by no means the first list of New Jersey ants to be published. In his 'Catalogue of Insects found in New Jersey,'[1] Prof. J. B. Smith records 66 species from the State. This list, however, includes the names, apparently derived from incorrectly identified specimens, of a number of European and tropical American ants. When we eliminate these, together with some synonyms and apocryphal names, about 44 legitimate entries remain. For the second edition of this work, entitled 'Insects of New Jersey,'[2] the list of ants was revised and extended by Dr. Wm. H. Ashmead till it comprised

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[1] From the Final Report of the State Geologist of New Jersey. Vol. II, 1890.

[2] Twenty-seventh Annual Report of the State Board of Agriculture, 1899. Trenton, N. J., 1900.

93 forms, the same number I have recorded in the following paper. But a critical examination of this list shows that it must have been compiled very largely from the literature and not from actual specimens, for it still contains a goodly number of synonyms cited as different species and several worthless names from authors like Say and Buckley who were incapable of describing an ant so that it could be recognized with certainty by any future entomologist. When Ashmead's list is revised it is seen to contain 68 valid forms, and only 53 that show evidence of having been actually taken in New Jersey.

Although my list is in all probability incomplete, it nevertheless bears witness to the richness of the ant-fauna of New Jersey in particular and of temperate North America in general. This is evident from a comparison with some of the well-known myrmecologies of Europe. Forel[1] cites 66 different forms from Switzerland, a country somewhat more than twice as large as New Jersey and of even greater physical diversity. From Sweden, which has 22 times the area of New Jersey, Adlerz[2] records only 36 different Formicidæ and from the vast territory of European Russia Nasonov[3] enumerates only 79. And this latter list even includes a number of Mediterranean forms like the species of *Myrmecocystus*, *Messor*, *Pheidole*, *Dolichoderus*, etc.

As a rule ants depend so intimately for their welfare on precise physical conditions that colonies which have not been established by their queens in proper soil, moisture, and sunlight grow slowly and, like plants under similarly unfavorable conditions, take on a more or less depauperate appearance. This is indicated by the small size of both colonies and individuals, and is most noticeable in species that have exceeded the limits of their normal geographical range. Within this range a species is usually confined to a particular station, so that the collector soon learns to associate species with very definite environments. Among our eastern ants we may recognize at least six such stations, each occupied by a series of species which are often so constantly associated with one another as to recall the plant societies of botanists. According to these stations, the New Jersey ants may be grouped as follows:

1. The *woodland*, or *silvicolous fauna*, comprising the species that inhabit our moist, shady forests. With the extinction or drainage

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[1] Les Fourmis de la Suisse. Zurich, 1874.

[2] Myrmecologiska Studier II Svenska Myror och deras Lefnadsförhållanden. Bihang till K. Svenska Vet.-Akad. Handlingar, Band 11, No. 8, 1886.

[3] Contributions to the Natural History of the Ants (Formicariæ). Publications of the Lab. Zool. Mus. Univ. Moscow, Vol. IV, No. 1, 1889, pp. 1–42; i–vi, Tab. i–ix (in Russian).

of these forests or the removal of the undergrowth, this characteristic and in many respects very primitive fauna is rapidly disappearing. It comprises the following forms:

Stigmatomma pallipes,
Proceratium silaceum,
Proceratium crassicorne,
Ponera pennsylvanica,
Myrmecina americana,
Protomognathus americanus,
Stenamma brevicorne,
Aphænogaster fulvum,
Aphænogaster piceum,
Myrmica punctiventris,
Leptothorax longispinosus,
Leptothorax curvispinosus,
Brachymyrmex depilis,
Lasius myops,
Lasius aphidicola,
Lasius speculiventris.

2. The *glade*, or *nemoricolous fauna*, comprising the ants that prefer open sunny woods, clearings, or the borders of woods. This fauna, a portion of which maintains itself even in the gardens and parks of our cities, includes the following:

Solenopsis molesta,
Cremastogaster lineolata,
Cremastogaster lutescens,
Cremastogaster cerasi,
Aphænogaster tennesseense,
Aphænogaster lamellidens,
Aphænogaster aquia,
Leptothorax schaumi,
Leptothorax fortinodis,
Dolichoderus plagiatus and its subspecies and varieties,
Tapinoma sessile,
Prenolepis imparis,
Lasius neoniger,
Lasius interjectus,
Lasius claviger,
Lasius subglaber,
Formica rubicunda,
Formica subintegra,
Formica integra,
Formica difficilis,
Formica exsectoides,
Formica schaufussi,
Formica incerta,
Formica nitidiventris,
Formica fuscata,
Formica subænescens,
Polyergus lucidus,
Camponotus castaneus,
Camponotus americanus,
Camponotus pennsylvanicus,
Camponotus ferrugineus,
Camponotus nearcticus,
Camponotus minutus,
Camponotus subbarbatus.

3. The *field*, or *cæspiticolous fauna*, comprising the ants that prefer to nest in grassy pastures and lawns in situations exposed to the full warmth and light of the sun. To this rather limited fauna belong the following:

Myrmica schencki,
Tetramorium cæspitum,
Lasius brevicornis,
Lasius latipes,
Lasius murphyi.

4. The *meadow*, or *pratincolous fauna*, comprising the following forms, which inhabit low grassy meadows or bogs:

Sysphincta melina,
Sysphincta pergandei,
Cremastogaster pilosa,
Myrmica brevinodis.

5. The *heath*, or *ericeticolous fauna*, includes the ants that inhabit rather poor, sandy, or gravelly soil exposed to the sun and covered with a sparse growth of weeds or grasses. To this fauna belong the following:

Pheidole pilifera,
Pheidole vinelandica,
Myrmica sabuleti,
Prenolepis parvula.

6. The *sand*, or *arenicolous fauna*, comprising the following ants, which prefer to nest in pure sand:

Monomorium minimum,
Pheidole morrisi,
Pheidole davisi,
Aphænogaster treatæ,
Myrmica pinetorum,
Pogonomyrmex badius,
Leptothorax davisi,
Trachymyrmex septentrionalis,
Dolichoderus mariæ,
Dolichoderus gagates,
Tapinoma pruinosum,
Dorymyrmex pyramicus,
Prenolepis testacea,
Prenolepis arenivaga,
Formica pallide-fulva.

A few of our species, like *Lasius americanus* and *Formica subsericea*, are so adaptable that they occur more or less abundantly in all or nearly all of the above stations. Owing to intergradation of these stations in some places, we, of course, have a corresponding mingling of faunas. Thus certain species, like *Monomorium minimum*, seem to belong indifferently either to the heath or sand fauna. In the deserts of the Southwestern States these two faunas may either mingle or be sharply separated from each other. In the Northeastern and Middle States a similar relation obtains between the glade and field faunas which it is often impossible to separate by a hard and fast line. *Formica schaufussi*, for example, seems to occur indifferently in either station.

Family FORMICIDÆ.

Subfamily PONERINÆ.

Stigmatomma *Roger.*

1. **S. pallipes** *Haldeman.*—Gloucester (Fox); Westville (Fox); Lakehurst (Wheeler); Palisades near Fort Lee (Wheeler).

This singular and primitive ant is subterranean and occurs only in rich, rather damp woods, under stones, leaf-mould, or more rarely under or in rotten logs. The colonies are very small, usually comprising less than 20, in extreme cases from 40 to 60 individuals. The males and females appear Aug. 20 to Sept. 17. The larvæ are slender, non-tuberculate, and covered with hair. They are fed by the workers on pieces of insect food, not by regurgitation. The cocoons are elongate, elliptical, dark brown. The ants are very timid and rather slow in their movements. When their nests are disturbed they are at first rather neglectful of their young but eventually return and carry them to a place of safety. For further notes on this ant see my paper: 'The Habits of Ponera and Stigmatomma' (Biol. Bull., Vol. II, No. 1, Nov., 1900, pp. 43–69, 8 figs.).

Sysphincta *Roger.*

2. **S. melina** *Roger.*—This rare ant probably occurs in New Jersey as it has been taken in Pennsylvania. Rev. P. J. Schmitt, O. S. B., found this and the following species under large stones in damp meadows.

3. **S. pergandei** *Roger.*—Like the preceding, and for the same reason, this species probably occurs in New Jersey.

Proceratium *Roger.*

4. **P. silaceum** *Roger.*—As this species has been taken in Pennsylvania by P. J. Schmitt and as I have taken it at Cold Spring Harbor, L. I., there can be little doubt that it occurs in New Jersey. The very small colonies live in rotten wood in damp, shady forests. The workers move slowly and have a habit of resting on their sides. The pupæ are enclosed in delicate cocoons.

5. **P. crassicorne** *Emery.*—There is a single worker of this species from Anglesea, N. J., in the collection of the Philadelphia Academy of Sciences.

Ponera *Latreille.*

6. **P. coarctata pennsylvanica** (*Buckley*) *Emery.*—Camden (Fox); Gloucester (Fox); Anglesea (Viereck); Glassboro (Viereck); Palisades near Fort Lee (Wheeler); Lakehurst (Wheeler); Halifax (Wheeler).

This form, like *Stigmatomma pallipes*, lives in small colonies under stones and vegetable mould and in rotten wood. It prefers rather open woods where there is shade and a fair amount of moisture. The males and winged females may be found in the small, irregularly excavated nests from Aug. 20 to Sept. 10. The larvæ have four pairs of glutinous tubercles on the dorsal surface of the third to sixth abdominal segments. Like the larvæ of *Stigmatomma* they are fed by the workers with fragments of insect food. The pupæ are enclosed in short, elliptical, sulphur yellow cocoons which have a black meconial spot at the posterior pole. When the nests are disturbed the ants are careful of the eggs and larvæ, but more neglectful of the cocoons. Ergatoid females are occasionally found. They have ocelli and larger eyes than the normal workers and a thorax intermediate in structure between that of the worker and the winged female. For further notes on the habits of this interesting species see my paper: 'The Habits of Ponera and Stigmatomma' (Biol. Bull., Vol. II, No. 1, Nov., 1900, pp. 43–69, 8 figs.).

Subfamily MYRMICINÆ.

Myrmecina *Curtis.*

7. **M. graminicola americana** *Emery.* — Riverton (Viereck); Lakehurst (Wheeler).

In the latter locality a single colony of this subspecies was found nesting in the sand in plesiobiosis with a colony of *Myrmica punctiventris* var. *pinetorum* var. nov. Usually *M. americana* nests in rotten wood or under stones in damp shady woods. It is a rare and local species.

Tomognathus *Mayr.*

(Subgen. *Protomognathus* Wheeler).

8. **T. (P.) americanus** *Emery.*—This rare species has been found in Pennsylvania and at Bronxville, New York, so that it can hardly be absent from New Jersey. It lives as a parasite in the colonies of *Leptothorax curvispinosus* Mayr. The female is winged and not ergatoid like the only other known species of the genus (*T. sublævis* Nyl.) of Europe. On this account I have thought it best to create a new subgenus for the American species.

Monomorium *Mayr.*

9. **M. pharaonis** *Linn.* — There can be little doubt that the statement in Dr. Smith's list that this cosmopolitan house ant occurs "throughout the State commonly," is correct. It lives only in houses, warehouses, ships, etc., and has been carried to the different seaports of the globe from its original home in the warmer regions of

the Old World. It is often confounded with our native *Solenopsis molesta* Say but can always be distinguished by its 3-jointed, instead of 2-jointed antennal club.

10. **M. minutum** *Mayr* var. **minimum** (*Buckley*) *Emery.* — Westville (Viereck); Riverton (Viereck); Lakehurst (Wheeler).

This tiny black ant is common in the pine barrens, where it constructs single or closely clustered craters two to three inches in diameter, often about the roots of the plants in the pure sand. The workers forage in files, visiting plants in search of honey-dew and the secretions of extrafloral nectaries. They also eat dead insects with avidity. The colonies in the pine barrens are quite as populous as those of Southern States, like Florida and Texas, where this ant is very abundant.

Solenopsis *Westwood.*

11. **S. molesta** *Say.*—Boonton (Viereck); Fort Lee (Wheeler).

This tiny species is recorded in Smith's list under the name of *S. debilis* Mayr. It is remarkable on account of its great diversity of habits, which exhibit a high degree of adaptability. It is often common in open, grassy places where it may live either in independent formicaries under stones or very rarely in diminutive crater nests, or as a thief-ant in the walls separating the galleries of the formicaries of our larger ants belonging to the genera *Formica, Myrmica, Stenamma* (*Aphænogaster*), etc. As a free lance it lives on dead insects but when living in cleptobiosis it devours the well-fed larvæ and pupæ of other ants. Under these conditions it escapes unnoticed by its hosts, either on account of its very small size or neutral nest-odor, and takes care to keep its own nests inaccessible to the species on which it preys. In these respects its habits resemble those of the allied European *S. fugax* and *S. texana* of the Southern States. The blackish males and yellow females, which are very much larger than the yellow workers, make their appearance in late August.

S. molesta presents, however, another set of habits on which Prof. Forel has thrown considerable doubt, though, in my opinion, without much justification. Since the settling of the country by man this insect has become a formidable house-ant in certain localities. It was found by Mr. Theo. Pergande in houses in Washington, D. C., and Mr. C. E. Brown has repeatedly taken it in the Milwaukee bakeries. I have myself seen enormous colonies in several residences in Rockford, Illinois, where it lives in the masonry and wood work of kitchens and annoys the house-wife by its assiduous visits to any foods containing fat. It is said not to eat sugar. These facts show that Forel's assertion that Say must have redescribed *Monomorium pharaonis* as *Myrmica molesta* instead of the species afterwards described by Mayr under the name of *Solenopsis debilis* is without foundation.

Still other aspects of this versatile little ant have been described by Prof. S. A. Forbes. I quote from his Seventh Illinois Report[1]: "It [*Solenopsis molesta*] was first found by us June 1–12, 1883, at Normal, Illinois, abundant in many fields of corn, both new and old, and afterwards, May 14–24, 1886, infesting seed corn in the fields at Champaign. In the corn field these ants were usually collected about the kernels in the earth, and frequently more or less hidden in little cavities in the softened grain. May 19, 1887, they were very abundant in a field of corn in sod in Champaign County, eating out the planted kernels. In autumn the same species has been detected by us indulging a similar appetite but in a way to do no harm. Sept. 11–21, 1893, it was found on and within kernels of corn at the tips of ears, which had evidently been injured previously by crickets and grasshoppers. The solid substance of the grains is not actually eaten by these ants, a fact which I demonstrated by dissection of the ants, but it is simply gnawed away, doubtless for the sake of the sweetish and oily fluids of the softened kernels. If plants start from seed thus injured, they are shorter than others adjacent, and have a stunted weak appearance.

"This species has also been several times noticed by us in September in attendance upon the root-louse of corn, *Aphis maidiradicis*, sharing with two other species of ants the cares and benefits of this association. It occurs more frequently, according to our observations, at this season of the year, with the corn-root lice infesting purslane than with those upon the corn itself."

Prof. Forbes's figure and description leave no doubt that the ant he observed was *S. molesta* (=*debilis* Mayr). He calls attention in a previous report to its eating strawberries. This and its corn-eating habits show its relations to the carnivorous and granivorous "fire ant," *S. geminata*, which I have seen eating strawberries and carrying away their seeds on Mr. Kleber's ranch at Corpus Christi, Texas.

Cremastogaster *Lund.*

12. **C. lineolata** *Say.* — Common throughout the State, according to Smith's list. I have seen fine colonies in such widely different

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[1] A Monograph of the Insects Injurious to Indian Corn, 1894.

localities as the Ramapo Mountains near Halifax and the sandy barrens about Lakehurst. In the former locality the ants were nesting under stones, in the latter under the bark of pine logs. There is a vestigial tendency in this ant to construct paper-like partitions in its nest, especially when nesting under stones. The workers have a disagreeable penetrating odor. They ascend trees in files and are much given to attending Aphides and Coccidæ. The males and females are very abundant in the nests at Lakehurst as late as Sept. 24.

13. **C. lineolata** var. **lutescens** *Emery.*—This variety is recorded from New Jersey by Emery (Beiträge, 1894, p. 282), and by Ashmead in Smith's list. I have seen typical specimens from Tinicum, Pa. (Viereck), which is very near the New Jersey boundary.

14. **C. lineolata** var. **cerasi** *Fitch.*—Anglesea, Clementon, and Riverton (Viereck); Medford (Phila. Acad.).

15. **C. lineolata pilosa** *Pergande.*—The types of this subspecies are from the District of Columbia and New Jersey. It is common at Lakehurst, nesting in rotten stumps and logs near or in cranberry bogs. In this locality it exhibits two interesting peculiarities, one of which is as flattering as the other is derogatory to its mental plasticity. Occasionally it constructs from particles of sphagnum moss agglutinated with saliva beautiful little "cow-sheds" over the clustered Coccidæ on the twigs of *Pinus rigida.* These sheds are usually elliptical in shape and about the size of a pecan nut or somewhat larger. They are entered by a little round hole, which is never in such a position as to enable the Coccidæ to escape. More than a dozen of these "cow-sheds" were found on one small pine tree about 6 feet high. Notwithstanding their ability to keep Coccidæ in well-constructed sheds, these ants are killed in great numbers by the pitcher plants (*Sarracenia purpurea*). They creep into the leaves, apparently for the purpose of getting at the water in their hollow bases, but are unable to return over the slanting hairs which point down the throats of the pitchers. In some places hundreds of these ants are found in a decomposing mass in the bottoms of the pitchers and probably constitute a valuable source of food to the plants.

Pheidole *Westwood.*

16. **Ph. pilifera** *Roger.*—Boonton (Viereck); Palisades (Davis); Great Notch (Wheeler); Lakehurst (Wheeler).

The androtypes and gynetypes of this species which, together with workers from Pennsylvania and other States, were described by

Mayr under the name of *Ph. pennsylvanica*, came from New Jersey. It nests in sandy or gravelly soil and usually constructs obscure craters with several openings. More rarely it may be seen nesting under stones. The huge-headed soldiers, which are rarely present in considerable numbers, are very timid and seek the remotest galleries whenever the nests are disturbed. As Morris (Amer. Naturalist, Sept., 1880, pp. 669–670) showed long ago, *Ph. pilifera* is a true harvesting ant, storing the chambers of its nests with seeds of grasses and other herbaceous plants. But like other harvesting species (*Pogonomyrmex* species, *Solenopsis geminata* and several species of *Pheidole* in the Western and Southwestern States) it is also very fond of animal food. I have seen the foraging workers of *pilifera* hurrying to their nests with small insects (Jassids, Aphides, etc.). A marriage flight was witnessed July 27 at Rockford, Ill.

17. **Ph. morrisi** *Forel.* — The types of this species were collected by Morris at Vineland, but it is common in the pine barrens as far north as Lakehurst. It prefers the pure sand and forms low diffuse and often very untidy moundlets sometimes covering one or two square feet and often about the roots of some plant. These nests are very different from the single compact dome-shaped craters in which Forel found this species in North Carolina and in which I have seen it nesting at Jacksonville, Florida, and Montopolis, Texas. The slender yellow workers are extremely active in their movements, the soldiers rather weak and timid. The species is carnivorous. Forel is clearly justified in separating it from *Ph. dentata* Mayr.

18. **Ph. vinelandica** *Forel.* — The types of this species, as the name indicates, came from Vineland, N. J. (Mrs. Mary Treat). It is not uncommon in the pine barrens where the soil contains some clay. The nests are diminutive scattered craters, rarely more than 1–1½ inches in diameter. This species occurs also at North Woodbury (Viereck), and even as far north as Bronxville, N. Y., where I have taken it in a single locality.

19. **Ph. davisi** sp. nov.

Soldier. — Length 3 mm.

Mandibles bidentate at the tip. Head, excluding the mandibles, hardly longer than broad, subquadrate, with slightly convex sides; occipital border deeply excised; upper surface convex, with the occipital groove extending forward to the middle. Eyes about one third the distance from the anterior to the posterior corner. Frontal carinæ short, not half as long as the antennal scape, rapidly subsiding behind. Clypeus short, flattened in front, somewhat convex behind, without a median keel; anterior border rather broadly excised in the middle. Frontal area subtriangular, about as long as broad, with rounded sides and a median carinula. Tips of antennal scapes reaching just beyond the eyes. Pronotum subhemispherical, about half as broad as the head, with prominent but rounded humeri and without a distinct promesonotal constriction. Mesoëpinotal constriction rather deep and broad. Epinotum with two stout spines which are further apart than long, rather blunt at their tips, directed upward and backward and somewhat outward, and each continued anteriorly and posteriorly into a prominent ridge. Epinotal declivity gradually sloping between the spines. Petiole from above somewhat violin-shaped, nearly twice as long as broad. In profile the node is high, with a rather sharp transverse border, long concave anterior, and short abrupt posterior declivity. Postpetiole twice as broad as the petiole and twice as broad as long, with a blunt conule in the middle on either side. Gaster somewhat smaller than the head. Legs with slightly incrassated fusiform femora.

Mandibles shining, with coarse, scattered punctures. Clypeus and frontal area shining; the former irregularly rugulose on the sides. Anterior two thirds of the head sharply longitudinally rugose, posterior third smooth and shining, with a few coarse punctures. Thorax subopaque, punctate-rugose, the rugæ on the pro- and mesonotum somewhat concentric on the sides and sometimes leaving a small smooth area in the middle of the dorsum; mesoëpinotal constriction and epinotal declivity shining, the latter with transverse rugæ. Petiole subopaque, densely punctate; postpetiole smooth and shining, with more opaque, punctate sides. Gaster smooth and shining.

Body and appendages clothed with sparse, rather long, suberect, yellowish hairs.

Head dark brown; mandibles and a broad band across the anterior portion of the head, reddish yellow; apical third of mandibles, petiole, postpetiole, and gaster black; thorax dark brown, mesoëpinotal constriction, epinotal declivity. legs, and antennæ reddish yellow.

Worker. — Length 1.5 — 1.75 mm.

Mandibles multidentate, with the two apical teeth most prominent. Head, excluding the mandibles, a little longer than broad, subquadrate, with slightly convex sides and nearly straight posterior border. Eyes a little in front of the middle of the sides. Clypeus short, convex, with its anterior border excised in the middle. Antennal scapes extending a little beyond the posterior corners of the head. Frontal area very distinct, impressed, rounded behind. Pro- and mesonotum evenly rounded above and on the sides, less convex than in the soldier. Epinotum with the basal and declivous surfaces of equal length, the latter very sloping; spines rather acute, about as long as their distance apart at the base, diverging upward, outward, and backward. Petiole very similar to that of the soldier, but proportionally narrower. Postpetiole a little wider than the petiole, as long as broad, with sides faintly angular in the middle.

Mandibles, head, postpetiole, gaster, and appendages very smooth and shining. Cheeks and front with a few longitudinal rugæ. Mandibles coarsely and sparsely punctate, thorax and petiole opaque, densely and very uniformly punctate.

Hairs on the body and appendages white, suberect, and rather sparse; tapering except on the thorax and pedicel, where they are somewhat enlarged towards their tips.

Mandibles yellow, with dark brown or black teeth; head and gaster black; thorax and pedicel black or very dark brown, with yellowish articulations. Antennæ and legs yellow, the former with the club more or less infuscated, the latter with the middle portions of the femora and tibiæ black.

The types are from Lakehurst. There is also a single soldier from Lucaston (Daecke) in my collection. This ant lives in small colonies in the pure, white sand of the pine barrens and makes small craters somewhat larger than those of *Ph. vinelandica.* It is allied to *Ph. bicarinata* Mayr and *Ph. vinelandica.* The soldier differs from that of *bicarinata* in its smaller size, darker color, shorter head, and more extensive sculpture of the head and thorax. The worker is at once distinguished by the opaque, densely punctate thorax, darker color, and smaller size. The soldier of *davisi* differs from that of *vinelandica* in its much darker color, less deeply emarginate clypeus, shorter head and frontal carinæ; while the differences between the workers of the two species are similar to those between *davisi* and *bicarinata.*

I take pleasure in dedicating this new *Pheidole* to Mr. Wm. T. Davis, the well-known naturalist of Staten Island, who introduced me to the interesting fauna and flora of the pine barrens.

Stenamma *Mayr.*

20. **S. brevicorne** *Mayr.*—I have seen five workers of the large typical form of this rare species from Riverton (Viereck). It nests under stones and dead leaves in rich, shady woods. For further notes on its habits see my paper: 'The North American Ants of the Genus *Stenamma sensu stricto*,' Psyche, Aug., 1903, pp. 164–168.

(Subgenus *Aphænogaster* Mayr.)

21. **S. (A.) tennesseense** *Mayr.*—This species in all probability occurs in New Jersey, since it is known from several localities in Pennsylvania, at least as far east as the Lehigh Water Gap. I have taken it also in Connecticut. It differs from our other species of *Aphænogaster* in having very small and very smooth females with huge epinotal spines. These aberrant females probably establish their colonies in nests of *S. fulvum*, in the same way that *Formica difficilis* var. *consocians* establishes its colonies in nests of *F. schaufussi* var. *incerta* (*vide infra*). At least *tennesseense* is known to occur only in regions where *fulvum* is unusually abundant, and several mixed colonies of the two species, containing queens of *tennesseense* only, have been recorded.

22. **S. (A.) treatæ** *Forel.* — The types of this species, which is readily recognized by the remarkable lobe on the base of the antennal scape in the worker and female, were taken by Mrs. Mary Treat at Vineland. I have seen many colonies in the pine barrens about Lakehurst. The nests, which are not readily found, except by following foraging workers, are in the sand in the shade of the oaks and pines. The entrance is sometimes produced upwards in the form of a little chimney and the earth or sand pellets removed by the ants while excavating the galleries are scattered about over a circular area 8 to 10 inches in diameter. The workers are very cowardly.

23. **S. (A.) lamellidens** *Mayr.* — A few colonies, found at Lakehurst, were nesting like the preceding species in rather shady places. Two isolated females were discovered in the act of establishing their formicaries in little cells about 3 inches below the surface of the sand. In one of these incipient nests there were a few larvæ and pupæ, in the other a few diminutive workers.

24. **S. (A.) fulvum** *Roger.* — Recorded from Caldwell (Cresson). I have always taken this the typical form of the species in rotten wood in rather dense forests. It is much less common than the following subspecies and variety.

25. **S. (A.) fulvum aquia** (*Buckley*) *Emery.* — Anglesea (Viereck); Clementon (Viereck); Westville (Phila. Acad.); Jamesburg (Davis); Halifax (Wheeler).

This form occurs under stones in shady woods, often in the same stations as the following variety.

26. **S. (A.) fulvum aquia** var. **piceum** *Emery.* — Very common in shady woods along the Palisades; also in the Ramapo Mountains, about Halifax. Careful studies of the habits of this ant have been recently published by Miss Adele M. Fielde in a series of papers.[1]

Myrmica *Latreille.*

27. **M. punctiventris** *Roger.* — Camden (Smith's List); Riverton (Viereck); Medford (Phila. Acad.); Fort Lee (Wheeler).

The worker of the typical form of this species is dark colored and has apically deflected epinotal spines which are longer than the epinotal declivity. The sculpture of the head, thorax, and pedicel is very coarse. The species, which is by no means common, nests in small colonies under stones in moist, shady woods. The males and

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[1] A Study of an Ant. Proc. Acad. Nat. Sci. Phila., Vol. LIII, 1901, pp. 425–449; Further Study of an Ant, *ibid.*, Vol. LIII, 1901, pp. 521–544; Power of Recognition among Ants, Biol. Bull., Vol. VII, 1904, pp. 227–250, etc.

winged females make their appearance during late August and early September.

28. **M. punctiventris pinetorum** subsp. nov.

The workers and females of this form are smaller, much paler in color and much less heavily sculptured than the corresponding phases of the typical species. The epinotal spines are shorter than the epinotal declivity and not deflected at their tips.

A single colony found nesting in pure sand in the pine barrens at Lakehurst.

29. **M. rubra brevinodis** *Emery.* — The *M. sulcinodis* Nyl. recorded by Mayr from New Jersey is probably *brevinodis* or its var. *sulcinodoides* Emery, which should occur in the State.

30. **M. rubra scabrinodis** *Nyl.* var. **sabuleti** *Meinert.* — New Jersey (Emery); Fort Lee (Wheeler).

This variety of the palæarctic *M. rubra scabrinodis* is reddish in color and in the male phase has a very long antennal scape which is somewhat more than a third the length of the funiculus. It nests in sandy or gravelly sunny places such as open pastures, road-sides, etc.

31. **M. rubra scabrinodis** *Nyl* var. **schencki** *Emery.* — New Jersey (Emery); New Brunswick (J. B. Smith); Lahaway (J. B. Smith); Lakehurst (Wheeler).

This form is cited in Smith's List under the name of the European form, *M. lobicornis.* The male has short, thick antennal scapes which are shorter than those of *sabuleti*, being rarely longer than one fourth of the funiculus.

Pogonomyrmex *Mayr.*

32. **P. badius** *Latreille.* — This ant, the "Florida harvester," is recorded in Smith's List as occurring at Caldwell (*teste* Cresson). This is certainly very far north but is not impossible as several Floridian insects have been taken in New Jersey.

P. badius is abundant in the vicinity of Jacksonville, Fla., where I have made a few observations on its habits. Its nests are flat circular craters, 5–10 inches in diameter, with a central perpendicular or somewhat inclined entrance and usually a lot of chaff about the rim. This chaff is stripped from the stored seeds by the workers. There is no circlet of living grass about the periphery of the craters, which may be single or in groups and resemble those of *P. comanche* in the sandy post-oak woods of Texas. The Florida species is peculiar in having polymorphic workers. The big-headed major workers, or soldiers seem to be no more vicious than the small and intermediate forms. Smaller nests contain very few or none of the big-headed individuals, which naturally increase in number with the growth of the colony.

Leptothorax *Mayr.*

33. **L. longispinosus** *Roger.* — This species is recorded from New Jersey by Emery. I have taken it in the woods about Fort Lee. It nests under small stones lying on large boulders, in the clefts of rocks, in stone walls, and more rarely under bark. It seeks its food on the low vegetation in the shade of the trees.

34. **L. curvispinosus** *Mayr.* — Clementon (Viereck); Riverton (Viereck); Lakehurst (Wheeler and Davis); Fort Lee (Wheeler).

This species usually nests in hollow twigs of the elder in shady woods. Two fine colonies were found at Lakehurst in oak-galls (*Amphibolips ilicifoliæ* Bassett and *A. confluentus* Harr.).

35. **L. schaumi** *Roger.* — There can be little doubt that this species occurs in New Jersey as it is known to occur in Pennsylvania and has been found near New York City. I have seen it nesting in the bark of large elms and willows.

36. **L. fortinodis** *Mayr.* — A small colony of this species was found at Lakehurst nesting in the bark of a living pitch-pine (*Pinus rigida*).

37. **L. texanus davisi** subsp. nov.

The worker of this form differs from that of the typical *texanus*, all three phases of which I described from Milano, Texas,[1] in the much less rugose surface of the head, thorax, and pedicel. This is especially noticeable on the thoracic dorsum, petiole, and postpetiole, where, instead of the deep reticulate rugosity of the typical form, the surface is finely and evenly reticulate and therefore much more shining. Corresponding differences are observable between the females of the two forms. The female *davisi* has the upper surfaces of the petiole and postpetiole shining though rugose. The epinotal spines are also longer and more robust than in the typical *texanus*.

Described from several workers and a deälated female taken at Lakehurst. Like the Texan form, *davisi* nests in pure white sand, forming slender galleries a few inches in length. It moves about rather slowly on the sunlit surface of the sand in search of small insects.

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[1] Proc. Phil. Acad. Nat. Sci., 1903, pp. 245–247.

Tetramorium *Mayr.*

38. **T. cæspitum** *Linn.* — Camden Co. (Daecke).—I have seen this species, the "lawn ant," only at Fort Lee. It is evidently imported from Europe and seems to be making but slow progress over the country. It occurs northward and eastward of New York as far as the Connecticut boundary, westward as far as Philadelphia, and southward as far as Virginia. Emery mentions its occurrence also in Tennessee and Nebraska, but I have never been able to find it in the Middle West.

Strumigenys *F. Smith.*

39. **S. pergandei** *Emery.* — This and the two following species are known to occur in Pennsylvania, and will doubtless be found also in New Jersey. They are all very rare ants and nest in the ground, often in plesiobiosis with larger species (*Formica*, etc.).

40. **S. pulchella** *Emery.*

41. **S. clypeata** *Roger.*

Atta *Fabricius.*

(Subgenus *Trachymyrmex* Forel.)

42. **A. (T.) septentrionalis** *McCook* (= ? *tardigrada* Buckley). — Vineland (Mrs. M. Treat, McCook); Toms River (Morris); Lakehurst (Wheeler).

This species, called the "northern cutting ant" by McCook, is the only one of the North American *Attii*, or fungus-growing ants, whose range extends into the Northern States. It is abundant in the pine barrens about Lakehurst, nesting in pure white sand. It moves very slowly and is so timid that it retreats into its nest at the slightest alarm. The nest is not easily found except during the spring and autumn when the ants are actively excavating. At such times one may find a circular nest-entrance about three sixteenths of an inch in diameter and an inch or two to one side of it a pile of sand brought out by the workers. The entrance leads into an oblique gallery which widens at intervals into two or three spheroidal chambers varying from 1–2 inches in diameter. Sometimes these chambers form the blind terminations of two or three different galleries branching off from the main or entrance gallery. The rootlets of plants are left spanning the chambers and from these fibrous supports the fungus gardens are suspended. They consist of a substratum of bits of leaves, buds, green seeds, and caterpillar excrement collected by the ants and woven together by the white hyphæ of a mould-like fungus, which is carefully cultivated by the insects and constitutes their only food. Since the culture of the fungus depends on definite degrees of moisture and temperature the ants are very careful of the ventilation of their nest. During the dry spells of midsummer the entrance is closed with bits of leaves and twigs to prevent the escape of the requisite humidity. At such times it is almost impossible to find the nests. In spring, however, when, after the first warm rains, the ants are clearing and renovating their chambers, and again in the fall after they have raised their brood and are preparing for the winter, the external architecture of the nest is more noticeable. The colonies of *A. septentrionalis* in New Jersey are feebler than those which I have seen near Miami, Florida, and near Austin, Texas. This somewhat depauperate character is evidently the result of unfavorable conditions at the extreme edge of the range of the species, which can hardly extend further north than the pine barrens.

Subfamily Dolichoderinæ.

Dolichoderus *Lund.*

43. **D. mariæ** *Forel.*—Vineland (Mrs. Mary Treat); Manumuskin (Daecke); Clementon (Viereck); Lakehurst (Davis and Wheeler).

This ant is one of the most beautiful insects of the pine barrens, where it nests in the pure sand in colonies comprising thousands of individuals. The nests are frequently excavated about the roots of grass (*Andropogon scoparius*) or turkey-beard (*Xerophyllum setifolium*). The workers remove nearly every particle of sand from the roots and dig a pot-shaped cavity from 12–18 inches in depth and 3–5 inches in diameter. The spaces between the root-fibers serve as galleries and in them the larvæ and pupæ are kept. The withdrawal of so much sand from the roots of the grass often destroys the vigor of the plant and prevents it from flowering. Bits of dead leaves, pine-needles, etc., are heaped over the surface between the grass blades, sometimes in sufficient quantity to form a flat mound, but quite as often the top of the nest is concave, owing to the withdrawal of the sand and its being only partially replaced by vegetable débris. The nests are most easily located by first finding the workers on the foliage of the oaks and pines, where they attend plant-lice and mealy-bugs, and thence tracing them as they move homeward in uninterrupted files often over considerable distances (30–50 ft.). It is probable that the number of plant-lice and mealy-bugs within a radius that can be conveniently patrolled by a single colony of *mariæ* is far from sufficient to supply its thousands of workers with food. Hence the colonies must from time to time move to new localities and establish fresh nests. This is easily accomplished owing to the ease and rapidity with which the sand can be excavated by a populous colony. *D. mariæ* is a pugnacious ant and when disturbed emits from its anal gland a peculiar volatile, smoky excretion which is unlike that of our other *Dolichoderine* genera (*Tapinoma*, *Dorymyrmex*). The males and winged females are found in the nests during the latter part of August. For additional notes on this and the following *Dolichoderi* see my paper: 'The North American Ants of the Genus Dolichoderus,' Bull. Am. Mus. Nat. Hist., Vol. XXI, 1905, pp. 305–319.

44. **D. mariæ davisi** *Wheeler.* — Jamesburg (Davis).

The worker differs from that of the typical form in having erect hairs on the head and thorax, which are also of a somewhat browner color. Only the base of the first gastric segment is yellow and the lateral spots on the second are barely indicated.

45. **D. taschenbergi** *Mayr* var. **gagates** *Wheeler.* — Iona (Daecke); Jamesburg (Davis); Clementon (Viereck); Lakehurst (Davis and Wheeler).

This form is as common in the pine barrens as *D. mariæ* and has very similar habits.

46. **D. plagiatus** *Mayr.* — Iona (Daecke); Jamesburg (Davis); Riverton (Viereck); Lakehurst (Wheeler).

Like *D. mariæ* and *gagates*, this species nests in the ground and attends Aphides on the leaves of trees and bushes. Its colonies are very small.

47. **D. plagiatus** var. **inornatus** *Wheeler.*—This variety, which occurs at Lakehurst, differs from the typical form in lacking the yellowish spots on the gaster.

48. **D. plagiatus pustulatus** *Mayr.*—This variety occurs at Lakehurst. It differs from the typical *plagiatus* in having the head and thorax more shining and less deeply foveolate.

49. **D. plagiatus pustulatus** var. **beutenmuelleri** *Wheeler.* — This variety occurs at Lakehurst. It differs from the typical *pustulatus* in the same way as the variety *inornatus* differs from the typical *plagiatus*, namely in lacking the yellowish spots on the gaster.

Tapinoma *Förster.*

50. **T. sessile** *Say.*—Camden Co. (Fox); Caldwell (Cresson); Clementon (Viereck); Cape May (Phila. Acad.); Fort Lee, Halifax, Lakehurst (Wheeler).

Probably very common throughout the State. It nests under stones, dead leaves, logs, bark, etc., usually in sunny places. The larvæ and pupæ are salmon colored. The workers emit a peculiar rancid-butter odor, the characteristic "Tapinoma odor," also observed in the two following species.

51. **T. pruinosum** *Roger.* — Atco (Viereck); Halifax (Wheeler); Lakehurst (Wheeler).

The occurrence of this species as far north as New Jersey has been overlooked hitherto. It is readily distinguished from *T. sessile* by its smaller size, paler color, and silvery or frosty appearance. At Lakehurst, it nests in pure, white sand, forming single or clustered craters somewhat like those of *Monomorium minutum.* I have also seen a colony nesting under a stone at Halifax and another near Ramapo in the Ramapo Mountains.

Dorymyrmex *Mayr.*

52. **D. pyramicus** *Roger.* — South Jersey (Smith's List); Lakehurst (Wheeler).

A few colonies belonging to a dark variety of this southern species, near var. *niger* Pergande, were seen nesting in the white sand at Lakehurst. It is probable that the species is really common in the southern portion of the State as claimed in Smith's List. The nest is a small regular crater 3 or 4 inches in diameter.

Subfamily CAMPONOTINÆ.

Brachymyrmex *Mayr.*

53. **B. heeri depilis** *Emery.*—Great Notch (Wheeler); Fort Lee (Wheeler).

This tiny ant is found nesting under stones in shady woods. The workers seem to be subterranean in their habits, rarely or never coming to the surface, at least during the daytime. They resemble the yellow species of *Lasius* in their habit of cultivating root-coccids in their subterranean galleries and chambers. The pupæ are not nude, like those of the following genus, but enclosed in cocoons. The males and relatively large females make their appearance in late August.

Prenolepis *Mayr.*

54. **P. imparis** (*Say*) *Emery.* — Caldwell (Cresson); Camden Co. (Fox); Halifax (Wheeler).

This is the largest and most widely distributed of the North American species of the genus. It prefers to nest in shady oak woods in soil containing more or less clay. It is almost never found nesting under stones but forms small circular craters consisting of earthen pellets. The workers visit trees for the purpose of feeding on the excretions of the extrafloral nectaries. I have seen them eagerly licking these organs on the leaves of *Ailanthus glandulosus.* After imbibing these liquids the gaster often becomes so distended that it is four or five times its normal size and the elegant gait of the insect becomes an awkward waddle. In this replete condition the *P. imparis* worker may be said to represent a temporary stage of the more extraordinary development of the gaster seen in the honey-ants (*Myrmecocystus*). The males and females of *P. imparis* often pass the winter in the parental nest and celebrate their nuptial flight in the spring.

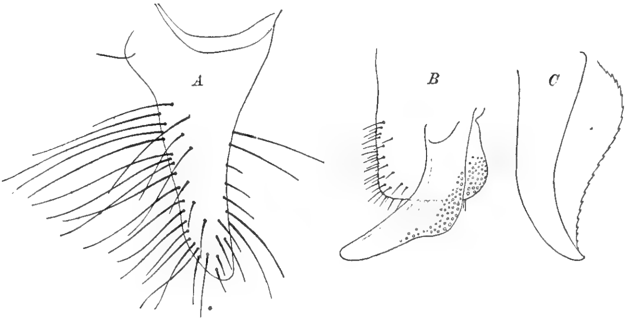

Fig. 1.—A outer, B median, and C inner genital valve of male *Prenolepis imparis* Say.

55. **P. imparis** var. **testacea** *Emery.* — Clementon (Viereck); Medford (Viereck); Lakehurst (Davis and Wheeler).

A pale variety which nests only in sandy regions and on this account is the only form of the species to be found in localities like the pine barrens. It is exceedingly common at Lakehurst but seems to be somewhat nocturnal in its habits. Once only during the daytime have I seen the workers leaving the nest in a file to visit some Aphides on a neighboring oak. They readily assume the replete condition, and owing to their yellowish color resemble the honey-ants even more closely than do the workers of the typical form.

56. **P. parvula** *Mayr.* — Atco (Viereck); Clementon (Viereck);

Brown's Hill Junction (Daecke); Halifax (Wheeler); Lakehurst (Wheeler).

This tiny species is not uncommon under stones in gravelly and sunny places. At Lakehurst it prefers to nest under the great patches of moss and lichen that spread over the sand in the dry woods. In this species, too, the males and winged females pass the winter in the parental nest and take their nuptial flight in the early spring.

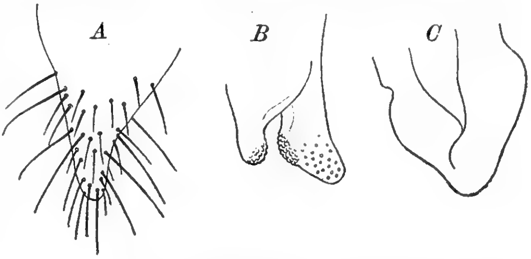

Fig. 2.—A outer, B median, and C inner genital valve of male *Prenolepis parvula* Mayr.

57. **P. arenivaga** sp. nov.

Worker. — Length, 2–2.5 mm.

Mandibles with oblique blades, 6–7 toothed, third and fifth tooth from the apex smaller than the others. Clypeus convex, carinate, with the anterior border faintly and sinuately excised in the middle. Head, including the mandibles, distinctly longer than broad, not narrower in front than behind, cheeks rather convex; occipital border very faintly excised. Antennæ slender; scape surpassing the posterior corner of the head by at least two fifths of its length. Funicular joints twice as long as broad, except the second to fourth, which are a little longer than broad. Thorax robust, mesoëpinotal depression pronounced, its floor somewhat longer than the transverse distance between the two metathoracic stigmata. Petiole small and narrow, cuneate in profile, inclined forward, its ventral surface slightly convex; its upper border blunt in profile, rounded when seen from behind. Gaster and legs of the usual structure.

Surface of body smooth and shining, antennæ and legs somewhat more opaque.

Body covered with very minute white pubescence which is dense on the antennæ and legs but sparse on the body. Antennal scapes, femora, tibiæ, and body with tapering erect or suberect hairs which have dark brown or black bases and white tips. These hairs are very conspicuous on the upper surface of the head, thorax, and gaster.

Pale yellow throughout, mandibular teeth and eyes black.

Male. — Length, 1.8–2 mm.

Mandibles well-developed but edentulous. Clypeus and head, except for the ocelli and more prominent eyes, in shape somewhat like that of the worker. Antennæ slender; scape extending nearly half its length beyond the posterior corner of the head. Mesonotum broad and convex anteriorly, but depressed just in front of the convex scutellum. Epinotum in profile rather sloping, with a but faintly indicated angle between its longer basal and shorter declivous surfaces. Petiole like that of the worker. Genital appendages all long and slender, outer pair triangular, nearly three times as long as broad at the base, tapering to a rounded tip; the bifurcated median pair are slender, digitiform, with the papillose surfaces at the tip; the inner pair are simple and triangular, with tapering rounded tips. Legs long and slender.

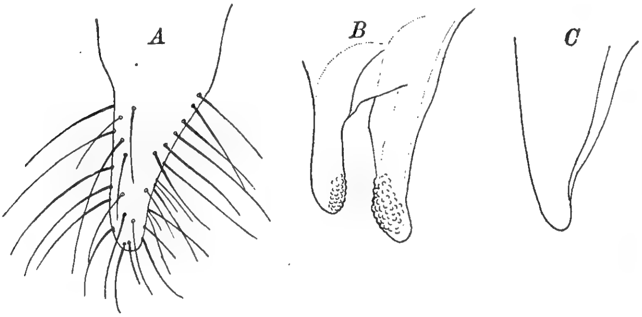

Fig. 3.—A outer, B median, and C inner genital valve of male *Prenolepis arenivaga* sp. nov.

Shining; the head and thorax a little more opaque than the gaster as their surfaces are somewhat shagreened. Appendages subopaque.

Pile and pubescence similar to those of the worker. Hairs on the outer genital appendages rather feeble.

Dark brown, gaster nearly black. Mouth parts, articulations of legs, wing-insertions, antennal funiculi, and genital appendages yellow or pale brown. Wings uniformly grayish hyaline, with very pale veins.

Described from several specimens taken in the pine barrens at Lakehurst, Sept. 25, 1904. This species occurs also in the sandy post-oak woods at Delvalle and Montopolis near Austin, Texas. In all these localities it lives in the pure sand and makes the same kind of nests, namely, flat craters about 1½ to 2 inches in diameter with a small central entrance. At Lakehurst the ants live in the pure white sand overlying a layer of ochre yellow sand. As they dig down into the latter the craters contrast in color with the surrounding white surface.

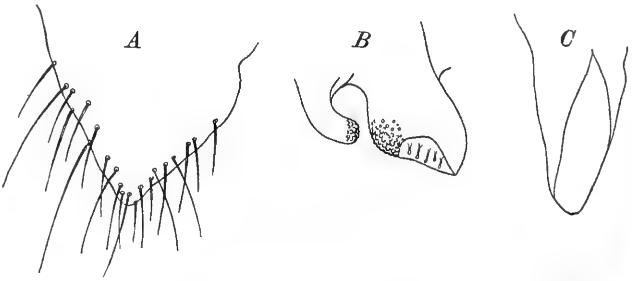

Fig. 4.—A outer, B median, and C inner genital valve of male *Prenolepis guatemalensis* Forel.

Although the worker of *P. avenivaga* resembles that of *P. guatemalensis* in its pale yellow color, the former species is nevertheless clearly distinct as shown by the genital valves of the male. For the sake of comparison I figure the valves of *guatemalensis* (Fig. 4) and of the three species enumerated from New Jersey (Figs. 1 to 3). The valves of two other North American species (*P. bruesi* Wheeler and *P. melanderi* Wheeler) are given in Psyche (June, 1903, pp. 104 and 107), and Emery (Beiträge, etc., 1893, pl. xxii, Fig. 24) has figured the outer genital valves of *P. fulva* Mayr.

Lasius *Fabr.*

58. **L. niger** *Linn.* var. **americanus** *Emery.*— Camden, Riverton, and Anglesea (Viereck); Cape May (Phila. Acad.); Jamesburg (Davis); Halifax, Lakehurst, and Fort Lee (Wheeler).

This form passes in much of our entomological literature as *L. alienus*, although Emery has given reasons for regarding it as distinct from the European form. It is not only the commonest of our numerous species of *Lasius* but the most abundant of our ants, and hence of all our insects. It occurs over the whole of North America except the extreme southern and southwestern portions, from timberline on the highest mountains to the sands of the seashore. Even in circumscribed localities it shows in its nesting sites great adaptability to different physical conditions, from the damp rotten wood of dense forests to the sandy soil of dry, sunny roads. Usually the workers living in the latter stations are much paler in color than the woodland forms and might be regarded as representing a distinct variety. The nests are indifferently under bark, logs, or stones, in rotten wood or in the soil. When in soil they are surmounted by small single or clustered craters. Like all of our other species of the genus, *L. niger* var. *americanus* is much given to cultivating root-coccids and root-aphids in the chambers and galleries of its nests, but, with the exception of the var. *neoniger*, it is the only one of our forms that is not exclusively subterranean in its habits. It may often be seen visiting the foliage of trees and bushes in search of Aphides and small insects. Prof. A. S. Forbes[1] has shown that this insect is of considerable economic importance on account of its noxious habit of cultivating the root-aphids of maize, or Indian corn (*Aphis maidiradicis*). His observations are well worth quoting, as they throw light not only on the habits of this and our other species of *Lasius* but also of other aphicolous ants:

"Seven kinds of ants have been found by us fulfilling the reaction

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[1] A Monograph of Insect Injuries to Indian Corn. Part I. Trans. Dep. Agr. Ill., Springfield, 1894.

of host, guardian, and nurse to the corn root aphis; viz., *Formica fusca*, *Formica schaufussi*, *Lasius niger*, *Lasius niger alienus*, *Lasius interjectus*, *Myrmica scabrinodis*, and *Solenopsis debilis*. The occurrence in this relation of all but the third and fourth just mentioned is, however, so rare that they need receive here no more than this passing mention, especially as their services to the aphis are, so far as observed, the same in character and value as those of the much more abundant species."

The following notes are given on the life-history, haunts, actions, and habits of the ant:

"The winged sexual forms, male and female, of this ant begin to appear each year, as early as the latter part of June (the 21st to the 27th), hatching from pupæ which may have formed late in May (27th and 28th, by our notes). The emergence of males and females from the pupæ continues throughout the season, certainly into October and probably to November, but the males perish before the winter. The females, however, having been fertilized and deprived of their wings, begin their separate excavations in fall, or continue with the workers in nests already established. There they hibernate, sometimes, at least, commencing to lay their eggs in fall and living in spring through April and May.

"The nests or burrows of this ant, in which these breeding operations are carried forward, are widely distributed in corn fields and grass lands,— especially in the latter, along the borders of roads and paths, — and also under stones and boards, in and under decaying logs, and in an indefinite variety of situations. In corn fields they are established almost wholly in the hills of corn, and remain here among the old corn roots throughout the season. As this is the commonest and most generally distributed of all our ants in Illinois, an exhaustive list of its places of habitation would have little present interest. It has never been found by us to form large settlements, or making mounds or conspicuous structures of any kind; but simply scattering its little burrows almost indiscriminately, living in small families rather than great colonies or city-like aggregations, and piling up only a small temporary heap of pellets around the mouth of its burrow. When its mines are explored they are found to consist of irregularly radiating and connected tunnels, rarely going to a greater depth than six or eight inches, or extending outward over a horizontal area of more than twelve or fifteen inches. Here and there in their course and at their extremities and at various depths are chamber-like enlargements in which their eggs and young and the eggs of the corn root aphis are preserved and cared for. Here also considerable collections of the worker ants are usually found, — especially in winter and in times of summer drouth, — and in these chambers the female resides and lays her eggs. . . .

"The fact has already been mentioned in this paper that the sexual egg-laying generation of the corn root aphis — the last to appear in fall — is born in the galleries of the nests or homes of the ants, and that here the sexes pair and the females drop their eggs. As one explores these nests in November, when the root louse eggs are being laid, he is struck with the relative independence of these oviparous adults, which are allowed to wander unattended through the burrows of their hosts as far as a foot or more from a corn root. We have found them, however, still feeding as late as November 5, and laying eggs November 21. These eggs, which are yellow when first deposited, but soon become shining black, and turn green just before hatching, are at first scattered here and there, as it happens, but are finally gathered by the ants for the winter in little heaps and stored in their galleries, or sometimes in chambers made by widening the galleries as if for storage purposes. If a nest is disturbed, the ants will commonly seize the aphis eggs — often several at a grasp — and carry them away. In winter they are taken to the deepest parts of the nest (six or seven inches below the surface in some cases observed) as if for some partial protection against frost; but on bright days in spring they are brought up, sometimes within half an inch or less of the surface, sometimes even scattered about in the sunshine, and carried back again at night—a practice probably to be understood as a means of hastening their hatching. I have repeatedly seen these ants in confinement with a little mass of aphis eggs, turn the eggs about one by one with their mandibles, licking each carefully at the same time as if to clean the surface. These anxious cares are of course explained by the use the ants make of the root lice, whose excreted fluids they lap up greedily as soon as the young lice begin to feed. They are not, however, wholly dependent on this food supply, at least in early spring, as I have seen them kill and drag away at that season soft-bodied insect larvæ, doubtless to suck their juices out as food. . . .

"That the young of the first generation are helped by the ants to a favorable position on the roots of the plants they infest is quite beyond question. It is shown (1) by the fact that in many cases the aphis could not get access to such roots unless these had been previously laid bare by the tunneling of the ants, and (2) by the behavior of ants with mines already constructed, when the root aphis is offered to them. We have repeatedly performed the experiment of starting colonies of ants on hills of corn in the insectary and exposing root lice from the field to their attentions, and in every such instance, if the colony was well established, the helpless insects have been seized by the ants, often almost instantly, and conveyed underground, where we would later find them feeding and breeding on the roots of the corn. In many cases in the field, we have found the young root aphis on sprouting weeds (especially pigeon-grass), which have been sought out by the ants before the leaves had shown above the ground; and, similarly, when the field is planted to corn, these ardent explorers will frequently discover the sprouting kernel in the earth, and mine along the starting stem and place the plant lice upon it. . . .

"I need hardly say that the relations above described between the corn root aphis and these ants continue without cessation throughout the year, the succeeding generations being quite as useful to the ants as those whose history I have thought it worth while to follow in detail. In order to determine more precisely the value of the services performed by their guardians, I arranged in several years a series of experiments designed to show to what extent the plant lice could help themselves if left unattended. Owing to the waywardness of the ants, which in most cases refused to content themselves in confinement, but one of these experiments came to a successful issue. April 13, 1889, corn root aphis eggs were placed in the earth among smart-weed roots to test the ability of the young lice hatching to find the roots for themselves. A check experiment was started at the same time with eggs placed in artificial cavities beside smart-weed roots. April 25 no insects could be found on the plants of the first experiment, while the cavities made in the second experiment contained young lice upon the roots in fine condition."

59. **L. niger** var. **neoniger** *Emery.*—This variety is characterized by having erect hairs on the legs and antennal scapes. It is much less abundant than the preceding and seems to have a northern or subboreal distribution. A few specimens from Anglesea (Viereck) and Hewitt (Davis) belong to this variety.

60. **L. brevicornis** *Emery.*—I have taken this species at Fort Lee, Halifax, Lakehurst, and near the Great Notch. It nests under stones, on hill slopes and in pastures, in rather small colonies, cultivates root-aphids, and, so far as I have been able to observe, is strictly subterranean like all of the remaining species of *Lasius* recorded in this list. The workers have a faintly pungent odor.

61. **L. myops** *Forel.*—Great Notch (Wheeler); Halifax (Wheeler). This is the American representative of the European *L. flavus*, under which name it is sometimes recorded in the literature. The bodies of the workers have a milky white appearance. According to my observations this ant always occupies a definite station, preferring to nest under stones, or leaf-mould in damp, shady woods. The colonies are rather small. The males and winged females may be found in the nests during the first week of August.

62. **L. umbratus mixtus** *Nyl.* var. **aphidicola** *Walsh.*—Caldwell (Emery); Woodbury (Viereck); Fort Lee (Wheeler); Great Notch (Wheeler).

This ant forms much larger colonies than the preceding species. It prefers damp, shady woods and in the Eastern States nests under large stones and in and about old logs and stumps. In the Middle West (Wisconsin and Illinois) it often builds considerable mounds of earth (1–5 ft. in diameter and ½–1 ft. high) around or over decayed stumps. These mounds are perforated with numerous openings and shot through with living grass blades. During winter and early spring, but especially during the latter season, the nests teem with snow-white Aphides and coccids which are cared for by the ants. The males and winged females appear Aug. 2–11.

63. **L. umbratus mixtus** var. **affinis** *Schenck.*—This European variety is recorded by Mayr from New Jersey. I have not yet been able to recognize it among any of my specimens collected in the United States.

64. **L. umbratus minutus** *Emery.*—This subspecies was described by Emery from specimens collected in New Jersey and Maine. In my collection there are three workers marked New Jersey, received from Mr. Pergande.

65. **L. speculiventris** *Emery.*—The types of this species are from Caldwell. I have taken it at Fort Lee and Great Notch. The colonies are very large, like those of *L. aphidicola*, and are found under stones or rotten logs in rich, shady woods. A populous colony found in the early spring at Fort Lee in a pine stump contained thousands of snow-white Aphides of all ages. The females of this species are unknown.

(Subgenus *Acanthomyops* Mayr.)

66. **L. (A.) interjectus** *Mayr.*—Caldwell (Cresson); Lakehurst (Wheeler).

The yellow *Lasii* of the subgenus *Acanthomyops* besides having only

3- instead of 6-jointed maxillary palpi in the worker and female phases, have a peculiar and rather agreeable odor like oil of citronella, quite unlike the odor of the typical *Lasii.* They all form large colonies and lead a subterranean, aphidicolous existence. *L. interjectus* is the largest species of the genus. It is found nesting in old logs and stumps in open woods and occasionally makes rough mounds or merely excavates its galleries under large stones. The mound nests, like those of *L. aphidicola*, often attain considerable dimensions in Wisconsin and Illinois where *interjectus* seems to be more abundant than in the Eastern States.

67. **L. (A.) claviger** *Roger.*— Caldwell (Cresson); Camden Co. (Smith); Merchantville (Daecke); Riverton (Viereck); Fort Lee, Lakehurst, and Halifax (Wheeler).

This is the commonest of our species of *Acanthomyops.* It nests under stones along the edges of woods where there is plenty of warmth and moisture. The males and winged females may be found in the nest as early as Aug. 25, though the nuptial flight may not occur till a month later.

68. **L. (A.) claviger subglaber** *Emery.* — As this subspecies is found near New York City I believe there can be no doubt of its occurrence on the western bank of the Hudson. It may be distinguished from the typical *claviger* in all three phases by its somewhat smaller size. The hairs on the gaster and thorax of the female are shorter and less abundant than in the type.

69. **L. (A.) latipes** *Walsh.*— Camden (Smith); Weymouth (Daecke); Fort Lee (Wheeler).

This species is rather common in grassy fields under large stones. Mr. J. F. McClendon and myself have shown [1] that some colonies have two kinds of females. One of these (the β-female) is very hairy, has much flattened femora and tibiæ, and the hind tarsus is shorter than the hind tibia. The other (α-female) is intermediate in structure between the β-female and the female of *L. claviger.*

70. **L. (A.) murphyi** *Forel.* — There can be little doubt that this interesting species, hitherto known only from North Carolina, occurs in New Jersey. In the Angus collection of the American Museum of Natural History there are a number of specimens of all three phases collected at West Farms, which is now a part of Greater New York, and I have taken females, that had just descended from their nuptial flights, at Cold Spring Harbor, Long Island, and at Mount Kisco, New York.

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[1] Dimorphic Queens in an American Ant (*Lasius latipes* Walsh). Biol. Bull., Vol. iv, pp. 149–163, 3 figs.

Formica *Linn.*

71. **F. sanguinea rubicunda** *Emery.*— Delaware Water Gap (Viereck); Woodbury (Phila. Acad.).

This subspecies of the holarctic blood-red slave-maker, or sanguinary ant, is less common than the next. Its nests are usually under stones in grassy places along the edges of woods. It obtains slaves, or auxiliary workers by kidnapping the young of *F. subsericea.*

72. **F. sanguinea rubicunda** var. **subintegra** *Emery.* — This variety is recorded from New Jersey by Emery. I have seen a single incipient colony of it at Lakehurst, but it is probably more abundant in the less sandy portions of the State. The slaves belong to *F. subsericea* as a rule, but the colony at Lakehurst contained instead workers of *F. schaufussi.* This is probably the normal auxiliary form in this region owing to a scarcity of *subsericea* colonies. In the vicinity of New York *subintegra* is the only form of *sanguinea* I have been able to find.

73. **F. rufa obscuriventris** *Mayr.* — This subspecies is mentioned by Mayr as occurring in New Jersey. I have not seen specimens of it from this State. It is probably a western ant.

74. **F. rufa integra** *Nylander.* — Caldwell (Cresson); Clementon (Viereck); Sea Isle City (Viereck); Jamesburg (Davis); Lakehurst (Wheeler).

Our largest and most conspicuous form of *rufa,* nesting in great colonies which often comprise several nests. These are in piles of large stones or old logs and stumps. The ants stuff all the crannies of their abodes with bits of dead grass, leaves, etc. Like most other species of *Formica, F. integra* is much given to attending Aphides. It is most abundant in hilly regions where it prefers sunny glades or clearings in the forests.

75. **F. difficilis** *Emery.* — Some of the types of this species were received by Emery from New Jersey. I have taken a few workers near Halifax in the Ramapo Mountains.

This interesting species has very small yellow females which are in all probability temporary parasites in the nests of *F. schaufussi* var. *incerta,* as I have shown to be the case in *F. difficilis* var. *consocians* of Connecticut. The young fertilized female of this variety seeks adoption in some depauperate and probably queenless colony of *incerta* and permits her hosts to bring up her young. Later the *incerta* workers die off, leaving the *difficilis* as a pure and independent colony which soon grows rapidly in size and shows no evidence of its parasitic origin. The nesting habits of *difficilis* resemble those of *F. integra* on a small scale, especially as a colony is confined to a single nest. See my paper: 'A New Type of Social Parasitism Among Ants,' Bull. Am. Mus. Nat. Hist., Vol. XX, 1904, pp. 347–375.

76. **F. exsectoides** *Forel.* — Newfoundland (Davis); Palisades (Beutenmueller); Alpine (Am. Mus. Coll.); Ramapo Mountains near Halifax (Wheeler).

This "mound-building ant of the Alleghanies," as McCook has named it, is found nesting in open glades or clearings in the more hilly portions of the State. The mounds which it constructs of earth and vegetable débris are regularly dome-shaped and usually vary from 3–4 ft. in diameter at the base and 1–2 ft. in height. They are exposed to the sun, though often covered with living grass except at the summit. The entrances are very numerous and mostly confined to a broad girdle around the base. A single colony often extends over several mounds. The workers, which are easily distinguished from those of all our other species of *Formica* by the excised posterior border of the head, are very pugnacious. Like the European *F. exsecta* they have a habit of sawing off the heads of other ants.

77. **F. pallide-fulva** *Latreille.* — Of this typical form of the species I have seen a single worker from Cape May (Coll. Phila. Acad.). This is probably very near the northernmost range of the form.

78. **F. pallide-fulva schaufussi** *Mayr.* — Caldwell (Cresson); Camden Co. (J. B. Smith); Da Costa (Fox and Daecke); Lucaston (Daecke); Clementon (Viereck); Alpine (Am. Mus. Coll.), Fort Lee, Halifax, and Lakehurst (Wheeler).

This is one of our commonest species of *Formica.* It forms rather small colonies and nests under stones or in small obscure mound-nests in sunny and grassy fields. In the barrens about Lakehurst, where there are no stones, it nests in the dry pine logs or in the pure sand. It is timid and runs very rapidly. Its food seems to consist very largely of the excrement of Aphides and the carcases of insects.

79. **F. pallide-fulva schaufussi** var. **incerta** *Emery.* — Recorded by Emery from New Jersey. This variety is common in the same localities as the typical *schaufussi* from which it differs merely in somewhat darker coloration and in having fewer hairs on the chin and border of the petiole.

80. **F. pallide-fulva nitidiventris** *Emery.* — Recorded by Emery from New Jersey. The workers are smaller than those of the two

preceding forms, dark colored, without hairs on the chin and petiolar border, and with a more shining and less pubescent gaster. The habits are similar to those of other forms of the species.

81. **F. pallide-fulva nitidiventris** var. **fuscata** *Emery.* — Near Halifax I have taken several workers evidently belonging to this variety, which is characterized by its dark color and rather opaque gaster. It occurs in woods and seems to be less fond of the open, sunny country than the preceding forms of *pallide-fulva.*

82. **F. fusca** *Linn.* var. **subsericea** *Say.* — Caldwell (Cresson); New Brunswick (Smith); Jamesburg (Davis); Fort Lee, Great Notch, and Lakehurst (Wheeler).

Next to *Lasius niger* var. *americanus* this is the commonest of our ants in particular and of our insects in general. Like that variety it ranges from timber-line in the Rocky Mountains to the sand of the seashore and from British America to the latitude of North Carolina. It prefers sunny, grassy places and either constructs dome-shaped mounds which are larger and more definite in outline in the Middle States, or excavates its galleries under stones, boards, the bark of stumps, etc. Except when living in large colonies it is a very cowardly species. Like the other members of the genus *Formica* it attends Aphides but is equally fond of feeding on the bodies of dead insects.

83. **F. fusca** var. **subænescens** *Emery.*—Emery mentions a New Jersey specimen intermediate between *subsericea* and the true *subænescens.* There can be little doubt that the pure form of the latter variety occurs in the hilly portions of the State. It is a woodland form, preferring damper soil and more shade than the var. *subsericea.*

84. **F. fusca subpolita** *Mayr* var. **neogagates** *Emery.* — Very probably occurs in the hilly portions of the State.

Polyergus *Latreille.*

85. **P. rufescens lucidus** *Mayr.* — Camden Co. (Smith's List); Clementon (Fox); Vineland (Mrs. Mary Treat).

This rare and beautiful species, the "shining slave-maker" of McCook, or "shining amazon" as it may be called, uses the workers of *Formica schaufussi* as slaves, or auxiliaries. These are bred from pupæ kidnapped from their maternal nests by the war-like *lucidus* workers. The latter are quite unable to feed themselves, excavate their nests, or care for their own brood, but have to depend for these important activities on the *schaufussi* workers. Hence the *lucidus* are quite unable to live an independent life and may be regarded as permanently parasitic on fragments of *schaufussi* colonies which they bring together with great skill. The sexual forms make their appearance during August.

Camponotus *Mayr.*

86. **C. castaneus** *Latreille.* — Caldwell (Cresson); Sea Isle City (Viereck); Fort Lee (Beutenmueller); Great Notch (Wheeler).

This species nests in the ground, under stones or logs, or in obscure mound-nests, like the typical species of the *Camponotus maculatus* group. It is common neither in New Jersey nor New York State. The latter probably represents the northernmost range of the typical form of the species.

87. **C. castaneus americanus** *Mayr.* — Manumuskin, Iona, and Da Costa (Daecke); Jamesburg and Paterson (Davis); Halifax and Lakehurst (Wheeler).

Similar in habits to the typical form but apparently more widely distributed and ranging as far north as Massachusetts. The colonies I have seen have all been of small size. The young larvæ are salmon-colored, like those of *Tapinoma sessile.*

88. **C. herculeanus pennsylvanicus** *De Geer.* — Caldwell (Cresson); Riverton (Viereck); Medford (Phila. Acad.); .Westville (Phila. Acad.); North Woodbury (Daecke); Newfoundland (Davis); Halifax (Wheeler); Fort Lee (Wheeler).

This is the common, entirely black form of the "carpenter ant." It nests usually in shady woods in old logs and stumps. Thence it migrates into old farmhouses and suburban residences and becomes a pest both by riddling the woodwork with its large anastomosing galleries and by visiting the pantries and kitchens for sweets.

89. **C. herculeanus pennsylvanicus** var. **ferrugineus** *Fabricius.* — Delair (Daecke); Camden (Viereck); Boonton (Viereck); Westville (Phila. Acad.); Fort Lee (Coll. Am. Mus.).

A beautiful color variety of *pennsylvanicus* confined, apparently, to the States east of the Mississippi River. Its habits are very similar to those of the typical form, but it seems to be much less abundant.

90. **C. herculeanus ligniperdus** *Latreille* var. **pictus** *Forel.* — Although I have seen no specimens of this variety from New Jersey, there can be little doubt that it occurs in the State, as it has been found in Pennsylvania, New York State, and Connecticut.

91. **C. marginatus** *Latr.* var. **nearcticus** *Emery.* — Boonton (Viereck); Lakehurst (Davis and Wheeler).

This, the largest and darkest form among the numerous American varieties of this ant, appears to have definite associations with pine trees. It is common at Lakehurst, nesting in the twigs and cones of *Pinus rigida.*

92. **C. marginatus** var. **minutus** *Emery.* — Great Notch (Viereck).

I have taken it at Halifax in the Ramapo Mountains and at Lakehurst, nesting in dead twigs of oaks and attending Aphides on the leaves.

93. **C. marginatus subbarbatus** *Emery.* — Westville (Schmitt); Riverton (Daecke).

In the collection of the American Museum there are specimens of all four phases of this subspecies from each of these localities. I have also taken colonies of it near Bronxville, New York, in the hollow stems of elder bushes.

Worker Ants with Vestiges of Wings.

By William Morton Wheeler.

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The Knickerbocker Press, New York

Article XXIV. — WORKER ANTS WITH VESTIGES OF WINGS.

By William Morton Wheeler.

Plate XIV.

In 1878 Dewitz published an important contribution to our knowledge of the postembryonic development of the appendages in insects.[1] Among the forms which he studied were the worker larvæ and pupæ of a common European ant (*Formica rufa*). He investigated their imaginal discs and discovered minute vestiges of wings which could be traced into the pupa stage. Concerning these structures he says (p. 82): "The imaginal discs of the vestigial wings arise later than those of the legs but nevertheless before the last larval ecdysis. They are situated on the sides of the two posterior thoracic segments, near their hind margins, and are drawn down close to the ventral surface [Pl. XIV, Fig. 1 *b* and *c*]. Hence they are much further from the row of stigmata than from the leg-discs and lie just above the broad muscle band that runs along each side of the ventral surface. An elongate thickening with its two ends directed towards the ventral and dorsal surfaces and having a long slit-shaped invagination, arises in the hypodermis. The disc enlarges while the invagination progresses inward, so that two parts are differentiated, as in the development of the legs: an enveloping membrane and lying within it a more massive portion, the rudiment of the wing."

The further development of these "wing-pockets corresponds exactly with that of the leg-pockets. Each is an invagination of the hypodermis towards the interior of the body and opens outward by means of an orifice. In both cases growth is accompanied by an enlargement of the enclosed appendage."

During the pupal stage of the worker "the wings do not increase in size, since they have reached the acme of their growth in the fully developed larva." Traces of the wings are still visible in the semipupa[2] but the little sacs finally flatten out and apparently become portions of the general hypodermis in the older pupa. Dewitz shows, nevertheless, a small vestige of the hind wing in a profile view of the thorax of a completed worker pupa (Pl. XIV, Fig. 2 *b*).

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[1] Beiträge zur postembryonalen Gliedmassenbildung bei den Insecten. Zeitschr. f. wiss. Zool., XXX, Suppl., 1878, pp. 78–105, Taf. V.

[2] According to Dewitz the term *semipupa* was introduced by Packard (Observations on the Development and Position of the Hymenoptera, with Notes on the Morphology of Insects. Proc. Boston Soc. Nat. Hist., Vol. X, Boston, 1866) and the term *pseudonymph* was subsequently given to the same stage by von Siebold (Beiträge zur Parthenogenesis der Arthropoden, Leipzig, 1871, p. 35). Although von Siebold's term seems to be the more generally used, especially in Germany Packard's term not only takes precedence but is simpler and more appropriate.

Owing to the high degree of variability so characteristic of vestigial organs, we should expect occasionally to find adult worker ants bearing these structures, especially traces of the larger anterior pair of wings, in a more or less imperfect state of development. And the probability of finding such workers would seem to be the greater on account of the vast number of these insects born into the world during every month of the warm season. Among the thousands of workers that have come under my observation during the past six years, I have, in fact, succeeded in finding four winged individuals belonging to two colonies of two different species. While this is a very small percentage of the total number of specimens examined, it must be borne in mind that the wing-vestiges are sometimes very minute and easily detached, so that workers actually hatched with these interesting appendages may rub them off while excavating, or have them torn off by their sister workers while undergoing final ecdysis, or while submitting to the mutual shampooing to which these insects devote so much of their leisure.

Sept. 5, 1904, I found at Bronxville, New York, a small colony of a form of *Myrmica rubra scabrinodis* near the variety *schencki* Emery. This colony comprised about 150 workers and a deälated female of rather small size. Three of these workers bear vestiges of anterior wings but are in every other respect perfectly normal individuals. In the structure of the thorax there is not the slightest approach to the female type. Each of the three specimens represents a different condition in the development of the wings. In one (Fig. 3) the wing vestiges are nearly 1.7 mm. long, spatulate in outline and very slender at their bases where they are furnished with small but distinct tegulæ. The appendages are yellowish brown, translucent and covered with minute hairs like those on the normal wings of females, but without any traces of venation. In another worker (Fig. 4) the wings are barely .4 mm. in length and are merely little opaque pads or sacs, without even a trace of hairs on their surfaces, although they have minute tegulæ at their bases. In the third specimen (Pl. XIV, Fig. 5) the wings are even more vestigial, the right being represented by a small nodular appendage and its tegula, the left by a minute papilla. In all of these workers the vestiges represent anterior wings, as is shown by their insertion just behind the suture which sharply separates the pro- and mesothoracic segments in the region of the pleuræ but not on the dorsal surface. It is very probable that the ants were quite unable to move these appendages. In the dead specimens they are applied to the mesopleuræ with their tips directed ventrally and posteriorly, like the wing-pads in the pupæ of normal males and females, and do not stand off at right angles from the thorax as represented, for the sake of clearness, in the figures. The two specimens with more considerable vestiges are a trifle larger than the majority of the workers in the colony, but this, apart from the wings, is the only character in which they approach the female.

The only other worker ant with wing vestiges in my collection is a soldier of *Cryptocerus aztecus* Forel taken Dec. 27, 1900, by myself from a normal colony that was living between the leaves of an epiphytic Tillandsia near Cuernavaca, Mexico. This specimen (Fig. 6) is in every respect a perfectly normal worker major, or soldier of its species, except that it bears on the external angles of the mesonotum a pair of symmetrical organs representing anterior wings. These are shaped very much like those in the first of the above-described *Myrmica scabrinodis* workers. They are .8 mm. long, spatulate, yellowish brown in color, opaque at the base but semi-transparent towards their tips. Their surfaces are transversely wrinkled but hairless. The tegulæ, if present, are extremely minute. In the dried specimen the vestiges are directed ventrally and posteriorly like the wing rudiments in the normal female pupæ of Myrmicine ants.[1]

We must assume that in all the above cases the wing vestiges which, in worker ant larvæ, are extremely minute and normally disappear in the pupa stage, have, so to speak, been fanned into greater activity of growth by some unusual and unknown stimulus during ontogeny and have persisted till the imaginal stage without, however, attaining to any functional significance.

The specimens above described not only confirm but emphasize Dewitz's conclusion that worker ants must once have possessed functional wings like those of the existing workers of social bees and wasps. This is evidently only a special case of what Dewitz expresses as a general law, now universally accepted by entomologists: "If only one of the sexes of an insect species is winged we must regard the wingless condition of the other as acquired during phylogenetic development." This statement is also clearly applicable to ants, provided we insert the words "one phase of a sex" in the place of "one of the sexes."

The above-described workers with vestigial wings evidently belong to the category of abnormal forms intermediate between normal worker and female ants, like the ergatoid females and pseudogynes.

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[1] This same winged soldier of *Cryptocerus aztecus* is also briefly described by my former pupil Miss Margaret Holliday in her paper entitled 'A Study of Some Ergatogynic Ants.' Zool. Jahrb. Abth. f. Syst., XIX, 4, 1903, p. 315.

While these latter, however, tend to resemble the normal female in the structure of the thorax but, like normal workers, lack wings, the workers above described have vestiges of wings but show no similarity to the female in the structure of the thorax. They therefore represent a distinct and hitherto apparently unknown group of gynæcoid abnormalities for which I would suggest the name *pterergates*.

POSTSCRIPT.

While this paper is going through the press I find in a collection of ants made in Isle Royale near the northern shore of Lake Superior and sent me by Dr. Chas. C. Adams of the University of Michigan, three peculiar workers of a new variety of *Myrmica rubra sulcinodis* Nyl. They resemble one another and approach the female in the structure of the thorax. The mesonotum is delimited anteriorly by a distinct suture, is larger and more convex than that of the normal worker, and has finer longitudinal rugæ. There is a small and indistinct scutellum but no traces of ocelli. Two of the specimens have vestigial fore wings but on the left side only. In one the vestige is a minute nodule like that on the left side in one of the *M. scabrinodis* workers above described (Pl. XIV, Fig. 5). In the other the vestige is about the size of those shown in the worker represented in Fig. 4, but more shrivelled. These three abnormal *sulcinodis* workers resemble a worker of the same species described by Wasmann (Die ergatogynen Formen bei den Ameisen und ihre Erklärung, Biol. Centralbl., XV, No. 16 u. 17, 1895, p. 609) except in possessing wing vestiges. I believe it would be best to regard them all as pseudogynes, although these forms, which are well known in certain Camponotine genera (*Formica*, *Polyergus*, and *Camponotus*) are described by Wasmann as "stets ungeflügelt" (*loco citato*, p. 606).

EXPLANATION OF PLATE XIV.

FIG. 1. — Anterior portion of adult worker larva of *Formica rufa* showing imaginal discs for legs at *a*, and at *b* and *c* vestigial imaginal discs for the hind and fore wings, respectively. After Dewitz.

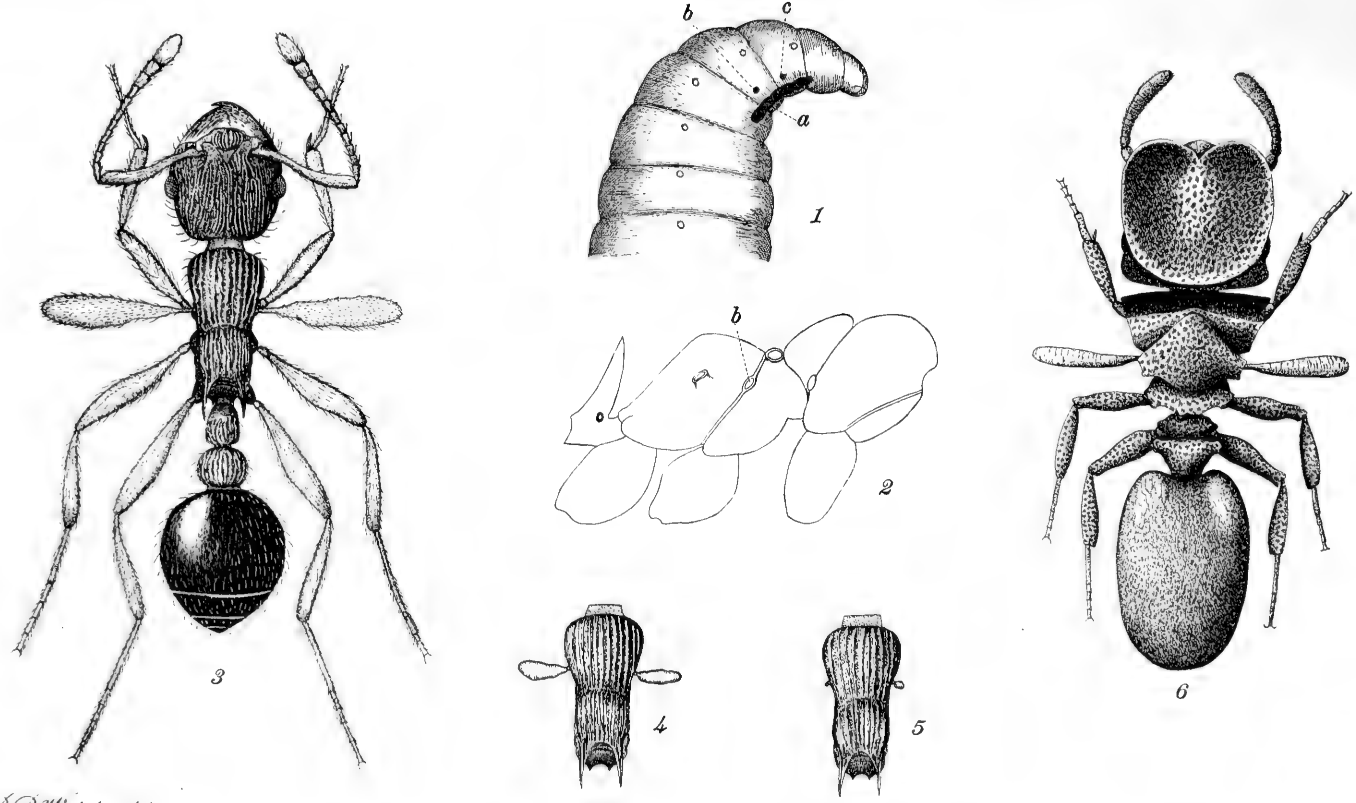
FIG. 2. — Thorax and petiole of adult worker pupa of *Formica rufa* showing vestige of hind wing at *b*. After Dewitz.

FIG. 3. — Worker of *Myrmica rubra scabrinodis* Nylander var. with vestigial fore wings.

FIG. 4. — Thorax of a second worker of the same ant with more reduced fore wing vestiges.

FIG. 5. — Thorax of a third worker with still more reduced fore wing vestiges.

FIG. 6. — Soldier of *Cryptocerus aztecus* Forel with vestigial fore wings.



P. B. Whelpley, del.

WORKER ANTS WITH VESTIGES OF WINGS.

6

The Habits of the Tent-Building Ant (Cremastogaster Lineolata Say).

By WILLIAM MORTON WHEELER.

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Article I. — THE HABITS OF THE TENT-BUILDING ANT (CREMASTOGASTER LINEOLATA SAY).

By William Morton Wheeler.

Plates I–VI.

The large cosmopolitan, but mainly tropical genus *Cremastogaster* is represented in the United States by some seven different species. These are confined to the Southern and Southwestern States, with the exception of the common *C. lineolata* which ranges over the whole country from the Atlantic and Pacific seaboards to an altitude of about 7000 feet in the Rocky Mountains. Like most of our widely distributed ants, it shows a remarkable tendency to vary. Emery[1] recognizes some ten different varieties and subspecies. He finds, moreover, that this number could be increased by recognizing some of the varieties which connect the subspecies. From the extraordinary variety of these ants that have been accumulating in my own collection, I should say that the number of subspecies and varieties hitherto recorded might readily be doubled. I must postpone, however, a detailed taxonomic study of these ants till some future time.

In such a protean form as *C. lineolata* we should expect to find marked variability in habits. While this is undoubtedly the case, this variability does not seem to be definitely correlated with particular color or form variations, but each single subspecies or variety exhibits a considerable range of adaptations, some of which may manifest themselves only in certain localities or at certain seasons. Thus, in its nesting habits, the beautiful yellow and black var. *clara* of Texas shows much the same range of adaptations as our common northern *lineolata* (typical) and its variety *cerasi*, for all of these forms may be found nesting either in the soil under stones, in

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[1] Beiträge zur Kenntniss der nordamerikanischen Ameisenfauna. Zool. Jahrb. Abth. f. Syst. VIII, 1894, pp. 280–286.

dead wood, or under bark, boards, etc. The workers of all of our forms have the same habit of climbing trees and plants in straggling files and of attending aphides and coccids. The excrement of these animals, popularly known as "honey dew," certainly constitutes a large portion of their food. All of our forms have a rank, indescribable odor. When in large colonies, they are often very courageous and sting and bite with great fury. Small colonies, however, or small groups of foraging workers are very timid and when disturbed take refuge in crevices in the bark or depressions in the soil. Like the other members of the genus, *lineolata* workers are able while walking or running to throw up and turn forward the tip of the gaster, so that its flattened dorsal surface becomes ventral and its convex ventral surface becomes dorsal in position. (Figs. 1 and 2.) This peculiar position, however, is not so readily or frequently assumed as in some of the tropical American species, like *C. minuta* and *C. ashmeadi*.

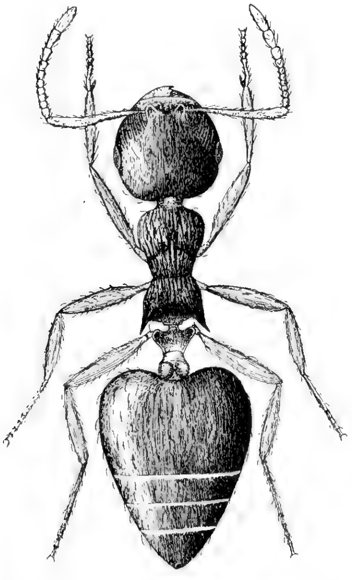

Fig. 1. Cremastogaster lineolata Say. Worker.

Among the habits of *C. lineolata* there is one that is as striking in its manifestation as it is obscure in its phylogenetic origin, — the habit of constructing, often at some distance from the ground or the nest, small enclosures, variously designated as 'tents,' 'pavilions' or 'cowsheds' over colonies of aphides or coccids. These structures, which consist of agglutinated earth or vegetable detritus, have been described by several observers, though they have neither been adequately figured nor satisfactorily explained. Such tents are erected by other ants, but those of *C. lineolata* seem to show greater perfection of workmanship and a higher degree of adaptation to special conditions.

One of the earliest accounts of these structures among our American ants was published by Baron Osten Sacken in 1862.[1] His

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[1] Entomologische Notizen. VII. Stallfütternde Ameisen. Stett Entomol. Zeitg., 23 Jahrg. 1862, pp. 127, 128.

article, which was translated and republished in 'Psyche' twenty years later,[1] is here quoted in full:

"On a horizontal twig of a juniper (*J. virginiana*), about five feet from the ground, I observed a colony of a species of *Lachnus*. A small reddish ant with a brown abdomen was diligently working at a tube-shaped structure of soft, grayish brown, felt-like material, enclosing the twig in a kind of sheath. The material probably consisted of short fibers of liber closely packed together; it had a pitchy smell, burnt well, the smoke having the same smell, but stronger. The structure was about an inch long and one third of an inch in diameter.

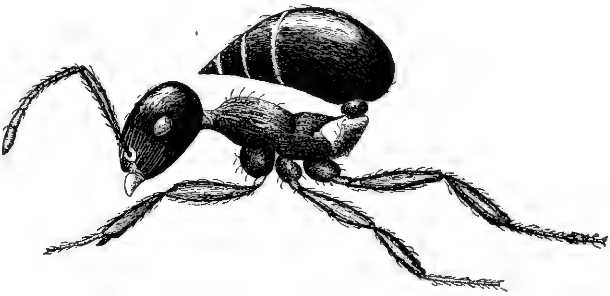

Fig. 2. Cremastogaster lineolata Say. Worker with the gaster turned up and directed anteriorly.

"The second case observed by me was near the Berkeley Springs, in Virginia. A black ant had built a globular structure of a sandy material, of about an inch and a half in diameter, around the stem of an *Asclepias*, which was closely packed with aphides. Although the sand was sufficiently mixed with clay to have the necessary consistence, and although several leafstalks served as supports, the structure was so brittle that I did not succeed in bringing it home. "

It is clear from Osten Sacken's description that the two aphis-tents which he observed were made of very different materials, one being of felted vegetable detritus, the other of sand and clay. As all the tents described by subsequent writers consist of one or the other of these two substances they may be distinguished as the carton and earthen types, respectively. In the original German paper Osten Sacken ascribes the felted or carton nest to a *Formica*, but it is very probable that both of the tents were constructed by forms of *C. lineolata*, for the term *Formica* need not be construed in the restricted modern sense; the fact that it was omitted in the translation may be taken to indicate that Osten Sacken may have employed it in a general sense as synonymous with the word 'ant.'

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[1] Ants and Aphides. Psyche, Vol. III, No. 97, May 1882, p. 342.

A year after the publication of Osten Sacken's paper, Couper described some tents of the carton type[1]:

"An ant occurs on the Homewood estate, near Toronto, U. Canada, that constructs a kind of *papier-mâché* tent over Aphides, parasitic on a species of alder. This structure is attached to the smaller branches of the tree, generally about two or three feet from the ground. The material used by the ants appears to be fine dust fallen from the interior of decayed hard-wood trees. They convert the dust into a sort of paste which is carried up in small particles. It is wonderful to notice the steadiness and rapidity of these little architects about their work. During the cooler portions of sunny days, the whole working force (neuters) of the nest are out at labor, running up and down on the main trunk of the shrub on which the Aphides are living. Each ant in its upward course, having a small particle of the ready-made building material in its mandibles, which it adds to the structure, and the work is continued daily until the extent of the colony of Aphides is under cover. The form of structure altogether depends on the position of the Aphides. It is sufficiently open interiorly to give the ants and plant-parasites plenty of room and ventilation, and there are also several holes leading from underneath the tent for the passage of the ants. I am led to mark this form of Insect Architecture as heretofore unnoticed in America, and although sufficiently familiar with the structure, the species, which is black, and about four lines long, is unknown to me."

A more detailed description of a carton tent of *Cremastogaster lineolata* than either of the preceding was published in 1882 by Professor William Trelease[2]:

"While collecting leaf-fungi on *Andromeda ligustrina*, in a sphagnum swamp at Woods Hole, Mass., in the early part of September, 1881, my attention was attracted by a small, rough mass, apparently of dried sphagnum, surrounding one of the twigs, at a distance of about a metre and a half above the ground. Curious to know how it had reached that unusual place, and what it really was, I went to it, and on closer examination found it to be a shelter erected by a colony of about a dozen worker ants and a numerous herd of small wingless brown aphides, which feed on the sap of this plant.

"The twig on which the nest was placed had a diameter of about 3 mm., branched once at the top, and again at about 8 mm. from the bottom of the nest; between these branchlets a single leaf was given

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[1] Remarks on Tent-building Ants. Proc. Entomol. Soc. Phila., Feb. 1863, pp. 273, 274.

[2] Unusual Care of Ants for Aphides. Psyche, Vol. III, No. 94, Feb. 1882, pp. 310, 311.

off. The nest was 3 cm. long, 1.3 cm. broad at the largest part, near the middle, tapering somewhat toward each end, where it was quite abruptly rounded off, running down the stem in a thin, solid layer for a very short distance. The walls, which had an average thickness of about 0.5 mm., also ran out in the same way, where the branchlets passed through. These decurrent portions formed the only support of the structure, which thus enclosed a capacious chamber surrounding the twig. On the inner surface, so far as seen, the wall was carefully smoothed off; the outer surface was quite irregular and rough. A small round opening existed at each end. That at the top was 3 mm. in diameter: the lower one was very minute, having a diameter of less than 1 mm. As I have said, the nest at first sight appeared to consist of dry bog-moss; a microscopic examination, however, showed the material to be chiefly small fragments of wood — evidently obtained from an old log lying at the foot of the shrub — with small quantities of the leaf-fragments of mosses and phænogams, the whole apparently glued together by the saliva of the ants. . . .

"The ants proved to be workers of *Cremastogaster lineolata* Say; not having winged individuals, I did not attempt to identify the aphides. Both, with the nest, have been placed in the biological collection of the Museum of Comparative Zoölogy at Cambridge, Mass."

In more recent years our entomologists seem to have paid little attention to the aphis-sheds of *C. lineolata.* Professor Comstock has found these structures repeatedly in the neighborhood of Ithaca, N. Y., and has kindly sent me a specimen of one of them together with a photograph of another. They are both of the earthen type and are reproduced in Figs. 1 and 2, Pl. IV. The specimen from which Fig. 1 was made is 3.5 cm. long, 2 cm. broad, and only 1.5 cm. thick. It is somewhat pyramidal in outline and has a circular opening 1.75 mm. in diameter, in its lower portion. Professor Comstock sends me the following field-notes concerning these tents: "The aphis-tents occurred upon dogwood growing on the banks of a stream. The dogwood was growing in a perfectly dry place, but only a few rods above a wet one. Although I collected these tents in several succeeding years, I never took the time to trace the ants back to their nest. The locality is a considerable distance from the University, and I visited it each year on an excursion with my class when there were many things to see, so that I had not much time to devote to these ants. These trips were made during the month of August of each year. I find one of my tents labelled Aug. 2d, '88, another

Aug. 25th, '96. On the 25th of July, '89, I found in another locality quite near the University some ant-tents built over *Kermes* on an oak sapling. This was growing in a dry place several rods from one of our streams."

Mr. E. Daecke has loaned me a fine carton tent of *C. lineolata* which he found October 23, 1903, near Hammonton, New Jersey. It is reproduced, nearly twice the natural size, in Fig. 2, Pl. III. Mr. Daecke writes me that "it was found about four feet from the ground on swamp huckleberry alongside of a wagon road. The spot, located in the typical pine-barrens, was rather moist on account of a small spring in the neighborhood."

Another tent of the carton type, but in a very dilapidated condition, was received from Mr. A. M. Ferguson, who found it near Columbia, Missouri, during the summer of 1903. This specimen, like the one mentioned by Professor Comstock, was built over some *Kermes* on an oak twig.

In the preceding paragraphs I have taken pains to bring together the scattered observations of previous authors for the reason that even in localities where *C. lineolata* abounds, it rarely constructs tents over the aphides and coccids. These structures are of local and sporadic occurrence, as if owing their origin to some unusual condition in the environment rather than to the normal instincts of the species. Though I have often sought for these structures, I have been able to find them in only one locality. August 20 and again September 5, 1905, while collecting insects in the sandy barrens about Lakehurst, New Jersey, I happened upon several fine carton tents built about the terminal twigs of some young pitch pines (*Pinus rigida*). The pines were scattered over an area of about an acre in a damp place that must have been a bog at some former time, as it was still partly overgrown with *Sphagnum* moss and studded with the stumps of larger pines destroyed by a forest fire. The *C. lineolata*, which belonged to the subspecies *pilosa* Pergande, were nesting in some of these stumps. The tents were widely scattered and probably represented the work of several colonies of ants, except in one spot where as many as fourteen were found on a single small pine only six feet high. At first sight they resembled the gray or whitish accumulations of a twig-boring tortricid caterpillar (*Retinia comstockiana* Fernald) which is destructive to the pitch pines. One of these accumulations with the hole from which the moth has escaped is shown in Fig. 1, Pl. I. Closer inspection, however, shows that the tents consist of a substance like coarse, pale gray blotting paper or dried paper-pulp. Under the microscope this resolves itself into bleached particles of *Sphagnum* moss agglutinated by some secretion from the cephalic glands of the worker ants. Several of these tents are shown in Figs. 2, 3, and 4, Pl. I, Pl. II, and Fig. 1, Pl. III. They completely envelop the terminal twigs a few inches from the tips and, though fragile, are evidently well protected from the wind and rain by the needles projecting through and a considerable distance beyond their walls on all sides. Some of the differences in the sizes and shapes of these tents are shown in the figures. The smallest specimens are 2.5 cm. long and 1 cm. in diameter, the largest 4 cm. long and nearly 3 cm. in diameter. Their walls are rarely thicker than ordinary blotting paper and as they are perforated and supported by the needles at a little distance from the surface of the twig, each tent encloses a space obstructed only by the bases of the needles, which thus answer the same purpose as the poles in a veritable tent. As a rule there is but one entrance, a circular hole about 1.5 mm. in diameter usually on one side and near the lower end of the tent, that is, the end nearer the ground or first reached by the ascending files of workers.

All of the tents contained herds of plump Coccidæ, 2–3 mm. in length, which sometimes completely covered the enclosed bark of the twig. There were also a number of *pilosa* workers busily imbibing the ejecta of their protégées or resting quietly in or among them as if loath to leave the pleasure pavilions. In Figs. 3 and 4, Pl. I, two of the tents are reproduced with a large portion of the wall removed to show the extent of the enclosed cavity, the way in which the walls are supported by the pine-needles, and the Coccidæ clustered on the bark of the twig.

The striking character of the tents described in the preceding paragraphs leads naturally to the question of their function and the study of the instincts of which they are an expression. There are several possible answers to such a question. We may suppose that *C. lineolata* builds these structures

1. for the purpose of preventing the escape of the aphides and coccids to other plants or to other parts of the same plant;

2. for the purpose of protecting these insects from their natural enemies or from other ants;

3. for the purpose of protecting them from the cold;

4. for the purpose of protecting themselves from exposure.

For some or all of these purposes the tents would seem to be most admirable contrivances. It is probable that the aphides and coccids make the same appeal to the ants' sense of ownership as their own larvæ and pupæ. This is certainly true of some other ants, like our species of *Lasius*, which are very fond of cultivating white root aphides and coccids in their subterranean galleries. Whenever the stones covering their nests are overturned, the workers seize their snowy charges in their mandibles and hurry away with them to a place of safety. It is natural, therefore, that ants should try to prevent the escape of their charges from a simple sense of proprietorship such as all ants display towards their own brood.

It is probable, moreover, that the protection of the aphides and coccids from other insects is an instinctive precaution not so much against the natural enemies of their charges, as against the larger and more powerful ants, which are quite as fond of honey dew as *C. lineolata.* This ant, being a weak and rather defenceless species, at least while foraging at some distance from its nest, must often be forced into competition with other aphidicolous and coccidicolous ants like our larger species of *Camponotus* and *Formica.* The fact that a herd of aphides or coccids is never attended by more than one species of ant at a time[1] shows that the different species of ants are quite as intolerant of one another on their feeding grounds as in their nests. It is not improbable, therefore, that *C. lineolata* in constructing tents over its charges merely emphasizes its sense of proprietorship in the presence of the larger and more powerful ants with which it has to compete in the struggle for existence; and it may well be that the tents are constructed only in localities where such competition is unusually severe.

That the tents may also serve to protect their occupants from the cold seems not to have been suggested by previous authors. Brandes[2] has shown that aphides — and the same is probably true of the coccids — are relatively inactive before dawn and do not begin to imbibe the juices of the plants till the diurnal temperature has risen sufficiently. The tents, by protecting their occupants from the cold night air, may thus prolong their feeding hours and increase the excretion of honey dew. This would, of course, be a decided advantage to the ants. In support of this supposition we may note the singular fact that the majority of authors above cited found the *lineolata* tents late in the season (August and September) and in damp localities. The cold, due to the greater evaporation in such places, coupled with the lateness of the season, would probably tend to inhibit the feeding

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[1] Except in the case of *Formica sanguinea* and its slaves, *F. fusca*, and then only when the two species belong to the same mixed colony.

[2] Die Blattläuse und der Honigthau. Zeitschr. f. Naturwiss., 66 Bd. 1893, pp. 98–103.

activities of the aphides and coccids at least during the night hours. Under such circumstances a paper or earthen tent would be of great service not only to the aphides or coccids, but also to the ants themselves, since the latter feel bound to spend so much of their time in the company of their charges. This time, of course, is not misspent, since it is obviously of advantage to the ants to be on hand to prevent any waste of the honey dew.

The tents of *C. lineolata* may seem to some to be admirable examples of foresight and reason on the part of their little builders. But although I have just shown how useful these structures may be, I am unable to maintain or even to believe that the ants are aware of these purposes. Like all ant structures, the tents undoubtedly exhibit a considerable degree of variability both in form and texture, but it is clear, nevertheless, that they are built on a common plan even in widely separated regions, so that instead of explaining them as the results of rational activity in the face of new conditions, there may be considerable justification in regarding them as due to an hereditary instinctive disposition, present in all the colonies of the species, but manifesting itself only under conditions formerly prevalent or universal but now of rare and sporadic occurrence. In order to obtain light on this matter, it will be necessary to inquire into the related instincts not only of other species of *Cremastogaster* but also of other genera of ants. In such inquiries the comparative method is of very great value. No instinct is known to be restricted to a single species, and in no two species is an instinct ever manifested in exactly the same way. Hence careful comparison of similar instincts in different species is apt to throw light on the phylogeny of animal behavior and often points the way to profitable observation and experimentation. Let us adopt this method in our study of the tent-building instincts of *C. lineolata*.

The tent-building instincts are not peculiar to the ant under discussion. In his incomparable work [1] published nearly a century ago, Pierre Huber gives the following account of the tents constructed by the "brown ant" (*Lasius niger*):

"One day I happened on a spurge plant that bore in the middle of its stem a little sphere of which the stem was the axis. This was a habitation that the ants had built of earth. They left it through a tiny opening made in its base, descended along the stem and passed into a neighboring formicary. I demolished a portion of this pavilion, built almost in the air, for the purpose of studying its interior.

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[1] Recherches sur les Moeurs des Fourmis Indigènes. Paris 1810, pp. 198–201.

It was a little chamber with vaulted, smooth, and continuous walls. The ants had taken advantage of the form of the plant, suspending their edifice so that the stem passed through its center while the leaves formed its only scaffolding. This retreat enclosed a numerous family of plant-lice to which the brown ants were peacefully resorting for the purpose of feeding on their ejecta in a shelter from the rain, sun, and alien ants. No insect could molest them, and the plant-lice were protected from their numerous enemies. . . .

"Several spurge stems laden with plant-lice rose from the very midst of a formicary of brown ants. These, profiting by the peculiar arrangement of the leaves of this plant, had built around each branch as many elongated chambers, to which they repaired in search of food. When I destroyed one of these domiciles, the ants straightway carried their precious animals into their nest. A few days later the structure was repaired by the insects under my very eyes and the herds were brought back to their pasture.

"These tents are not always so near the earth. I have seen one five feet above the ground, and this one merited a description. It consisted of a blackish, rather short tube surrounding a small poplar branch where it left the trunk. The ants entered it from the hollow interior of the tree in such a way that, without exposing themselves, they could reach their plant-lice by means of an opening at the very base of the branch. The tube consisted of rotten wood from the tree itself, and I saw the ants repeatedly bringing particles in their jaws in order to repair the breaches I made in their pavilion. This particular act is not very common and is not one that can be attributed to the routine of habit.

"There are also some ants that obtain their food from the plant-lice on the common plantain. These insects are usually stationed under the flower spike, but when this has faded and the stem begins to wither — and this occurs towards the end of August — the aphides retire beneath the root-leaves of the plant. Thither they are followed by the ants, which cloister themselves with their protégées by walling up with damp earth all the openings between the edges of the leaves and the ground. Then they excavate the earth underneath, in order to gain access to the aphides and be able to pass from them to their nest through covered galleries."

Huber's observations have been confirmed by Forel,[1] who has shown that in Europe tents are constructed by various species of *Lasius* (*niger*, *alienus*, *brunneus*, and *emarginatus*) and *Myrmica*

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[1] Les Fourmis de la Suisse. Zürich, 1874, pp. 204, 205.

(*lævinodis*, *scabrinodis*, etc.). *L. brunneus* is especially devoted to attending "enormous bark aphides, which it covers with vaulted galleries made of detritus." The forms of *Myrmica* above cited "make earthen cells on plants for the purpose of covering their aphides. Some of these communicate with the nest by means of vaulted passages running along the stem, others are built freely in the air without a covered communication with the soil. It is especially the latter which with Huber we may call pavilions. The aphides, and particularly the coccids, are literally immured by the ants, although their prison is rather roomy, and the ants can enter and leave it through a little opening. I have seen a pavilion of *M. scabrinodis* situated a few centimeters above the soil on an oak branch. It was 1.5 cm. long and shaped like a cocoon. It enclosed some *Chermes* which the ants were carefully attending. When these pavilions communicate with the formicaries, the ants often carry their larvæ into them so that they become a simple dependence to the nest. I have seen a pavilion thus built about a plant stem by *Lasius emarginatus*. This pavilion also enclosed *Chermes*." Forel[1] has also observed *Brachymyrmex heeri* constructing vaulted passage-ways of vegetable débris between its nests and the coccids which it attends.

Our common American form of *Lasius niger* (*L. niger* var. *americanus*), which is very closely related to the European *alienus*, occasionally builds detritus tents around the stems of plants. One of these which I found during the past summer at Colebrook, Connecticut, is represented in Fig. 3. A small colony of *americanus*, nesting under a flat stone, was keeping aphides on a prostrate stem along which a broad and very irregular gallery had been excavated. Around the stem at the point where it emerged from under the stone, the ants had woven a cylindrical tube of fine vegetable detritus about 1½ inches in length and closed at the outer end, as if to prevent the aphides from escaping from the nest.

Both Huber and Forel have described the much larger detritus tents constructed around the stems of plants at a level with the ground by *Formica rufa*. Very similar structures are built by our fine large *F. integra*, a subspecies of *rufa*. In one locality near Colebrook I found several of these tents about the roots of some sapling paper birches (*Betula populifolia*). Two of these tents are shown in Figs. 1 and 2, Pl. VI. One of them had been built around an abandoned bird's nest which happened to occupy the center of a cluster of young trunks. Within these tents, which were about fifty feet

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[1] Études Myrmécologiques en 1875. Bull. Soc. Vaud. Sc. Nat., XIV, 1875, pp. 39, 40.

from their formicary, the ants were guarding a few large black membracids (*Vanduzea arcuata* Say). Late in the summer, in a very different locality, near Lakehurst, New Jersey, I found a number of *integra* workers attending a herd of large lead-colored aphides on the leaves of some small oaks (*Quercus obtusiloba*) around the roots of which they had constructed tents exactly like those seen at Colebrook. The ants had evidently been keeping aphides or membracids in these tents earlier in the season.

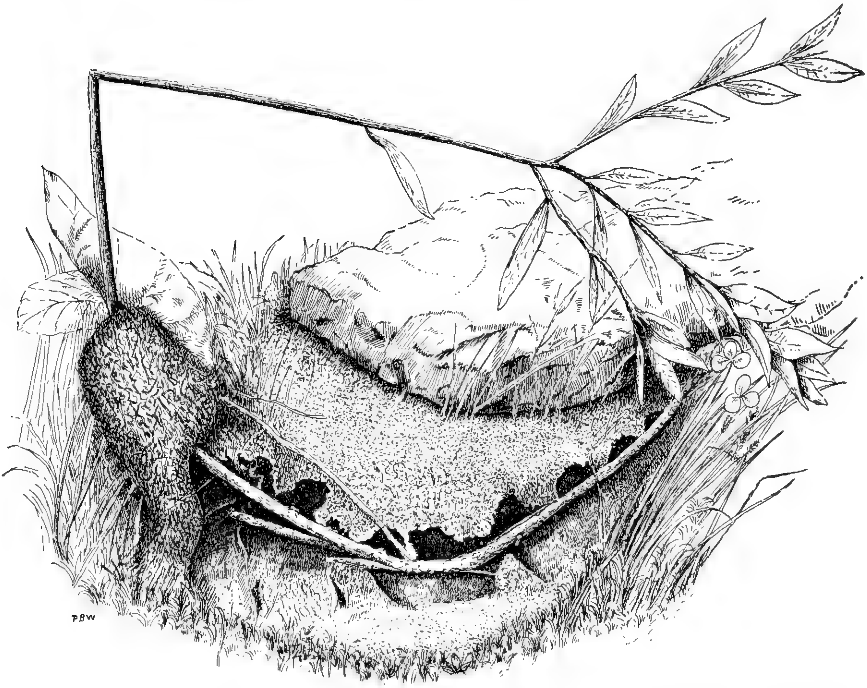

Fig. 3. Nest of *Lasius niger* L. var. *americanus* Emery under stone. The stone has been removed, showing a prostrate plant-stem along which the ants have constructed an irregular gallery. An aphis tent of vegetable detritus is shown on the left-hand side of the figure where the plant-stem rose from under the stone.

F. rufa and its subspecies *integra* may be regarded as typical of a large number of species and genera of ants and show very clearly the intimate connection between the construction of tents and that of the nest proper. The tents are, in fact, merely detached portions of the nest set aside for a particular purpose. Ants are apt to be regarded as mere excavators in soil or wood and their mounds as mere accumulations of the excavated materials. While such a view truthfully represents the conditions in certain species, it is, nevertheless, a very partial view of the nesting instincts of ants in general. For in addition to the excavation of galleries and chambers, the workers of many species, like *F. rufa*, range far afield in search of vegetable débris such as twigs, bits of dead grass, leaves, pine-needles, pellets of earth, etc., and with these construct large mounds, in which the young can be more rapidly incubated than in the cold soil. These building instincts, which may be called positive and centripetal as distinguished from the negative and centrifugal excavating instincts, are so widely distributed among ants as to suggest very forcibly that the primitive ancestral forms of the family must have been architects like the wasps and bees, working the soil or vegetable débris up into rude nests and attaching them to plants and the sides of stones. From such a condition a great number of species have lapsed into mere excavators of the soil, a change the more easily accomplished because the under surfaces of stones and logs furnish such excellent roofs for their galleries and chambers as to render the constructive instincts superfluous. Whether this has been the universal tendency in the Formicidæ can be decided only after further investigation. That it has been the tendency in the genus *Cremastogaster* appears to be satisfactorily shown by the following observations.

The most elaborate and perhaps the most primitive form of architecture among ants is found among the species that use carton in the construction of their nests. These species are members of the genera *Camponotus*, *Polyrhachis*, *Lasius*, *Azteca*, *Liometopum*, *Dolichoderus*, and *Cremastogaster*, and represent three of the five subfamilies of ants. The carton-building species of *Cremastogaster*, with which alone we are here concerned, are nearly all confined to the tropics. As they are distributed over both hemispheres, however, we may infer that the instinct to agglutinate vegetable detritus, dried cow-dung, etc., and build it up into the form of spherical or subspherical nests, is fundamental and of long standing in the genus. Among the Indian species, these carton nests, which are suspended to the branches of trees like the nests of certain hornets in more northern latitudes, were long ago described and figured by Sykes[1] for *C. kirbyi*. Kirby has reproduced Sykes's figures in the Seventh Bridgewater Treatise.[2] Later Mayr, Wroughton, and Rothney called attention to similar habits in two other Indian species (*C. rogenhoferi* and *ebeninus*).[3]

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[1] Descriptions of New Species of Indian Ants. Trans. Ent. Soc. London, I, 1836, pp. 99–103, pl. xiii, fig. 1.

[2] On the Power, Wisdom, and Goodness of God as Manifested in the Creation of Animals and in their History, Habits, and Instincts. Second Am. Edit., Phila., 1837, pl. xi.

[3] *Mayr*, Beiträge zur Ameisenfauna Asiens. Verhandl. k. k. Zool. bot. Gesell. Wien, 1878, pp. 39, 40; *Wroughton*, Our Ants. Journ. Bombay Nat. Hist. Soc., 1892, p. 23; *Rothney*, Notes on Indian Ants. Trans. Ent. Soc. London, 1895, Pt. II, p. 205.

Another species (*C. artifex*), according to Mayr,[1] builds paper nests in Siam and Singapore. In Madagascar *C. ranavalonæ* Forel builds spherical carton nests 3 dcm. (1 foot) in diameter and *C. tricolor* of the same island has a very similar habit.[2] In Africa no less than three species (*C. inconspicua*, *margaritæ*, and *stadelmanni* var. *intermedia*) have been shown by Mayr and Aurivillius to construct large paper nests.[3] These authors describe an *intermedia* nest that was 68 cm. long, 37 cm. broad, and 80 cm. in circumference.

In tropical America there are several carton builders among the species of *Cremastogaster*. F. Smith long ago figured the paper nests of the Mexican *C. montezumia*[4] and Forel has more recently shown that similar structures are made by *C. sulcata*, its variety *ramulinida* and *C. stolli* in Central America and Colombia.[5] *C. stolli* also makes long vaulted galleries which wind about on the tree trunks and along the small branches in the thickets. The ants move about in these galleries and rarely expose themselves to the open air. This species is of particular interest in connection with the tent-building habits of *C. lineolata*.

Turning from these strictly arboreal species of *Cremastogaster*, we are led to inquire whether there are any indications of the carton-building instinct in the terrestrial species like *C. lineolata*. McCook several years ago briefly described the nesting habits of this ant as follows[6]: "The favorite nesting place is under stones or underneath and within the decayed matter of old logs and stumps. This material is sometimes prepared by the ant as a paper-like pulp, and arranged into cells and chambers, which are attached to the surfaces of logs." Similar carton constructions are often built under stones. Fig. 4, Pl. IV, shows the surface chambers of a large *C. lineolata* nest found under a stone in a pasture near Colebrook, Connecticut. In the center of the figure, to the left of the main opening leading into the subterranean galleries, there is a large chamber containing pebbles and traversed by a branching rootlet which is covered with irregular masses of black carton. In other nests somewhat greater accumulations of this substance are occasionally found.

In a variety of *lineolata* not uncommon in the mountains of Colo-

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[1] Loco citato, pp. 40, 41.

[2] *Crandidier.* Histoire Physique, Naturelle et Politique de Madagascar. XX Hymenoptères, 2. Partie. Les Formicides par A. Forel, 1891, pl. vii.

[3] *Mayr, G.* Beiträge zur Kenntniss der Insektenfauna von Kamerun. Formiciden. Entomol. Tidskr., Årg. 17, H. 3, 1896, pp. 253–255. Taf. 4, 5.

[4] Catalog. Hymenopt. Insects, in Coll. Brit. Mus., Pt. VI, Formicidæ, 1858, pl. i.

[5] Biol. Centrali-Amer., Hymenoptera, Vol. III, Formicidæ, 1899–1900, pp. 83, 84, pl. ii, figs. 1 and 2. The nest of *C. sulcata* is also described by Emery in his Studii sulle Formiche della Fauna Neotropica. I, Bull. Soc. Ent. Ital., XXII, 1890, p. 53.

[6] Formicariæ in Comstock's Report upon Cotton Insects. Washington, 1879, p. 188.

rado at an altitude of 6000 to 7000 feet, where the scrub oaks grow among the red volcanic rocks, I have found a much greater tendency to construct masses of carton in the nests under stone. One of these masses of about $\frac{3}{4}$ the natural size is shown in Pl. V. A stone had rolled down on to a lot of dead oak leaves and the spaces between these had been built into a series of inosculating and slightly concentric chambers by means of black carton partitions carried up to the lower surface of the stone. In other nests the pebbles or twigs on which the stone happened to lie were similarly covered with irregular masses of carton. A fragment of this material from such a nest is shown in Fig. 3, Pl. IV. In all these cases the surface of the carton was covered with a delicate blue mould which probably derived its nutriment from the glandular secretion used by the ants as a mortar in agglutinating the fine particles. A similar mould has been observed by Lagerheim[1] covering the carton plates in the nests of the European *Lasius fuliginosus*, and is said to be eaten by the ant-larvæ. In the case of the Colorado *lineolata*, the layer of mould would be an entirely inadequate food supply for the thousands of larvæ found in one of these nests, and there is nothing to indicate that it is of the slightest use to the ants. The blackness of the carton in these nests is due to the large amount of soil used in its construction.

It is difficult to understand why the ants build masses of carton in these nests under stones unless they are exhibiting a merely vestigial instinct which may be called into activity whenever they find leaves or twigs — the very objects about which their arboreal ancestors built carton nests — in the way while they are excavating. The covering of the rootlets with carton in the Colebrook nest above described may also be taken to indicate that contact with vegetable surfaces acts as a stimulus to which the ants respond with an ancient and abortive instinct. This response may, however, assume extraordinary proportions in *lineolata* colonies that are compelled to return to a strictly arboreal life like their tropical ancestors, as shown in the following observation published several years ago by Atkinson[2]:

"The nest was built several feet from the ground on a bush, in the marshes bordering Broad Creek, Hyde County, N. C. . . .

"This nest is about eighteen inches long by twelve inches in circumference at its greatest diameter. I made a longitudinal section of it, and had a photograph taken, so as to represent both the

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[1] Ueber Lasius fuliginosus (Latr.) und seine Pilzzucht. Entomol. Tidskr., Årg. 21, pp. 17–29, 4 figs.

[2] Singular Adaptation in Nest-Making by an Ant, *Cremastogaster lineolata* Say. Am. Naturalist, Vol. XXI, 1887, pp. 770, 771, pl. xxvi.

external form and internal structure. The ants were alive in the nest when I received it. They were chloroformed before sectioning the nest. I took from the nest about one-fourth pint of adults, pupæ and larvæ. They were collected in a mass through the chambers within a space four inches in length of the nest. This space is about two-thirds the distance from the lower end. The material composing the cells in this space is lighter in color than the other internal parts. . . .

"The material used in making the nest seems to be the same as that used by the ant in making its nest under stones, etc. Beside the woody pulp, a microscopic examination seems to reveal also some portions of dried grass. The nest is supported by the branches of the bush; a vine and some stalks of marsh-grass are fastened in it. Upon the outside the material is of a light gray color, much like that of the nest of the white-faced hornet. In the interior it is darker, in some places almost black. Probably the high tides, causing the creek to overflow, forced the ants to build their nest above the high-water mark instead of under stones and within logs."

In this exceptional instance, as shown by the figure accompanying Professor Atkinson's article, the ants had constructed a large carton nest of the same kind as the tropical species above mentioned. We may regard this occurrence as an interesting case of atavism and as demonstrating that instincts like structures may become latent and manifest themselves with almost pristine intensity after an apparent disappearance during many generations. Such conditions, which are apt to prove embarrassing when the potential aspects of instinct are ignored and only its manifestation as "instinct action" is taken into consideration, lead inevitably to the assumption of "dispositions" in the sense in which this term is used by some modern human psychologists.[1]

An explanation of the tents of *C. lineolata* is to some extent implied in the preceding consideration of the carton-building instinct of this species. They may obviously be regarded as small but detached portions of the nest, constructed in a specific environment which at one time, in the possibly not very remote phylogenetic history of the species, led to the building of carton nests. The worker ants, finding themselves detained by their strong appetite for honey dew in exposed situations on the stems of plants, build these small succursal

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[1] These cases of the revival of instincts are particularly suggestive in connection with Hering's view recently elaborated by Semon in his interesting volume "Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens." Leipzig, Wilhelm Engelmann, 1904.

nests, primarily, perhaps, for their own comfort and protection, but at the same time admirably suited to a number of other purposes, as I have shown on p. 7. The presence of the aphides and coccids must also act as a stimulus akin to that which is exercised by the presence of larvæ and pupæ, in calling forth as a response the protective and philoprogenitive, and hence also the nest-building instincts of the species. Originally the tents may have been connected with the main nest by covered galleries such as are still built by *C. stolli*, *Brachymyrmex heeri*, some of the species of *Formica* of the *rufa* group, and many termites, as a means of avoiding exposure to light and enemies. Sometime it may be possible to test the truth of these conclusions experimentally by isolating and exposing colonies of *C. lineolata* on the stems of plants without depriving them of an abundant supply of food and the materials from which carton can be made.

EXPLANATION OF PLATES I–VI.

PLATE I.

FIG. 1. — Accumulation of resin on twig of pitch-pine (*Pinus rigida*) produced by the boring caterpillar of a Tortricid moth (*Retinia comstockiana* Fernald). x 1¾.

FIG. 2. — Carton coccid-tent built by *Cremastogaster lineolata pilosa* Pergande around a twig of pitch-pine, exposed by cutting away part of the needles and showing the opening through which the ants enter and leave the tent. x 1½.

FIGS. 3 and 4. — Similar tents cut open to show the coccids on the twigs and the way in which the carton walls are supported by the pine needles. x 1½.

PLATE II.

A carton coccid-tent built by *Cremastogaster lineolata pilosa* around a twig of pitch-pine. x 1½.

PLATE III.

FIG. 1. — Unusually large coccid-tent built by *Cremastogaster lineolata pilosa* around a twig of pitch-pine, showing the entrance near the base of the lower branch on the right side. x 1½.

FIG. 2. — Carton aphis-tent built by *Cremastogaster lineolata* on twig of swamp huckleberry. x 1¾. From a specimen in the collection of Mr. Erich Daecke.

PLATE IV.

FIG. 1. — Earthen aphis-tent built by *Cremastogaster lineolata* on dogwood. x 1½. From a specimen collected by Professor J. H. Comstock near Ithaca, N. Y.

Fig. 2. — Similar tent, natural size. From a photograph made by Professor Comstock.

Fig. 3. — Piece of black carton built over twigs under a stone by a Colorado variety of *Cremastogaster lineolata.* $\frac{3}{4}$ natural size.

Fig. 4. — Surface chambers of nest of *Cremastogaster lineolata* under a large stone, showing black carton covering rootlets. $\frac{1}{5}$ natural size.

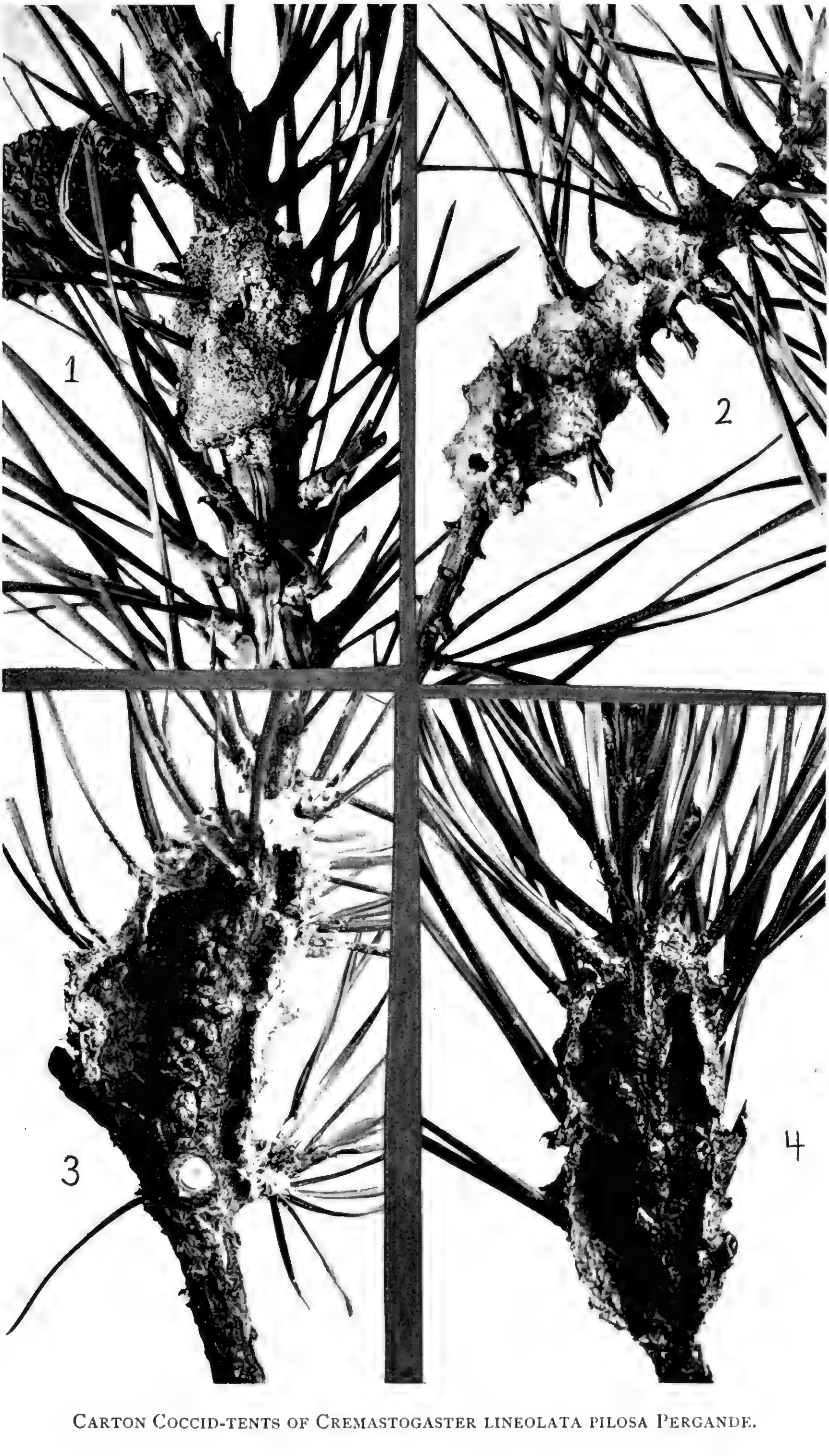
PLATE V.

Nest of a Colorado variety of *Cremastogaster lineolata* built of dead oak-leaves and black carton under a stone. $\frac{2}{3}$ natural size.

PLATE VI.

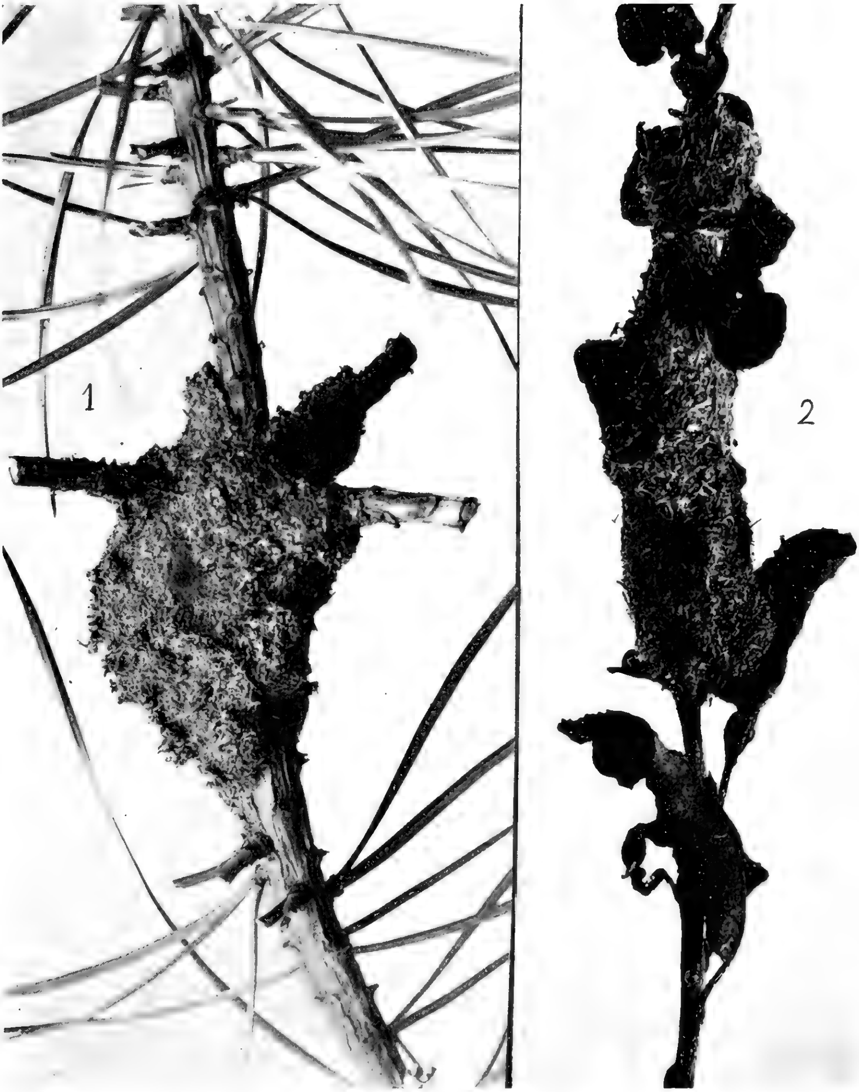
Fig. 1. — Membracid-tent of *Formica rufa integra* Nyl. built about the roots of a young birch (*Betula populifolia*). $\frac{1}{2}$ natural size.

Fig. 2. — Similar tent built around a bird's nest. $\frac{1}{5}$ natural size.

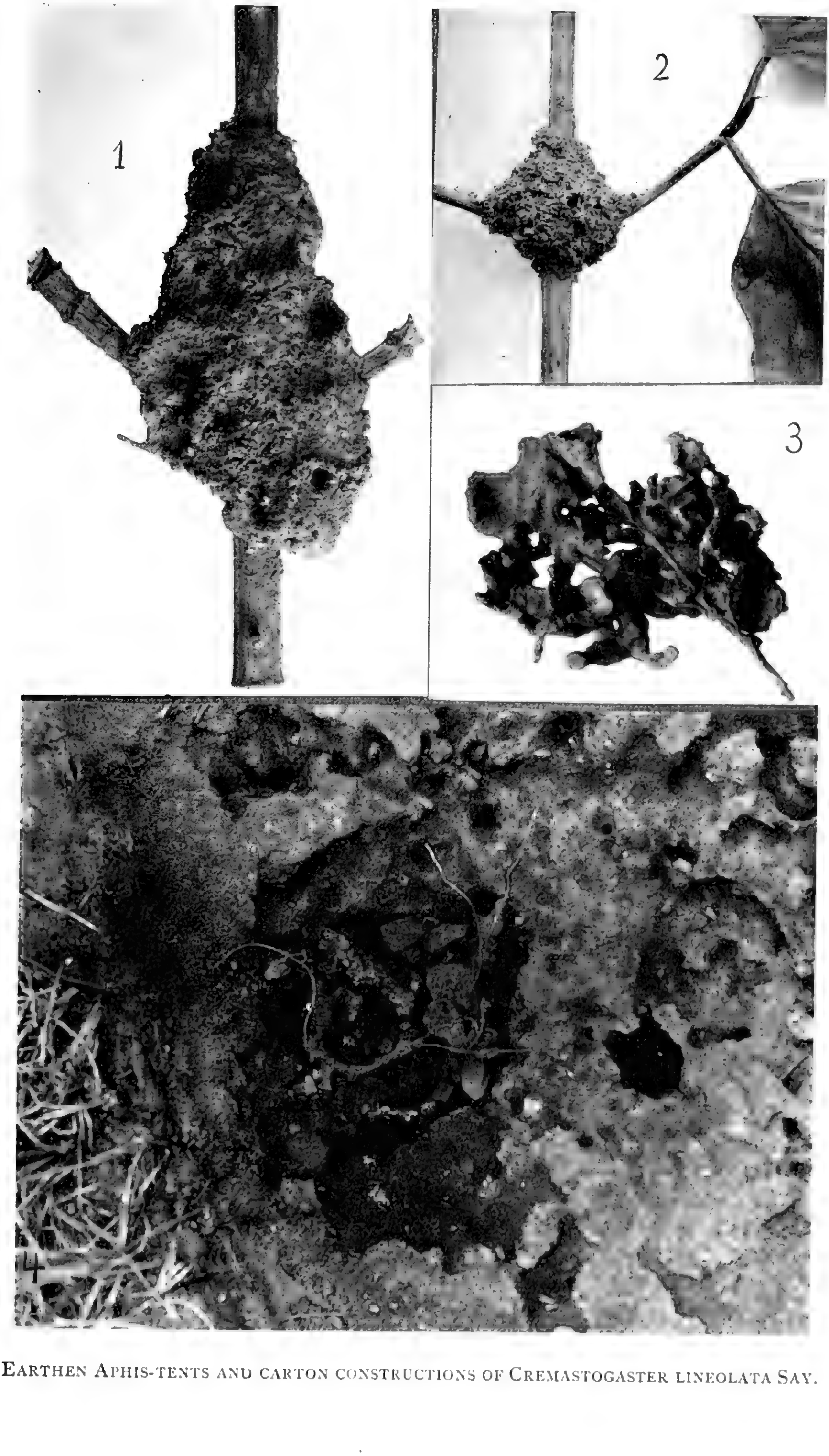


CARTON COCCID-TENTS OF CREMASTOGASTER LINEOLATA PILOSA PERGANDE.

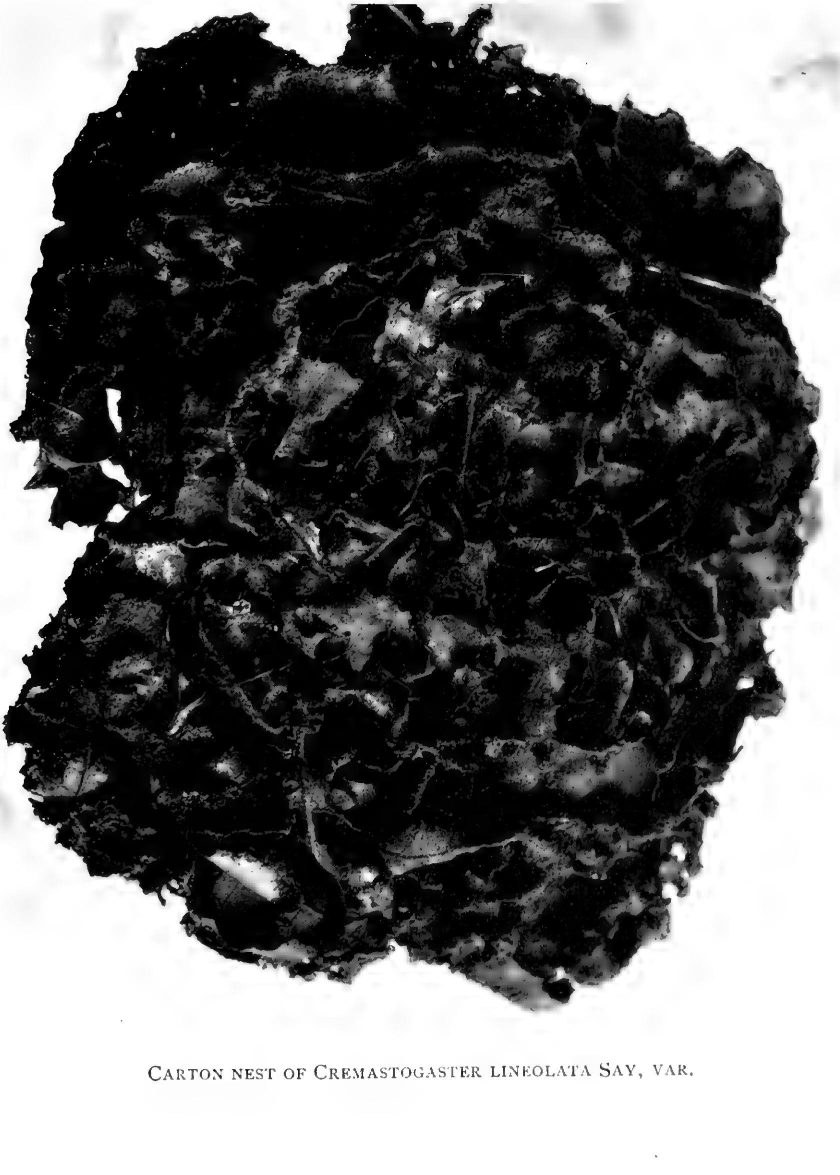
CARTON COCCID-TENT OF CREMASTOGASTER LINEOLATA PILOSA PERGANDE.



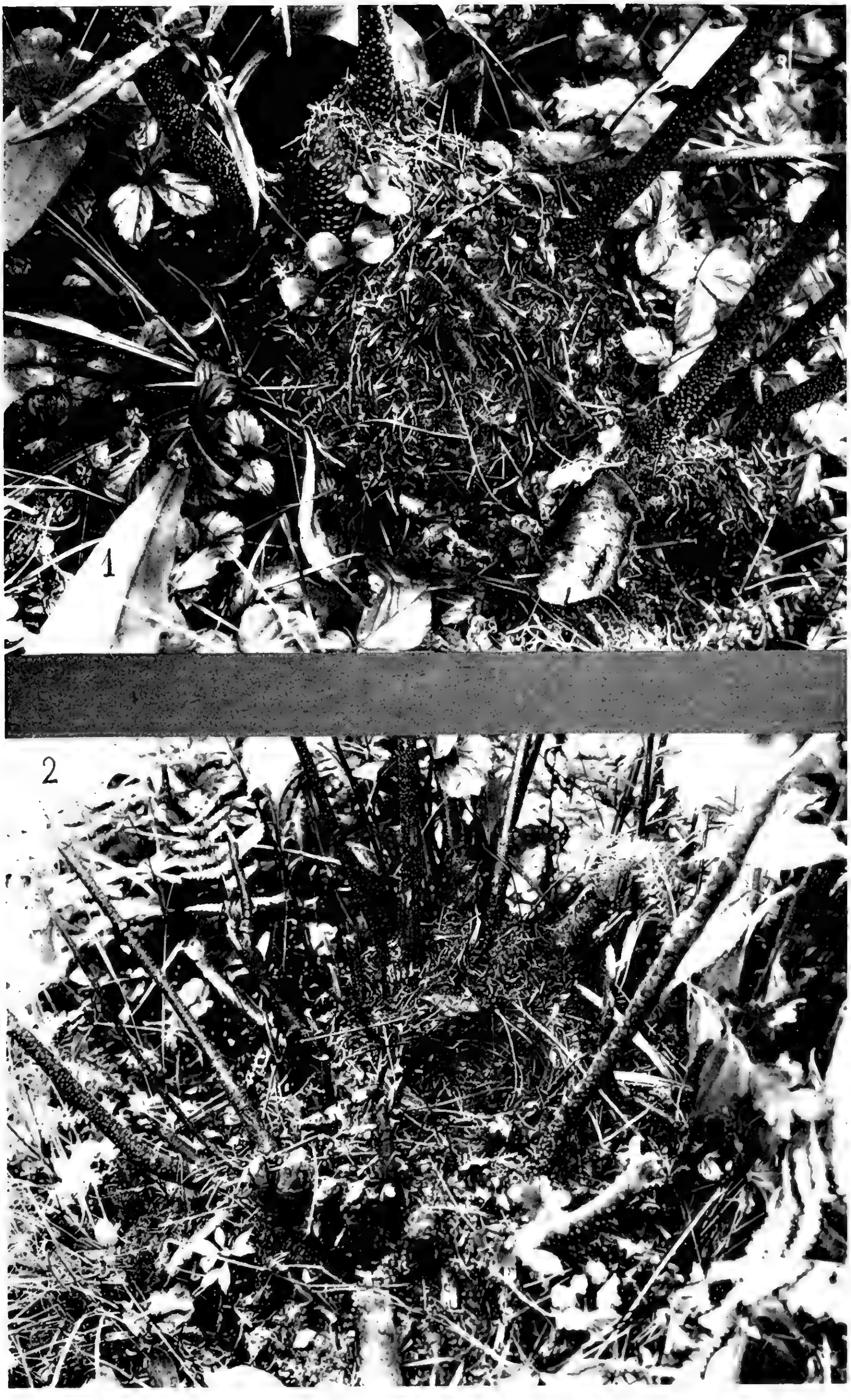
CARTON COCCID- AND APHIS-TENTS OF CREMASTOGASTER LINEOLATA SAY.



EARTHEN APHIS-TENTS AND CARTON CONSTRUCTIONS OF CREMASTOGASTER LINEOLATA SAY.



Carton nest of Cremastogaster lineolata Say, var.



MEMBRACID-TENTS OF FORMICA RUFA INTEGRA NYL.

On the Founding of Colonies by Queen Ants, with Special Reference to the Parasitic and Slave-Making Species.

By William Morton Wheeler.

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Article IV. — ON THE FOUNDING OF COLONIES BY QUEEN ANTS, WITH SPECIAL REFERENCE TO THE PARASITIC AND SLAVE-MAKING SPECIES.

By William Morton Wheeler.

Plates VIII–XIV.

Introduction.

The following paper is a continuation of work previously published on our North American symbiotic ants. It comprises a series of observations and experiments made during the past summer while I was on a month's vacation in the Litchfield Hills of Connecticut, a locality abounding in interesting Formicidæ. Somewhat later in the season the work was continued at my home in Bronxville, New York. I had planned to devote all my time to ascertaining the method of colony formation adopted by young queens of our common slave-making ants (*Formica sanguinea* subspecies and varieties), but the opportunity to renew my study of *Formica consocians*, the discovery of another interesting and probably parasitic species (*F. nepticula*) with diminutive females, and the opportunity of performing some experiments on still other species of the *F. rufa* group, induced me to enlarge the scope of my work. As the habits of all these species have been hitherto very imperfectly known, I have included some illustrations of their nest architecture.

While the exclusive and intensive study of the structure and ethology of a single type is unquestionably of great value if only as a guide to what we may expect to find in allied but as yet unstudied forms, this method is, nevertheless, sometimes misleading and illusive, for the very reason that it may lead us to prejudge a field of inquiry. It would be difficult to find a better illustration of the truth of this statement than the study of the honey-bee. The remarkable conclusions reached from the long and painstaking investigation of this economic insect, have been again and again extended, either unconsciously or intentionally, to the other groups of social insects. And it is especially the instincts of the queen bee that have been thus adopted as a paradigm of the female instincts in other Hymenoptera such as the ants. A moment's reflection, however, shows the error involved in any such generalization even when extended to insects as closely related to the honey-bee as the humble-bees and the wasps.

[*May, 1906.*]

The queen bee is a degenerate organism—a perambulating ovary, incapable of founding a colony unaided, shorn of the primitive pollen-collecting apparatus and instincts of the ancestral wild bees, no longer capable of visiting the flowers and of feeding either herself or her offspring. The worker bee, on the other hand, apart from her normal infertility, is more like the ancestral female bee in still retaining all the attributes of that sexual form. While the queen bee has thus, as it were, delegated to her workers all the female functions and structures except those of normal reproduction, the great majority of female ants, as the following paper will abundantly show, have lost very few or none of the primitive female instincts of the species. In fact, the instincts of the ant-species have their center of gravity, so to speak, in the female and not, as is usually supposed, in the worker. That nearly all writers on these insects should be more or less biased by the study of the honey-bee, is due to the fact that the female ant is apt to be stolid and very slow to respond to the stimuli of her environment, while the instincts of the workers are persistently and conspicuously manifested. Yet the fertilized and isolated female ant is self-sufficient in structure and instincts, since she is able to reproduce the whole colony—males, females, and workers—from her own substance. She is not only the winged germ of the species, but the epitome of its instincts, and, unlike the females of most Hymenoptera, she undoubtedly adds to her inherited capacities the results of individual experience and imitation gained during her prenuptial sojourn in the maternal nest.

Female, or queen, ants in founding their colonies resort to one of three methods, which may be known as the usual or typical, the redundant, and the defective. In the first method there is a manifestation of instincts of the ordinary and undoubtedly primitive type, as displayed by nearly all the species of Formicidæ; in the second there are adventitious instincts leading to a more complicated activity, and in the third method there is a lapsing of original instincts and a substitution of others. More explicitly, these different methods may be described, as follows:

1. The female ant is able by herself alone to start her colony; that is, under favorable circumstances she can produce and bring to maturity the first brood of workers and thus insure the further growth and development of the colony. She is capable of passing many months without nourishment even while she is feeding her offspring. Her voluminous fat-body, built up during her larval life in the maternal nest, together with her degenerating wing-muscles, furnish the sub-

stances that are converted into food for the young. Although so arduous that few of the many queens of all that celebrate their nuptial flight during a season ever succeed in establishing a colony, this method is, nevertheless, the one adopted by the great majority of ants.

2. The female is not only able to accomplish all that is implied in the usual method of founding a colony, but in addition she can carry over to her colony and cultivate certain plants that have been grown as food for countless generations by the stock from which she sprang. This is the case in the remarkable fungus-raising ants (*Attii*) of tropical and subtropical America.

3. The female ant, owing to her small and delicate stature or delayed fertility, is quite unable to found a colony without the aid of workers of another species. This method which is resorted to by parasitic species—using that term in a very broad sense—appears under three different aspects:

A. As *temporary social parasitism.* The female seeks and obtains adoption in a small queenless colony of another species and permits its alien workers to bring up her young. When these have matured, they emancipate themselves and become an independent colony, either by emigration or, more probably, only through the natural death of the host species.

B. As *permanent social parasitism.* The female seeks and obtains adoption in a colony of some other species and there permanently resides together with her offspring. Examples: *Anergates*, *Strongylognathus*, *Protomognathus*, *Wheeleria*, etc.

C. As *dulosis, or slavery.* The solitary female enters a small colony of another species, kills the workers, and seizes and rears the progeny (larvæ and pupæ) as a first step towards bringing up her own young. The workers produced by the female subsequently make forays on other colonies of the host species and appropriate their offspring. While they use a portion of these as food, they permit another portion to develop as "auxiliaries" or "slaves," so that the colony preserves its "mixed" character. This method is adopted by some, if not by all, the forms of the sanguinary ant, or blood-red slave-maker (*Formica sanguinea*). The amazon ants (*Polyergus*) appear to combine this with the preceding method.

Although in this paper we are especially concerned with temporary social parasitism and dulosis, it may not be amiss to discuss a few matters, mainly of a historical nature, concerning the usual and redundant methods of colony formation.

Pierre Huber was the first to call attention to the method of colony formation adopted by the great majority of female ants. In his remarkable book[1] published nearly a century ago, he writes (pp111–113):

"As soon as they [the female ants] have dropped their wings, they are seen running about over the ground in search of a lair. It would be difficult indeed to follow them through their devious courses and detours in the midst of fields and lawns. Although I have failed to see them establish themselves, I have nevertheless convinced myself, after some trials, that these females, which were required to do no labor in the parental formicaries, and seemed incapable of initiative, become, nevertheless, when inspired by maternal affection and the need of employing all their faculties, industrious and care for their young quite as well as do the workers. I confined several fertilized females in a box full of light, damp earth. They knew how to dig galleries, which they inhabited either singly or in common; they laid and cared for their eggs, and notwithstanding the inconvenience of being unable to regulate the temperature of their dwelling, they reared some of the eggs, which became larvæ of considerable size but perished through my negligence.

"Hereupon I assembled some other females in a similar apparatus and gave them some worker pupæ for the purpose of ascertaining whether their instinct would lead them to open the cocoons; and although these females were virgins and still bore wings, they worked to such good purpose that on the following morning I found three workers in their midst. A few days later I surprised them in the act of liberating other workers from their final envelope; in this they behaved like workers and seemed not to be embarrassed by the occupation in which they were engaged for the first time.

"It is evident, therefore, that the females are able, when necessary, to rear a family quite by themselves. If I endeavored to convince myself of this fact by still more positive proofs, it was less for the purpose of dispelling all my doubts on this matter, than to satisfy my curiosity concerning the composition of these incipient formicaries. After long search I succeeded in discovering the hiding place of these females and the nascent colonies which they had established. These were situated at a slight depth in the soil. There were a few workers with their mother and some larvæ which they were feeding. I have seen two examples of such recently established formicaries. Then, too, one of my friends [M. Perrot of Neufchatel, an excellent naturalist] whose observations are worthy of implicit confidence, one day discovered, in a small subterranean cavity, a female ant living alone with four pupæ, for which she appeared to be caring."

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[1] Recherches sur les Mœurs des Fourmis Indigènes. Paris and Geneva, 1810.

While we must still admire, in the light of our present knowledge, the accuracy of Pierre Huber's statements, we must not forget that he largely inferred the method of colony formation and did not actually observe the female ant bringing her firstling brood of workers to maturity. Subsequent authors have not failed to notice this important hiatus in the work of that gifted naturalist. As late as 1874 we find Forel (pp. 417–419)[1] still balancing the views of St. Fargeau, Ebrard, and Lepeletier with those of Huber and reaching the conclusion, which was really no conclusion at all, that "There is left to us only Lepeletier's supposition, but I believe that we must refrain from accepting it as an established fact. Nor am I of the opinion that we are justified in absolutely discarding Huber's conception."

Although Mayr[2] in 1864 observed isolated female ants with eggs, the actual founding of a colony by a single queen was first witnessed by an American of somewhat doubtful reputation as a myrmecologist, Dr. Gideon Lincecum.[3] His work seems to have been overlooked by those who have considered this subject. In 1866 he wrote as follows of the Texas agricultural ant (*Pogonomyrmex barbatus* var. *molefaciens*):

"When one of the young queens, or mother ants, comes to maturity, and has received the embraces of the male ant, who immediately dies, she goes out alone, selects a location, and goes rapidly to work excavating a hole in the ground and carrying out the dirt with her mouth. As soon as she has progressed far enough for her wings to strike against the sides of the hole, she deliberately cuts them off. She now, without further obstruction, continues to deepen the hole to a depth of 6 or 7 inches, when she widens the bottom of it into a suitable cell for depositing her eggs and nurturing the young. She continues to labor outdoors and in, until she has raised to maturity 20 to 30 workers, when her labor ceases, and she remains in the cells, supplying the eggs for coming millions, and her kingdom has commenced. But very few of the thousands of mother ants that swarm out from the different kingdoms two or three times a year succeed in establishing a city. However, when one does succeed in rearing a sufficient number of workers to carry on the business, she entrusts the management of the national works to them and is seen no more outside. . . .

"The workers increase the concealment which has been kept up by the mother ant during the period of her personal labors, of the passage, or gateway to their city, by dragging up and covering it with bits of

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[1] Les Fourmis de la Suisse. Zürich, 1874.

[2] Das Leben und Wirken unserer einheimischen Ameisen. Wien, 1864.

[3] Proc. Phil. Acad. Nat. Sci., 1866, pp. 323, 324

stick, straw, and the hard black pellets of earth, which are thrown up by the earthworms, until there is no way visible for them to enter; and the little litter is so ingeniously placed, that it has more the appearance of having been drifted together by the wind than to have been the work of design.

"In about a year and a half, when the numbers of the community have greatly increased, and they feel able to sustain themselves among the surrounding nations, they throw off their concealment, clear away the grass, herbage, and other litter to the distance of 3 or 4 feet around the entrance of their city, organize an efficient police, and, thus established, proclaim themselves an independent city," etc.

Essentially the same account was published by Lincecum in 1874 in another article[1] and is repeated in McCook's larger work on the Texan agricultural ant (pp. 146 *et seq.*).[2]

My own observations on this same ant confirm Lincecum's in every important detail, except that I have never seen the female return to the surface after she had excavated her burrow. She closes it behind her and, thus shut off from the world, devotes herself to bringing up her brood, like the females of most ants. I am glad to record my nearly complete agreement with Lincecum in this matter because I am unable to accept his account of some of the other instincts of *Pogonomyrmex.*[3]

The first to witness the founding of a colony in an artificial nest, that is, under conditions accurately controlled, was Sir John Lubbock. His account, originally published in 1879,[4] is reproduced in the various editions of his well-known book on ants, bees, and wasps. On Aug. 14, 1876, he isolated two pairs of *Myrmica ruginodis* and succeeded in keeping them in a perfectly healthy condition through the winter. The males died during the following April and May. The females laid during the latter part of April. Some of the young had pupated by the first of July and the firstling workers appeared and began to care for the remainder of the brood by the end of that month and the first week in August. This demonstrated, as Lubbock said, "that the queens of *Myrmica ruginodis* have the instinct of bringing up larvæ and the power of founding communities."

In 1883 McCook[5] published a number of careful observations by

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[1] The Agricultural Ant. Am. Nat., Vol. VII, 1874, No 9, pp. 514, 515.

[2] The Natural History of the Agricultural Ant from Texas. Philadelphia, 1879.

[3] See my paper: A New Agricultural Ant from Texas, with Remarks on the Known North American Species. Am. Nat., Vol. XXXVI, Feb., 1902, pp. 91 et seq.

[4] Observations on Ants, Bees, and Wasps. Part V, Ants. Journ. Linn. Soc., Vol. XIV, 1879 pp. 265–290.

[5] How a Carpenter Ant Founds a Colony. Proc. Phila. Acad. Nat. Sci., Vol. XXIV, 1883, p. 303.

Edward Potts to show that young females of *Camponotus pennsylvanicus* "when fertilized, go solitary, and after dispossessing themselves of their wings, begin the work of founding a new family. This work they carry on until enough workers are reared to attend to the active duties of the formicary, as tending and feeding the young, enlarging the domicile, etc. After that, the queens generally limit their duty to the laying of eggs," etc.

To any one who has given even a little attention to the insect life of our northern woods, it seems strange that the founding of colonies by this ant should not have been recorded till 1883. Certainly no observation could be more easily made, for in many localities it is hardly possible to tear a strip of bark from an old log without finding one or more females of *C. pennsylvanicus* or of the allied varieties *ferrugineus* and *novæboracensis*, each in her little cell brooding over a few eggs, larvæ, cocoons, or minim workers. Usually the cell is carefully excavated just under the loose bark in the decayed wood, but where pine logs are abundant these females often prefer to take possession of the deserted pupal cavities of a longicorn beetle (*Rhagium lineatum* Oliv.). These cavities are surrounded by a regular wall of wood fibers arranged like the twigs in a bird's nest (Pl. VIII, Fig. 1).

Within more recent years the observations of Lincecum, Lubbock, McCook, and Potts have been repeatedly confirmed by continental authors. Blochmann,[1] Forel,[2] Janet,[3] von Buttel-Reepen,[4] and Emery[5] have all published interesting notes on colony formation by isolated females of ants belonging to the common genera *Myrmica*, *Cremastogaster*, *Formica*, *Lasius*, and *Camponotus*.

On more than one occasion during the past six years I have myself been able, both in the field and in the laboratory, to test the truth of these observations. In fact, a catalogue of the North American species, in which I have seen evidence of the founding of colonies by isolated females, would comprise nearly all of our common ants. I have observed it in members of all the subfamilies except the Dorylinæ. Even the Ponerinæ, which I at one time supposed to be an exception, conform to the general rule, for I have found isolated female of *Odontomachus clarus* and *hæmatodes* in the act of establishing their

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[1] Ueber die Gründung neuer Nester bei Camponotus ligniperdus Latr. und anderen einheimischen Ameisen. Zeitschr. f. wiss. Zool., Bd. XLI, 1885, pp. 719–727.

[2] Origine d'une Fourmilère de Camponotus ligniperdus Latr. Ann. Soc. Ent. Belg., XLVI, 1902, pp. 180–182; and Suite de l'Histoire de mon Camponotus ligniperduso. *Ibid.*, XLVI, 1902, pp. 294–296.

[3] Observation sur les Fourmis. Limoges, 1904, 68 pp. 7 pl.; and Études sur les Fourmis, Troisième Note. Bull. Soc. Zool. France, Vol. XVIII, 1893, pp. 168–171.

[4] Sociologisches und Biologisches vom Ameisen- und Bienenstaat. Wie entsteht eine Ameisen kolonie? Arch. f. Rassen u. Gesell. Biol., 2 Jahrg., 1. Heft, Jan. u. Feb., 1905.

[5] Sur l'origine des fourmilières. Compt. Rend. 6me Congrès intern. de Zoologie, Session de Berne, 1904, May 25, 1905, pp. 459–461.

formicaries. During the past May (1905) I observed an unusually striking case of colony formation by queens of the Californian harvester (*Pogonomyrmex californicus*) on the edge of the Mojave Desert. This observation recalls the above quoted passage from Lincecum on the Texan harvester. I arrived at Needles, California, May 23, a day or two after the nuptial flight of *P. californicus.* This was proved by the thousands of isolated females of this species, in the act of establishing their formicaries. The country in which I observed them was the sandy bottom on the right bank of the Colorado River and the adjacent low escarpment of the desert. The latter is interrupted by numerous short 'draws,' which are more or less sandy like the river bottom into which they open. The surface of the escarpment, however, is very hard and stony, but it, too, is furrowed by very small 'draws' often only a few inches wide and containing sand washed from the surrounding surfaces by the winter showers. After their nuptial flight myriads of *Pogonomyrmex* females had rained down over the whole hot, dry country for a distance of at least three miles to the south and as many to the west of the Needles. After losing her wings, each female sought out the regions of pure sand, avoiding the hard surfaces, and set to work digging a hole. The earth was brought out to one side of the burrow so as to form a diminutive fan-shaped mound, which when completed was about two inches in diameter (Pl. VIII, Fig. 2). On May 23, during the hot morning hours the females could be seen at work everywhere in the 'draws' and river bottom, often within a few inches of one another. Many had already completed their burrows, which extended down obliquely to a depth of three or four inches, and had closed the opening behind them. It was an easy matter to dig a deälated female from each spot indicated by a small fan-shaped mound or to tempt her to the surface by inserting a straw into her burrow. A wind- or rainstorm would have obliterated at once all traces of the whereabouts of these females. That they actually sought the pure sand, which is also the substance in which the adult colonies are found, was seen on the top of the escarpment. There each tiny draw was literally filled with incipient nests, although none could be found on the hard intervening spaces often hundreds of feet wide. The ants would, in fact, be quite unable to excavate in such hard soil. The comparatively small number of adult colonies in the vicinity proved that but few of these isolated females ever succeed in rearing a colony. They are doomed to rigid, all but catastrophic, elimination, which only the best endowed and most favorably situated can survive.

In the foregoing paragraphs attention has been repeatedly called to the fact that an ant colony is started by a single isolated female. This requires some qualification, since under very exceptional circumstances a couple of females from the same maternal nest may meet after their marriage flight and together start a colony. During August, 1904, I found two deälated females of *Lasius brevicornis* occupying a small cavity under a clump of moss on a large boulder near Colebrook, Connecticut. They had a few larvæ and small cocoons and a couple of tiny callow workers. The colony was transferred to an artificial nest and kept for several days. Both females were seen to take part in feeding and caring for the single packet of larvæ and freeing the remaining callows from their cocoons. Without doubt these twin females were sisters that had accidentally met under the same bit of moss and had renewed the friendly relations in which they had lived before taking their nuptial flight. This case is of considerable interest because, as a rule, even sister ants seem averse to such postnuptial partnerships. This is indicated by some of the observations on *Formica consocians* recorded in the sequel.

We wonder at the extraordinary endurance which enables the female of our common ants to live so many months without food while she is metabolizing her fat-body and functionless wing-muscles into eggs and the salivary secretion with which to feed her first brood of workers, but the huge female of the American species of *Atta* (in the restricted sense) not only accomplishes this difficult and complicated task, but simultaneously cultivates a fungus garden as a means of providing herself and progeny with food. The founding of colonies by the females of the larger Brazilian leaf-cutting ants has been studied by Sampaio de Azevedo,[1] von Ihering,[2] Goeldi,[3] and Jakob Huber.[4]

Sampaio, on digging up an *Atta* female ten days after the nuptial flight, found her in a cavity with two small white masses, one consisting of 50–60 eggs, the other of a filamentous substance which was the young fungus garden though not recognized as such. Three and one half months after the nuptial flight he excavated another nest which had an opening to the surface of the soil. He found numerous workers of three different sizes but all smaller than the corresponding castes in adult colonies. They were already cutting leaves and had a fungus garden about 30 cubic centimeters in volume. He estimated

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[1] Saúva ou Manhúaára. São Paulo, 1894

[2] Die Anlage neuer Kolonien und Pilzgärten bei Atta sexdens. Zool. Anzeig., XXI, pp. 238–245.

[3] Forel. A., Einige Biologische Beobachtungen des Herrn Prof. Dr. Goeldi an brazilianischen Ameisen. Biolog. Centralbl., XXV, März, 1905, pp. 170–181. Goeldi, Beobachtungen über die erste Anlage einer neuen Kolonie von Atta cephalotes. C. R. 6me Congr. internat. Zool. Berne, 1905, pp. 457, 458; also Myrmecologische Mittheilung das Wachsen des Pilzgartens bei Atta cephalotes betreffend, *ibid.*, pp. 508, 509.

[4] Ueber die Koloniengründung bei Aatta sexdens. Biolog. Centralbl., XXV, 1905, pp. 606–619, 625–635, 26 figs.

the number of workers at 150 to 170, that of the larvæ and pupæ at about 150, and the eggs at 50.

The much more important observations of von Ihering, including his brilliant discovery of the method of transfer of the fungus culture from the maternal to the daughter colony, deserve fuller consideration. According to this observer there are repeated nuptial flights of the Brazilian *Atta sexdens* from the end of October to the middle of December. His account of these flights shows that they are essentially like those of other ants, so that his supposition that the female may be fertilized in the parental nest is without foundation. His account of the founding of the colony is so interesting that I cannot refrain from quoting it.

The fertilized female "rids herself of her easily detached wings by quick motions of her legs and then begins to dig her burrow in some spot more or less free from vegetation. This canal is nearly or quite vertical and measures about 12–15 mm. in diameter. It is so narrow that the 'Içca' cannot turn round in it, but is compelled to walk backwards whenever she returns to the surface. She bites off lumps of earth with her powerful jaws, makes them into a pellet by means of loose threads of saliva, brings them up and deposits them a short distance from the entrance to the burrow. The earth thus brought up forms a circular wall, thickened in front and interrupted behind, about 4–5 cm. broad in front and at that point 3 cm. from the entrance. The burrow varies in length according to circumstances from 20–30 cm. and ends in a small laterally placed chamber about 6 cm. long and somewhat less in height. As soon as the chamber is completed, the ant closes the upper portion of the burrow to a distance of 8–10 cm. from the entrance with pellets of earth and this closure becomes more and more compact in the course of weeks, probably through the action of the rain.

"If the nest be opened in one or two days, the female will be found in the empty chamber unchanged, only more lethargic, as if exhausted. A few days later one finds near the ant a little packet of 20–30 eggs undergoing segmentation. Beside them lies a flat heap of loose white substance, only 1–2 mm. in diameter. This is the earliest rudiment of the fungus garden. Microscopical examination shows that it consists of compact masses of the well-known fungus-hyphæ, but no traces of "kohlrabi" corpuscles. As time goes on the fungus garden grows rapidly and becomes more voluminous till it reaches a diameter of about 2 cm. It seems to consist of closely aggregated spherules about 1 mm. in diameter. As soon as it has attained this size the transparent pyriform globules bud out, which Moeller called "kohlrabi" and the ant is seen to eat them frequently. She always keeps close to the fungus garden and in it embeds her eggs. The larger of these soon become larvæ. The eggs are not spun over with fungus hyphæ but have the chorion smooth and shining. Eggs are also found in the interior of the fungus mass, which the ant keeps rearranging and redistributing from time to time. It was easy, for purposes of observation, to transfer the ant to a terrarium. Without excavating anew she remained with her garden on the fresh layer of earth. The garden did not grow, but rather diminished in volume, for it is difficult to imitate the conditions, especially the precise degree of moisture, in which it grows and develops in its cavity. I failed, therefore, to keep the ant and her garden till the first workers appeared.

"The time required to accomplish this must be between two and three months. Presumably the last phase of this first brood period is very precarious, since leaves must be brought in to serve as a substratum for the further growth of the fungus garden. In any event, the development of the garden is in need of further elucidation. According to my investigations, which need fuller confirmation, the organic substratum is provided in the form of malaxated eggs, but perhaps the soil, which is rich in vegetable mould, may itself contain nutrient substances. . . .

"As soon as the first workers appear, the colony may be regarded as established and the opening up of the burrow, the enlarging of the first chamber, carrying in of leaves, etc., lead to the well-known conditions of the adult colony. . . .

"The preceding description is hardly complete without an answer to the question: Whence come the fungus germs for the establishment of the new garden?" After searching the queen for fungus spores concealed about her person, von Ihering made the important discovery that "every *Atta* queen, on leaving the parental nest, carries in the posterior portion of her oral chamber a loose pellet, .6 mm. in diameter, consisting of hyphæ of *Rhozites gongylophora*, small fragments of bleached, *i. e.*, chlorophylless leaves, and chitinous bristles. The last are undoubtedly derived from the larvæ undergoing ecdysis in the parental nest." Von Ihering is of the opinion that the female keeps the pellet of hyphæ, etc., in her mouth till she has excavated her chamber and then spits it out where it will serve to kindle the fungus garden of the new colony.

The observations of Goeldi are little more than a confirmation of those of von Ihering. He maintains that the fungus is actually grown on some of the malaxated eggs of the *Atta* queen, who would thus be sacrificing a part of her offspring as a culture medium for the fungus that i to nourish both herself and her workers in their larval and adult stages.

None of these investigators succeeded in rearing an *Atta* colony from its very inception till the hatching of the firstling workers and the bringing in of the leaves for the purpose of keeping up the fungus culture. This has been accomplished very recently by Jakob Huber, who, besides correcting a few errors in the work of his predecessors, has added a number of new and important observations. His paper, from which the following abstract is taken, also contains several interesting figures from photographs of the *Atta* female, her progeny, and fungus garden.

The female expels the pellet from her buccal pocket the day following the nuptial flight. It is a little mass .5 mm. in diameter, white, yellowish, or even black in color, and consists of fungus hyphæ imbedded in the substances collected from the ant's body by means of the strigils on her fore feet and thence deposited in her mouth. By the third day 6 to 10 eggs are laid. At this time also the pellet begins to send out hyphæ in all directions. The female separates the pellet into two masses on this or the following day. For the next 10 to 12 days she lays about 10 eggs daily, while the fungus flocculi grow larger and more numerous. At first the eggs and flocculi are kept separate, but they are soon brought together and at least a part of the eggs are placed on or among the flocculi. Eight or ten days later the flocculi have become so numerous that they form when brought together a round or elliptical disc about 1 cm. in diameter. This disc is converted into a dish-like mass with a central depression in which the eggs and larvæ are henceforth kept. The first larvæ appear about 14 to 16 days after the *Atta* female has completed her burrow, and the first pupæ appear about a month after the inception of the colony. By this time the fungus garden has a diameter of about 2 cm. There are no "kohlrabi" corpuscles in the earlier stages, and when first seen they are at the periphery of the disc. A week later the pupæ begin to turn brown and in a few days the first workers hatch. Hence the time required for the establishment of a colony under the most favorable conditions is about 40 days. After this rapid survey of the matter, Huber asks the important question: How does the Atta female manage to keep the fungus alive? Obviously the small amount of substance in the original pellet must be soon exhausted and the growing hyphæ must be supplied with nutriment from some other source. His interesting answer to this question may be given in his own words:

"After carefully watching the ant for hours she will be seen suddenly to tear a little piece out of the fungus garden with her mandibles and hold it against the tip of her gaster, which is bent forward for this purpose. At the same time she emits from her vent a clear yellowish or brownish droplet which is at once absorbed by the tuft of hyphæ. Hereupon the tuft is again inserted, amid much feeling about with the antennæ, in the fungus garden, usually not in the same spot from which it was taken, and is then patted in place by means of the fore feet. The fungus then sucks up the drop more or less quickly. Often several of these drops may be clearly seen scattered over the young fungus garden. According to my observations this performance is repeated usually once or twice an hour, and sometimes, to be sure, even more frequently. It can almost always be observed a number of times in succession when a mother ant that has no fungus, as sometimes happens in the cultures, is given a piece of fungus belonging to another *Atta* female or from an older colony. The mother ant is visibly excited while she explores the gift with her antennæ, and usually in a few minutes begins to divide it up and rebuild it. At such times she first applies each piece to her vent in the manner above described and drenches it with a fecal droplet."

From these observations Huber concludes that the droplet must be liquid excrement and that the fungus owes its growth to this method of manuring. A direct use of malaxated eggs for this purpose was never observed and could not be detected by microscopical examination, although a number of observations show that the same result may be accomplished indirectly, namely by the female eating her own eggs. This habit is so common and apparently so normal that Huber estimates that 9 out of every 10 eggs are devoured by the mother, often as soon as they are laid. The life of the *Atta* female in her little cell during all this time is very rhythmical. At regular intervals she conscientiously examines the walls of the cavity, flattens out the earth, etc. She devotes more time to licking and manuring the fungus garden and, of course, lavishes most care on the brood.

As soon as the larvæ appear they are fed directly with eggs thrust into their mouths by their mother. Huber concludes that this is their normal diet till the first workers hatch. He never saw the female either eating the fungus mycelium herself or feeding it to the young. As a proof of his contention he cites the case of one of his *Atta* queens who brought up a brood without a fungus garden. With the appearance of the firstling workers, which are minims, that is members of the smallest worker caste, a change comes over the colony. They begin to usurp the functions of the mother ant. They manure the garden, which at the time of their appearance measures hardly more than 2.5 cm. in diameter, and feed the larvæ with their mother's eggs. The workers themselves, however, feed on the "kohlrabi" which has been developing on the hyphæ for some time. After about a week some of the workers begin to dig in the earth, and ten days after the appearance of the first worker and seven weeks after the inception of the colony, they break through to the surface of the soil and surround the entrance of the nest with a tiny crater of earthen pellets. They now begin to bring in pieces of leaves, knead them up into minute wads, and insert them in the fungus garden. The method of manuring the garden with fecal droplets seems now to be abandoned. The mother *Atta* henceforth pays no attention to the development of the garden or to the brood, but degenerates into a sluggish, egg-laying machine, while the multifarious labors of the colony devolve on the workers. In the meantime the "kohlrabi" has become so abundant that it can be fed to the larvæ.

In concluding his paper Huber makes the important observation that fertile females of *Atta sexdens* are readily adopted by strange workers of their own species. Such adoptions may be frequently resorted to in a state of nature and would perhaps account for the enormous size and great age of some of the formicaries of the larger species of *Atta*, which in this respect resemble the colonies of *Formica rufa* and *F. exsectoides* in the north temperate zone.

In marked contrast with the elaborate habits and great independence of the *Atta* females are those of certain ants which are unable to establish their colonies without the assistance of alien workers. Some of the most remarkable examples of this inability are found in the typical genus *Formica*.

Our American species of *Formica* may be separated into at least five groups, all but one of which may bear the name of a well-known European species. America is, without doubt, the geographical center of the genus and hence an American type for each group would seem to be more appropriate. Nevertheless, both because the European species were first and more thoroughly studied and because they are less variable than their American congeners, they should maintain their position as reference types. The five groups of species are the following:

1. The *fusca* group. European type: *F. fusca* Linn. Typical and most widely distributed American form: *F. fusca* var. *subsericea* Say. Additional varieties: *subæneseens* Emery, *argentata* Wheeler, *gnava*

Buckley, *neorufibarbis* Emery, *neoclara* Emery, *montana* Emery. Additional species: *F. subpolita* Mayr with the varieties *neogagates* Emery and *perpilosa* Wheeler; *F. cinerea* Mayr var. *neocinerea* Wheeler; *F. lasioides* Emery and its var. *picea* Emery; *F. rufibarbis* Mayr var. *occidentalis* Wheeler and *F. pilicornis* Emery.

2. The *pallide-fulva* group. Not represented in Europe. Typical and most widely distributed form: *F. pallide-fulva* Latr. subsp.*schaufussi* Mayr, with the varieties: *incerta* Emery, *nitidiventris* Emery, *succinea* Wheeler, *meridionalis* Wheeler and the typical *pallide-fulva*.

3. The *sanguinea* group. European type: *F. sanguinea* Latr. The common American forms are the subspecies *rubicunda* Emery and its var. *subintegra* Emery. Additional subspecies: *puberula* Emery, *obtusopilosa* Emery, *subnuda* Emery. Additional species: *F. pergandei* Emery and *munda* Wheeler.

4. The *rufa* group. European type: *F. rufa* Linn. Additional European forms: *F. pratensis*, *truncicola* and *pressilabris*. The species is represented in America by *F. rufa* subsp. *integra* Nyl. and its var. *hæmorrhoidalis* Emery, subsp. *obscuriventris* Mayr, and its varieties: *integroides* Emery, *rubiginosa* Emery, and *melanotica* Emery and the subsp. *obscuripes* Forel. Additional species: *F. difficilis* Emery and its var. *consocians* Wheeler, *F. oreas* Wheeler, *dryas* Wheeler, and its var. *gymnomma* Wheeler, *ciliata* Mayr, *impexa* Wheeler, *montigena* Wheeler, *nepticula* Wheeler, *nevadensis* Wheeler, *microgyna* Wheeler and its variety *rasilis*Wheeler, *dakotensis* Emery and its variety *wasmanni* Forel.

5. The *exsecta* group. European type: *F. exsecta.* Nyl. American forms: *F. exsectoides* Forel and its var. *opaciventris* Emery. Additional species: *F. ulkei* Emery.

With respect to the method of establishing their colonies these five groups may be arranged under three heads:

1. The ants of the *fusca* and *pallide-fulva* groups agree in having large females that adopt the usual method of colony formation. I have observed this in most of the varieties of both species.

2. Many, if not all, the ants of the *rufa* and *exsecta* groups seem to be temporary social parasites; that is, their young fertilized females are unable to rear a first brood without the assistance of workers belonging to the *fusca* or *pallide-fulva* groups. In several of the species this inability is very clearly indicated by the diminutive stature of the females, which may be actually smaller than the largest workers of their own species and seem to be much less immediately fertile than the females of the *fusca* and *pallide-fulva* groups.

3. The females of some of the species of the *sanguinea* group, such as *F. pergandei* and the different subspecies and varieties of *F. sanguinea*, are dulotic and appear to secure the workers needed for bringing up their first brood by robbing the young of ants belonging to the *fusca* or *pallide-fulva* groups.

Thus the colonies of the ubiquitous, very cowardly, highly adaptable and extremely fertile *F. fusca* and *F. schaufussi* furnish a wide-spread substratum, so to speak, on which at least many of the species of *Formica* belonging to the *rufa*, *exsecta* and *sanguinea* groups have molded their parasitic habits. These species have learned to exploit the *fusca* and *schaufussi* in manifold ways — to use them either merely as nurses for their firstling progeny (temporary social parasitism), or as a permanent food supply and source of auxiliary workers (dulosis). The parasitism thus inaugurated in the genus *Formica* has been developed to its extreme in the allied highly dulotic genus *Polyergus*, the members of which are abjectly dependent on *fusca* or *schaufussi* workers for their food, for the care of their young, and even for the excavation of their nests.

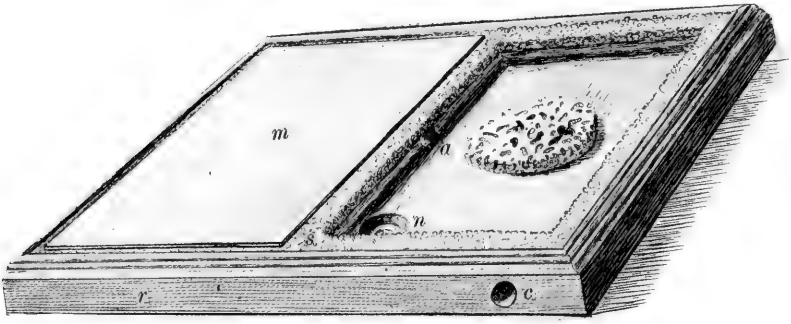

Fig. 1. Artificial ant nest, constructed on the combined principles of the Fielde and Janet nests; with one of the roof-panes removed. *r*, plaster of Paris base, cast in a single piece; *c*, entrance to be plugged with cotton after the admission of the ants from the Forel arena: *m*, glass roof-pane, resting on Turkish towelling (*s*); *a*, opening between the two chambers; *n*, manger; a cup-shaped depression in the plaster base; *e*, slice of sponge, which is kept wet. The plaster base measures 20 × 25 cm.

Inasmuch as the parasitic instincts of these various ants are traceable to the very first foundation of the colony, and since this, as has been abundantly shown in the preceding paragraphs, is the work of the female ant, I have concentrated my experiments on the instincts of this sex, although some miscellaneous notes on nesting habits and other ethological matters which fell under my observation at the same time, have been included in the following pages.

For purposes of study I have used an artificial nest combining the Fielde and Janet patterns (Fig. 1). Of the former I have retained the shape and arrangement of the chambers, the towelling, sponge-slices, roof-panes and the method of roofing the passage-ways between the chambers, but for the glass floor and walls I have substituted a plaster of Paris base and sides cast in a single piece. The dry plaster was mixed with a pale reddish pigment and, after being cast and thoroughly dried, was coated with varnish to prevent undue absorption of water from the damp sponges. These nests are very easily made, are almost as light and portable, and quite as satisfactory in all other respects as the original Fielde nests.

My simple experiments, which consisted in introducing female ants into small colonies of workers of alien species, are open to certain objections which may be briefly considered. *Ex hypothesi* I should have used either incipient or depauperate, that is, very small wild colonies of workers, and fertilized females that had just descended from their nuptial flight, or had passed a few days roaming about the country thereby ridding themselves of more or less of their parental nest-odor. It may be contended, furthermore, that the experiments should have been performed under conditions permitting of the voluntary escape of females that failed of an amicable reception among the alien workers. None of these conditions could be realized for obvious reasons. Although young fertilized females of the various species considered in this paper are occasionally seen running over the ground just after the nuptial flight, one cannot rely upon obtaining such specimens of a particular species when they are wanted, and a systematic search for them would consume no end of time and patience. Incipient and depauperate nests, too, become as rare as hen's teeth as soon as one begins to search for those of a particular species. I was compelled, therefore, either to adhere rigidly to the conditions implied in the hypothesis concerning the founding of colonies by *Formica* species of the *rufa*, *exsecta* and *sanguinea* groups, and plan the work for several summers after locating colonies and studying the exact dates of the nuptial flights, or to use unfertilized and artificially deälated females and small numbers of workers taken from adult colonies of other species. I chose the latter course and soon found that the results were very nearly the same as would in all probability have been obtained by the former with its almost insuperable difficulties. Contrary to what might be expected, the act of fecundation has little effect on the subsequent instincts of the females, and a small number of workers when isolated from a flourishing colony, either through what may be called an awareness of lack of backing by numbers, or for some other reason, are often as cowardly and conciliatory as the firstling workers of incipient colonies. And finally, unless the experiments were to be performed in the open country, where they would hardly be practicable, it was necessary to compel the females to reveal as much as possible of the resources of their instincts by preventing their escape from the alien workers. In some cases the nests were large enough to enable the females to keep at a safe distance from the spot on which the workers had settled with their cocoons.

OBSERVATIONS AND EXPERIMENTS.

1. **Formica difficilis** *Emery* var. **consocians** *Wheeler.*

Owing to the lateness of my arrival in Colebrook during the summer of 1904, I failed to find the males and virgin females of *F. consocians* and was therefore unable to complete my observations on the habits of this interesting ant. During the past summer I arrived as early as June 27, and at once began a search which resulted in my finding not only the colonies which had been seen in former years but several additional ones in different localities. The species is, however, by no means common. It certainly occurs only in stations occupied by colonies of its temporary host, *F. schaufussi var. incerta* Emery. Unlike several members of the *rufa* group, *consocians* is monodomous, that is, its colony is confined to a single nest. The sexual individuals, which were found only in the larger colonies, began to hatch July 3 to 5. The males seemed to make their appearance earlier than the females, and the summer brood of workers did not appear till after the latter had hatched. Most of the colonies contained both sexes, but one was always much more abundant than the other. The opened nests present a very pretty appearance. The males are deep black, the females rich fulvous yellow with black wings, the workers have a dull orange red head and thorax and an opaque brown and somewhat glaucous gaster. The small size of the females and their parasitic habits would lead one to suppose that they must be produced in greater numbers than the much larger females of *F. subsericea*, *schaufussi*, etc., and this is certainly the case. Some of the colonies must have contained as many as 800 females, since fully half that number hatched from part of the cocoons taken from a single colony and kept in one of my artificial nests. As the weather during the past July was extremely warm, the males and females hatched and matured in this and other artificial nests with great rapidity. They became very actively phototropic just before July 20 and, had they been permitted, would have escaped into the air. That this was approximately the date for the nuptial flight for some of the colonies during 1905 was also shown by an observation on a wild colony of *F. incerta-consocians* found July 22 under a stone fully half a mile from any locality in which I had previously seen *consocians* colonies. This colony consisted of some fifty *incerta* workers, about a dozen callows and a number of worker cocoons. The most careful search failed to reveal a female of this species, but instead there was a fine deälated female of *consocians* that must have been very recently adopted. As all the cases of a similar character recorded in my former paper[1] were found later in the summer, and as males had been found as late as Aug. 12 during 1901, I conclude that the season of 1905 was unusually far advanced. In all probability the nuptial flight commonly takes place somewhat later, perhaps during the last days of July or the first days of August.

While the observations recorded in my former paper leave little doubt that *F. incerta* is the normal temporary host of *F. consocians*, they do not, of course, exclude the possibility of other species assuming this rôle under certain conditions or in certain localities. To test this matter I introduced artificially deälated females of *consocians* into small colonies of workers belonging to different species of *Formica*. The results, which, with a single exception, were all negative, may be briefly stated.

Experiment 1. Aug. 10, 6 P.M. A female *consocians* was placed in a nest with 40 workers of *F. subpolita var. neogagates.* Several of the latter at once seized her by the legs and antennæ, dragged her about, and although they were individually inferior in stature, succeeded in killing her by the following morning. A similar experiment with a smaller colony of *neogagates* workers gave the same result.

Experiment 2. July 6. A female *consocians* introduced into a small colony of *F. subsericea* workers was dispatched by a single large worker as soon as she was encountered.

Experiment 3. July 10. A female *consocians* placed in a nest containing a few medium sized workers from a young colony of *F. exsectoides* was at once seized by one of the workers. She managed to get the worker's fore leg between her mandibles and pinched it till she was released. She then ran frantically about the nest, trying to escape, but was at once seized by another worker, that proceeded to saw off her head. This was not quite accomplished, but the female died on being released a few minutes later.

Experiment 4. July 11, 11.30 A.M. Placed successively two *consocians* females in a nest containing 17 workers of the typical *F. schaufussi* and several worker pupæ. The first female was at once attacked and killed by a worker

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[1] A New Type of Social Parasitism among Ants. Bull. Am. Mus. Nat. Hist., Vol. XX, Oct., 1904, pp. 350, *et* seq.

that used both her mandibles and formic acid batteries. The second female was attacked jointly by two workers, but managed to escape to the light corner of the nest, where she was found lurking at 2 P. M. By 4 P. M. she had been discovered and killed. A very similar experiment with another small colony of *schaufussi* gave the same result.

Experiment 5. July 11, 11 A.M. A female *consocians* was placed in a nest containing 12 workers and a queen of *F. schaufussi* var. *nitidiventris* together with several worker cocoons and larvæ. The female *consocians* was ignored by the female *nitidiventris*, but not by the workers, who kept dragging her about by the legs and antennæ. July 12 to 14 the female was being pulled away from the *nitidiventris* queen and brood by the workers but kept returning to them whenever she was released. At 1.40 P. M. on the latter date she was found dead. Two more *consocians* females were at once placed in the nest. Not only were these also attacked and pulled about by the workers, but they began to attack each other although before deälation they had been living amicably side by side in the parental nest. July 15, 7 A. M. One of the *consocians* was dead; the other kept lingering about the brood, apparently seeking adoption. July 16 the same behavior was observed and was interrupted from time to time by the workers pulling her away by the legs and antennæ. On July 17, 7.30 A.M., she was found dead in one corner of the nest. At 8.45 A.M. a fourth female was introduced. From time to time till 4 P.M. the usual tugging and persistent returning of the female to the stack of cocoons were observed. July 18, 1 P.M. the *consocians* female was resting peaceably beside the *nitidiventris* queen on the pile of cocoons. No attacks on the former were seen during the afternoon, but on the following day she was repeatedly pulled away by the workers. July 20, 6.30 A.M. she was lying dead in a corner some distance from the brood. At 8 A.M. a fifth female *consocians* was introduced. At 6.30 P.M. she was resting with the brood and *nitidiventris* queen. Although the colony was carefully watched on the following days, from July 21 to 26, no attacks on this female were observed. She had been adopted without remonstrance and behaved and was treated as if she had always been a member of the colony.

This experiment indicates that *F. nitidiventris*, though very closely related to *incerta*, does not readily adopt *consocians* females, but that this can be brought about by keeping the colony constantly supplied with these females. In the experiment four were killed before one was adopted. The perfectly indifferent attitude of the *nitidiventris* female toward the intrusive *consocians* is very suggestive. It is possible that the presence of the mother of the workers may have delayed the adoption of a stranger. The var. *nitidiventris* seems to be very rare in the Litchfield Hills. At any rate, I could not find another colony on which to try the experiment without a *nitidiventris* queen.

The results of experiments 1 to 5 seem to eliminate several species of *Formica* from the list of possible hosts of *F. consocians*. It is so improbable that the other members of the genus occurring at Colebrook, namely *F. integra, nepticula* and the different forms of *sanguinea*, can be temporary hosts of *consocians*, that I have not thought it necessary to consider them in this connection. *F. incerta*, therefore, remains as the only host species.

The experiments recorded in my former paper were avowedly incomplete, since they were all performed with *consocians* females that had, during some portions of their lives at least, been living with *incerta* workers. It was necessary, therefore, to observe the behavior of *incerta* in the presence of recently hatched *consocians* females. From a number of experiments performed with such females during the past summer I select a few of the more suggestive.

Experiment 6. July 21, 4.30 P.M. An artificially deälated *consocians* female was placed in a nest with 20 *incerta* workers and several worker cocoons taken from one of the most vigorous colonies found during the entire summer. he workers were unusually large and more like the workers of pure *schaufussi* but with the coloration and pilosity of *incerta*. The female seemed disinclined to approach the workers which were brooding over their cocoons, but she moved towards them when the illumination of the chamber was reversed. She was at once seized by a worker and showered with formic acid. She escaped to a corner of the nest. By 5.15 P.M. she had returned, mounted the pile of cocoons and was licking the workers, who were submitting to this treatment as if it were a matter of course. A few moments later she fed one of the workers and then kept alternating between feeding and caressing the *incerta* with comical rapidity and perseverance. The colony was watched till 7.45 P.M. but no further hostilities were seen. July 22, 7 A. M. The previous night had been cold and the female seemed to have passed it hanging from the roof-pane in a corner of the nest. Later as it grew warmer she returned to the *incerta* and their brood, caressed and fed the workers and took food from their lips. Only once during the day was a worker seen to tug for a few moments at one of her antennæ. On the four following days (July 23 to 26) no hostilities were observed. The *consocians* female had been definitively adopted.

Experiment 7. July 8, 4 P.M. Three artificially deälated female *consocians* (Nos. 1, 2, and 3) were introduced into a nest containing 20 *incerta* workers and numerous worker and male cocoons. About half of the workers were callows. Very little hostility was displayed towards the intruders. July 9, 8 A.M. One of the females (No. 1) was found dead in the light chamber and the remaining pair were quarrelling with each other. On separating, one of them mounted the pile of cocoons and began assiduously to feed and lick the callows. This female was finally pulled away from the brood by an *incerta* worker. At 11.35 A.M. the two females were seen rolling about in a fierce scrimmage. They finally separated no worse for the struggle and one of them was dragged about the nest by an *incerta* worker. The other went to the pile of cocoons but soon returned and pounced on the dragged queen, biting her thorax and petiole and then pulling her legs till she squirmed with pain. The female then released her hold and a worker *incerta* came up and pinioned her by the hind leg. At 1.15 P.M. the two females were again detected in the act of fighting, while one of them was being simultaneously pulled by an *incerta*. At 5 P.M. one of the females (No. 2) was found dead in a corner of the nest. At 6 P.M. two more females (Nos. 4 and 5) were introduced and were soon being pulled about the nest by the *incerta* workers. They were also set upon by female No. 3, who fought them with greater animosity than she had displayed towards Nos. 1 and 2. At 6.30 P.M. all three females were fighting one another, while a single *incerta* was tugging one of them (No. 4) by her antenna. Then another *incerta* fell upon the same female and while she was being stretched out between them, one having hold of her antenna, the other of her hind leg, females Nos. 3 and 5 came up and savagely bit at nearly every part of her body. Then the two free females faced about and fought with each other, even making use of their formic acid batteries. 8 P.M. Fighting still continued among the three females but none of them seemed to be injured. July 10, 6 A.M. One of the females (No. 4) was dead in a corner of the nest. Nos. 3 and 5 were still fighting but were not molested by the *incerta* workers. July 11, 4.20 P.M. Two more females (Nos. 6 and 7) were introduced. At 5.30 P.M. female No. 3 was fighting No. 7, which had been pinioned by an *incerta*. Female No. 6 was ingratiating herself with the callows and workers. July 12, 11.30 A.M. Female No. 3 had lost one antenna during the night; the remaining females (5, 6, and 7) were at peace with one another. At 4.30 P.M. three more females (Nos. 8, 9 and 10) were introduced, so that there were seven altogether. July 13, 8 A.M. Two more females were dead (Nos. 9 and 10). One of them was being carried about by an *incerta* worker. Another died at 1.45 P.M. July 14 and 15 no struggling of the females either with one another or with the *incerta* was observed. Workers of *incerta* were hatching in great numbers. July 16, 1 P.M., 9 deälated and 8 winged females were introduced, making altogether 21 females in the nest. July 17, 7 40 A.M., all these females were alive and in good condition. There were no hostilities. Even the wings were unruffled. July 18, 7 A.M., 6 deälated females were dead and had been deposited in the light chamber. There was some pulling of the remaining females by the workers. A few of the former had lost some or all of their wings. In some the tips of the wings had been torn off, indicating hostilities. 3.30 P.M. One of the deälated females was being pulled by three *incerta* while another female was trying to saw off her gaster. Thereupon there was a struggle between two other females. In the light chamber some of the winged individuals were quietly eating sugar while the remaining deälated females were feeding and licking the callows or brooding over the cocoons. Many male *incerta* began to hatch. July 19, 7 30 A.M. There were a few struggles between females and workers. Both the *incerta* males and winged *consocians* females were very restless and ran about the light chamber. At 12 M. three deälated females were fighting with one another like three angry viragos. July 20. There were no dead females. The winged individuals still tended to congregate in the light chamber even when they had lost all but the basal portion of their wings, while the deälated individuals stuck to the brood and lavished their attention on the callows and any adult workers that seemed inclined to be licked and to exchange ingluvial food. There were no important changes in the nest during July 21 and 22. July 23, 1 P.M. A single deälated female was found dead on the refuse heap. During July 24 to 26 perfect amity pervaded the nest. On the latter date, when I was compelled to close the experiment, only one of the females still retained wings and all of them were busy licking the workers and being fed by them. These females no longer visited the manger. All of the females used in this experiment were sisters taken from the same wild colony.

Experiment No. 8. July 6, 5 P.M. Four deälated *consocians* females (Nos. 1, 2, 3, and 4) were introduced into a nest containing a dozen *incerta* workers and many larvæ and pupæ taken from a flourishing wild colony. These females at once ascended the brood-pile, begged for food, and commenced licking the *incerta* workers. In the evening one of the females was seen to attack another and drag her around the nest. July 7, 8 A.M. Three of the *consocians* (Nos. 1, 2, and 3) were dead and had been deposited in the light chamber. The fourth was living peaceably with the *incerta*. Two more females (Nos. 5 and 6) were placed in the light chamber. As soon as they entered the dark chamber and attempted to ascend the brood-pile they were attacked by female No. 4 and so persistently persecuted that they fled to the light chamber, leaving their irate sister in full possession of the *incerta* colony. The two banished females returned to the dark chamber but were again driven out. Meanwhile the *incerta* workers remained quite indifferent to these bickerings and kept nursing their larvæ and cocoons. Females Nos. 5 and 6 were again returned to the dark chamber and the entrance was closed with earth. No. 4 now attacked No. 5 and bit her thorax so severely that she was injured and kept dropping on her knees when she tried to walk. Then No. 4 began to drive No. 6 around the nest, tweaking her legs and antennæ and trying to cut off her head till she managed to escape to the light chamber by burrowing through the earth in the entrance. Females Nos. 5 and 6 were again returned to the dark chamber and the entrance was plugged with cotton. Late in the evening all was quiet in the nest, the three females having come to rest in different parts of the chamber. No. 4 was busily licking the *incerta* workers. July 8, 8 A.M. Females Nos. 5 and 6 were dead and No. 4 was in undisputed possession. Two more females (Nos. 7 and 8) were introduced and the plug was removed from the entrance, No. 4 made no effort to attack them, but they were pulled about a little by the *incerta* workers and finally escaped into the light chamber. The entrance was again closed and they were returned to the dark chamber. They ran about but showed no inclination to associate with the *incerta* or with female No. 4 though they were very conciliatory whenever they happened to meet one of the workers. They lapped the surface of the sugar with avidity. July 9, 8 A.M. Female No. 7 was found dead in the manger. Female No. 8 was hovering around the edge of the brood-pile. There must have been some fighting during the day, as at 7 P.M. female No. 4 had an injured hind leg and walked with difficulty. She was dead at 8 P.M. Two more females (Nos. 9 and 10) were introduced. Females 8, 9, and 10 quarrelled among themselves. No. 8 was seen to move the cocoons whenever the chamber was illumined. This was the first and almost the only time one of these females was seen to pay any attention to the cocoons of her hosts. There were no battles between the females and workers. Late in the evening females Nos. 9 and 10 were feeding and caressing each other. July 10, 6 A.M. The three females 8, 9 and 10 were huddled together, licking and intergurgitating with the *incerta* workers. A little pulling of these females by the workers was observed from 1 to 5 P.M. July 11 there was peace and this remained unbroken till 5 P.M. on the following day (July 12), when six more artificially deälated *consocians* females were introduced, making a total of nine in the nest. The six new females were all placed in the light chamber, but as soon as they could find the opening they entered, crossed the dark chamber and at once ascended the pile of cocoons where the *incerta* workers were brooding. There was a little rather half-hearted resistance on the part of the *incerta*, but after a few moments all nine females were peaceably elbowing each other on the brood-pile while they cleaned one another and the *incerta* and fed and received food from the latter. At 7 P. M., however, two of the females engaged in a fierce combat, while all the others remained undisturbed. One of the pair escaped, whereupon the victorious individual went up to another female and began to pick a quarrel with her. In these combats one of the females always tried to bite through the other's thorax. July 13, 8 A.M. two of the females were dead, but one of them had evidently died from an injury received while she was being placed in the nest. The remaining 7 females were to all appearances living in perfect amity, with the *incerta* and with one another. At 12 M. three deälated and three winged females were introduced, making a total of 13. No hostilities were observed during the remainder of the day. July 15. One deälated female died during the course of the morning. The three winged females sought the light chamber, where they huddled side by side on the lower surface of the roof-pane. They showed no interest in the *incerta* or in their deälated sisters. From July 16 to 26 no hostilities were observed. The dozen females had been adopted by the *incerta* and had settled their differences with one another. The winged females retained all their wings and exhibited the behavior peculiar to their sex before deälation, till July 26, when I had to close the experiment. The females used in this experiment were taken from two widely separated wild colonies.

These experiments disclose several interesting facts:

First, it is clear that, though the introduced *consocians* females are recognized as aliens, they nevertheless often succeed in overcoming the hostile instincts of the *incerta* and acquiring adoption. When *consocians* females are persistently kept before the *incerta*, the latter become reconciled to their presence and will tolerate a considerable number of them in the nest.

Second, there is a pronounced tendency for the females to war on one another. These struggles are much fiercer than those between the *consocians* and the *incerta*. This fact is surprising because the females used in the above experiments were usually taken from the same colony and had been amicably snuggling together as daughters of the same mother before they were introduced to the *incerta*. I am inclined to believe that this mutual hostility of the females is a useful adaptation to prevent, as it must in a state of nature, the over-peopling of an *incerta* nest with these parasites. If this is the case it is perhaps difficult to understand why the hostility subsides and even ceases altogether when the number of females in an *incerta* colony is artificially augmented. Perhaps this dog-in-the-manger instinct on the part of the *consocians* is still in process of development, or being controlled or rendered in part unnecessary by the unwillingness of the *incerta* workers to receive these females into the colony. At any rate, a second female entering an *incerta* nest must meet with greater opposition than the first, since she must overcome both the hostility of the *incerta* and that of the adopted *consocians*.

Third, the above experiments show very clearly that mere artificial deälation at once produces an interesting change in the instincts of the female. She becomes forthwith negatively phototropic, less inclined to feed herself, and shows great interest in the *incerta* workers. In other words she behaves as if she had been fertilized, and, instead of resting or moving indolently about the nest, seems to have suddenly awakened to an appreciation of thes erious tasks of her existence as the mother of a future colony.

While the preceding experiments show that *consocians* females fresh from the maternal nest are quite readily adopted by *incerta* workers which to all appearances have had no previous experience with these parasites, it is clear that the possibility of such experience has not been eliminated. In other words, it may be objected that the *incerta*, having lived in a locality inhabited by *consocians*, must be familiar with this species and, for aught we know to the contrary, may have been hatched and reared in or very near a colony of the parasitic species. The cogency which any one unfamiliar with the ways of ants might find in this objection is completely destroyed by the two following experiments, which at the same time strengthen the conclusions drawn from my previous observations:

Experiment 9. July 5. A number of worker pupæ and a just hatched callow from a wild *incerta* nest were isolated. By July 7 eleven workers had hatched and had reached maturity by July 10. At 12 M. on the latter date a single deälated *consocians* female was introduced into the nest. She ran about a moment till she stumbled on the group of workers brooding over their cocoons. She touched the head of one of them and at once began to quicken the vibrations of her antennæ, while the remaining workers clustered around her and responded with a similar acceleration of their antennal beats. Only one worker showed a trace of hostility by opening her mandibles. The *consocians* female at once fell to licking one of the workers, while the others turned away apparently satisfied that the female was good company. Though the nest was watched repeatedly on this and the following day (July 11), no sign of hostility could be detected. July 12, 2 P.M. Two more females were introduced. They were carefully scrutinized, pulled a little and then licked by the workers. They stood their ground and at once began to caress the *incerta*. At 4 P.M. four more females were introduced, making seven altogether. Like the others they were received with barely noticeable signs of hostility and much licking, and forthwith settled down on the cocoons as members of the colony in good standing. At 7 P.M. two of the females were quarelling with each other, while the others were quietly brooding over the cocoons. July 14. During the morning there was perfect peace in the nest. At 12 M. four winged females were introduced. They were slightly pulled but soon adopted. The colony remained in the same peaceful condition till July 23 except that on July 19 the winged females became very restless and ran about the light chamber as if impatient to take their nuptial flight. At 2 P.M. July 23, ten more deälated females were added, bringing the total number up to 21. These females were adopted by the *incerta* without hesitation, but there was some bickering between the females from 3 to 5.30 P.M. There was perfect peace, however, on the following days from July 24 to 7 P.M. July 26, when the experiment was closed. All the females employed in this experiment were sisters from the same colony.

In this case the *incerta*, of course, could have had no previous experience with *consocians*. Although the weather was very warm during the first days of the experiment it occurred to me that the workers might not have reached maturity in three or four days and that the introduction of the females should have been postponed for at least twice that period of time. On returning to Bronxville, N. Y., during August I therefore repeated the experiment with this in mind. A number of *consocians* females had been brought from Colebrook and were introduced to *incerta* workers bred from cocoons taken from nests at Bronxville in a locality where the typical *difficilis* is very rare and its variety *consocians* is not known to occur.

Experiment 10. Aug. 17, 6 P. M. an artificially deälated *consocians* female (No. 1) was placed in a nest with nine *incerta* workers, all of which had hatched in isolation 6 to 8 days previously, and a number of worker cocoons. The workers threatened the female with opened mandibles but did not seem courageous enough to attack her. She kept approaching and touching them with her antennæ. Aug. 21, the female contrived to escape from the nest during the night. Another (No. 2) was introduced at 6 P. M. There were now 12 *incerta* workers, three having hatched since Aug. 17. She was seized by three workers and pulled about. They also bent their gasters forward between their legs and deluged her with formic acid. One worker dragged her to the manger and tried to throw her into it. She freed herself but seemed to be lame. She continued, however, to accost the workers with rapidly vibrating antennæ and without signs of fear or resentment. The workers were unrelenting in their attacks. They seized the poor female with a jerking, almost vindictive movement. She mounted the brood-pile and stood her ground while the workers kept nibbling at her body and legs. Some of them licked her from time to time. By 6.15, although she was still threatened by some of the workers, most of them passed without tweaking her. Several of them were evidently much interested in her. At 6.30 she began to lick the heads and backs of the workers with great assiduity. Some of them still pinched her legs from time to time. At 7.10 P.M. she showed signs of weakness, and died soon afterwards. At 8 P.M. another female was introduced. She was at once threatened by several workers and pulled across the chamber. She was soon released, however, and ascended the brood-pile, where she was attacked by a callow. She was seen to feed one worker and to attempt to repeat the same performance with a second when she was attacked by a third. The proffered droplet was distinctly seen at the tip of her tongue while she opened her mandibles to their fullest extent. At 8.45 P.M. she was passing from one worker to another, licking, feeding and being fed. At 9 P.M. there was very little bickering. The female seemed to be quite at home on the stack of coccons and was being licked and fed by the workers. Aug. 22, 7 A. M. she was still alive and resting on the brood-pile, which the ants had moved to a different part of the nest. A worker pulled her by the antenna but soon released her. Two more callows were hatching, so that by 6 P.M. there were 14 workers in the nest. During the following days, from Aug. 23 to 27, there were few or no hostilities, so that female No. 2 seemed to be definitively adopted. Aug. 27, 11 A.M. another female (No. 3) was introduced. For some time she remained unnoticed, resting on the towelling at the edge of the chamber. By 12 M. she had entered the cluster of workers and brood and was being pulled by the legs and antennæ. She stood her ground and offered food but was seized by the mandibles. At 12.30 P.M. female No. 3 had a lame antenna, and at 1.35 a fierce combat was in progress between the two females, female No. 2 being the aggressor. By 6 P.M. peace was restored and by 8.35 female No. 3 had been adopted. Two more females (Nos. 4 and 5) were introduced. No. 3, and somewhat later No. 4, was attacked and pulled by three workers. There was also some fighting between Nos. 2 and 3. The workers soon began to lick No. 4. Aug. 28, 7 A.M. Female No. 3 was dead. She had probably been injured by the tweezers during her introduction into the nest. Three more females (Nos. 6, 7 and 8) were introduced. They were threatened and pulled a little by the workers. At 8 P. M. there were lively combats between pairs of females. From time to time these begged the workers for food. Four more females were introduced, making a total of ten. 9 P.M. There was much fighting between pairs of females and those latest introduced were being pulled by the workers. As many as three pairs were fighting at the same time. While fighting two females met face to face with open mandibles and made rapid lunges at each other, trying to grab the opponent's antenna or fore-leg. When one of them was hard pressed she backed but kept facing her opponent. While in this position they often bent the gaster forward between their hind legs and discharged formic acid into each others' faces. The workers paid no attention to these combats. Aug. 29, 7 A.M., three females were dead and the remaining seven were fighting with one another. On the following days (from Aug. 30 to Sept. 2) six of the females remained alive and kept fighting from time to time. Peace was restored Sept. 3 and continued till Sept. 9. During this period there was a conspicuous tendency for the six females to huddle together in the midst of the *incerta* workers. Sept. 10, 8.30 A.M. six more females were introduced. They were all received with signs of hostility on the part of the *incerta*. One of them was attacked by four workers simultaneously. The new females had all been put in the light chamber, but they soon entered the dark chamber of their own accord. Within twenty minutes most of the attacks on them by the workers had subsided and by 9 P.M. they were being licked and fondled by their hosts. Some fighting between the older and more recently introduced females took place and increased in frequency and violence till 6 P.M. One of the females died Sept. 11, another Sept. 18, and only 7 remained alive Sept. 19. During this time there was more or less fighting between females but not between females and workers. Sept. 22, 7.30 A.M. six more females were placed in the nest. These were amicably received by the workers but were attacked by the old females. At 7 P.M. several couples were chasing each other around the nest. By Sept. 23 the fighting had become much less frequent and violent. Oct. 1 there were still 13 living females in the nests and this number was maintained till Nov. 30, when 11 of them and some of the *incerta* died because the nest was permitted to dry out. The remaining two females were still living, Feb. 6, 1906. All the females used in this experiment were sisters.

The ease with which the *consocians* females are adopted by *incerta* workers is in marked contrast with the refusal of *consocians* to receive females of their own species from other colonies and the refusal of the workers of either species to adopt workers of the other.

Experiment 11. July 6, 12 M. Into a colony consisting of several hundred *consocians* workers two deälated *consocians* females from another colony were introduced. They were suddenly and violently seized by the workers and dragged into the dark chamber, where they were enveloped by a mass of workers that showed as much active interest in them as they had in house-flies introduced into the nest: they licked and bit them persistently. One of the females had been killed by 4 P.M. and the other was found dead the following morning. July 9 a winged and a deälated female, together with two workers from the same colony, were introduced. The workers were at once adopted but the females were soon killed. July 10 two more deälated females, added to the colony at 8 P.M., were killed within an hour. July 13, three deälated females were introduced. July 14, 6.30 A.M. two of these were found dead. July 16 the remaining one was still living, at 7.30 A.M. At 1.30 P.M. three more females were introduced, so that there were four altogether. July 18 one of these had been killed. The three females were permitted to live till July 20, when all had been killed and thrown into the light chamber. Four more added July 21 were killed by 8.30 A.M. and by July 23 another had been dispatched, leaving only one alive. This female also died some time between July 26 and Aug. 1.

Experiment 12. July 10, 4.30 P.M. Three *consocians* workers were placed in the dark chamber of a nest containing a number of *incerta* workers and cocoons and two *consocians* females that had been adopted. The intruders were fiercely attacked by the *incerta* and ran wildly about the nest trying to escape at the corners of the chamber. Again and again three or four of the *incerta*, that seemed to be much excited by the peculiar odor of the *consocians*, would seize a worker and pull its legs and antennæ. At 5.40 P.M. the *consocians* workers had managed to escape into the light chamber, whither they were followed by a few *incerta*. These at once began to close the entrance to the dark chamber with pellets of earth and thus prevented any further visitations.

The views of the phylogenetic origin of slavery advanced by Wasmann and myself almost simultaneously[1] suggested some experiments to ascertain whether there is any tendency for adult *consocians* colonies to seize the larvæ and pupæ of *incerta* for the purpose of eating them or rearing them as auxiliaries. In nature there is absolutely nothing to indicate that these two species ever form mixed colonies except under the conditions already described in this and my previous paper, although colonies of both species were sometimes found very close together; often, indeed, in the same stone-pile. The two following experiments certainly show an unusually pronounced aversion on the part of either species to adopting the young of the other.

Experiment 13. June 28 a number of cocoons and larvæ from a large *consocians* colony were placed in the light chamber of a nest containing about twenty *incerta* workers with a *consocians* female that they had adopted. The ants removed the larvæ to the dark chamber, but left the cocoons untouched and exposed to the light for eight days till I removed them from the nest. The *consocians* larvæ were gradually eaten.

Experiment 14. June 30 one hundred *incerta* cocoons and 16 larvæ were placed in the light chamber of a nest containing a number of *consocians* workers. The larvæ and thirteen cocoons were slowly taken into the dark chamber, the remaining cocoons were ignored. The larvæ were eaten and the cocoons that had been carried away were restored to the light chamber. None of the *incerta* young hatched, and had to be removed when the nest was cleaned five days later.

A point on which I have been unable to throw much light during the past summer is the emancipation of the young *consocians* colony from the colony of *incerta* by which it has been reared. That this emancipation takes place by the gradual and natural death of the *incerta* workers rather than by the sudden emigration *en bloc* of the *consocians* is indicated by the following observation, which is similar to those made on nests No. 15 and 16 of my former paper. July 16 I found under a large stone on the eastern slope of Mt. Pisgah a small pure colony of *consocians* comprising about fifty workers, nearly all of small stature, a few nearly full grown and three packets of young larvæ and a fine female. The nest architecture, however, was unmistakably of the pure *incerta* type although no workers of this species were present. There could be no doubt that this represented a *consocians* colony in its second or third year. It corresponded exactly with the *truncicola-fusca* nest found by Wasmann during March, 1905.

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[1] An Interpretation of the Slave-making Instincts of Ants. Ursprung und Entwickelung der Sklaverei bei den Ameisen. Biol. Centralbl., 15 Feb, bis 1 Mai, 1905, p. 291.

Before concluding what I have to say about *F. consocians* I would insert a few notes on three colonies that have been kept in artificial nests since August, 1904. They may be designated as Colonies A, B, and C.

Colony A consists of some 500 *consocians* workers nearly all of which hatched in a Fielde nest from cocoons taken from a large colony during August, 1904. Although kept in a cool room (50°–60°F.) all winter, the workers began to lay eggs in great numbers as early as the first of February. The nest was white with eggs during February and March, and many larvæ began to hatch during April. The nest was unfortunately much neglected during May while I was absent in Arizona and many of the eggs and young larvæ had been eaten. On my return June 3 I found 16 pupæ, all males and of normal size and structure but not enclosed in cocoons. Most of these hatched during July.

Colony B, which was installed Aug. 19, 1904, consists of three deälated *incerta* queens and a few workers together with a fertile *consocians* queen which they had adopted.[1] The four females have lived together in perfect amity throughout the year. From time to time eggs and young larvæ appeared in the nest, but they were always eaten, so that I was unable to determine which species produced them. By July 1 all but one of the workers had perished. From this time forth the *incerta* females took entire charge of the young, carrying them away in their mandibles or standing guard over them when the nest was exposed to the light. The *consocians* female never exhibited the slightest interest in these young. During July, 1905, this diminutive colony was given a few *incerta* cocoons which soon produced workers. These were, of course, adopted by the queens, who now no longer looked after the young. Up to the present writing (Oct. 1) the colony has not succeeded in bringing any of its larvæ to maturity.

The observations on this colony together with those recorded above for *F. nitidiventris* (p. 52) show that the presence of the queens of the host species may be a matter of indifference in the adoption of a *consocians* female. If such a queen is present in a wild colony at the time it receives the *consocians*, she must be dispatched by her own workers under conditions as yet unexplained.

Colony C. This colony, also installed in August, 1904, consisted of a fertilized *consocians* female and about 40 *incerta* workers. It passed the winter successfully. The gaster of the female increased greatly in size and took on a whitish hue from the eggs and fat-body shining through the integument. During the spring and summer of 1905, eggs and young larvæ were continuously present in the nest, but none of them ever matured. This colony died of neglect during September, 1905.

The only myrmecophiles seen in the nests of *F. consocians* at Colebrook, Conn. were the larvæ of an undetermined species of *Microdon*. These were found July 7 in a single nest under a large stone lying on a

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[1] See A New Type, etc., pp. 354, 355.

lot of twigs, grass-roots, etc. Three larvæ were seen at this time, one nearly mature and one only about a quarter grown. On the twigs and lower surface of the stone there were some twenty empty puparia from which the flies had already escaped. The three larvæ were placed in a Fielde nest containing several hundred *consocians* workers. The two older ones at once applied their flat creeping-soles to the glass bottom of the nest and with their hard rough backs resisted the attacks of the workers. The small larva was not so successful. The ants turned it over on its back and for two days kept licking and biting it till it was killed and reduced to a small granule. The two large larvæ kept crawling slowly about the nest. They raised the anterior end of the body a little distance from the glass surface and moved the small pointed head, which is just beneath it, from side to side apparently in search of food. They showed signs of uneasiness when exposed to strong light. They remained in good condition till Aug. 23, when one of them disappeared. It had probably been eaten by the ants. The other lived till Sept. 10. Some days previously it had begun to shrivel, and finally dried up without losing its hold on the glass. I have failed to ascertain the nature of the food of these larvæ. July 25 I again visited the wild *consocians* nest but found that the ants had moved away. On the twigs there were two more half-grown but rather emaciated *Microdon* larvæ which had been left behind by the ants. These together with a couple of old puparia are shown in Pl. X, Fig. 2. The fact that these larvæ were so emaciated, and died soon after they were placed in the same Fielde nest with the others, shows that the presence of the ants is in some way essential to the well-being of these singular synœketes.

2. **Formica difficilis** *Emery.*

The typical *F. difficilis* like its variety *consocians*, is a rare and local ant. Judging from my experience during the past summer it is even rarer then its variety, since I have hitherto been able to find only two colonies, one near Mt. Vernon, N. Y., the other at Bronxville, N. Y. Each of these was nesting under an isolated stone. The ants of the Bronxville colony, which was found Aug. 12, had heaped up a quantity of dead leaves, bits of grass, etc., and were guarding, partly in this pile of débris and partly under the stone, a great number of worker pupæ. Dozens of these were naked, a condition which is rare in ants of the *rufa* group and had not been observed in the colonies of the Connecticut variety. The minim workers in this colony were very dark and smaller than the smallest commonly found in the *consocians* colonies. They measured only 3–3.5 mm. while the largest workers were 5.5–6 mm. in length. The nest was discovered too late in the season to contain males and females. Both this and the Mt. Vernon colonies were located on the sunny border of some open woods where the typical *schaufussi* and its var. *incerta* are unusually abundant. There can be little doubt that one or the other of these ants functions as the temporary host of *difficilis*. This species occurs also near Halifax in the Ramapo Mountains of northern New Jersey, where I captured a few workers attending aphides on trees at an altitude of about 800 feet. Mr. Wm. T. Davis has brought me several specimens taken at Inwood, N. Y., a locality in which the last traces of the original ant-fauna of Manhattan still linger at the northernmost end of the island.

3. **Formica nepticula** *Wheeler.*

This species, which I have described in a recent paper,[1] is of unusual interest because it has females even smaller than those of *F. difficilis;* quite as diminutive, in fact, as those of *F. microgyna* and *nevadensis*. A single colony of *nepticula* was located during August, 1904, at Colebrook, Conn., but as at that time it appeared to contain only workers it was regarded as a colony of *F. dryas* or of some form of *rufa*. June 30 of the current year when I again visited the nest, which was under a large stone banked with vegetable débris like the nests of *F. consocians*, I was surprised to find several diminutive, mostly callow females and a considerable number of cocoons all of about the same size. A large part of the colony was transferred to an artificial nest. During the first week in July many of the little females but only two males made their appearance. The workers of the season did not begin to hatch in numbers till July 9 to 21. The date of the nuptial flight is approximately July 11.

The small size of the females indicates that this species, like *consocians*, *microgyna*, *montigena*, etc., is a temporary parasite on some other species of *Formica* of the *fusca* or *pallide-fulva* groups, but we can only conjecture which of the species nesting in the same locality is used for this purpose. These species are: *F. subsericea*, *neogagates*, *incerta*, *nitidiventris*, and the typical *schaufussi*. The coloring of the *nepticula* female is remarkably like that of certain workers of three of these forms, namely: *neogagates*, *incerta*, and *nitidiventris*. The only colony of *nitidiventris* I found during the summer was used for experiments with *consocians*. The results of my attempts to get the other species of *Formica* to adopt *nepticula* females are here given in condensed form:

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[1] New Species of Formica. Bull. Amer. Mus. Nat. Hist., Vol. XXI, 1905. p. 270.

Experiment 15. July 2, 2 P.M., a mature deälated female *nepticula* was placed in each of two *incerta* nests containing only workers and their cocoons. The presence of the *nepticula* greatly excited the *incerta*. They seized and pulled her about and sprayed her with formic acid. Their whole behavior was decidedly more vehement than on the introduction of *consocians* females. In both nests the females were found dead at 4 P.M. Essentially the same results were obtained by placing *nepticula* females in nests with workers of the typical *schaufussi*.

Experiment 16. July 5 a deälated female *nepticula* was placed in a nest with a number of *subsericea* workers. She was at once seized and in a few moments terribly mutilated. One of her antennæ was extirpated, one mandible was completely torn from its socket, the funiculus of the other antenna was cut off and some of her legs were cut in two, so that she died in a few moments.

Of the following three experiments with *F. neogagates* one terminated with the adoption of a female *nepticula :*

Experiment 17. July 7, 8 A.M., four deälated *nepticula* females (Nos. 1, 2, 3, and 4) were placed in a nest with 12 small *neogagates* workers and a number of nude pupæ. These workers had been taken from a young wild colony consisting of not more than 50 small workers and their queen. The *nepticula* were vehemently attacked. Female No. 1 was killed during the afternoon; two others (Nos. 2 and 3) wandered about the nest, ate the sugar in the manger and fed each other, but gave no heed to the *neogagates* workers which had collected their pupæ and were occupying a corner of the nest. The fourth female, however, remained with the *neogagates* workers and was seen to adopt the same conciliatory tactics towards them as are shown by the *consocians* females towards the *incerta*. The callows were beginning to hatch from the nude pupæ. July 8, 8 A.M., a worker tried to drag No. 3 and then No. 4 away from the pupæ but soon desisted, whereupon the females again returned. At 11.30 A.M., another female (No. 2) was found dead. July 9, females Nos. 3 and 4 showed no desire to mingle with the *neogagates* but wandered about the dark chamber partook of the sugar from time to time and fed each other. Although No. 3 had lost an antenna she persisted in foisting herself on the *neogagates*. By noon No. 4 had also lost an antennal funiculus. Both females were being pulled about by the workers. July 11, No. 3 was dead. The pulling continued. July 12. At 6 P.M. two more females (Nos. 5 and 6) were introduced. They had escaped from the parental nest and had been flying about the room. A few minutes later female No. 5 settled near the pupæ and was being licked from head to foot by a *neogagates* worker. Then she was pulled a little by the antenna. Female No. 6 was also licked and pulled. Female No. 4 (with the injured antenna) kept returning and seeking adoption. Some of the callows which had hatched since she was placed in the nest licked her, but the older workers dragged her about. Whenever she was approached by a *neogagates* worker she crouched with flexed legs and antennæ. July 13, female No. 4 wandered about the light chamber all day, while females 5 and 6 kept lurking near the *neogagates* and their brood. At 3 P.M. female No. 5 was seen to go up to a worker and beg for food, which she received without signs of hostility. July 14, 6.30 A. M. female No. 4 was found dead. Females 5 and 6 still hung about the workers. No. 5 was seen licking a nude pupa. No. 6 was pulled about considerably but was very conciliatory. By reversing the illumination at 5.30 P.M. the *neogagates* were made to move to the diagonally opposite corner of the nest. Females 5 and 6 at once followed them and stopped within an inch of the brood, thereby showing a craving to join the colony. July 15 female No. 5 was removed from the nest, as she seemed to be too fond of the company of No. 6. The latter, now the only female in the nest, was seen, feeding a callow. At 6.30 P.M. she was found dead in the nest. Another female (No. 7) was at once introduced. July 16, 7 A.M. she was resting peacefully with the workers and their brood. No hostilities were witnessed till 4.30 P.M., when she was being pulled about. She was soon released and again pushed herself into the cluster of resting workers. Her attitude when approached by the workers was extremely conciliatory: she crouched and folded her antennæ. From July 17 to 19 she was occasionally dragged about by an antenna and then left quite unmolested for long periods or was even fed and licked by some of the workers, especially by the callows. The number of workers had risen to 21 by July 19. From July 20 to 26, when the experiment was closed, no hostilities were witnessed. Female No. 7 had been definitively adopted and was on the best of terms with the workers, which now numbered 24. During this time the behavior of the *nepticula* female was much like that of *F. consocians*: she was constantly licking or feeding the workers or being fed by them.

Experiment 18. July 14, 1.15 P.M., a deälated female *nepticula* (No. 1) was placed in a nest containing only five *neogagates* workers and some nude pupæ. These workers were of small size and had been taken from a depauperate wild colony comprising only about 15 individuals and a few male and worker pupæ. No female was found in the nest. At 1.40 P.M. the *nepticula* was fiercely attacked by a worker and driven away from the pupæ which were in a corner of the nest. She wandered restlessly about. July 15, 7 A.M. she was lurking near the workers and their brood. At 7.30 she was pulled away by the largest worker. At 2 P.M. she was dying with outstretched limbs. Another female (No. 2) was introduced. At 6.30 P.M. she was seen hanging about the workers and brood and furtively feeling of the latter. July 16 7 A.M., she was resting with the brood, at 7.20 she was dragged away by an antenna. July 17 and 18 she was resting at the diagonally opposite corner of the chamber from the *neogagates*. At 9 A.M. on the latter date she was very faint, and died at about noon. Another female (No. 3) was introduced. July 19. She persisted in hanging about the *neogagates* and their brood as if begging for adoption, but was pulled about considerably during the day. At 5 P.M. she was dead. Another female (No. 4) was at once substituted. This female remained alive in the nest till July 26 but was not adopted. She was pulled about from time to time, but nevertheless evinced a strong desire to join the little colony, as was shown by her returning again and again to the brood. It is probable that she would have been adopted had it been possible to continue the experiment.

Experiment 19. Aug. 9, 7 P.M., two mature and naturally deälated *nepticula* females were placed in a nest containing 30 small and medium-sized *neogagates* workers, most of which had been hatching in an artificial nest since Aug. 1. Each of the females was at once attacked and pulled about sometimes by as many as five or six workers at a time. They endured this treatment passively, with flexed legs and antennæ, and never attempted to bite their tormentors. Occasionally they were sprayed with ormic acid, although this severe treatment was resorted to only during the first encounters. At 9.30 P. M. one of the females was dying while being licked all over by the workers; the other was still living. Aug. 10, 7 A. M. both females were dead. Another female was introduced. She was found dead at 6 P. M. The experiment was abandoned at this point.

These experiments, while not completely satisfactory, show nevertheless that the female *nepticula*, like the female *consocians*, is very conciliatory and adaptable and has a pronounced fondness for associating with alien workers. They show that *neogagates* is not inclined to adopt *nepticula* females but may be induced to do so occasionally. It is probable that experiments 18 and 19 would have given the same result as 17 had it been possible to carry them further. The workers in the colony of experiment 19 were larger and more aggressive than those employed in experiments 17 and 18. The latter represented more nearly such incipient and depauperate colonies as *nepticula* probably selects as the most suitable in which to seek adoption. The resemblance of the *nepticula* female to a small or medium-sized *neogagates* worker is so great that she can be detected in a mixed colony only by close scrutiny. *F. neogagates* is a subboreal species and at Colebrook rarely occurs below an altitude of 1000 ft. The single colony of *nepticula* was also found at such an altitude (1400 ft.) as to indicate a connection between these species. All of these facts point to *neogagates* rather than to *subsericea* or one of the forms of *schaufussi* as the temporary host of *nepticula*.

4. **Formica rufa integra** *Nylander.*

Very little has been published on the habits of our North American forms of the holarctic fallow ant (*F. rufa*). The only form of the species which I was able to draw into the scope of my studies during the past summer was *F. rufa integra*. This beautiful insect is common in some localities in the more hilly portions of the Eastern States (above 1000 ft.), but is manifestly rarer at lower altitudes and seems to be lacking in the prairie regions of the Middle West. It prefers open, sunny glades in the woods and, so far as my observations go, occurs only in localities where its probable temporary host, *F. subsericea*, is abundant. Its colonies are often of enormous size and extend over a number of nests, each of which may contain thousands of workers. In the immediate vicinity of Colebrook, Conn., I have found two colonies, one consisting of four or five, the other of fully a dozen such nests. These are in large logs, stumps, or piles of stones, never in the shape of mounds as in the European and some of the American *rufa* forms to be considered presently. The workers collect great quantities of straws, dead leaves, pine needles, etc., and work all this vegetable débris into the crevices of the wood or between the stones. This is clearly seen in Pl. IX., Figs. 1 and 2, and Pl. X., Fig. 1. When the nests are disturbed the ants bite furiously or congregate in numbers on the surface of the nest, face the intruder, throw their heads back, and, directing the tips of their gasters forward between their hind legs, emit a shower of formic acid.

Although *F. integra* seems to be absent in the Mississippi Valley, one of its varieties—*hæmorrhoidalis*—occurs in the mountains of Colorado at an altitude of 7000–8000 feet. I have observed this form at different points in the Ute Pass and the Garden of the Gods, near Manitou. The workers are quite as large as those of the typical *integra*, but they seem to be covered with a peculiar glaucous bloom. Their habits are very much like those of the eastern form. They do not build mounds, but nest in great logs or stumps or piles of stones in the open woods. The largest nest I have seen was at Woodland Park, where the ants were occupying a prostrate pine log 12 ft. long and 1½ ft. in diameter. They had piled up débris to a height of 8–10 inches all around this log. Another nest, apparently belonging to this same colony, was in an old stump. Around this the ants had built a mass of débris 5 ft. in diameter at the base and 3 ft. high. This was connected by a run-way with another large nest in a log a few yards away. Like the true *integra*, the var. *hæmorrhoidalis* occurs in the same localities as a form of *fusca*, in this case not var. *subsericea* but var. *argentata*, a more silvery form with reddish legs and antennae.

The closely allied forms of *rufa* known as *obscuriventris*, *obscuripes*, *rubiginosa* and *melanotica* build mound nests, which in Colorado are large dome-shaped accumulations of débris 3 or 4 ft. in diameter at the base and 1 to 2 ft. high, and hence rivalling the nests of the European *rufa*. In Colorado these nests sometimes occur in colonies in the open pine woods. In the Middle West (Wisconsin and Illinois), however, the nests of *obscuripes* and *melanotica* are much smaller and of a different shape, as Father Muckermann has shown.[2]

In 1884 McCook published a number of observations[1] on the mound nests of *F. obscuripes* or an allied form of *rufa* . These nests were found

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[1] The Structure of the Nests of some North American Species of Formica. Psyche, Vol. IX, June 1902, pp. 355-360.

[1] The Rufous or Thatching Ant of Dakota and Colorado. Proc. Acad. Nat. Sci. Phila. 1884-1885. pp. 57-65. 5 figs.

scattered over the rolling country of Dakota and in Colorado to an altitude of 11,300 feet near Leadville. They ranged from 8 inches to 1½ ft. in height and from 2 to 10 ft. in diameter at the base, and were thickly covered or thatched with "bits of wood, fallen needles and broken sprigs of pine." The center of each mound was occupied by "a ball of twigs about eight inches in diameter; the sticks are longer and thicker than those used upon the roof, some of them being two and a half and three inches long. They were found unmixed with soil or any other substance. Several galleries, about one-fourth of an inch in diameter, led upward from this billet-globe to the surface, having their outlet by circular openings through the thatch." "Beneath the faggot ball a series of galleries, seven in number, extended downward to at least the distance of four and a half feet, the extent of the excavation made by Dr. De Puy." McCook believes that this faggot ball may serve as a "general nursery and common living barracks for the family." His paper also contains observations on the swarming of the ants, the destruction of their nests by prairie fires, their use in ridding garments of vermin, etc.

To any one acquainted with the magnificent adult colonies of *F. integra* and our western forms of *rufa* it must seem improbable that the queens of these species should start their families in the nests of some other ant. I am convinced, nevertheless, that this is the case and that *F. subsericea* is the species commonly employed for this purpose. The difficulties mentioned in the introduction to this paper have prevented me from securing incipient colonies of *F. subsericea*, so that I have introduced my *integra* queens to small batches of workers taken from larger colonies. Only five experiments were performed and in only one of these was the female adopted. But this would certainly be a very large proportion of success even among wild colonies. I record all of the experiments because even the least successful of them indicates that the female is inquilinous in her habits.

Experiment 20. July 4, 8 A.M. A deälated female *integra* was placed in a nest containing a dozen *subsericea* workers. She was seized and pulled about the nest by from one to three of them at a time during the entire day. July 5, the same performance was continued. The female remained uninjured. She never defended herself, but when the workers approached, crouched and made rapid supplicating movements with her antennæ. July 6. During the morning one of her hind tibiæ was torn off. She finally escaped to the light chamber, where she concealed herself under a lump of earth. July 7 she was still hiding under the earth. In the afternoon she was removed from the nest.

Experiment 21. July 14. At 1.10 P.M. a fine deälated *integra* female was placed in a nest with 19 *subsericea* workers and many nude worker pupæ, all taken from a medium-sized wild nest. She was at once pinioned by six of the workers and kept in a corner for some time. At 5.15 P.M. she was found dead. None of the *subsericea* workers had been injured.

Experiment 22. July 11, 12 M., an *integra* female was placed in a nest containing 10 large *subsericea* workers with two males, a number of larvæ and some nude pupæ taken from an old mound nest. She was at once attacked and pulled about the nest by her legs and antennæ. She made no attempt to retaliate, but remained perfectly passive, while making rapid and apparently conciliatory movements with her antennæ. The movements were very much like those of the female *consocians* on entering an *incerta* nest and meeting one of the workers. The workers finally succeeded in dragging her out into the light chamber, where she was killed and abandoned by 2 P.M.

Experiment 23. July 23, 8 A.M., a fine female *integra* was placed in a nest with 16 *subsericea* workers of different sizes and many naked pupæ from a rather large colony. She was soon seized by her legs and antennæ and dragged about the nest. She submitted with great docility, and whenever her antennæ were free kept them in constant and rapid motion, as if begging for more merciful treatment. There was so little excitement on the part of the *subsericea* not engaged in maltreating the female that they did not even remove their pupæ. At 1 P.M. the female was found dead.

Experiment 24. July 4, 10 A. M., a female *integra* was placed in a nest with three very small *subsericea* workers, 25 worker cocoons and a few larvæ. The workers attacked the female very gingerly and soon released her. They finally settled down with their brood in one corner of the nest. The female kept hanging about them. These conditions were maintained till July 9, when the female was found to have taken up her station about an inch away from the corner occupied by the *subsericea* and their brood. She had secured five small larvæ and was guarding them carefully. Whenever light was admitted into the nest she carried them away and tried to conceal them. Later in the day both the female and the workers were snuggling together in a corner. From July 10-13 these conditions remained unchanged: the female had been definitively adopted by the workers. July 14, one small callow *subsericea* had hatched during the night and another during the afternoon. On the following day (July 15) three more callows appeared and by 8 A.M. there were in all 10 workers. The illumination of the two chambers of the nest was reversed. There was no movement of the ants during the morning, as the light was rather subdued. At 12 M. the nest was placed near a window. One of the three original workers entered the dark chamber but soon returned and began to pull the female by the mandible and then by the fore leg, whereupon she again ran into the dark chamber, returned and dragged the queen into it. This demonstrated the complete adoption of the female. During the remainder of the month the worker cocoons slowly hatched: by July 18 there were 12 *subsericea* workers, by the 23d, 14, by the 25th, 18, and by Aug. 1, 23. At the present writing (Oct. 12) the queen and her colony of small workers are in excellent condition and, although they occupy only a small portion of the nest are always together. The queen is fed and cleaned by the workers as if she were their own mother.

One matter that is clear from these experiments is the docile and passive behavior of the female and its resemblance to the behavior of *F. consocians* under similar conditions. Such behavior is certainly significant in an ant like *integra* whose workers are so aggressively pugnacious. The last experiment was probably more successful than the others because it was performed with a very few small and timid *subsericea* workers, that is, with just such workers as the female *integra* probably selects in the wild state as nurses for her brood. The experiment at least lends plausibility to the view that the female *integra*, not withstanding her robust stature, is nevertheless, like *consocians*, a temporary parasite. It should be possible to test the truth of this statement by a careful examination of very small *subsericea* nests in localities where *F. integra* abounds.

5. **Formica exsectoides** *Forel.*

The geographical range of *F. exsectoides* seems to be coextensive with that of the true *F. integra*, and, like that subspecies, it has a variety (*opaciventris* Emery) in Colorado. The range, however, has not been accurately determined except in the Eastern States, where it is known to extend along the hills and mountains of the Appalachian system from Maine to North Carolina. Although I have never been able to find *exsectoides* in Illinois or eastern Wisconsin, Father Muckermann, S. J., has taken it in the southwestern corner of the latter State in the vicinity of Prairie du Chien. But Father Muckermann's account shows that the Wisconsin form must be very distinct ethologically. He says that its nests in his neighborhood "sometimes resemble heaps of dirt dumped out at random. Besides they consist for the most part of earth, although the latter is often mixed with vegetable remains. . . The nest entrances are distributed without any apparent order. At any rate, they are not located merely at the base and about the periphery. . . *Formica exsectoides* is one of the ants most frequently met with in this region, and often their colonies consist also of ten and more nests."[1] Parts of this description differ greatly from McCook's account of the nests of the Pennsylvania *exsectoides*, which are regular conical mounds with their entrances arranged in rows around the base. Their size must be much greater than that of the nests described by Muckermann. But *exsectoides* exhibits still another variation in the form of its nests. All of these structures which I have seen near the

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[1] The Structure of the Nests of Some North American Species of Formica. Psyche, June, 1902, p. 357.

Atlantic seaboard, as for example in the Ramapo Mountains, on Staten Island, in the Litchfield Hills of Connecticut, and in the pine and beech woods near Woods Holl, Massachusetts, are dome-shaped and do not taper to a blunt point above like those figured by McCook. They are often very low, rarely attaining a height of a foot or 18 inches, and are usually surrounded by a broad circle of grass at the base, which may be 3 or 4 feet in diameter. (Pls. XII.–XIV.). The entrances, however, are nearly all aggregated in a broad belt around the base. The average mounds studied by McCook were 2½ to 3 feet high, and he mentions nests 12 and 15 feet across the top, and one, the largest observed, 24 feet across the top, 58 feet around the base, and about 42 inches high. On Staten Island there are about a dozen of the nests in a colony, but in Connecticut and Massachusetts I have found them singly and often at long intervals. All of these facts indicate that the species is in a decidedly more depauperate condition in these different regions than near Hollidaysburg, where its nesting habits were studied by McCook. This author mentions colonies of these ants of as many as 1800 mounds, and he describes the process by which new hills are produced by a kind of nidamental budding or proliferation. After the marriage flight "some of the fruitful females, it is known, are seized by the workers upon the mounds and others upon the neighboring grass-stalks and weeds, and are thence forced into the hill. But there must be some who drop upon secluded spots, and unobserved begin measures for the establishment of new families, according to their instinct. These families eventually erect independent hills, which in turn become the mother hills of new hill-clusters. Thus ant colonies, like some groves and forests, grow from the parent stock by shoots."

This observation, together with others recorded in McCook's paper, indicates that new nests of *exsectoides* may be formed like those of *F. rufa* in Europe. In a former paper I have given my reasons for believing that the *exsectoides* colony is originally started by temporary parasitism on *F. subsericea*. Schmitt, Forel and myself have all found small mixed colonies of these two species under circumstances which, in the light of my observations on *F. consocians*, certainly justify such an inference. Experiments with artifically deälated females of *exsectoides* introduced into small colonies of *subsericea* workers gave practically the same results as those above recorded for *F. integra*. In all except one of seven experiments the results were negative, but they revealed, nevertheless, some of the inquilinous instincts of the *exsectoides* female. Only three of the experiments are here recorded.

Experiment 25. July 13. A winged female *exsectoides* that was being dragged about in the galleries of a wild colony of *F. sanguinea* var. *subintegra* by the *subsericea* slaves was released and at 3 P. M. deälated and introduced into the dark chamber of a nest containing 12 *subsericea* workers and many cocoons. As soon as her presence was perceived the workers snatched up their cocoons and fled with great precipitation into the light chamber. Soon the female found the opening and also escaped into the same chamber. The *subsericea* approached her from time to time but seemed to be afraid to attack her. At such times she crouched, folded her antennæ, and rapidly titillated the workers' heads with their tips. Sometimes she begged for food, but her appeals were ignored. Her whole behavior could only be described as humble and supplicating, and recalled very vividly the behavior of the *F. consocians* female in the presence of alien *incerta* workers. Soon, however, the *subsericea* began to seize the tips of her antennæ and then a leg, pulling mildly and spasmodically at first, but growing bolder, apparently on becoming aware of the inoffensive attitude of the female. At 5.30 P. M. she was released and at once began to lick the mouth-parts of one of the workers in a most affectionate manner while rapidly vibrating her antennæ. July 14, 6.30 A. M., the female was found dying in the light chamber, with a hole gnawed in her gaster. The workers had devoured her viscera during the night. Her legs and antennæ, however, were still intact.

Experiment 26. July 16. 3.20 P. M. A fine active *exsectoides* female was placed in a nest with 14 medium-sized *subsericea* workers and many nude pupæ. She was at once attacked and dragged about by her appendages. Without resisting, she folded her appendages close to her body and allowed herself to be pulled about passively, making slow appealing movements with her antennæ. At 4.30 P. M. she was still being maltreated by a number of the workers, but made no attempt to retaliate, though she bit my finger when I tried to remove her from the nest. The workers endeavored to force their mandibles into her body, but they slipped from her polished integument. Then they tried to saw off her legs at their coxal articulations. By 7.20 P. M. they had amputated one leg. July 17, 7.30 A. M. The female was still alive, but had been shorn of both antennæ and several legs. Two workers were busily gnawing at her hips. The experiment was discontinued.

Experiment 27. July 23, 1 P. M. A fine female *exsectoides* was placed in a nest with 7 *subsericea* workers and 14 nude worker pupæ nearly ready to hatch. She was not at once attacked by the workers, who approached her rather timidly, opened their mandibles a little in a menacing attitude and then turned away. She showed no signs of fear but stretched forth her long antennæ and caressed each worker when it approached. From 2.50 to 5 P. M. she was being pulled about by one of her antennæ or legs. July 24, 8 A. M., the female was snuggling quietly in a corner with the workers and their brood. No signs of hostility were witnessed during the day. From that day to the present writing (Sept. 5) the female has lived in perfect amity with the seven original workers and ten others that had hatched soon after her adoption. She is fed by the workers, and, though the tiny colony occupies but little space in the nest, is always found in their company.

6. **Formica sanguinea rubicunda** *Emery.*

Two forms of the sanguinary ant are pretty generally distributed over the northern portion of the United States: *Formica sanguinea rubicunda* Emery and its variety *subintegra* Emery, the former with a black, the latter with a brown or even yellowish, gaster. In most localities, so far as I have been able to observe, the var. *subintegra* is the more common and often the only form represented. This is certainly true of the region about New York where I have hitherto found only *subintegra.* At Colebrook, Conn., where both occur in the same localities, there is also another much rarer form, which agrees very closely with Forel's description of the subspecies *aserva* and with types of this form which he kindly sent me some years ago. I have used females of all three of these forms in my experiments, but the results obtained with *subintegra* and *aserva* leave much to be desired.

During the last days of June I found a large army of *rubicunda* in the act of plundering a nest of *F. subsericea.* I followed the cocoon-laden workers a distance of about seventy feet to their nest, which was on a sunny slope under two large stones. On removing these many fine female pupæ were found in the galleries and were carefully transferred to an artificial nest, where they soon began to hatch. The young females were abundantly fed with sugar, houseflies, etc., and were not used for the experiments till fully mature. In all twenty-one experiments were performed. These may be divided into three groups: nine were failures, two were partially and the remaining ten completely successful. Two thirds of these experiments are given below for the sake of emphasizing the typical reactions of the female *rubicunda.* It is most improbable that this insect would respond to an artificial environment with such a regular series of reactions unless these are the very ones she habitually displays while establishing her colonies in a state of nature.

Experiment 28. July 13. At 2.15 P.M. a *rubicunda* female was introduced to 17 *subsericea* workers with worker pupæ taken from a wild colony of average size. They at once fell upon her, four and six at a time, and succeeded in killing her by 3 P.M.

Experiment 29. July 14, 7.30 A. M. a female *rubicunda* was placed with 12 *subsericea* workers and about 150 worker cocoons. She was immediately attacked by several of the workers and dragged about the nest on her back. Often the *subsericea* were so excited that they kept tugging at a leg or antenna of one of their own sisters that happened to be pulling one of the female's legs. The female was singularly passive, but was finally so thoroughly aroused by the pulling and tweaking that she killed three of the workers by 12 M. In these struggles she lost one antenna and died at 2 P.M.

Experiment 30. July 11. At 11 A.M. a *rubicunda* female was placed in a nest containing 30 large and medium-sized *subsericea* workers with naked worker pupæ and semipupæ from a rather large mound nest. She was at once seized by eight workers and pulled about by all her legs and antennæ. She resented this treatment, threw off her assailants and by 11.30 A.M. had killed nine of them. She herself, however, succumbed a little after 12 M.

Experiment 31. July 23, 11 A.M., a fine female *rubicunda*, that lost her wings while she was being taken out of her own nest, was placed with 12 large *subssericea* workers, two males, and a number of larvæ and nude worker pupæ taken from a large mound nest evidently of several years' standing. She ran about in dismay, trying to avoid the workers, but at 11.10 A.M. her legs and antennæ were pinioned by two and then by four workers. She shook them off adroitly but was soon held fast by three others. This so thoroughly aroused her that she killed them by biting them one by one through the head or thorax. Almost at once, however, two workers fell upon her, stretched her legs and sprayed their articular membranes with formic acid till she succumbed at 11.30. She had been overcome in a surprisingly short time.

These experiments show very conclusively that *rubicunda* is received with great hostility and may be quickly dispatched by even a small number of *subsericea* workers. It is certain that she would stand no chance of survival if she attempted to enter a large colony of these ants. The experiments also show that the female resents the treatment she receives, but this is more clearly manifested in the following cases:

Experiment 32. July 7. 10 A.M. A female *rubicunda* was introduced into a nest containing 12 large *subsericea* workers with a number of worker cocoons. As soon as she was perceived, some of the workers snatched up their cocoons and fled to the light chamber, just as they are in the habit of doing when their nests are attacked by *rubicunda* workers; while others fell upon her and began to tug at her legs and antennæ. This she endured patiently for some minutes, but finally succeeded in shaking off her assailants and, thoroughly aroused, began to prance back and forth in the chamber, pouncing on any worker that came within her reach. She killed two of them in rapid succession and then at once began to collect the cocoons and tuck them away in one of the corners of the nest. She collected 18 of them, mounted the pile, and with wide open mandibles, stood guard over them. The *subsericea* hurriedly carried the remainder of the cocoons into the light chamber and plugged up the entrance between the chambers with some pellets of earth. July 8 matters remained *in statu quo* during the entire day. The female never left the brood she had appropriated and the *subsericea* made no attempt to recover it. During the night, however, there must have been such an attempt, as the female was found dead at 8 A.M., July 9, and the workers had carried the 18 cocoons into the light chamber and had placed them with the others.

Experiment 33. July 10, 9 P.M., a female *rubicunda* was placed in a nest with 8 medium-sized *subsericea* workers and about 100 larvæ and pupæ. She was attacked, but killed 2 of the workers and then ran into the light chamber with a single small larva, which she continued to hold in her mandibles till I retired at 11 o'clock. At 6 A.M. on the following morning I found that she had killed all the workers during the night and had carried about two thirds of the brood into a corner of the dark chamber. At 6.30 A.M. a callow worker had hatched from one of the nude pupæ. The female remained with the brood during the day but was very sluggish. July 12, 6.30 A.M. another callow had hatched during the night. The female had left the brood and was clinging to the wet sponge. She seemed to be very weak. At 4 P. M. she was dead.

In experiments 32 and 33 the *rubicunda* female was interrupted in the display of her instincts by death, caused without doubt by injuries received while killing off the *subsericea* workers. I believe that such deaths are due to spraying of the distended articular membranes of the limbs with formic acid. Probably at these points the acid is absorbed, and, thus admitted in small quantities into the blood, causes a slow paralysis which, as in the last experiment, overtakes the female in the midst of her catenary reflexes, or instincts. At any rate, in these and most other cases where the females succumb after struggling with alien workers, death is certainly not due to wounds or mutilation. In the following experiments the females, either because of their exceptional strength and agility or the weakness of the *subsericea* with whom they were confined, survived and were able to display the whole series of their colony-establishing instincts.

Experiment 34. July 8, 9 A.M. A *rubicunda* female was placed in a nest containing 33 *subsericea* workers, small and large, 150 cocoons, and a few larvæ. The workers at once seized their cocoons and fled into the light chamber. One or two of them attacked the female, but she shook them off and killed one of them. In the meantime some of the workers kept stealing into the dark chamber for the purpose of securing cocoons and carried them to the remotest corner of the light chamber. As the morning wore away the female gradually became more and more excited. By 1 P.M. she had killed five more workers and was busy carrying the cocoons back from the illuminated into the dark chamber, where she had already stored most of them in a corner. In a few minutes she had secured all the cocoons in the light chamber, 36 in number. She interrupted this task twice, each time for the purpose of killing a worker that came within her reach. Finally she retired to the dark chamber and began to collect the cocoons into a more compact pile. Two of the workers persisted in stealing in and hurrying back with cocoons taken from the edge of the pile. The female soon perceived this, however, and dispatched both of them. The whole performance resembled a dulotic expedition in miniature, carried out by a single virgin female instead of by an army of *rubicunda* workers. In killing the *subsericea* workers, she was quite as ruthless as the workers of her own species but much surer on account of her larger size and greater strength. She exhibited very beautifully what may be called the "prancing" movement, so characteristic of the females in this stage of their activities. She moved in a jerky fashion, taking a few steps in one direction, then turning the body and taking a few steps more. July 9, 8 A.M., only two of the workers survived. They had regained possession of 30 of their cocoons, however, and were guarding them in a remote corner of the light chamber while the female was watching over the great bulk of the brood in a corner of the dark chamber. By 10.30 she had entered the light chamber, recaptured all but 6 of the cocoons, carried them into the dark chamber and placed them on her pile. The two workers were wandering about in a state of "abulic dejection." At 11.30 one of them was seen to enter the dark chamber and approach the female, but the latter opened her mandibles and the worker fled. The female had stacked her cocoons in a compact heap and was bent on defending them. Apparently she had not forgotten the 6 cocoons still remaining in the light chamber. At any rate, she secured 4 of them by 12 M. She took up her position on the pile of cocoons, and whenever light was admitted into the dark chamber, opened her mandibles and went to prancing about as if looking for an enemy. By 1.15 P.M. she had secured one of the two remaining cocoons in the light chamber. July 10, 6 A.M. In the night the female killed the two remaining workers and took their last cocoon. Throughout the day she kept closely to the brood, prancing whenever the light was admitted into the chamber and fiercely seizing a straw or my finger whenever either was held near her. She seemed to display a much greater interest in the pupæ than in the larvæ. July 11 to 15 she remained *in statu quo*. Whenever the nest was uncovered she hastily took up a cocoon and tried to conceal it. July 16, 7 A.M., 5 callow workers had hatched during the night. One larva had been partially eaten by the female. At 1.40 she was surprised in the act of opening a cocoon. She used her fore and middle feet to hold the cocoon while she tore a large elliptical hole with her mandibles in the portion of its wall overlying the concave ventral surface of the pupa. Through this hole the worker was later drawn after it had thrust out its antennæ and legs. Whenever the nest was uncovered throughout this and the following of the first days, the female could nearly always be detected in the act of either opening a cocoon or removing the pupal envelope from a callow just released. By the afternoon of July 16 some of the callows began to assist the female in releasing their sister workers. The number of callows now began to increase rapidly. On the morning of July 17, there were 19 altogether, by 5 P.M. 24, by 7.30 A.M., July 18, 30, and by 7.30 A.M., July 19, 50. On the following days the numbers ran thus: July 20 about 60; July 21 about 75; July 22 about 100; July 23 and 24 about 130. This completed the callow brood, as some of the cocoons failed to hatch. The female took the greatest interest in her black family and they bestowed on her every attention. Soon after they had begun to feed and clean her another marked change supervened in her instincts. Instead of defending herself and brood when the nest was uncovered she slunk away, or at any rate attempted to conceal herself among the mass of workers. She had become highly photophobic and behaved exactly like the old queens, that invariably make for the galleries whenever the nest is disturbed or illuminated. This experiment was concluded and the ants liberated in the garden on July 26, as I had to leave Colebrook for New York on the following day.

Experiment 35. July 9, 10 A.M. Placed a *rubicunda* female in a nest containing only 4 *subsericea* workers and about 200 worker and two female cocoons. The workers at once grabbed cocoons and fled into the light chamber. The female ran about the dark chamber and escaped into the light chamber, but at once returned, forcing her way through the entrance, which was much obstructed with earth, and began to collect and pile up the cocoons in a corner. The workers kept returning and stealthily snatching cocoons from the edge of her pile and hurrying away with them into the light chamber. She perceived one of these returning workers, pounced on her and killed her with a blow of her mandibles. This first murder thoroughly aroused her and she began to prance to and fro. Another worker returned, but before she could be grabbed had seized one of the female's antennæ. The two ants now began to pull in opposite directions, while the remaining workers made haste to carry the cocoons into the light chamber. At 11.30 the female had killed the worker and freed herself without losing her funiculus and was in the act of killing a third worker. She at once began to bring the cocoons back to the corner in the dark chamber. She removed 80 of them in 30 minutes, that is at an average rate of 2⅔ per minute. Only four cocoons were overlooked and left in the light chamber. Then she returned to the dark corner and began to stack up the cocoons. Meanwhile the single surviving worker ran about in great trepidation, fleeing whenever the female approached her, and endeavoring to escape from the nest without making any attempt to carry away the cocoons. Whenever the dark chamber was uncovered the female at once tried to secrete her cocoons in some other part of the nest, thus showing a clear sense of proprietorship. By 2 P.M. she had also secured three of the four cocoons remaining in the light chamber. July 10 to 11. The female had built all the cocoons into a more compact pile and was resting on them with half-open jaws ready to attack any comer. July 12. During the night a callow worker and callow female *subsericea* hatched. Two more callow workers and several naked pupæ from a wild colony were placed in the light chamber. These were found by the female and carefully removed to her pile. She paid no attention to the *subsericea* female. The callows joined the female *rubicunda* in caring for the pupæ. At 5 P.M. one of the older callows was seen in the act of freeing a young callow from its cocoon. July 14 another callow hatched. The female *rubicunda* was very solicitous about the cocoons whenever the dark chamber was uncovered. There were now one female and five worker *subsericea*. This female also at times helped in stacking up the cocoons. July 15, 7 A.M. There were 8 workers and one callow in the act of hatching and by evening others had been divested of their pupal envelopes. July 16, 7 A.M. there were 25 workers. At 2.30 the *rubicunda* female was surprised in the act of licking a callow and carrying it a short distance as if to hide it. By 4.30 P.M. there were 34 callows. At 7 P.M. the female was seen to open a cocoon. She held it firmly in her two fore feet while she made a rent in the center of its ventral surface with her mandibles. July 17, 7.30 A.M. there were 45 workers altogether, most of them still very callow. The female *rubicunda* spent most of her time opening cocoons and freeing the callows from their pupal envelopes. By 5 P.M. there were 55 workers and by the following morning (July 18, 7.30 A.M.) 63 were counted. The number rose to 80 by 7.30 A.M. July 19. The female still tried to hide her cocoons whenever the nest was uncovered. Many of the workers were busy assisting the callows to hatch. July 20, 8 A.M., there were about 100 workers in the nest and several were hatching. A large number had matured. July 21 and 22 the female *rubicunda* no longer attended to the brood or hurried away with a cocoon when the nest was opened, but slunk away and tried to conceal herself in the mass of workers, behaving exactly like the old females one finds in wild nests. By July 22 more than 125 mostly mature workers were counted. The *subsericea* female had lost her wings during the night. By evening the number of workers was nearly 150 and during the following 4 days (July 23 to 26) it rose to 175 approximately. Both females were living peacefully side by side. The colony was released in the garden at 6 P.M., July 26.

Experiment 36. July 14, 5.30 P.M. A female *rubicunda*, mature but with small, shrivelled wings, was placed in a nest with 11 *subsericea* workers of medium and large size, a few worker and 3 female cocoons and a few larvæ, taken from a rather small colony. The female was attacked and almost at once succeeded in killing 3 workers (5.55 P.M.) At 6 P.M. she disabled one, and killed another a minute later. She dodged whenever she encountered a worker. July 15, 7 A.M. The female was loitering in a corner far from the brood and the workers. By 2.30 P.M. one of the female *subsericea* had hatched. During the whole day the *rubicunda* rested quietly on the sponge at some distance from the workers, that huddled in a corner with their brood. July 16, 7 A.M. one more worker was killed by the female during the night, so that only 5, the largest individuals, remained alive. The female was resting near the brood. By 12 M. only 4 workers remained and the female had driven the workers from their corner and was in possession of 19 cocoons. Another female *subsericea* had hatched. The 4 workers and 2 *subsericea* females had taken refuge with a few cocoons in a lighted corner of the chamber. They seemed to be possessed with the desire to get as far as possible from the *rubicunda* female. This female had become very alert and was much interested in the cocoons. At 2.40 P.M. when the nest was uncovered she tried to hide her cocoons, of which she now had only 4, all the others having been recovered by the *subsericea* and carried to the diagonally opposite corner, which was strongly illuminated. Fear of the female *rubicunda* appeared to be stronger than the instinct which compels these ants to keep their brood in the dark. The female began to run about wildly as if suddenly filled with a craving to get cocoons. She pranced around with half-open mandibles ready to attack any worker. She flew at a worker that was coming up to steal a cocoon and pulled the mandibles of one of the callow *subsericea* females. She killed one worker, thus reducing the number to three. Although these were the largest individuals, they fled in great trepidation whenever she approached. At 4.30 P.M. the female *rubicunda* had collected 11 cocoons and was guarding them with raised head and open mandibles. By 6.50 P.M. she had secured 23, including the unhatched female cocoon. She was no longer molested by the 3 workers. These were trying to escape by gnawing at the towelling in the light corner. July 17, 7.30 A.M. During the night the workers had recovered some of their cocoons, leaving only 17 worker cocoons and a larva with the female *rubicunda*. July 18, 7 A.M. She had regained all her pupæ during the night. The 3 workers were still alive. The female was very sluggish. At 8.30 the *subsericea* workers were opening the third and last female pupa. By 12 M. the female *rubicunda* had recovered all the cocoons and was guarding them in company with the 3 callow *subsericea* females.

Another worker had been killed. The remaining 2 were wandering about aimlessly and not endeavoring to recover their cocoons. One of them had lost an antenna. At 1.30 P.M. they tried to associate themselves with the *rubicunda* and *subsericea* females. The latter were a link between the two inimical factions represented by the workers and *rubicunda*. July 19, 7.30 A.M. the colony was *in statu quo* except that one of the *subsericea* females was dying. July 20, 7.30 A.M. During the night the *rubicunda* had killed one of the workers and injured another. She was now in full possession of the brood and two surviving *subsericea* females. July 21 the experiment was discontinued.

Experiment 37. July 14, 2. P.M. A vigorous and active *rubicunda* female was placed in a nest with 9 *subsericea* workers and about 150 worker cocoons. By 2.17 P.M. she had killed 6 workers and was rushing wildly about the nest, apparently more in fear than in anger. Two of the three remaining workers were callows. By 5.20 P.M. she had carried nearly all of the cocoons to a corner of the nest and was standing guard over them with open mandibles. At 6 P.M. one of the callows associated herself with the female. July 15, 7 A.M. the other callow had joined the female, who had transferred all the cocoons to another corner of the nest. The single mature worker was lurking in the diagonally opposite corner. The dead *subsericea* which were scattered about the nest yesterday had all been collected (by the female?) and placed in a pile near the cocoons. Whenever the nest was uncovered the female endeavored to conceal the brood. July 16, 8 A.M., 3 callows had hatched in the night. The mature worker was with the brood, but ran away and hid when the nest was uncovered. The female was very alert and showed great solicitude for the brood. At 2.20 P.M. the single adult worker kept away from the brood and tried to escape from the nest by gnawing at the towelling. July 17, 7.30 A.M., this worker had joined the callows and all the ants were living peacefully together. Later in the morning the total number of workers had risen to 12. At noon the single mature worker deserted the brood and went to stay in the light chamber, the entrance to which had been closed on the previous day. July 18, 8 A.M., there were 27 *subsericea* workers altogether. The single mature worker had again joined the colony during the night and mingled with the callows. Henceforth she became a permanent member of the colony. The number of workers increased to 36 by noon. July 19, 7.30 A.M., there were 51 *subsericea*. The female was very timid when the nest was uncovered. Although she seemed to be much interested in the callows she was not seen to care for the cocoons after the callows had begun to aid one another in hatching. The number of *subsericea* increased as follows: July 20 there were about 60; July 21 about 80; July 22 about 90; July 23 more than 100. At 12 M. on the date last mentioned the colony was given 150 worker cocoons of *F. rufa integra.* They at once seized them and began to carry them to the pile of unhatched cocoons of their own species. July 24, 8 A. M., there were about 125 *subsericea* in the nest. They were carefully hoarding the *integra* cocoons mingled with a few remaining cocoons of their own species. July 25, 7.30 A.M., the *subsericea* took a few of the *integra* pupæ out of their cocoons, killed them and threw them on the refuse heap. Two callow *integra* were walking about the nest. July 26 both of these callows had been killed. The nest was transported to New York and not examined till August 6, when nearly all the *integra* had hatched and most of them had matured. They have since formed a part of this triple mixed colony and are living in perfect amity with the *rubicunda* female and the *subsericea* workers (Sept. 12).

Experiment 38. July 15, 7.30 A. M., a female *rubicunda* was placed in a nest containing 11 medium-sized *subsericea* workers with more than 100 naked worker pupæ and semipupæ from a rather small colony found under a stone. The female was not molested during the day, but at 6 P. M. was quietly resting at some distance from the workers and their brood. July 16, 7 A. M., the female was still resting at the edge of the brood. Two workers had been killed during the night. While the nest was under observation a worker approached the female and seized her by the antenna. She at once curled her body about the worker and killed her. The morning, like the preceding night, was cold, so that the ants were very sluggish. At 12 M. the female seemed to be seeking adoption among the *subsericea*. Whenever the nest was uncovered she was found hanging about the workers and their brood. The workers seemed to be on the defensive. At 6.50 P. M. the female suddenly took possession of the pile of pupæ in the corner of the nest and was prancing about. This alert and excited behavior was extraordinary after her lethargy during the whole day. Whenever a worker entered the corner she was driven away or killed. Seven of the workers were killed between 6 and 6.50 P.M. The survivors fled to the light end of the chamber with some of their pupæ and at 7.20 P. M. were dragging pellets of earth to the corner and trying to barricade themselves from the female. July 17, 7.30 A. M., the female had killed the remaining 4 workers and had collected all the nude pupæ and semipupæ in a compact pile. At 8.40 the corner in which the female was guarding the brood was brightly lighted and another corner of the chamber was darkened. By 9.45 she had carried all the brood into the dark corner and was guarding them with open mandibles. At 11 A. M. another female *rubicunda* from the same colony was introduced. This female (B) was readily distinguished from the first female (A) in the following observations by her wing stumps. B on approaching A was at first violently attacked, but she was soon recognized and permitted to pass. July 18, 7 A. M., female B seemed to be less attached to the brood than A. One callow had hatched during the night and at 8.45 another appeared and was being licked by female A. By 7.30 A. M. female B had come to take as much interest in the brood as A. When the nest was uncovered both females hastened to conceal the pupæ and semipupæ, and when a straw or the finger was brought near the brood both females thrust their mandibles into it. The callows were beginning to assist the females in freeing the young from their pupal envelopes. July 19, 7.30 A. M., the *rubicunda* sisters behaved as on the preceding day and carried the pupæ to the same dark spot when their corner was exposed to the light. July 20, 7.30, 2 callows had hatched during the night and two appeared on the following day, July 21. Two more hatched July 23, but no others had appeared by July 26, when the experiment was discontinued.

Experiment 39. July 18, 8 A. M., a *rubicunda* female was placed in the dark chamber of a nest with 12 medium-sized *subsericea* workers and about 150 nude worker pupæ and semipupæ. The adjoining chamber was then opened and the illumination reversed. The workers began to move their brood into the other (now darkened) chamber, and succeeded in getting about 50 of their pupæ through the entrance when the female became suddenly much interested in the brood. She killed 2 workers in quick succession and began to collect the pupæ in the light (previously dark) chamber and tried to conceal them, at first in the entrance and then in one of the corners which I darkened for her. The pupæ in this chamber were at first much scattered, but the female had collected all of them by 8.40 A. M. Meanwhile one worker kept stealing into the chamber and making off with some of the pupæ into the dark chamber. At 9 A. M. the female caught one of the workers *in flagrante delicto* and nearly killed her with a blow of her mandibles. She released the worker and went to look after the pupæ. Later, on passing, she noticed that the worker was still moving and dispatched her. By 9.10 the female had collected all but 2 of the pupæ, 37 in number, and was carefully guarding them at 12 M. July 19, 7.30 A. M., she was surprised in the act of removing the pupal skin from the limbs of a hatching callow. She was still very alert and pugnacious and during the night had evidently successfully protected the pupæ from all incursions of the *subsericea* workers in the adjoining chamber. Another callow hatched at 4 P. M., July 20. Matters were *in statu quo* except that a third callow had made its appearance during the night. The female was not molested by the *subsericea* workers, that remained in their own chamber after plugging up the entrance with pellets of earth. At 6.30 P. M. the female had 7 callows and by 7.30 A. M. on the following morning an eighth had made its appearance. Matters remained *in statu quo* during the two following days, when the female was released in the garden.

Experiment 40. July 19, 8 A. M. Two *rubicunda* sisters, A and B, distinguished by a difference in size, were placed in a nest containing 6 mature, medium-sized *subsericea* workers, 12 callows two days old but able to run about and carry pupæ, and about 125 nude pupæ, all with pigmented eyes and some of them brown and nearly ready to hatch. The workers at once fled with their brood. Female A began to prance about as soon as her antennæ had explored the fine assortment of pupæ. She went from one worker to another pinching and when necessary killing them. Even the young callows tried to defend themselves and their brood, but were soon (8.15 A. M.) driven to the other end of the nest. A at once began to move the pupæ into a corner. B was less excitable and very listless; she at first tried to escape from the nest by biting at the towelling; then she dug a hole in the earth, and finally took to carrying pellets of earth, dead *subsericea* workers, etc., for short distances in a desultory manner. At last, however, she joined A in defending the pupæ and even tweaked the workers when they ventured into her neighborhood. Both of the females seemed to be very lenient with the callows and seriously injured only 2 of them, while they killed 4 of the mature workers outright. The workers, however, succeeded in recovering about a dozen of their pupæ. Female B now set about collecting the young callows and carrying them to the pile of pupæ, and then began to take the pupæ away from the workers at the farther end of the nest. By 8.30 both females were equally excited and busy and working in unison. The two opposite ends of the chamber were darkened and the middle portion exposed to the light for the purpose of ascertaining whether the females would establish separate nests. 11 A. M. With the exception of the two youngest callows, every *subsericea* in the nest had been killed and their bodies had been placed by the females at one end of the nest, while they had collected all the pupæ and the two young callows in a single pile at the other end. Both females fondled and licked the callows and tried to conceal them and the pupæ whenever the nest was uncovered. By 4 P.M. 4 pupæ had hatched. Whenever one of the callows tried to crawl away from the pile of pupæ, female B would follow her, seize her in her mandibles and bring her back, much as a cat carries her kitten. Both females were equally solicitous about the young. They had even brought back some of the youngest of the dead callows from the opposite end of the nest and had placed them with the pupæ. On the succeeding days the number of callows increased as follows: July 20 there were 13; July 21, 23; July 22, 32; July 23, 36; July 24, 40; July 25, about 50. During all this time the females showed no tendency to establish different colonies by dividing the brood, nor any signs of hostility towards each other. At 6 P.M., July 26, they were set free

Experiment 41. July 23, 1.15 P.M., a *rubicunda* female was introduced into a nest containing 21 medium-sized and large workers of *subsericea* with a number of semipupæ and naked pupæ from a large colony nesting in a mound. She was at once attacked but promptly killed two of the workers, then a third, and then angrily pulled one by the mandibles. By 5.30 P.M. she had killed all but one of the workers and was busily collecting the brood and storing it in a dark corner of the nest. July 24, 8 A.M. The single worker was still alive but wandering dejectedly about far from the female and the brood. Two callows had hatched during the night. July 25, 7.30 A.M. The single worker had been killed during the night and the female was in undisputed possession of the pupæ. A third callow had appeared and by 2.15 P.M. two more had been freed from their pupal envelopes by the female. On the following day (July 26) a sixth callow hatched. The little colony was set free in the garden at 6 P.M.

The above series of successful experiments shows very clearly that the female *rubicunda*, when placed with a small number of *subsericea* workers and their pupæ, displays a chain of instincts that result in her gaining possession of the latter. To all appearances she is quite ready to be amicably adopted by the *subsericea*, but when received with marked hostility, as is probably almost invariably the case, her animosity is very quickly kindled, and she slays the *subsericea* with all possible dispatch, thus manifesting instincts very similar to those of her own workers when engaged in a dulotic raid. Owing to her powerful mandibles and closely knit frame she is always a match for several workers and may kill as many as 21 of these (Experiment 41) in a very short time. Before she has killed them all, however, she becomes much interested in their brood, eagerly collects and secretes it in some favorable corner and guards it with open mandibles till the callows are ready to hatch. These she skilfully divests of their cocoons and pupal envelopes. Their advent in considerable numbers appears to be the signal for another marked change in the instincts of the female. She now becomes very timid, fleeing whenever the nest is disturbed and taking refuge in the darkest and remotest corner of the nest. In this instinct phase the female remains throughout the remainder of her life. The reactions displayed in the foregoing experiments are, moreover, so definite, uniform and purposeful even in artificial nests that one can hardly doubt that they are similarly manifested in a state of nature. It is evident that, especially in timid incipient wild colonies of *F. subsericea*, the females may meet with less opposition and therefore with greater and more immediate success. Still the fact that *rubicunda* is a local ant and by no means one of our most abundant species shows that the successful establishment of colonies in a state of nature must be attended with considerable difficulties. The search of the *rubicunda* female for weak or incipient *subsericea* colonies, even in regions where the latter ant is very abundant, must often be vain or illusory. This is tantamount to saying that the element of chance must enter very largely into the life of the *rubicunda* queen, just as it does into the lives of most parasitic animals.

7. **Formica sanguinea rubicunda** var. **subintegra** *Emery.*

The females of this form are much smaller than those of *rubicunda* proper. A few of them were taken July 10 from a flourishing colony containing many *subsericea* slaves, and were used for experiments like those performed with *rubicunda*. They gave negative results, however, for in every case the female was killed by the workers before she could show an interest in the cocoons or try to collect them. It is, of course, quite possible that these small females may be less pugnacious than those of the pure *rubicunda* and rely on amicable adoption by the workers of incipient *subsericea* colonies rather than on killing the workers and appropriating the young. The following may serve as an example of the experiments performed with *subintegra.*

Experiment 42. July 17. At 11.45 P.M. an artificially deälated female *subintegra* was placed in a nest with 7 *subsericea* workers and 10 pupæ (5 nude and 5 in cocoons). One of the workers at once seized her by an antenna, but the others at first sought to avoid her. She grabbed the irate worker by a leg and tried to amputate it. While the two ants were in this predicament, a worker came up and began to lick the female's head and mandibles effusively. Then another worker came up and did the same, but soon departed. The female tried to cut off the gaster of the worker pulling at her antenna. Meanwhile another worker approached and licked the female's head. At 1.05 P.M. she killed the worker that was holding her, and succeeded in extricating her antennal funicle. She was very alert and examined all parts of the nest very carefully. The workers, annoyed and frightened by the female, tried to conceal their brood in the manger. While running about the nest the female felt into the manger and was at once attacked by 3 workers simultaneously. She managed to shake off two of them and to catch the third by the hind leg. She dragged this worker about, stopping from time to time to curl her body as if to spray her victim with formic acid. The worker finally escaped. The others seemed to be much afraid of the female and fled whenever she approached. She did not seem to be at all interested either in them or their brood, but settled down on a lump of sugar and began to lick it eagerly. July 18, 7 A.M., the female was lying dead but unmutilated some distance from the workers and brood. Six of the workers were still living.

This unsatisfactory experiment proves little more than that the *subintegra*, like the *rubicunda* females, resent the attacks of *subsericea* workers. It throws no light on the method of colony formation unless, perhaps, the caressing behavior of the workers in the early part of the experiment may be taken to indicate amicable adoption of these females by feeble colonies of *subsericea*.

8. **Formica sanguinea aserva** *Forel.*

Of what I take to be this ant I have found only two colonies at Colebrook, Connecticut. These were about a mile apart and each was in a large prostrate log. The galleries besides permeating the wood extended into the soil, in one case to a distance of about 8 ft., where they terminated in another nest under a large stone. Although there were several hundred large workers in each of these colonies I failed to find more than 5 or 6 *subsericea* slaves in either of them. Exactly the same condition was observed in one of these colonies during the summer of 1904. Neither colony was very large, not nearly as large as the *rubicunda* colony from which the females were taken for the experiments above recorded. That one of them was still in its prime was shown by the great number of female cocoons which I took from it during July. These were kept in an artificial nest with several workers till they had hatched and matured. The workers, and especially the females, have the head and thorax dark brown instead of blood red as in the common forms of *sanguinea*. In many of the females the head is almost or quite black. At first sight the ant resembles *F. pergandei* Emery but is much more robust, the head is broader and the petiole has an acute instead of a blunt border. The workers vary much in size and the females are smaller than those of the typical *rubicunda*, but somewhat larger than those of *subintegra*. *F. aserva* seems to be a distinct and constant form and to be widely distributed in New England. Mrs. Annie Trumbull Slosson has recently sent me a couple of deälated females taken on the summit of Mount Washington and another from Franconia, New Hampshire.

Four experiments with fine mature females of this subspecies placed with a few workers of *subsericea* all gave unsatisfactory results, like the following:

Experiment 43. July 21, 6 P. M., a female *aserva* was placed in a nest containing 11 small *subsericea* workers and some nude pupæ taken from a small colony under a stone. The female was at once attacked by a worker but curled her body and tried to kill her assailant. At first she could not free herself and soon had two more workers pulling at a leg and antenna. She finally succeeded in extricating her antenna, but by 6.30 had lost both hind tibiæ and was being pulled about by 3 workers. At 6.45 she killed one worker and ran about with another dead one dangling from her antenna. By 7 P. M. she had cast off this encumbrance and was resting on the sponge. As her hind legs had been seriously injured she was removed from the nest and the experiment was discontinued. In another similar experiment the *aserva* female was promptly dispatched by the *subsericea* workers after she had killed two of their number.

These cases show that the female *aserva*, like the female *rubicunda* and *subintegra*, is by no means a patient inquiline like *consocians*, but when severely tweaked is always ready to defend herself with her mandibles and formic acid batteries. Further inferences in regard to the founding of colonies by this form can hardly be drawn from the above experiments.

9. **Polyergus rufescens lucidus** *Mayr.*

On returning to my home at Bronxville, New York, early in August, 1905, I at once visited a large colony of *Polyergus lucidus* with *F. schaufussi* slaves, which I had had under observation during the summers of 1903 and 1904, in the hope of finding a number of virgin females to use for my experiments. I was not to be disappointed, for the nest contained a lot of females and males, fully mature and ready for their nuptial flight. Thirty of the females were secured and confined in an artificial nest with several of their slaves. During the month of August I tried 12 experiments with as many of these females, but in no instance could I observe an adoption of these insects by strange *schaufussi* workers. The results are varied and conflicting, but as they are suggestive and can be briefly reported, I transcribe several of them from my note-book

Experiment 44. Aug. 6, 5.30 P.M., a female *Polyergus lucidus* was placed in a nest with 15 *Formica schaufussi* workers, small and medium-sized, taken from an average colony, together with 100 cocoons and 26 larvæ. After running about the nest for some time she was seized by a worker, which she killed by running her mandibles through its head. Then further struggles ensued between the two species and resulted in the crippling of two of the workers. By 9 P. M., however, the female showed signs of having been injured. Though still able to walk, she was found from time to time lying on her back with sprawling legs. Aug. 7, 6 A. M., there were 7 maimed workers in the nest, showing that the female had had many struggles during the night. She was lying on her back and appeared to be very weak. As she showed no signs of recovering, the experiment was discontinued.

Experiment 45. Aug. 7, 12 M. Into the nest used for the preceding experiment and still containing 8 *schaufussi* workers, another *Polyergus* female was introduced. At 6 P.M. she was still in excellent condition though she had killed 3 of the workers. Aug. 8, 7 A.M. Another worker had been killed during the night. The female seemed to have no inclination to associate with the survivors and showed no interest in their brood, but rested quietly on the sponge. Aug. 9, 7 A.M., she was resting near the workers and their brood and at first it looked as though she might be adopted, but at 6 P.M. she was found dead.

Experiment 46. Aug. 6, 9 A.M., a fine *Polyergus* female was placed in a nest with 9 rather small *schaufussi* workers and about 100 cocoons. One of the workers was a very young, another an older callow able to carry cocoons. The female ran about the nest and was soon attacked by a worker, which she promptly disabled by piercing one of its eyes and optic ganglia, so that it kept turning around in a counter-clockwise direction. Then she was attacked in succession by 4 other workers. She killed one of these and maimed the three others. Whenever one of them tweaked her legs, she ran her mandibles through its head. Two of the three injured workers kept gyrating, one in a clockwise, the other in a counter-clockwise direction, showing that in the former the left, in the latter the right side of the head had been pierced by the female's mandibles. At 10 A.M. she was attacked by two workers, one of which she had previously wounded. This one she killed in the usual manner. Throughout the day she showed neither interest in the brood nor fear of the *schaufussi.* By noon there were only 3 uninjured workers in the nest and these kept attacking the female from time to time. During the greater part of the afternoon she rested quietly on the sponge. Aug. 7. 6 A.M., she was resting on the cocoons with the workers, of which only 4 survived uninjured. At 6 P.M. she was dead.

The above experiments show that the female *Polyergus lucidus* is not adopted without, at least, considerable reluctance on the part of the *schaufussi* workers, and that she manifests no interest in the brood and is ready to kill the workers in self-defense. There is none of the strange excitement and keen interest manifested by *F. rubicunda.* It seems certain that the female *Polyergus* would accept adoption if the workers showed any disposition to confer it upon her, but they have no such inclination. The two following experiments show very clearly the female's lack of interest in the brood.

Experiment 47. Aug. 27, 11 A.M., a female *Polyergus* was placed in a nest with 3 *schaufussi* workers of medium size and a number of worker cocoons. She seized one of the workers at once and perforated its head. The worker began to gyrate in a counter-clockwise direction, but still endeavored to carry a cocoon to a place of safety. The female soon injured another aggressive worker, that nevertheless kept returning again and again to the attack. This worker died at 12 M., and the single remaining one had lost an antenna and was staggering along with a cocoon. By 6 P.M. this worker had also been killed and the female was resting quietly on the moist sponge. During this and the two following days she paid no attention whatever to the cocoons which were scattered about the nest. At 6 P.M., Aug. 29, she was returned to the parent nest and the experiment was concluded.

Experiment 48. Aug. 27, 12 M., a fine female *Polyergus* was placed in a nest with 4 large *schaufussi* workers and about 100 worker cocoons, all taken from a large wild colony. The female at once killed a worker that she encountered while running about the nest, and a few moments later dispatched two others in quick succession. The single remaining worker ran about with a young larva in its mandibles, trying to escape from the female. The latter returned again and again to the murdered workers and thrust her mandibles through their bodies. She paid no attention to the cocoons. By 9 P. M. she had killed the last surviving worker. During the two following days she ran about the nest or rested for long periods on the moist sponge, but never gave the least heed to the cocoons which lay scattered about the nest as they had been dropped by the demoralized workers. At 6 P. M., Aug. 29, she was removed from the nest.

In the two preceding experiments the *Polyergus* females were very aggressive and showed much of the insensate eagerness to kill alien workers so characteristic of the *Polyergus* workers. Neither in these nor in the succeeding experiments was a female ever seen to touch a cocoon with her mandibles, though often compelled to feel them with her antennæ and to walk over them while moving about the nest. In the two following experiments the behavior of the female *Polyergus* presents still another aspect, as passive as the preceding was agressive.

Experiment 49. Aug. 27, 11.30 A.M. A fine *Polyergus* female, placed in a nest with 14 large *schaufussi* workers and several cocoons, was soon seized by a worker. She pierced its cranium with her mandibles and compelled it to release its hold. While she was extricating herself from the jaws of this worker she was attacked by another, but did not offer to defend herself. Some of them pulled her about by the legs or antennæ while others fired volleys of formic acid into her face. She eventually escaped and without any signs of fear or resentment ascended the pile of cocoons. Here the workers seized her again and dragged her away. She drew her limbs up against her body and remained in a quiescent, pupal attitude while they tried to pierce her shining integument with their sharp mandibles. At noon she was still being dragged about passively. At 1.35 P.M. she was attacked simultaneously by 5 workers. By 6 P.M. they had succeeded in injuring her and she was so weak that she was removed from the nest.

Experiment 50. Aug. 27, 6.20 P.M. Another *Polyergus* female was placed in the nest employed in the last experiment, which still contained 13 *schaufussi* workers. There was a great commotion among the latter as they fled with their cocoons. She was seized by one of the workers but did not retaliate. She was almost at once released and went to rest in a corner. Aug. 28, 7 A.M., she was still alive, quietly resting on the moist sponge at some distance from the workers and their brood. At 9.15 P.M. she was walking about the nest. Whenever she passed workers they threatened her with half-open mandibles but went no further. She was not in the least aggressive. Aug. 29, 7 A.M., matters were *in statu quo.* A worker came up and pulled the female's leg, but soon released her. She rested near the workers and spent much of her time cleaning herself. By 6 P.M. there were 3 dead workers in the nest, showing that she must have resented some of the indignities to which she had been subjected during the day, for the workers seized her from time to time and dragged her about the nest by a leg or an antenna. When released she escaped to a corner of the chamber but soon returned to the workers and brood as if seeking adoption. Often the workers came up and felt of her and then passed on without molesting her. Aug. 30, 7 A.M., during the night another worker had been killed. The female was still in excellent condition. She was pulled about by a large worker but offered no resistance. Others repeatedly pulled her away from the brood, but as soon as she was released she returned to the workers' corner. Aug. 31, 7 A.M., she was uninjured and hung about the workers' corner all day. By 6 P.M. she had lost her left antennal funiculus and was so weak that there was no hope of her survival. She had lived 5 days in a nest with 9 to 13 unusually large *schaufussi* workers.

In these two experiments the behavior of the *Polyergus* female was much like that of *F. consocians* in *incerta* nests and strongly suggested adoption as the method of colony formation. I planned a number of other experiments in the hope of gaining a clearer insight into the peculiar behavior of the *Polyergus* females, but was prevented from carrying them out by the rapid dying off of these insects in their own nest. Hence this portion of my work, like that on *F. subintegra* and *aserva*, will have to be continued another summer under more favorable circumstances.

GENERAL CONSIDERATIONS.

The foregoing simple experiments, which consisted in compelling female ants, mature but mostly unfertilized, and artificially deälated, to consort with small colonies of alien workers, all go to confirm, what has long been known, that worker ants of one species are hostile to females of another species. It is clear, however, that this hostility is not always manifested with uniform intensity. Towards the females of the *Formica rufa* and *exsecta* groups, it is often feeble or even evanscent, so that in these cases mixed colonies can be produced consisting of adult individuals of both species. Under normal conditions such colonies are necessarily temporary, since they are destined, after the death of the original workers, to resolve themselves into pure colonies of the species to which the fertile queen belongs. Towards the females of *F. sanguinea* and *Polyergus* the hostility of alien workers is so pronounced and persistent that mixed colonies cannot be produced as in the former case. The females are obliged to exterminate the old workers and to take possession of the brood in order to rear a colony of loyal auxiliaries; it being well known that ants hatched in the presence of adult individuals of another species are less liable to attack these even when they are recognized as aliens.

Of the rather numerous species of the *rufa* and *exsecta* groups, *F. consocians* has furnished us with the clearest case of temporary social parasitism through the immediate adoption of the fertilized female by *incerta* workers. Not only is the *consocians* female apt to arouse little or no hostility in the *incerta*, but she displays in her own behavior a pronounced instinctive adaptation to an inquilinous or parasitic mode of life. When placed in an empty chamber communicating with one occupied by *incerta* workers and their brood, she does not hesitate to enter and approach the workers with fearless and conciliatory gestures. She at once manifests a keen interest in the persons of the workers and their callows, and if driven away or persecuted returns again and again without signs of fear or resentment. Her attitude throughout is consistently insinuating. She licks the workers continually and effusively, and, at least till she has been definitively adopted, will even deign to feed them from her own crop. Her behavior is often surprisingly like that of the workers of *Leptothorax emersoni*, a highly inquilinous ant described in two of my former papers.[1]

This unusual behavior of the *consocians* queen endows some of her physical characters, which would otherwise be difficult of explanation, with a peculiar significance. I allude especially to her diminutive stature and uniform yellow coloration. Both of these peculiarities may be mimetic, since they must enchance her resemblance to the *incerta* workers, and may therefore facilitate an alliance between the two species. The fulvous yellow hairs on the body of the *consocians* female are also suggestive of myrmecophily, since it is known that many myrmecophilous arthropods, especially beetles, belonging to the most diverse taxonomic groups, present a peculiar convergent character in the form of tufts of yellow hairs connected with osmateria. These hairs are licked by the ants with unmistakable signs of satisfaction.

It is probable that the diminutive stature, though it may be regarded as a mimetic character, has not been developed as such, but is rather a result of precocious development. This, in turn, must be due to underfeeding during the larval stages. I have shown (p. 50)

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[1] The Compound and Mixed Nests of American Ants. Am. Natur., XXXV, 1901, p. 431 *et seq.*; and Ethological Observations on an American Ant (*Leptothorax emersoni* Wheeler). Archiv f. Psychol u. Neurol., II, 1903, pp. 1–31.

that in wild nests the *consocians* females make their appearance in great numbers and before the summer brood of workers hatches. This fact, taken in connection with the observation that colonies of our other species of *Formica*, notably those of the *fusca* and *pallide-fulva* groups, annually produce comparatively few but very large queens, indicates that the stature of the female ant must depend on the colonial food-supply and the manner of its distribution to the larvæ. While each of the large females has her gaster well stored with adipose tissue carried over from larval life, voluminous wing muscles that may be disintegrated after deälation to form additional nutriment, and ovaries containing mature or nearly mature eggs, the tiny female *consocians* is conspicuously lacking in all of these particulars and is therefore compelled to associate with worker ants in order to secure food not only for her prospective brood but for her own frail body.

The foregoing considerations satisfactorily account for the belated fertility of the female *consocians*. In one of my colonies (Colony C, *vide supra* p. 62), which was kept from August, 1904, till September, 1905, the ovaries of the queen did not enlarge and produce eggs till late in the spring, although the ants were so abundantly supplied with honey and hashed meal-worms that the gasters of the *incerta* workers were full and tense throughout the fall and winter months. This belated fertility under what seemed to be unusually favorable conditions is in marked contrast with what may be observed in some other ants. Thus Emery[1] found that the female *Pheidole pallidula* laid a great number of eggs on the day following the nuptial flight, and that a female of *Liometopum microcephalum* fertilized July 1, laid some 20 eggs four days later. The above-cited observation of Jakob Huber (p. 44) shows that the female *Atta sexdens* lays on the third day after her nuptial flight. I have observed that the females of *Pogonomyrmex molefaciens* will begin to lay within four days after fertilization. In all of these cases the females are very large compared with their workers. It is probable that great variations will be observed in the length of time that elapses in different species of ants between fecundation and laying. These variations are, of course, easily explained as due to differences in the amount of food stored up during larval life. If we regard the female ant as the winged germ of the colony, we are led to look upon her size as we look upon the size of the eggs in various animals. It is well known that the more numerous the eggs produced by an organism, the smaller they are apt to be and the greater or more numerous the

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[1] Sur l'Origine des Fourmilières, *loc. cit.*, p. 460

vicissitudes to which they are subjected during their development. This is especially true of parasitic animals like the Cestodes, Meloid beetles, etc. Similarly in ants, the larger the females the smaller the number of them produced by a single colony, and the fewer the vicissitudes they must encounter in founding their colonies. The analogy holds good also in respect of parasitic species like *F. consocians*.

It is, I believe, admissible, as I have asserted in a former paper, to extend the conclusions derived from a study of *F. consocians* to several other species of *Formica* belonging to the *rufa* group and having similarly diminutive or otherwise aberrant females. The species of *Formica* which I have described under the names of *microgyna*, *montigena*, *nevadensis*, *impexa*, and *nepticula* all have diminutive females, and small colonies of the two first mixed with *F. subsericea* workers have been actually observed. The females of *F. oreas*, *ciliata*, *dakotensis* and its var. *wasmanni* are aberrant in coloration and, though larger than the females above mentioned, are nevertheless smaller than those of the *fusca* and *pallide-fulva* groups. The very long yellow hairs of the female *ciliata* are especially remarkable and indicate that this insect must be a genuine inquiline. Mixed colonies of *wasmanni* with *subsericea* have been observed by Muckermann. Even *exsectoides* and the various varieties and subspecies of *rufa*, which have larger queens than the preceding species, are in all probability temporary social parasites. Several young colonies of *exsectoides* mixed with *subsericea* have been observed, and Wasmann has found, as I predicted, that the European *F. truncicola* presents essentially the same conditions as *consocians*. The behavior of *F. integra*, as shown in the above experiments, is clearly suggestive of inquilinism. I have also added a Myrmicine ant, *Stenamma* (*Aphænogaster*) *tennesseense* to this series of forms, since there is evidence that its diminutive, very glabrous and bright red females start their colonies with the aid of workers of *S.* (*A.*) *fulvum* or some one of its varieties.

Questions concerning the phylogenetic origin of parasitic habits are notoriously difficult to answer. The obstacles to an explanation of certain cases of social parasitism, however, like those seen in *F. consocians*, *truncicola*, etc., seem to have less weight than in the case of ordinary, or nonsocial parasitism. From the very nature of social organization in ants, the female may be regarded, throughout a large portion of her life, as a parasite on the workers of her own species. As a virgin she is a parasite on the maternal colony, as a mother, on her own offspring; so that both by instinct and tradition she has a pronounced proclivity to seek the society of workers and to rely on them both for her own sustenance and that of her brood. Hence it is not surprising to find that the females of some species may return after the marriage flight to seek readoption in the parental nest. In other cases fertilization may take place within the nest and the females, after losing their wings, remain as so many additional mothers to re-enforce the reproductive energies of the colony. One or both of these methods is adopted by most of our species of *Formica*, and must, indeed, be assumed in order to account, first, for the normal occurrence of more than one deälated female in nearly every large colony; second, for the multiplication of nests by a single colony and third, for the longevity of certain colonies far exceeding that of individual queens. From single colonies of *F. gnava* in Texas I have taken from 30 to 50 deälated females, and Wasmann[1] dug 60 old females from a single nest of the European *rufo-pratensis*. He also publishes a number of notes on the great tendency of *F. rufa* to form nests by a process of budding, so to speak, from a single original formicary, a phenomenon that had been previously observed by Forel and others, and also in the North American *exsectoides* by McCook. (*Vide supra* p. 72) Forel[2] mentions a colony of *F. pratensis* which he has had under observation for nearly forty years. It is extremely populous and has taken possession of a whole pine grove. On digging into this nest recently he found fertilized and unabraded females that certainly must have been much younger than the colony.

We may conceive that the next step in the phylogenetic development of temporary social parasitism was taken when, after descending from their nuptial flight, the females sought adoption in nests of their own species but belonging to alien colonies. As such adoption may be easily effected in artificial nests of some species of ants, there is no reason to suppose that it does not occur in wild colonies. In fact, Wasmann's observations[3] go to show that in Europe such adoptions not infrequently occur between workers of one and females of another variety or subspecies of *F. rufa*. He says that "in *rufa* and *pratensis* colonies, but especially in *rufo-pratensis*, *rufo-truncicola*, etc. females with *rufa*, *pratensis* or *truncicola* coloration are often found together."

Such conditions, which can be explained only as the result of adoption, lead to the final phylogenetic stage represented by the adoption of a female of one species by workers of another. It must be admitted

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[1] Ursprung u. Entwickelung der Sklaverei bei den Ameisen, *loc. cit.*, p. 196.

[2] Ueber Polymorphismus und Variation bei den Ameisen. Zool. Jahrb. Suppl., VII, 1904, p. 580.

[3] Ursprung u. Entwickelung, etc., *loc. cit.*, p. 198.

that at this point the difficulties in the way of adoption become more serious. There is unquestionably a pronounced antipathy among ants to the formation of mixed colonies by consociation of adult individuals, unless the insects themselves have exceptional characters or happen to be living under exceptional conditions. The female, on the one hand, must have instincts that lead her to behave in a conciliatory manner when she is surrounded by alien and hostile workers, and in all probability also a peculiar neutral, agreeable, or, at any rate, pacific odor. On the other hand no prosperous ant colony adopts females of alien species. They could be tolerated only by small, depauperate or effete colonies which had lost their queen or queens and were on the verge of extinction, or by incipient colonies under similar untoward circumstances. Even under these conditions adoption may be rare and exceptional, so that it may chance to occur only in the nests of very abundant and widely distributed species like *F. fusca* and *pallide-fulva.* But the good fortune of being able to found a colony with the aid of alien workers, though so rare, may still be sufficiently frequent to insure the survival of the species of the *rufa* and *exsecta* groups, especially as these insects, when once established in a neighborhood, are able to produce enormous and long-lived colonies.

Miss Fielde[1] has recently published some observations and conclusions which would seem to contradict not only the views which I have advanced in this and several other papers, but also those of Forel and Wasmann. She sums up her experience in the following sentences: "In no species of ant have I found workers that would tolerate the presence of any queen of unfamiliar odor, nor any queen that would willingly remain among workers of unfamiliar odor. Although all species of ants have not been tested we may well assume that what is shown to be a fundamental trait in a few species will manifest itself in all species of the tribe."

While I do not doubt the accuracy of Miss Fielde's observations I am not prepared to accept her conclusions in the comprehensive and somewhat schematic form in which they are stated, since they seem to me to be subject to the following limitations:

First, although simple at first sight, Miss Fielde's hypothesis becomes very complicated on closer scrutiny. If I understand her correctly she recognizes definite reactions to odors which differ with the species (specific odors), a "nest aura," an odor of the trail, a female and worker odor, that is, an odor which undergoes progressive change during the life of each individual, at least in the workers (progressive

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[1] The Progressive Odor of Ants. Biol. Bull. X, No. 1, Dec., 1905, pp. 1–16.

odor). She assumes on the part of the ants not only a highly developed associative memory for these various odors, but also a transmission of odors by heredity. In other words, we must suppose that every worker has an individual odor, which is continually changing with age, and identical only with the odor of the other workers of the same age and lineage in the same colony. I am not prepared to deny the existence of all these odors, although I find it difficult to understand how animals even as highly endowed as ants can behave with anything approaching diagrammatic accuracy in the presence of such a bewildering multiplicity of stimuli. The facts certainly appear to be much simpler than the hypothesis which Miss Fielde advances for their explanation. It would seem that the specific and nest odors and the reactions which they call forth would be amply sufficient to prevent two or more colonies of the same or different species from fusing to form a single colony. This interpretation, which is really the basis of Miss Fielde's elaborate schema, has long been accepted by myrmecologists and repeatedly applied to particular cases.

Second, while so much of Miss Fielde's contention may be granted, there can be no question that she has failed to account for the numerous exceptions which Forel, Wasmann and myself have been endeavoring to elucidate. These she practically ignores. The species used in her experiments, at least so far as they are mentioned in her paper, are well known nonsymbiotic species. Nor does she refer to any of the recorded cases in which female ants have been shown to be readily adopted by adult workers of the same species from very different colonies. In some of our species such adoptions may be immediate and complete, for example in *Stigmatomma pallipes*, *Pogonomyrmex molefaciens*, *Eciton schmitti*, *Leptothorax emersoni* and *Myrmica brevinodis*, according to my own observations, and in *Atta sexdens* according to Huber (*vide supra*, p. 46).

Third, the cases just cited, together with the adoption of queens by adult workers of alien species, of which several examples are recorded in this paper, are *facts*, and can only be explained by assuming on the part of the adult ants a very considerable amount of plasticity and adaptability to unfamiliar odors. It seems to me that Miss Fielde fails to make due allowance for this factor in her interpretation. This plasticity is conspicuously attested and exploited by the hundreds of myrmecophilous insects known to science. The toleration and adoption of the females of ants like *Anergates atratulus* and other workerless species, which are not only obligatory but permanent inquilines, *Leptothorax emersoni* and *Formica consocians*, which have unmistakable inquilinous instincts, not to mention other species, are to be interpreted in the same manner as the toleration and adoption of myrmecophiles. These ants are, in a word, merely myrmecophilous insects.

Fourth, animosities among ants are certainly not, in all cases, reactions to unfamiliar odors. The tactile sensations, which are associated with those of odor in these insects, may be very important and cannot be readily isolated in experiments like those undertaken by Miss Fielde. In several of my experiments on *F. consocians* it was seen that sister queens that had been living in perfect amity in the parental nest attacked one another furiously when placed in a nest containing *incerta* workers. Such animosity could hardly be aroused by odors. If something akin to this mutual hostility in deälated and fertilized females were not the general rule among sister ants, they would often establish their colonies in partnership, but only one such case has hitherto been observed in a state of nature. (*vide supra* p. 41).

Contrary to the hypothesis advanced almost simultaneously by Wasmann[1] and myself,[2] I now believe that slavery, or dulosis, has no direct ontogenetic or phylogenetic connection with the condition I have called temporary social parasitism. Although only one of the forms with which I experimented, namely *F. sanguinea rubicunda*, gave positive and clean-cut results, the behavior of the others, *F. sanguinea aserva* and *subintegra* and *Polyergus lucidus*, though much less satisfactory, was deficient rather than opposed to the results derived from *rubicunda*. That *aserva*, *subintegra* and *Polyergus*, in founding their colonies, may present conditions intermediate between those of *rubicunda* and *consocians* is, of course, possible. I have given reasons for believing that under natural conditions the recently fertilized female of *F. rubicunda* enters some small colony of *subsericea*, a species with which, of course, she has been familiar during her whole prenuptial life in the parental nest, kills the workers, if they attack her, seizes the larvæ and pupæ, stands guard over them and helps them to hatch. These workers then function as so many loyal nurses in feeding the queen and rearing her young as soon as they are brought forth. When the latter have reached maturity, they show the dulotic instincts of their mother in a modified and exaggerated form, making concerted forays on neighboring *subsericea* colonies, kidnapping their brood, and thereby perpetuating the mixed colony.

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[1] Ursprung und Entwickelung der Sklaverei, etc., *loc. cit.*

[2] An Interpretation of the Slave-making Instincts in Ants. Bull. Am. Mus. Nat. Hist. XXI, Feb. 14, 1905, pp. 1–16.

While the incipient dulotic colony is, to all appearances, very similar to that of a temporary parasite like *F. consocians*, there is an important difference in the comparative ages of the personnel in the two cases: In the incipient dulotic colony the workers are all younger than the queen, whereas in the incipient *consocians* colonies some or all of the workers are older than the queen. In the case of *rubicunda*, the *subsericea* workers kidnapped as pupæ by the queen are in full vigor and may live for three or four years, thus constituting a most efficient *entourage* for the education of the firstling *rubicunda* brood. In the colony of the temporary parasite, on the contrary, the conditions after adoption are less favorable, but there is a compensatory advantage to the species in the comparative ease with which adoption may be effected. The *rubicunda* queen is bound to retain her large stature, vigor and pugnacity. She may be conciliatory or indifferent towards the *subsericea* till she is attacked, but then the fiery temper, so characteristic of her species, asserts itself and she makes short work of the hostile workers. In the above experiments the series of actions of which this massacre is the first, is so constant, precise, and purposeful that it must represent a perfectly normal episode in the life of the female *rubicunda*, whenever she is subjected to the proper stimulus in the form of a small colony of hostile *subsericea* workers with their brood.

Since my experiments were concluded I have received from Prof. Emery a paper[1] in which he predicts for *Polyergus* a method of colony formation similar to that observed in my artificial nests of *rubicunda*. He says: "And what of the parasitic and slave-making ants like *Polyergus* ? Wasmann has formulated for this species an hypothesis which is not altogether satisfactory. He assumes the formation of the colony by alliance between a female *Polyergus* and alien workers of *Formica fusca* or *rufibarbis*. I would hazard a different supposition. Forel's observations seem to show that the instincts of the female *Polyergus* are less degenerate than those of the worker; he has even seen a female aiding a hatching callow to escape from its pupal envelope. Moreover, both Forel and I have seen virgin females taking part in slave-making expeditions. I surmise, therefore, that the female *Polyergus*, after losing her wings, is able to plunder from some feeble *Formica* colony one or more worker pupæ, which will then give rise to her first auxiliaries." So far as they go, my observations on *P. lucidus* are in accord with this hypothesis. It is certainly remarkable, however, that my queens were never seen to

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[1] Sur l'Origine des Fourmilières, *loc. cit.*, p. 461.

manifest the slightest interest in the larvæ or pupæ, even after all the workers in the nest had been dispatched. One of these insects could perhaps succeed in founding a colony if, after killing all the *schaufussi* workers in a small nest, she simply remained with the brood till some one of the pupæ hatched. This, however, could not occur without the aid of the female unless the pupa happened to be naked or very young callows happened to be present.

It is clear, just as in the cases of temporary social parasitism, that a *sanguinea* or *Polyergus* queen could not enter a flourishing colony of the auxiliary species with any prospect of being tolerated, much less of being permitted to establish a colony of her own. In addition to the two kinds of colonies available for this purpose, the incipient and the moribund, which were postulated in the cases of temporary parasitism, there is also a third possibility, namely, the fragment of a dispersed colony. In regions where *Polyergus* and *sanguinea* occur one often finds that the workers of *subsericea* and *schaufussi* colonies that have just been plundered by the dulotic ants scatter and again congregate in small clusters, each with such larvæ and pupæ as it has been able to rescue, under the dead leaves or stones, to remain for hours or days in a state of "abulic dejection." One of these clusters would afford every opportunity to a young *sanguinea* or *Polyergus* queen in search of a brood. It is highly probable that on the approach of one of these queens, such a cowardly colony-fragment would take to flight and surrender at least a portion of its cocoons.

If dulotic colonies are founded as here maintained, it follows as I have said before, that we can hardly look to temporary social parasitism as the phylogenetic basis of dulosis. Hence I ought perhaps to be well satisfied when Wasmann[1] calls my former view "eine nur undeutlich erfasste Hypothese," in order that his own "allseitig durchdachte und abgerundete Theorie" may shine forth with greater effulgence. That he should indulge in such boasting after reading my foot-note on the behavior of the *rubicunda* female shows that he failed to grasp the full import of my paper.[2] The present paper will, I believe, make it apparent that he forgot to round off at least one very important side of his "Theorie."[3]

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[1] Nochmals zur Frage über die temporär gemischten Kolonien und den Ursprung der Sklaverei bei den Ameisen. Biol. Centralbl., XXV, Oct. 1, 1905, p. 648.

[2] Some Remarks on Temporary Social Parasitism and the Phylogeny of Slavery among Ants. Biol. Centralbl., XXV, Oct. 1, 1905, pp. 639, 640 *nota*.

[3] It would be unnecessary to return to this controversy, since Wasmann concedes the only point I had a right to demand, namely the acknowledgment of my priority in the discovery of temporary social parasitism as a regular occurrence in ants of the *rufa* and *exsecta* groups, were it not that he seeks to deflect his reader's attention from this single matter, which constituted the whole issue. He is, of course, at liberty to say that he made the discovery independently, but the fact remains that he had received and read my paper by October 21 and did not send his manuscript to the editor of the "Biologisches Centralblatt" till the early part of December, as is perfectly clear both

Wasmann, who has for years been studying the typical *sanguinea* in a region where it seems to be very abundant, has concentrated his attention on the dulotic instincts of the workers. To discuss the views he has advanced on this subject is unnecessary, because I believe that they are the result of seeking answers to questions that should have been propounded in a different way. The same is true of much of the general discussion which some years ago culminated in a well-known controversy between Weismann and Herbert Spencer on the all-sufficiency of natural selection. All along it has been tacitly assumed that the workers have peculiar instincts of their own, differing qualitatively from those of the queens of the corresponding species; and since the workers are normally infertile, there was great difficulty in accounting for the adaptive structures and behavior inherited through an organism that did not exercise nor even manifest them. The first question should really be: Does the worker have any physical or psychical characters that are not somehow represented in the female? In other words, are not the worker characters adaptively correlated excess or defect, that is, merely quantitative characters of the queen, characters differing from those of the queen after the manner of fluctuating variations and not of mutations? Had such questions been asked at the outset, a painstaking and comprehensive study of the female ant would probably have been inaugurated. And had this been done, I feel sure that much less would have been written about the differences in intelligence, instincts, etc. between workers and queens. The idea that the fertile female contains all the potentialities of the species would have been familiar. It would have been seen that in the workers characters such as structures, instincts, physiological reactions as expressed by longevity, resistance to maxima and minima of temperature, moisture, poisons, etc., are commonly less developed than in the queens. Some characters, however, are more strongly developed in the workers. It is true, for example, that some of the worker instincts, such as the foraging instincts, are supposed to be absent in the queens, but I have seen old, deälated females of *Trachymyrmex septentrionalis* not only in the act of excavating the nest in company with the workers, but actually collecting and carrying in caterpillar excrement on which to grow the fungus garden. Emery and Forel long ago observed *Polyergus* females accompanying the dulotic expeditions of the workers. It is also well known that young

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from his own statement and that of the editor. I still maintain that observations on mixed colonies comparable to those of *F. consocians* were far too meagre, prior to the appearance of my paper to justify Wasmann's claim of independent discovery. It certainly does not help his case to write at length about all kinds of adoption among ants when there was only one kind under discussion.

female ants sometimes behave like the workers in caring for the young, feeding other members of the colony, etc. Because female ants are slow to manifest certain reactions, or fail to do so entirely, except under the stress of unusual stimuli, we should not say that the capacity is absent, any more than we admit the absence of an hereditary character which remains latent during one or more generations. To use the language of the neovitalist, the entelechy of the worker ant is involved in that of the female. While the instincts of the worker ants are very important in all that relates to the inheritance and maintenance of the colony—its *Betriebsfunktionen*, to use a German word—the instincts of the female are of supreme significance in all that relates to the reproduction of the species; to the ontogenetic and hence also to the phylogenetic development of colonies. This seems to have been overlooked in all previous attempts to explain social parasitism and dulosis. Wasmann, for example, continually stresses the dulotic activities of the workers and the impossibility of explaining them except as manifestations of an inordinate fondness for rearing the larvæ and pupæ of an alien ant, on the part of an enterprising and pugnacious species which would seem to be well able to hold its own in the struggle for existence without resorting to any such methods for the enlargement of its colonies.

There are obviously some further bearings of these general considerations on the subject of dulosis. It is possible, in the light of the experiments on *rubicunda*, to regard the slave-making instincts of the workers of this species as at most only exaggerations of similar instincts in the female. In the former, however, they are more suffused with the instinct to forage in files. As Forel and I have shown, a large portion of the larvæ and pupæ kidnapped by *sanguinea* workers must be eaten, although some of them are reared in obedience to the threptic instincts, which the workers, of course, share with the queens. It is not even necessary, however, to regard these instincts as unusually developed in the workers of the slave-making species. In the *rubicunda* queen, they naturally predominate, although in one experiment a single small *subsericea* larva was eaten. Unfortunately I failed to give much attention to the larvæ used in my experiments, which should therefore be repeated with a view to ascertaining whether the female *sanguinea* does not satisfy her hunger occasionally with some of the *fusca* larvæ if she is required to wait too long for the hatching of the pupæ.

As I have already intimated, there seems to be no way to derive the dulotic instincts from a condition of temporary social parasitism like that of *F. consocians*, *truncicola*, etc. Dulosis is rather to be regarded as a distinct manifestation, which has probably arisen independently from the same basis as temporary social parasitism. This basis, as we have seen, is the instinct to form polydomous colonies, like those of *rufa*, *exsectoides*, etc., by adopting females of the same species and multiplying nests. Wasmann has shown that the European *sanguinea* is very prone to proliferate over several nests. This seems to be true also of some of our American varieties and subspecies, although I have seen indications of it only in certain localities. Wherever it occurs it may be taken to indicate that some of the females after fecundation either remain in or return to colonies of the parental species. In founding new colonies, however, the females obey the same instinct which impels them to return to the parental nest, namely to enter colonies in which they find the already familiar *fusca* workers. To this extent, and, I believe, no further, have dulosis and temporary social parasitism a common phylogenetic origin.

Now if we regard the worker instincts as derived from those of the queen, instead of as activities *sui generis*, the matter will appear in a clearer light. The dulotic tendencies of the worker are then referable to the instincts which the female has occasion to display only while she is founding her colony. The differences are largely due to the fact that the workers make their forays not singly and but once in their lives but in companies and repeatedly and on populous *fusca* colonies which the females could not enter. Wasmann has explained the fact that the workers select the *fusca* colonies as the objects of their raids because this species happens to be a very familiar one, since it reared them in the parental nest. This is probably true, but it is even more evident in the case of the queen, since the tendency to invade such a nest is in her reinforced by the traditional purpose of establishing a colony.

Pursuing the matter still further, however, we come to deeper and more general instincts. At first sight the catenary reflexes manifested by the *rubicunda* in the experiments recorded on pp. 75 to 83 appear to be very unusual and quite in harmony with the unique and exceptional character commonly attributed to dulosis. It is probable, however, that young and vigorous females of nearly all species of ants, when confronted with a small number of hostile workers and their brood, either of the same or of an alien species, would behave very much like the queens of *rubicunda*: they would, in other words, slaughter the workers and take possession of the brood. The attacks of the workers would naturally goad the queen to self-defence and violence while the presence of the undefended brood would arouse her philoprogenitive cravings. These suppositions are worth testing by specially devised experiments. The behavior of the queens of the *rufa* and *exsecta* groups obviously constitutes a striking exception to these statements, since some of these in my experiments failed to resent the hostile tweaking and spraying with which they were received by the workers. It is probable, however, that in these species the instincts of self-defence are latent, or rather adaptively inhibited in the presence of workers of the host species. Through founding colonies with the aid of adult workers these females have become so completely socialized as to have lost nearly all hostile initiative.

It is not surprising to find that the psychologist and physiologist have followed the ethologist in concentrating their attention on the worker to the neglect of the female ant. The workers are, of course, more abundant, much simpler and more responsive to certain stimuli. The female ant, however, as the epitome of the species, not only presents a fresher and more extensive field for the study of formicid instincts, but one to which we must more and more resort in tracing the worker instincts back to their origins and meanings. While worker ants undoubtedly can and often do reproduce, and are therefore able to transmit their characters to the species as a whole, at least through male offspring, it is nevertheless certain that the specific characters are commonly and often exclusively transmitted by the queens.

The taxonomist, like the physiologist and psychologist, has unduly stressed the importance of worker ants and for the same reasons, namely that they are more abundant and often, indeed, the only procurable specimens of a species. As myrmecography progresses, however, the specific and generic characters will certainly be drawn more and more from the males and females and less from workers and soldiers. It is evident that the same rule will apply to the termites, as Sjöstedt[1] and Desneux[2] have shown in their opposition to Wasmann's tendency to establish genera on the characters of soldiers.

The results of ethological study should be an abiding source of suggestion to the comparative physiologist and psychologist. Not only is such suggestion one of the greatest contributions of ethology, but this science should itself continually welcome and utilize the results of physiology and psychology. In this connection the experiments on *F. consocians* and *rubicunda*, showing that the phototropism

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[1] Monographie der Termiten Afrikas. K. Svensk, Akad. Handl., XXIV., 4. Stockholm, 1900.

[2] Remarques Critiques sur la Division Systematique des Termitides. Ann. Soc. Ent. Belg. XLVIII, 1904, pp. 372–378.

and instincts of the female ant can be changed or modified by such a simple and definite stimulus as artificial deälation have a peculiar interest. Some years ago my friend Prof. Loeb in an important paper[1] called attention to the fact that female ants (*Lasius niger*) are negatively phototropic till the time of the nuptial flight, when they become positively phototropic to a high degree, only to return to the negative state after they have lost their wings. The latter state is accompanied by a positive stereotropism, which induces the insects to work their way into crevices, under stones, into the soil, etc. One would be inclined to regard fertilization as responsible for this change from positive to negative phototropism, but mere removal of the wings with tweezers not only produces the same peculiar inversion of reaction towards the light, but also changes other reactions as well. Before deälation the insects exhibit many instincts supposed to be peculiar to workers; they eat from the manger and, like workers, may be very aggressive to strange ants, though they usually pay little attention to the workers or to the brood. After extirpation of the wings, however, they become interested in the brood and solicit food from their offspring. Later still they become exceedingly timid and sensitive to light, so that they conceal themselves at once when the nest is opened or disturbed. The physiologist would naturally seek the cause of these changes in metabolic processes. Obviously the primary stimulus to which the insect reacts is a privitive one, the absence of the wings; but the secondary, or true stimulus must be sought within the organism, and since, in this case, the female ant reacts the same with an empty as with a replete spermatheca, fertilization cannot be the cause of the conspicuous differences in behavior before and after deälation. Apparently metabolic changes in the thoracic musculature, initiated by the mere absence of wings and leading to fatty degeneration of the muscles and their replacement by gases, may be the secondary or true stimulus. This, however, would seem to be a purely physiological problem.

To some it may appear that in the foregoing general considerations I have unduly exaggerated the importance of the female ant. It must be admitted that one can hardly fail to be biassed by merely concentrating one's attention on a particular object of investigation, for specialization must of necessity mean limitation and undue emphasis. While I do not flatter myself that I have escaped such influence in the present instance, I believe I have shown that we must gain a

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[1] Der Heliotropismus der Thiere und seine Uebereinstimmung mit dem Heliotropismus der Pflanzen. Würzburg, 1890, p. 64 *et seq.*

deeper insight into the activities of female ants before we can hope to solve many of the problems suggested by the instincts of the workers.

POSTSCRIPT.

While the foregoing pages have been going through the press, a few facts of considerable interest in connection with both temporary and permanent parasitism among ants have come to light.

Mr. A. P. Morse has sent me a number of ants which were apparently living as a mixed colony under the bark of a pine tree at Sherborn, Massachusetts. The specimens comprise workers of *Formica fusca* var. *subænescens* and workers and a female of *F. impexa*, which I originally described from the Porcupine Mountains of northern Michigan. The female is very small and closely resembles the females of *F. microgyna*, *nevadensis*, and *nepticula*. Probably, therefore, *F. impexa* is a temporary parasite like *F. consocians*.

Forel has just published the interesting observations of Dr. Santschi of Kairouan, Tunis, on the workerless ant *Wheeleria santschii*, which is a permanent parasite in the nests of *Monomorium salomonis*. (Mœurs des Fourmis Parasites des Genres Wheeleria et Bothriomyrmex. Rev. Suisse Zool., XIV, pp. 51–69, 6 figs.) The young fertilized *Wheeleria* females were seen to enter the *Monomorium* nests, and were at first pulled about by the workers. In the course of a few hours, however, these females were definitively adopted. Santschi has made the very significant observation that the *Monomorium* workers kill their own queen and transfer their allegiance to the parasites. It now seems probable that the absence of the *incerta* queens in colonies that have adopted *consocians* queens may be due to similar matricidal instincts on the part of the workers.

Forel in his 'Fourmis de la Suisse' described a mixed colony of the Dolichoderine *Bothriomyrmex meridionalis* and *Tapinoma erraticum* without being able to explain its origin. Santschi has just made several observations which indicate that the *Bothriomyrmex* females seek adoption in the *Tapinoma* nests, but as pure colonies of each of these species are common, it is probable that the parasitism is of the temporary type seen in *F. consocians*.

EXPLANATION OF THE PLATES.

PLATE VIII.

FIG. 1. — Queen of carpenter ant (*Camponotus pennsylvanicus*) with incipient colony consisting of three minim workers and a packet of young

larvæ, nesting in the deserted pupa case of a longicorn beetle (*Rhagium lineatum*) under pine bark. Slightly enlarged.

FIG. 2. — Incipient nest crater formed immediately after the nuptial flight by a queen of the California harvester (*Pogonomyrmex californicus*). Mojave Desert, near Needles, California. Nearly ½ natural size

FIG. 3. — Nest of young colony of *Lasius niger* var. *americanus* under stone, presumably in its second year, showing the original queen chamber after its extension by the workers. Colebrook, Connecticut. ⅔ natural size.

PLATE IX.

FIG. 1. — Nest of *Formica rufa integra* in a huge pine stump, showing vegetable débris accumulated by the workers in the crevices of the bark and around the roots. Colebrook, Conn.

FIG. 2. — Nest of same species in a large pine log, showing accumulation of débris stopping up the hollow end. Colebrook, Conn.

PLATE X.

FIG. 1. — Nest of *Formica rufa integra* under and between a pile of stones lying on a large boulder. In this case the workers had carried the débris to a height of nearly six feet above the ground and packed it in between the stones. Colebrook, Conn.

FIG. 2. — Superficial nest chambers of *Formica difficilis* var. *consocians* under a stone. ½ natural size. At *a* and *c* two *Microdon* larvæ are seen, at *e* and *n* two puparia of the same insect. The imago has left the puparium at *e*. Colebrook Conn.

PLATE XI.

FIG. 1 — Nest of *Formica schaufussi* var. *incerta* under the edge of a stone. The nest entrance is at *x*. About ⅛ natural size. Colebrook, Conn.

FIG. 2. — Surface galleries of a nest of the same ant under a stone. *x*, entrance to nest, *v*. opening of one of the galleries into the large surface chamber. About ⅕ natural size. Colebrook, Conn.

PLATE XII.

FIG 1. — Young nest of *Formica exsectoides*, hardly a foot in diameter and still covered with long grass. Colebrook, Conn.

FIG. 2.—Larger nest from the same locality, showing straws on the dome-shaped summit and small openings about the base.

PLATE XIII.

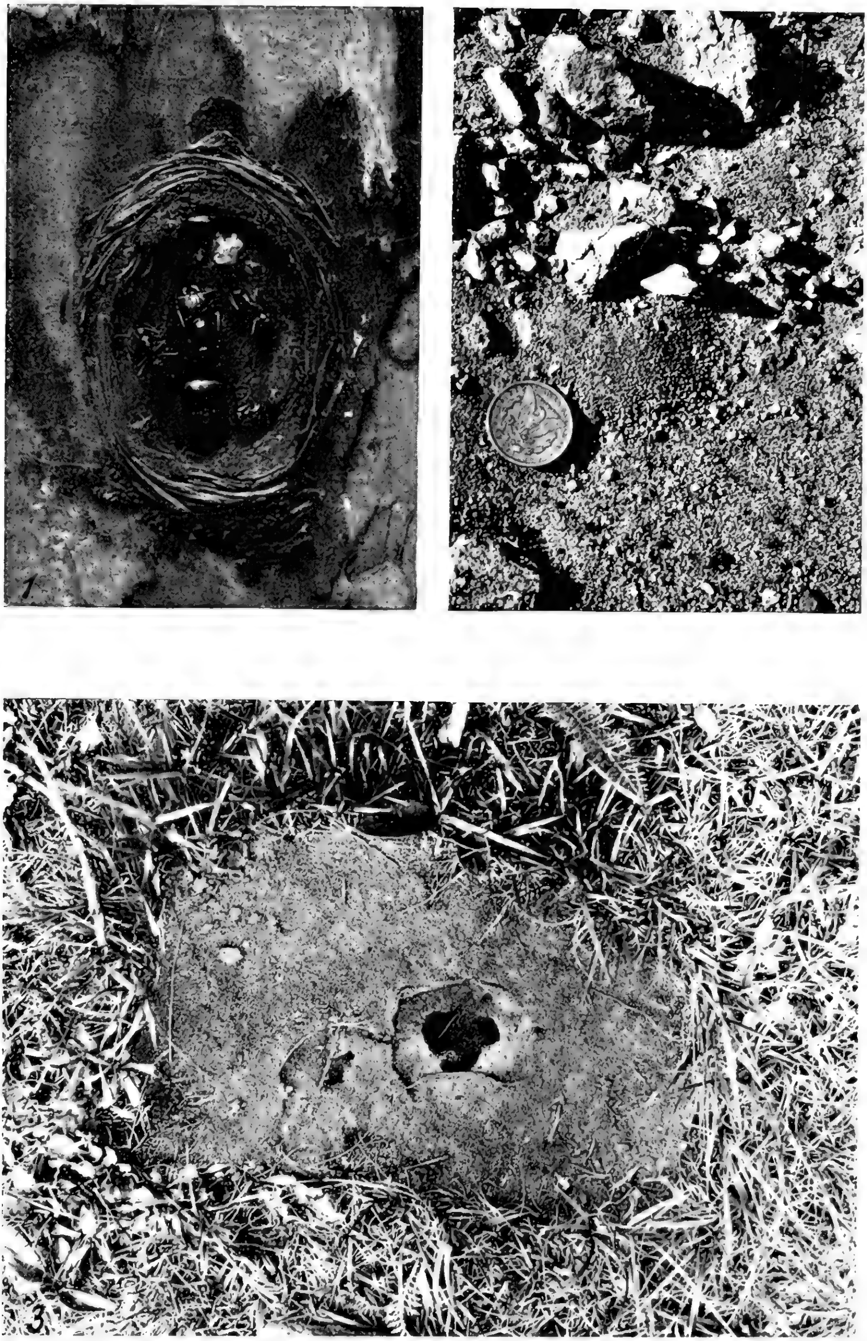
FIG. 1.—Nest of *Formica exsectoides*. Staten Island.

FIG. 2.—Nest of same species from the same locality, showing zone of green grass around the base and covering the entrance

PLATE XIV.

FIG. 1.—*Formica exsectoides* mound shot through with the stems of plants that have been killed by the ants. Staten Island.

FIG. 2.—Large mound nest of *Formica exsectoides*, showing the numerous entrances around the base, Colebrook, Conn.



INCIPIENT ANT NESTS.

2.

NESTS OF FORMICA INTEGRA.

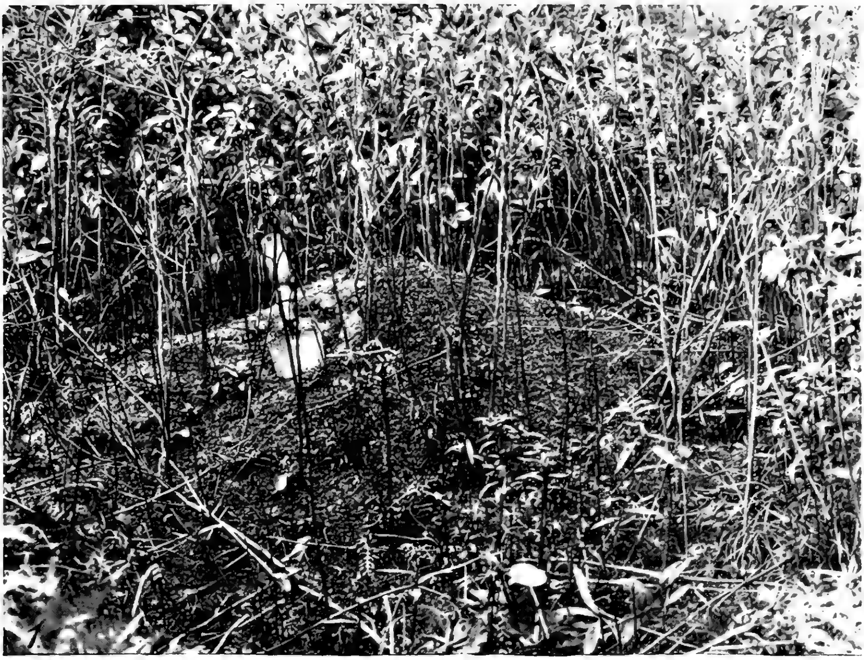
Nests of Formica integra and F. consocians.

2.

NESTS OF FORMICA INCERTA.

SMALL NESTS OF FORMICA EXSECTOIDES.

LARGE NESTS OF FORMICA EXSECTOIDES.



LARGE NESTS OF FORMICA EXSECTOIDES.

A New Wingless Fly (Puliciphora Borinquenensis) from Porto Rico.

BY WILLIAM MORTON WHEELER.

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59, 57, 72 P (727.5)

Article XIV. — A NEW WINGLESS FLY (*PULICIPHORA BORINQUENENSIS*) FROM PORTO RICO.

By William Morton Wheeler.

Plate XXXIV

The genus *Puliciphora* was established by Dahl in 1897 for some wingless and halterless flies which he had collected in the Bismarck Archipelago on dead birds and the carrion-scented flowers of the Aroid *Amorphophallus*. Being of the opinion that these flies would shed a new light on the phylogenetic origin of the fleas (Aphaniptera) from dipterous insects, he named the new species *P. lucifera*, and assigned it to the well-known family Phoridæ. In the following year, Wandolleck, while studying the types or co-types of *P. lucifera*, found that Dahl had described two species under the same name; that he had, in fact, designated as the male of *P. lucifera* the female of another wingless and halterless species. As if to show his distaste for Dahl's views on the phylogeny of the fleas, and in utter disregard of all precedent among systematic naturalists, he brushed aside the name *Puliciphora lucifera* and substituted two new generic and specific names, calling the female of *P. lucifera*, *Stethopathus ocellatus*, and the supposed male, *Chonocephalus dorsalis*. These two insects, together with a third which in the meantime Cook had described from specimens collected on a Liberian land-snail (*Achatina*) as *Wandolleckia* (since named *W. cooki* Brues), were removed from the Phoridæ by Wandolleck and elevated to the rank of an independent family, the Stethopathidæ.

It is only too evident that Wandolleck's *Stethopathus ocellatus* is merely a synonym of Dahl's *Puliciphora lucifera*. It follows also that the word Stethopathidæ must be abandoned even if Brues had not shown that the three wingless genera supposed to constitute this group are closely related to two older genera of subapterous flies (*Psyllomyia* Loew and *Ænigmatias* Meinert), and to several subapterous genera first described by Brues himself (*Ecitomyia*, *Commoptera*, *Xanionotum*, and *Aconstistoptera*). Brues's further discovery of the male of *Ecitomyia wheeleri*, which has well-developed wings with typical Phorid neuration, makes it very probable that all the other genera, which happen to be based on females only, have similar winged males. It is even doubtful whether we should follow the example of Melander and Brues and include all the apterous and subapterous Phoridæ in an independent subfamily. If this is insisted on, however, the group should be known as the Puliciphorinæ, unless, indeed, we revert to Loew's *Psyllomyia testacea* as the type. In that case, the subfamily should, of course, bear the name Psyllomyinæ.

There is opportunity for some difference of opinion in regard to the systematic position of the singular termitophilous and physogastric genera *Termitomyia* and *Termitoxenia* recently described by Wasmann. According to this author they represent an independent family which should be inserted between the Eumyid and Pupiparous sections of the order Diptera. He bases his opinion on his discovery that these insects are protandric hermaphrodites and develop directly, that is, without metamorphosis, from very large eggs. Brues regards these termitophiles as very aberrant Phoridæ, allied to the above-mentioned apterous and subapterous genera. While there can be little doubt that the forms in question have arisen from Phorid-like ancestors, it seems to me that the arguments adduced by Wasmann for regarding the Termitoxenidæ as a distinct family are not easily set aside. It may be contended, however, that we know nothing as yet of the development of the apterous and subapterous Phoridæ. The eggs of some of these insects seem to be very large, like the eggs of the Termitoxenidæ, so that it is not impossible that their development may be ametabolic or at least much abbreviated. This is most probable in some of the extreme forms like *Wandolleckia*, *Puliciphora*, and *Ænigmatias*.

The genus *Puliciphora* remained monotypic till 1903 when Melander and Brues found specimens of a second species (*P. occidentalis*) running on the ground in the immediate neighborhood of *Halictus* burrows at Wood's Hole, Massachusetts. As in the case of *P. lucifera*, only female specimens were taken. I am able to add a third species, which I recently captured in Porto Rico. On March 16, Professor N. L. Britton, Director of the New York Botanical Garden, handed me a large beetle (*Stratægus julianus* Burmeister) which he picked up while we were walking through the streets of Utuado. The beetle, which was nearly dead, was placed in a tin box with a perforated lid and left in my room at the hotel. On opening the box the following day I found that a lot of "crazy ants" (*Prenolepis longicornis* Latr.), together with a number of small Phoridæ, which I at first took to be *Podurans* allied to *Sminthurus*, had entered it through the small apertures. There was nothing to indicate any myrmecophilous relationship between the ants and the Phorids. Probably both had been independently attracted to the box by the strong odor of the decomposing beetle. The Phoridæ, which on closer examination were found to belong to an undescribed species of *Puliciphora*, were running about on the surface of the beetle and the adjacent walls of the box with a rapid skating gait, interrupted by quick turns and sudden halts. The beetle was examined at intervals of a few hours during the three following days, but though from one to half a dozen *Puliciphora* females were taken on each of these occasions, no males were to be found. It is not improbable that these have well-developed wings with a typical Phorid neuration like the males of *Ecitomyia wheeleri* Brues. I subjoin a description of the new species from the types in the American Museum of Natural History, and a list of the literature pertaining to the apterous and subapterous Phoridæ.

Puliciphora borinquenensis sp. nov.

(Pl. XXXIV.)

Female. Length, .7–1 mm.

Head slightly broader than long, with subparallel sides, straight posterior border and slightly convex and projecting front. Ocelli present. Eyes small, flattened, distinctly hairy. Antennæ set in deep frontal concavities, as in the other species of the genus; basal joint globose, second and third joints very small, cylindrical, subequal and, like the long arista, distinctly plumulose. Palpi long, projecting beyond the head when the latter is seen from above; in profile, their upper surfaces are straight or slightly concave, their lower surfaces convex. Proboscis well developed, projecting, laterally compressed, as long as the height of the head. The head has the following chætotaxy: There are four or five long macrochætæ on the outer apical surface of each palpus, four close together and projecting forward on the middle of the front, one on each side of the anterior ocellus, two between the posterior ocelli, and one at each of the extreme posterior corners of the head.

Thorax shorter than the head, but about twice as broad as long, a little narrower in front than behind, with feebly convex sides. It is as broad as the head, but hardly a third of the width of the greatest transverse diameter of the abdomen. There are no traces of either wings or halters. The pleuræ are steep and flattened, the three segments being very short and indistinctly indicated. On each side of the notum there are three macrochætæ, which increase in length from before backwards; the middle one is inserted further dorsally than the other two, the posterior higher than the anterior. Between the posterior pair, which occupies the extreme posterior corners of the thorax, there is a smaller pair near the posterior edge and about as far apart as each of them is from the posterior corner. There are very few hairs on the pleuræ.

Abdomen very voluminous, egg-shaped. The chitinous investment is thin and finely and very regularly chagreened, except on the dorsal surface, where there are six thickened sclerites, the first being very narrow, the last reduced to a minute lunule, the second as long as the subequal third and fourth together, the fifth narrow and with a large crescentic glandular opening in its middle. There are no ventral sclerites. The seventh, eighth, and ninth segments are suddenly attenuated, and the last bears a pair of small foliate flaps. The dorsal sclerites are covered with short uniformly distributed hairs; the remainder of the abdomen, except a large patch on each side just back of the hind leg and extending over about four segments, is covered with similar hairs, each of which arises from a small but conspicuous, elliptical brown spot. There is a circlet of macrochætæ along the posterior edge of the sixth and on the anterior portion of the much smaller seventh segment.

Legs rather stout, covered uniformly with short hairs except the coxæ which are nearly bare. Tips of hind coxæ with a row of bristles. Tibiæ with prominent spurs. Empodia fimbriated. Hind metatarsus slightly flattened and bearing on its plantar surface six transverse rows of bristles.

The body and legs are yellowish; abdomen white, except the dorsal sclerites and the spots from which the hairs arise, which are dark brown. Upper surface of head and thoracic dorsum light brown, the former with a dark brown, V-shaped mark with its angle over the ocelli, the latter with two indistinct longitudinal dark brown bands.

Described from nineteen specimens taken at Utuado, Porto Rico, March 17 to 19, 1906.

This species differs from both *P. lucifera* and *P. occidentalis* in having the hind metatarsi somewhat dilated and furnished with rows of bristles, and in the shape of the thorax, which is much longer than in *lucifera* and without the lateral sinuosities of *occidentalis*. From the former it differs also in the wider distribution of the stout hairs on the membranous portions of the abdomen. There are also important peculiarities in the chætotaxy of the new species, as may best be seen by comparing the figures accompanying this article with those of Wandolleck and Melander and Brues. It is, perhaps, worth noting that all the bristles of *P. borinquenensis* are bare, that is, non-pubescent, just as they are in *lucifera* and *occidentalis*.

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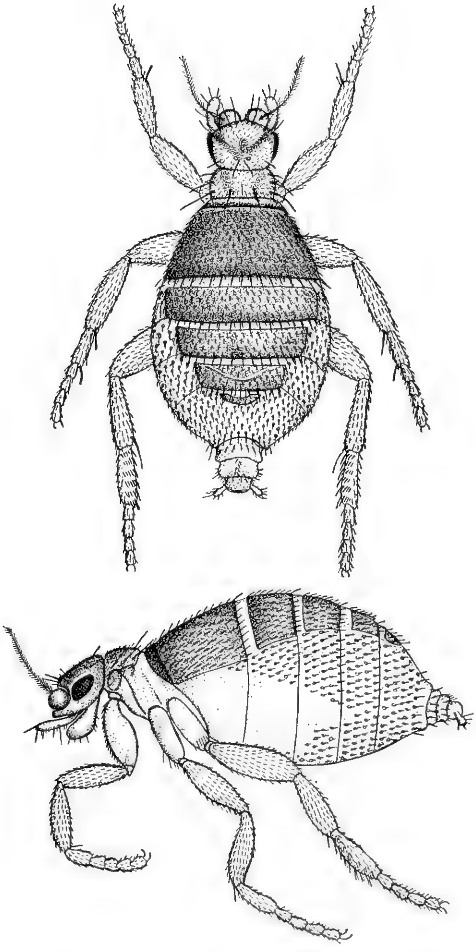

Puliciphora borinquenensis sp. nov.

The Ants of Japan.

BY WILLIAM MORTON WHEELER.

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59.57.96 (52)

Article XVIII.—THE ANTS OF JAPAN.

By William Morton Wheeler.

Plate XLI.

The following paper is based on a larger collection of ants made by Mr. Hans Sauter, mainly at Okayama, Kanagawa, and Yamanaka during the summer of 1904 and the spring of 1905 and sent me by Mr. Alan Owston of Yokohama, and some smaller collections from Misaki and other localities, sent me by Professor J. F. Abbott and Dr. W. H. Ashmead. Although this material has enabled me to recognize a number of the forms described by previous myrmecographers and to add several new ones, it is nevertheless true that our knowledge of the Japanese ant-fauna still remains very meager and unsatisfactory. Of very few of the species are all the castes known, and the published descriptions have often been drawn from a few or even single specimens. Moreover, ants have been collected in only a few localities of the Japanese archipelago. Probably, therefore, the described species and varieties will suffer considerable amendment when more material becomes available. The Japanese themselves seem to have paid little attention to the ants, unless perchance the results of their studies on these insects are embodied in works in their own language inaccessible to the occidental student.

Meager as are the materials at hand, however, they nevertheless throw considerable light on the geographical distribution of the Formicidæ in Eastern Asia. Forel called attention to the fact that the ant-fauna of Japan "consists of a mixture of palearctic and Malayan stocks, the latter confined for the most part to the southern portion of the archipelago." He fancied he could detect also "certain very interesting nearctic affinities, for example in *Camponotus pennsylvanicus* var. *japonicus* and *Formica fusca* var. *nipponensis.*" I believe that these affinities are somewhat doubtful. *C. japonicus*, being probably as closely related to certain Old World forms of *herculeanus* as it is to our common North American forms, should probably constitute a distinct subspecies of *herculeanus* independent of *pennsylvanicus*, and *F. nipponensis* is certainly as distinct from our North American var. *subsericea* as it is from the typical *fusca* of Europe.

There is, of course, no question as to the closer relationship between the Japanese ant-fauna and that of the adjacent East Asiatic continent. The complexion of the former, however, is altered by the intrusion, mainly, as Forel suggests, in the southern part of the archipelago, of a number of forms with strong Malayan or Indian affinities, in some cases even identical with the species of southern Asia. Such are the following:

Euponera solitaria,
Pheidole nodus,
Monomorium floricola,
Monomorium nipponense,
Monomorium triviale,
Vollenhovia emeryi,
Pristomyrmex japonicus,
Strumigenys lewisi,
Iridomyrmex itoi,
Iridomyrmex abbotti,
Technomyrmex gibbosus,
Colobopsis rothneyi,
Polyrhachis lamellidens.

The relationship of the Japanese to the European and North Asiatic ant-faunas is beautifully shown in the following list of identical species:

Myrmecina graminicola,
Solenopsis fugax,
Cremastogaster sordidula,
Myrmica lævinodis,
Myrmica lobicornis,
Tetramorium cæspitum,
Lasius umbratus,
Lasius niger,
Lasius fuliginosus,
Lasius flavus,
Formica rufa,
Formica sanguinea,
Formica fusca,
Camponotus herculeanus,
Camponotus marginatus.

In the majority of cases the subspecies or varieties which represent these species in Japan are much more closely related to the European types than to the North American subspecies and varieties.

The following list embraces forms which are known only from Japan, though in many cases these have pronounced affinities with other palearctic species, subspecies and varieties:

Sysphincta watasei,
Ectomomyrmex japonica,
Pseudoponera sauteri,
Brachyponera solitaria,
Ponera japonica,
Myrmecina nipponica,
Pheidole nodus,
Pheidole fervida,

Messor aciculatus,
Leptothorax congruus,
Leptothorax spinosior,
Pristomyrmex japonicus,
Monomorium nipponense,
Monomorium triviale,
Cremastogaster laboriosa,
Cremastogaster osakensis,
Stenamma owstoni,
Vollenhovia emeryi,
Aphænogaster famelica,
Iridomyrmex itoi,
Iridomyrmex abbotti,
Technomyrmex gibbosus,
Prenolepis flavipes,
Formica yessensis,
Formica fusciceps,
Formica nipponensis,
Camponotus obscuripes,
Camponotus vitiosus,
Camponotus 4-notatus,
Camponotus brunni.

Perhaps the most interesting of the new forms described in the following pages are *Sysphincta watasei*, *Myrmecina nipponica*, *Stenamma owstoni*, and *Vollenhovia emeryi*. These forms, with the exception of the last, have decidedly palearctic and nearctic affinities.

In working over the materials for the following revision of the Japanese ants I have been greatly aided by Professor Emery, who has taken the trouble to compare several of my specimens with the types of allied species in his extensive collection and has generously given me his expert opinion on the status of some of the new forms.

Family FORMICIDÆ.

Subfamily Ponerinæ.

1. **Sysphincta watasei,** sp. nov.

Worker (Plate XLI, Fig. 5). Length 4 mm.

Mandibles with oblique blades, 5–6-toothed; the three basal teeth blunt. Head, excluding the mandibles, longer than broad, with rounded posterior angles. Cheek with a short carina anteriorly. Eyes very small, near the middle of the lateral surface. Clypeus very short, its compressed middle portion projecting in front as a prominent blunt tooth between the high and approximated frontal carinæ. Antennal scapes thickened towards their tips and somewhat curved, reaching to the posterior corners of the head; joints 1–10 of the funiculus about as long as broad, terminal joint barely as long as the three preceding joints together. Thorax in profile convex in front, flattened behind, laterally compressed, much broader in front than behind. Epinotum with two indistinct teeth above, connected by a transverse ridge and each continued down on the side as a ridge bordering the concave epinotal declivity. Petiole from above longer than broad, broader behind than in front; in profile with a convex rounded node above, and below near its middle with a sharp tooth. Postpetiole campanulate, twice as broad as the petiole, not longer than broad; in profile flattened above, especially in front. First gastric segment somewhat broader and twice as long as the postpetiole, convex above; remaining gastric segments prominent, forming a cone which is bent forward and has a base occupying the posterior $\frac{2}{3}$ of the ventral surface of the first gastric segment. Sting well developed. Legs rather long and robust.

Mandibles, appendages and body opaque, with the exception of the gaster which is shining. Mandibles finely striated. Head, thorax and pedicel densely punctate or granular, the surface becoming more uneven on the epinotum, petiole and postpetiole. Upper surface of postpetiole almost rugulose. Gaster very finely punctate.

Body and appendages covered with rather long yellowish pubescence, interspersed with longer, suberect hairs of the same color.

Rich ferruginous red, gaster somewhat paler, mandibular teeth, edges of clypeus and frontal carinæ blackish.

Female (deälated). Length 4.8 mm.

Resembling the worker except in the usual sexual characters, namely, the presence of the ocelli, the larger eyes and the structure of the thorax. The wing insertions and thoracic sutures are black. The ventral tooth of the petiole is in the middle of the segment as in the worker. The first gastric segment is distinctly broader than the postpetiole.

Described from single worker and female specimens collected by Mr. H. Sauter, the former at Okayama, Bizen, the latter at Kamakaur on the Sagami Gulf "under drift-wood on the sea-beach." This species, which I take pleasure in dedicating to my old friend Professor Sho Watasê of the Imperial University at Tokio, very closely resembles the other known species of the genus, namely the three Mediterranean species *S. europæa*, *algirica*, and *mayri*, and the two North American species *melina* and *pergandei*. The Japanese species may be distinguished from all of these except *S. algirica* by its flatter postpetiole, from *algirica* by the position of the ventral petiolar tooth, which is in the middle and not at the anterior end of the segment.

2. **Pachycondyla (Ectomomyrmex) japonica** *Emery.*

Emery, Rendic. R. Accad. Sci. Ist. Bologna, Ann. 1901, p. 12 (sep.) 1, ☿

This ant, of which I have seen no specimens, was described from the Island of Tsushima, between Japan and Corea.

3. **Pachycondyla (Pseudoponera) sauteri** sp. nov.

Plate XLI, Fig. 66, *a*.

Worker. Length 3–3.5 mm.

Head longer than broad, narrower in front than behind, with straight posterior border. Eyes very small, of one or two ommatidia, situated about $\frac{1}{6}$ the distance from the anterior to the posterior corner. Mandibles broad, triangular, 7–8-toothed, with rather straight outer borders. Clypeus short, its anterior border nearly straight, its middle portion projecting between the carinæ as a small rounded protuberance. Frontal groove distinct, extending back beyond the middle of the head. Antennal scapes incrassated at their tips and not reaching the posterior corners of the head by a distance equal to twice their greatest diameter. First funicular joint nearly as long as the three preceding joints taken together; second joint as long as broad, joints 3–7 distinctly broader than long; joints 8–10 as broad as long; terminal joint nearly as long as the three preceding joints and forming with them a 4-jointed club, which is much thicker than the basal portion of the funiculus. Thorax with pronounced promesonotal and mesoëpinotal sutures; pronotum somewhat narrower than the head, rounder in front and on the sides, nearly twice as broad as long; mesonotum shorter and narrower than the pronotum, slightly convex; epinotum as long as the pronotum, but only half as broad, laterally compressed, its basal surface in profile straight, slightly lower than the mesonotum, distinctly longer than the declivity which is abrupt and has rounded lateral edges. Petiole from above as broad as the epinotum, somewhat broader than long, broader behind than in front; in profile a little higher than the epinotum, narrower above than below, with flattened and vertical anterior, truncated upper, and somewhat convex posterior, surfaces. Constriction between the first and second gastric segments rather indistinct. Legs stout; those of the middle and hind pairs, each with a pectinated and a simple spur; middle tibia and metatarsus bristly on their extensor surfaces, the latter joint much shorter than the hind metatarsus.

Clypeus and mandibles very smooth and shining, the latter sparsely and coarsely punctate. Head opaque, densely and finely punctate, frontal groove shining. Thorax, abdomen and appendages subopaque or in some specimens shining, more sparsely punctate than the head.

Body and appendages covered with yellow pubescence and suberect hairs of the same color, which are most conspicuous on the gaster and legs.

Mandibular teeth black, remainder of the body uniformly ochraceous.

Female, Length 4 mm.

Differs from the worker in color, the upper surface of the head, except its anterior third, the petiole and gaster dark brown or blackish. In some specimens this color extends over the sides of the mesonotum and the upper surface of the pronotum. Wings opaque, distinctly and uniformly infuscated.

Described from a number of workers and females (mostly deälated) taken by Mr. Hans Sauter, March 25, '05 at Yamanaka, Suruga ("1700 ft.; under stones"), and April 15, '05 at Takakiyama, near Kanagawa on the Sagami Gulf.

This species is closely allied to the palearctic *P. ochracea* Mayr, of which Professor Emery has sent me a worker and a female specimen. The Japanese species is darker in color and has a shorter head, which is broader behind with its sides converging anteriorly and thicker antennæ with more club-shaped funiculi.

4. **Euponera (Brachyponera) solitaria** *F. Smith.*

PLATE XLI, FIG. 13.

Ponera solitaria F. SMITH, Trans. Ent. Soc. London, 1874, p. 404, ☿

Ponera solitaria MAYR, Verh. zool. bot. Ges. Wien. XXXVI, 1886, p. 363.

Ponera solitaria FOREL, Bull. Soc. Ent. Suisse, X. 7, 1900, p. 267 and 284, ☿ ♀

Euponera (*Brachyponera*) *solitaria* EMERY, Ann. Soc. Ent. Belg., XLV, 1901, p. 47.

Several workers and deälated females collected by Mr. Hans Sauter during March and April 1905, at Kanagawa near Yokohama. Forel's specimens of the workers and females arrived in Hamburg in a living condition with plants (*Prunus*) imported from Japan. As Forel has shown, this species is allied to the two Indian species, *luteipes* Mayr and *jerdoni* Forel. It differs from both of these in having the posterior border of the head less deeply excised.

5. **Ponera japonica** sp. nov.

Worker. Length 2–2.25 mm.

Mandibles with three larger apical, and numerous minute basal teeth. Head excluding the mandibles, fully 1½ times as long as broad, nearly as broad in front as behind, with subparallel sides; occipital border slightly concave. Antennal scapes not reaching the posterior corners of the head by a distance equal to their greatest transverse diameter. All the funicular joints, except the first and last, distinctly broader than long; basal joints very short and narrow, four terminal joints forming a thickened club, which is distinctly longer than the remainder of the funiculus. Last joint about as long as the three preceding subequal joints. Eyes minute, consisting of only a few ommatidia and situated about ⅕ the distance from the anterior to the posterior border of the head. Thorax from above much broader in front than behind, in profile with straight dorsal surface and distinct promesonotal and mesoëpinotal sutures. There is also a distinct suture between the mesonotum and mesopleuræ. Mesonotum about ½ as long as the pronotum; basal surface of epinotum about as long as the declivity, which is distinctly flattened but hardly marginate on its sides. Petiole thick, nearly as long as broad, from above broader behind than the epinotum; in profile as high as the epinotum and gaster, flattened in front and behind and above, laterally compressed below and armed with a small median ventral tooth. Gaster and legs of the usual shape.

Head subopaque, very finely and densely punctate, thorax and abdomen more shining, more sparsely and more finely punctate.

Pubescence and hairs grayish yellow, longest and most conspicuous on the upper surfaces of the head, thorax, and gaster.

Reddish brown; upper surface of body dark brown; mandibles, clypeus, frontal carinæ, antennæ, and legs yellow.

Female. Length 2.7 mm.

Resembling the worker, but the body is darker in color and the petiole is proportionally shorter, with flatter anterior and posterior surfaces. The upper surface of the thorax is almost as coarsely punctate as the head but more sparsely. The basal surface of the epinotum is only about half as long as the declivity.

Described from two deälated females and several workers taken by Mr. Hans Sauter at Yamanaka, Suruga, on the western slope of the Hakone Mountains.

This species is closely related to the palearctic and nearctic *P. coarctata* Latr., but differs in its smaller size, thicker petiolar node, and shorter antennæ. The scapes do not reach so far back on the head, and the funiculus has much shorter basal and more club-shaped terminal joints. The sculpture and pilosity closely resemble those of *coarctata.*

Subfamily MYRMICINÆ.

6. **Myrmecina graminicola nipponica** subsp. nov.

The worker of this subspecies, like that of the typical European form, has well-developed median and lateral clypeal teeth, and the two pairs of teeth on the epinotum are similar, except that the posterior pair are somewhat broader and blunter in the Japanese specimens. The sculpture of the head, thorax and pedicel is much more pronounced than in the European and North American forms. It consists of coarse longitudinal, more or less anastomosing rugæ, especially on the head and thorax. Pilosity and color as in the European type. Length 3 mm.

Two workers collected by Mr. Hans Sauter at Yamanaka, Suruga.

7. **Solenopsis fugax** *Latreille.*

This well-known European species is cited by Ernest André as occurring in Japan. (Bull. Mus. d'Hist. Nat. Paris, 1903, p. 128, ☿)

8. **Pheidole nodus** *F. Smith.*

Pheidole nodus F. SMITH, Trans. Ent. Soc. London, 1874, p. 407, ♃
Pheidole nodus MAYR, Verhandl. zool. bot. Ges. Wien, XXXVI, 1886, p. 363.
Pheidole nodus FOREL, Bull. Soc. Ent. Suisse, X, 7, 1900, p. 268, ♃ ☿

Soldier (Plate XLI, Fig. 8). Length 4-4.5 mm.

Allied to *Ph. striativentris* Mayr of India. Mandibles convex, flattened on the outer surface towards the base, with two apical teeth and a small basal tooth. Head, excluding the mandibles, but little longer than broad, somewhat narrower in front than behind; posterior angles rather acute, posterior border broadly excised, median dorsal surface convex. Eyes one third the distance from the anterior to the posterior corner, convex. Clypeus short, very flat or slightly concave in the middle, with a deep median notch in the anterior border and a distinct median keel. Frontal area carinulate in the middle, concave, fused with the clypeus. Frontal carinæ low, but very long and diverging, extending to within a short distance of the posterior corners of the head and forming shallow scrobes as long as the antennal scapes. Antennæ slender; scape curved at the base, very slightly enlarged towards its tip, which reaches half way between the eye and the posterior corner of the head; funicular joints 1–8 a little longer than broad; three terminal joints subequal, slender, together longer than the remainder of the funiculus. Thorax less than half as broad as the head, hardly broader through the pro- than through the epinotum, constricted in the mesothoracic region; pronotum rounded on the sides but with distinct humeri. There is a well-marked transverse depression across the posterior pronotal surface and also a distinct promesonotal depression. Epinotum with two sharp spines directed upward and outward, twice as far apart as long and longer than broad at their bases. The basal and declivous surfaces of the epinotum form almost a continuous sloping surface between the spines. Petiole barely half as broad as the epinotum, 1½ times as long as broad and distinctly broader in front than behind, with sides slightly concave in the middle; node transverse, in profile high and rather acute, with long concave anterior, and short concave posterior slope. Postpetiole more than three times as broad as the petiole, about 1½ times as long as broad, with very convex and much rounded dorsal surface and the sides produced in the middle as blunt angles. Gaster about twice as broad as the postpetiole, much smaller than the head. Legs rather long and slender.

Mandibles smooth and shining, with coarse, scattered punctures; on the outer surface near the base with coarse longitudinal rugæ. Clypeus shining, longitudinally rugose on the sides. Head subopaque, coarsely, longitudinally and reticulately rugose throughout. Even the antennal scrobes are crossed by rugæ. Between the rugæ the surface is finely punctate. Pronotum and base of epinotum transversely rugose, the latter more delicately, the remaining surface more irregularly; epinotal declivity and petiole smooth and shining; postpetiole finely reticulate; summit of the node with delicate transverse rugæ. Gaster smooth and shining, except the basal fourth or third of the first segment, which is sharply longitudinally rugose. Legs shining, coarsely and sparsely punctate.

Body with coarse, yellow, erect hairs, which are especially long and conspicuous on the head, thorax, pedicel and gaster. There are similar but much more reclinate hairs on the legs, antennæ and mandibles.

Ferruginous brown; head and gaster darker, the latter sometimes paler at the base. Legs, and in some specimens also the thorax and pedicel, yellow. Edges of mandibles and anterior border of clypeus black.

Worker. (Plate XLI, Fig. 9). Length 2.3–2.5 mm.

Mandibles slender, with two prominent apical and several minute basal teeth. Head, excluding the mandibles, but little longer than broad, elliptical, without posterior corners. Eyes prominent and convex, in front of the middle of the head. Clypeus convex, with a median keel and an entire, broadly rounded anterior border. Frontal carinæ rather short, high and far apart.

Frontal area depressed, triangular, not fused with the clypeus. Antennæ very slender, scapes, when turned directly back, extending about $\frac{1}{3}$ their length beyond the head; all the funicular joints longer than broad; three terminal joints subequal, very long and slender. Thorax resembling that of the soldier, but with rounder and more sloping humeri and no transverse depression on the posterior portion of the pronotum. Mesonotal depression deep and rounded at the bottom. Basal epinotal surface convex, especially in front; spines short, hardly longer than broad at their bases. Petiole like that of the soldier but with a more conical node; postpetiole three times as broad as the petiole, slightly longer than broad, convex above, pyriform, broader behind than in front. Gaster about the size of the head, with a rather straight anterior border. Legs slender.

Smooth and shining; cheeks and front with a few longitudinal rugæ. Meso- and metapleuræ reticulate-rugose, subopaque.

Hairs white or pale yellow, erect or suberect, sparse on the body, more abundant on the legs and antennæ.

Brownish yellow, head and gaster somewhat darker; teeth of mandibles black.

Female (deälated). Length 5.5–6 mm.

Head resembling that of the soldier. Thorax somewhat narrower than the head, longer than broad, with very flat mesonotum and scutellum. Epinotal spines robust, blunt, longer than broad at their bases, more than twice as far apart as long, directed backward and outward and very slightly upward. Petiole from above similar to that of the soldier, broader in front than behind, with sharp anterior corners and straight sides; node much compressed antero-posteriorly so that its summit is a sharp blade, deeply notched in the middle. In profile the anterior slope is long and straight, the posterior short and abrupt. Below, the petiole is produced in the middle into a compressed keel, gradually increasing in height posteriorly. Postpetiole about $2\frac{1}{2}$ times as broad as the petiole, straight and broadest in front, semicircular behind, so that its sides appear to be produced anteriorly as blunt or somewhat truncated projections. In profile the node is high and evenly rounded. Gaster broad and flat.

The sculpture of the head is like that of the soldier. Pro- and mesonotum, paraptera, scutellum and sides of thorax with regular longitudinal rugæ; base of scutellum smooth and shining; petiole and epinotal declivity shining and obscurely punctate-rugulose. Postpetiole subopaque, node transversely rugose. Gaster shining except the basal half of the first segment, which is opaque and covered with regular longitudinal striæ.

Pilosity like that of the soldier.

Deep reddish brown; legs, antennal funiculi and epinotal declivity more yellowish.

Described from several females, soldiers and workers taken by Mr. Hans Sauter from colonies nesting under stones near Okayama, Bizen. The types from Hiogo were very inadequately described by Smith. According to Forel, who received soldiers and workers from Osaka, this species is very closely related to the Indian *Ph. rhombinoda* Mayr, "but the head of the soldier is more elongated, the antennal scrobe shallower, the thorax smoother, the epinotal spines more slender and pointed. In the worker the epinotum is shorter."

9. **Pheidole fervida** *F. Smith.*

Pheidole fervida F. Smith, Trans. Ent. Soc. London, 1874, p. 406, 407, ♃ ☿

Pheidole fervida Mayr, Verhandl. zool. bot. Ges. Wien, XXXVI, 1886, p. 363.

Pheidole fervida Forel, Bull. Soc. Ent. Suisse, X, 7, 1900, pp. 268 and 285, ♃ ☿

A single soldier and six workers taken by Mr. Hans Sauter at Yamanaka, Suruga, and four workers taken by him at Kanagawa, near Yokohama, seem to belong to this species, which was very inadequately described by Smith. As Forel says, it closely resembles *Ph. megacephala*, but the head of the soldier has a faint scrobe for the antennal scape, which is shorter than that of *megacephala*, and the rugæ extend further back. More material of this form is necessary before the status of *Ph. fervida* can be accurately determined. According to Forel living specimens have been imported into Hamburg in bamboo plants.

10. **Monomorium floricola** *Jerdon.*

Monomorium intrudens F. Smith, Trans. Ent. Soc. London, 1874, p. 406. ☿

Monomorium intrudens Mayr, Verhandl. zool. bot. Ges. Wien, XXXVI, 1886, p. 363.

F. Smith's *M. intrudens* may be regarded as a synonym of the well-known tropicopolitan *M. floricola* on the authority of Prof. Emery (*in litteris*) who remarks that Smith's description "agrees in every point" with specimens of the latter species.

11. **Monomorium nipponense** sp. nov.

Worker. Length 1.3 mm.

Head longer than broad, oblong, with parallel sides and straight posterior border. Eyes small, distinctly in front of the middle of the head. Clypeus and frontal area convex, the former with broadly rounded anterior margin. Antennæ 12-jointed, scapes not reaching to the posterior corners of the head; first funicular joint about twice as long as broad, joints 2–8 very small, much broader than long, joints 9 and 10 subequal, as long as broad, together decidedly shorter than the terminal joint. Prothorax half as broad as the head, pro- and mesonotum evenly rounded, hemispherical, separated by a sharp but not very deep constriction from the epinotum which is also evenly rounded and sloping, without any angle between the base and declivity. Petiole barely twice as long as broad, pedunculate in front, broader behind; node in profile high but evenly rounded. Postpetiole no broader than the petiole; globular, but little broader than long; in profile lower than the petiole. Gaster flattened, somewhat larger than the head.

Body smooth and shining throughout.

Hairs yellow, very sparse, erect on the upper surface of the body, delicate and appressed on the antennæ and legs.

Pale yellow; gaster black with a small yellow spot, the size of the postpetiole, at its extreme base.

Described from seven workers taken by Mr. Hans Sauter at Kanagawa near Yokohama. *M. nipponense* is allied to *M. destructor* but differs in its smaller size, much more compact antennæ, shorter and stouter pedicel, proportionally smaller head, etc.

12. **Monomorium triviale** sp. nov.

Worker. Length 1.3–1.5 mm.

Head nearly 1½ times as long as broad, rectangular; occipital border feebly excised. Clypeus broadly rounded in front Eyes in front of the middle of the head. Antennæ 12-jointed; tip of scape reaching about halfway between the eye and the posterior corner of the head; joints 2-8 of the funiculus narrower than the elongated first joint, much broader than long; two basal joints of club subequal, much narrower than the terminal joint and together hardly half as long. Thorax rather slender, anteriorly about half as broad as the head; mesoëpinotal constriction distinct but shallow; epinotum small, rounded, without any angle between the basal and declivous surfaces. Petiole hardly half as broad as the epinotum, nearly twice as long as broad, distinctly pedunculate in front; node in profile high with longer concave anterior and shorter convex posterior slopes. Postpetiole hardly broader than the petiole, a little broader than long, in profile much smaller and lower than the petiole, evenly rounded above. Gaster somewhat smaller than the head. Legs slender.

Surface of body smooth and shining throughout.

Hairs yellow, sparse and erect on the head, thorax and abdomen; shorter and more appressed on the appendages.

Pale yellow throughout; mandibular teeth brownish.

Described from seven workers taken by Mr. Hans Sauter at Kanagawa on a "heath on the margin of a pond."

At first sight this species appears to agree with the Indian *M. atomus* Forel, with which I at first identified it, but Prof. Emery, who has compared some of my specimens with one of Forel's types, writes me that the Japanese insect is smaller, has a narrower head, and shorter antennæ, the scape not reaching so far back and the funiculus being more slender than in *atomus*.

13. **Cremastogaster sordidula** *Nylander* var. **osakensis** *Forel.*

Forel, Bull. Soc. Ent. Suisse, X, 7, 1900, p. 269, ☿

Several workers collected by Mr. Hans Sauter at Kanagawa agree with Forel's description of this yellow form of the palearctic *sordidula.* The types are from Osaka, as the name indicates.

14. **Cremastogaster laboriosa** *F. Smith.*

F. Smith, Trans. Ent. Soc. London, 1874, p. 407, ☿

The types of this inadequately described species are from Hiogo.

15. **Cremastogaster laboriosa** *F. Smith* var. **matsumurai** *Forel.*

(Plate XLI, Fig. 1.)

Forel, Ann. Soc. Ent. Belg., XLV, 1901, p. 372, ☿

Described by Forel from Sapporo in the island of Yezo. It seemed certain to him that his specimens, coming from a locality so far from Hiogo, must represent a distinct variety. I find however that a number of workers collected by Hans Sauter at Kanagawa and Yamanaka agree perfectly with Forel's description of the variety *matsumurai* though these localities are in southern Japan near Hiogo. It is probable, therefore, that the characters which Forel regards as varietal are merely omitted in Smith's brief and slipshod description.

A deälated female from Yamanaka, Suruga, is 6 mm. long, dark brown, with yellowish mandibles, legs and antennæ. Body smooth and shining, very sparsely and finely punctate; anterior half of head subopaque, finely and longitudinally striated. Head broader than long. Epinotal spines very short, stout and blunt. Petiole and postpetiole similar to those of the worker, the latter segment with a faint median depression.

According to a note accompanying the specimens, this ant lives "in small colonies under the bark of pines and Cryptomerias."

16. **Vollenhovia emeryi** sp. nov.

Worker. (Plate XLI, Figs. 10 and 11.) Length 2–2.3 mm.

Head longer than broad, rectangular, with straight, subparallel sides and broadly concave posterior border. Eyes rather large, in front of the middle of the head. Mandibles with 5 graduated teeth. Clypeus short, with transverse anterior border, not produced in the middle, and with two longitudinal, rather thick ridges, diverging anteriorly and separated by a depression. Antennæ 12-jointed; scape short, swollen distally, its tip reaching half the distance between the eye and the posterior corner of the head. Funiculus exceeding the length of the scape by the length of the terminal joint; the three terminal joints forming a distinct club; first funicular joint as long as joints 2–5 together; joints 2–8 broader than long; 9th joint half as long as the 10th, 10th less than half as long as the terminal joint. Prothorax broad in front but distinctly narrower than the head, sides of meso- and epinotum compressed. Dorsal surface of thorax flattened, with a very faint mesoëpinotal depression. Epinotum as high as the mesonotum, with long slanting basal, and much shorter, concave declivous surface and bearing two small teeth widely separated at their bases. Petiole from above 1½ times as long as broad, subrectangular, with sides slightly convex, in profile triangular, with a pointed node, the anterior and posterior declivities of which are subequal, the former slightly concave, the latter nearly straight. The petiole is compressed below and carinate and terminating in a large blunt tooth anteriorly. Postpetiole from above about as long as broad, slightly broader behind than in front, in profile hemispherical above, flattened and toothless below. Gaster long and narrow without basal angles, somewhat flattened dorsoventrally. Legs rather short, femora and tibiæ distinctly thickened.

Mandibles, clypeus, and frontal area shining, the first with scattered punctures. Head subopaque, covered with longitudinal rows of large umbilicate, piligerous punctures or foveolæ, except in the middle where there is a narrow, smooth, shining streak running from the frontal area nearly to the occiput. Thorax and petiole subopaque, pronotum longitudinally rugose and umbilicately punctate; epinotum densely punctate or granular; upper surface of petiole and postpetiole similar to that of the pronotum, the middle of the latter smooth and shining. Gaster and legs shining, with scattered, coarse, piligerous punctures.

Whole body, including legs and antennæ, covered with pale yellow, suberect or reclinate hairs.

Reddish brown; a large elongate spot on the front; the epinotum, upper surface of postpetiole, sides and posterior dorsal surface of gaster blackened. Mandibles, clypeus, antennæ and legs brownish yellow.

Female. Length 3 mm.

Resembling the worker. Mesonotum and scutellum each with a large elongate shining area in the middle, the former also with a shining spot over each parapsis. Postpetiole less shining above in the middle than in the worker. Gaster with large and more numerous piligerous punctures. Wings gray, densely pilose, with brown stigma and veins.

Described from several workers and two females taken by Mr. Hans Sauter at Negishi near Yokohama (Feb. 25, 1905) and numerous workers taken at Yamanaka and Kanagawa. The specimens taken in Kanagawa are marked as taken on a heath.

This species of *Vollenhovia* differs from its Indian and Malayan congeners in its peculiar sculpture and in having a distinctly armed epinotum. In size and general appearance it approaches *V. subtilis* Emery from Papua, but this species has a shining, unarmed epinotum and smoother petiole and postpetiole.

17. **Stenamma owstoni** sp. nov.

Worker. Length 3.25-3.5 mm.

Head, excluding the mandibles longer than broad, sides rather straight, subparallel, posterior corners rounded. Clypeus short, depressed, its anterior border emarginate in the middle, behind fused with the deeply impressed frontal area. Frontal carinæ short, but prominent. Eyes moderate, with 7-8 ommatidia in the longitudinal diameter. Antennal scapes reaching to the posterior corners of the head. Funiculus with a 4-jointed club, first joint twice as long as broad, joints 2-4 nearly as long as broad, 5-7 as long as broad, joints 8-10 slightly longer than broad, terminal joint as long as the two preceding joints together. Thorax with the pro- and mesonotum rather convex, higher than the epinotum and separated from it by a pronounced constriction. Basal epinotal surface in profile straight, longer than the concave declivity; spines small, a little longer than their distance apart at the base, directed upward and backward. Petiole narrow, 3½ times as long as broad, seen from above gradually widening posteriorly, in profile unarmed below, with a very low, rounded node above. Postpetiole 1½ times as broad as the petiole, nearly twice as long as broad, regularly elliptical from above, in profile with a low, regularly rounded node and a slightly concave ventral surface.

Mandibles subopaque, rather coarsely striatopunctate, clypeus and frontal area smooth and shining, head and thorax subopaque, the former rather finely, the latter more coarsely, longitudinally reticulate-rugose. Epinotal declivity smooth and shining. Petiole punctate-rugulose, opaque, except the upper surface of the node which is smooth and somewhat shining. Postpetiole and gaster smooth and shining, the former more opaque and rugose on the sides and below. Legs and antennæ subopaque.

Body and appendages covered with abundant, suberect whitish hairs, which are longest on the gaster.

Reddish brown; head and first gastric segment blackish. Mandibles, clypeus, antennæ and legs, posterior border of first gastric segment and all the remaining segments yellowish.

Described from three specimens collected by Mr. Hans Sauter, at Yamanaka, Suruga, at an altitude of 2000 ft. "in rotten wood." The three specimens appear to have been taken from as many different colonies.

This species is closely related to the European *S. westwoodi* Westw. and the North American *brevicorne* Mayr. From the former it differs in having much larger eyes, longer joints in the base of the antennal funiculus, a lower, less angular and smoother petiolar node, a longer postpetiole and longer and more abundant hairs. From the North American species it differs in these same characters, except that the eyes are of about the same size and the sculpture distinctly finer.

18. **Stenamma (Aphænogaster) famelicum** *F. Smith.*

Ischnomyrmex famelicus F. Smith, Trans. Ent. Soc. London, 1874, p. 405, ☿
Aphænogaster famelica Mayr, Verhandl. zool. bot. Ges. Wien, Jahrg. 1878, pp. 669, 670, ☿
Aphænogaster famelica Forel, Bull. Soc. Ent. Suisse, X, 7, 1900, pp. 267, 268, ☿
Aphænogaster famelica Forel, Mitth. naturhist. Mus. Hamb., XVIII, 1901, p. 61.

Of this species, originally described from Hiogo, I find no specimens among my material. Forel records it from Hozuyama, Majori Tamba. The species has been redescribed by Mayr who calls attention to its close resemblance to the nearctic *S.* (*A.*) *fulvum* Roger and the palearctic *striola* Roger.

19. **Stenamma (Messor) aciculatum** *F. Smith.*

Aphænogaster aciculata F. Smith, Trans. Ent. Soc. London, 1874, p. 405, ☿ ♀
Aphænogaster aciculata Mayr, Verhandl. zool. bot. Ges. Wien, 1878, p. 670.

According to Mayr, who examined one of Smith's type specimens, this species is probably the same as *Aphænogaster obsidiana.* See the following variety.

20. **Stenamma (Messor) aciculatum** *F. Smith* var. **brunneicorne** *Forel.*

(Plate XLI, Fig. 14.)

Forel, Mittheil. naturhist. Mus. Hamburg, XVIII, 1901, pp. 60, 61, ☿

Forel described this form, which he somewhat doubtfully referred to Smith's *A. aciculata*, from Hozuyama, Kuwadagori Tamba. Among my material I find three workers taken from as many colonies at Takakiyama near Kanagawa by Mr. Hans Sauter. They agree very well with Forel's description, except that all the funicular joints are longer than broad, a character which brings them closer to the well-known *S.* (*M.*) *barbarum.* Forel notes the resemblance of the Japanese form to *S. barbarum* var. *rugosum.* It is not improbable that more material may lead us to change the name of the form to *S.* (*M.*) *barbarum* var. *aciculatum.*

21. **Myrmica rubra lævinodis** *Nylander.*

Forel (Ann. Soc. Ent. Belg., XLV, 1901, p. 371) mentions a female of this subspecies from Sapporo, Yezo, as being "absolument typique."

22. **Myrmica rubra lobicornis** *Nylander* var. **jessensis** *Forel.*

Forel, Ann. Soc. Ent. Belg., XLV, 1901, p. 371, ☿

According to Forel, the worker of this variety has "the antennal lobe a little shorter than the type, the epinotal spines shorter and the petiolar node more rounded, almost as in the var. *schencki* Emery, so that I cannot decide, notwithstanding the characters of the male, to assign it to *scabrinodis*. It has the deep color of the *lobicornis* of the northern Alps. Its antennal lobe is much more developed than in the variety *fracticornis* Emery of the United States."

It is a significant fact that none of the forms of the circumpolar *M. rubra* are represented in Mr. Sauter's collections from southern Japan.

23. **Leptothorax congruus** *F. Smith.*

F. Smith, Trans. Ent. Soc. London, 1874, p. 406, ☿

Worker. Length 2–2.5 mm.

Head, excluding the mandibles, longer than broad, with slightly convex sides and straight posterior margin. Eyes a little in front of the middle. Clypeus convex with nearly straight anterior border, without a median depression or emargination. Antennæ 12-jointed; tip of scape not reaching the posterior corner of the head by a distance equal to its transverse diameter; first funicular joint 3 times as long as broad, joints 2–8 distinctly broader than long, subequal, joints 9–11 forming a club, the terminal joint of which is as long as the two preceding subequal joints together. Thorax in front nearly two-thirds as broad as the head, with rounded and sloping humeri, in profile straight above, with barely indicated mesoëpinotal constriction. Epinotal spines short, acute, about a third the length of the straight basal surface, a little further apart at their bases than long, directed outward, backward and a little upward. Petiole from above nearly half as broad as the epinotum, more than twice as long as broad, gradually widening anteriorly; in profile with a well developed node, whose anterior slope is slightly concave and hardly longer than the convex posterior slope. Postpetiole from above $1\frac{1}{3}$ times as broad as the petiole, a little broader than long, rectangular, in profile convex dorsally, especially in front. Gaster flattened dorsoventrally, with straight anterior border. Legs rather robust, femora incrassated in the middle.

Mandibles coarsely striato-punctate. Clypeus longitudinally rugose, smoother and more shining in the middle. Head, thorax and pedicel subopaque; head rather finely and longitudinally rugose-punctate; thorax irregularly and coarsely rugose on the dorsal surface, pleuræ and epinotum more finely and reticulately rugose, as are also the petiole and postpetiole. Gaster smooth and shining.

Hairs white, obtuse, erect and rather short on the trunk; delicate, tapering and appressed on the appendages.

Dark brown; head and gaster nearly black; mandibles, legs and antennæ yellowish brown; antennal scapes and clubs, middle portions of femora and tibiæ darker and in some specimens almost black

Female (deälated). Length 3-3.75 mm.

Resembling the worker. The thorax is robust, flattened and rather shining above; the mesonotum and scutellum regularly longitudinally rugose, the latter smoother behind. Epinotum and pedicel opaque, very coarsely rugose; epinotal spines short and blunt. Color like that of the worker except that the thorax is almost black.

Described from three females and numerous workers collected by Mr. Hans Sauter at Takakiyama, Kanagawa and Yamanaka, Suruga. F. Smith's types of this species were from Hiogo.

24. **Leptothorax congruus** *F. Smith* var. **spinosior** *Forel.*

FOREL, Ann. Soc. Ent. Belg., XLV, 1901, p. 371, ☿

According to Forel this variety, of which he obtained specimens from Sapporo, Yezo, has the epinotal spines "long and curved inward, as long as the basal epinotal surface and longer than their interval, reddish at their tips." Four workers and a deälated female collected by Hans Sauter at Yamanaka at an altitude of 900 ft. agree with Forel's description. They are all smaller and much paler in coloration than the corresponding phases of the typical *congruus* above described The epinotal spines diverge but are bent downwards at their tips. Forel calls attention to the similarity of this variety to the European *L. tuberum* Fabr.

25. **Tetramorium cæspitum** *Linn.*

Forel (Bull. Soc. Ent. Suisse, X, 7, 1900, p. 268) mentions two varieties of this common European ant from Osaka, "one paler and smaller, the other black and larger." Among my specimens two workers collected by Professor J. F. Abbott near the Marine Biological Laboratory at Misaki belong to the large, dark form. Six others collected by Mr. Hans Sauter at Kanagawa are decidedly smaller but of the same dark color.

26. **Pristomyrmex japonicus** *Forel.*

(PLATE XLI, Fig. 7.)

FOREL, Bull. Soc. Ent. Suisse, X, 7, 1900, pp. 268, 269, ☿
FOREL, Ann. Soc. Ent. Belg., XLV, 1901, p. 371.

The types of this species are from Osaka, but Forel mentions its occurrence also at Sapporo, Yezo. Twelve workers collected by Professor J. F. Abbott near the Marine Biological Laboratory at

Misaki agree well with Forel's description. The long epinotal spines are distinctly divergent and the funicular joints 2–7 are broader than long. These characters serve to distinguish the species from the closely allied *P. pungens* Mayr of Ceylon and Malacca.

27. **Strumigenys godeffroyi** *Mayr* var. **lewisi** *Cameron.*

Strumigenys lewisi CAMERON, Proceed. Manchester Lit. Phil. Soc., XXV, 1886, pp. 229, 230, ☿ ♀

Strumigenys godeffroyi MAYR var. *lewisi* MAYR, Verhandl. zool. bot. Ges. Wien, XXXVII, 1887, p. 569, *nota*, ☿ ♀

Strumigenys godeffroyi MAYR var. *lewisi* MAYR, Termeszétrajzi Füzetek, XX, 1897, pp. 431, 432 (pseudogyne?).

Strumigenys godeffroyi var. *lewisi* FOREL, Journ. Bombay Nat. Hist. Soc., XIV, 1902, p. 707.

Strumigenys lewisi BINGHAM, Fauna Brit. India, Hymenopt, II, 1903, p. 149, ☿

This ant (Plate XLI, Fig. 12), which is known to occur also in Burma and Ceylon, was originally described by Cameron from Nagasaki. Later Mayr showed that it is hardly more than a variety of the Samoan *S. godeffroyi*, from which it differs in having curved instead of straight mandibular blades. I have before me a number of workers and a few deälated females collected by Mr. Hans Sauter in the following localities: Negishi, Kanagawa and Yamanaka (1700 ft.). According to a note accompanying the specimens they were taken "in siftings in pine woods."

Subfamily DOLICHODERINÆ.

28. **Iridomyrmex itoi** *Forel.*

FOREL, Bull. Soc. Ent. Suisse, X, 7, 1900, p. 269, ☿

I have not seen the typical form of this species, which is allied to the Australian and Indian *I. glaber* Mayr. It differs mainly in the structure of the epinotum, the basal surface of which "is much longer than in *glaber*, nearly twice as long as broad, with a transverse impression which makes it appear a little concave in profile. The declivous surface is more inclined than in *glaber;* it is not longer than the basal surface nor overhung by its posterior edge." The types are from Osaka.

29. **Iridomyrmex itoi abbotti** var. nov.

Worker. (Plate XLI, Fig. 3.) Length 1.75–2.25 mm.

Head, excluding the mandibles, a little longer than broad, with straight posterior and rather convex lateral borders. Clypeus rather convex in the middle behind, flattened laterally, with a pronounced median excision in its anterior border. Eyes a little in front of the middle of the head. Frontal area distinct, triangular; frontal groove tenuous but distinct, not interrupted in the middle. Antennal scapes reaching to the posterior corners of the head. Thorax in profile with perfectly straight dorsal surface, interrupted by a deep but narrow mesoëpinotal depression. Basal surface of epinotum flat, decidedly shorter than the declivity which is concave and separated from the base by a sharp angle. Petiole vertical, as high and as broad as the epinotum, much compressed anteroposteriorly, somewhat thinner below than above, slightly flatter behind than in front; edge sharp, broadly and evenly rounded when seen from behind.

Mandibles shining, very finely striated, and coarsely and sparsely punctate. Whole body shining, distinctly reticulate, except the gaster which is very glabrous.

Hairs white, erect and much scattered on the vertex, gaster and mandibles. Legs and antennæ with sparse white pubescence.

Black; mandibles dark brown, legs dark brown or black, with yellow knees and tarsi; antennæ yellow with the tips of the scapes and the funiculi brown or blackish. Gaster with metallic violet reflections. In some specimens, possibly immature, the head and thorax are dark brown.

Described from numerous specimens collected by Professor J. F. Abbott at Itajima Aki.

I was at first inclined to regard this variety as a distinct species but Prof. Emery informs me that *abbotti* differs from the typical *itoi* only in the metallic violet color of the gaster.

30. **Technomyrmex gibbosus** sp. nov.

Worker. (Plate XLI, Fig. 4.) Length 2–2.5 mm.

Mandibles rather large, with straight multidenticulate blades. Head longer than broad; posterior border straight; sides rather convex. Clypeus convex, with a deep notch in the middle of its anterior border. Eyes large, flattened, in front of the middle of the head. Antennal scapes reaching a little beyond the posterior corners of the head; second funicular joint twice as long as broad, remaining joints, except the terminal, hardly longer than broad. Clypeal and antennal foveæ confluent. Frontal area obsolescent, frontal groove lacking. Thorax in front $\frac{2}{3}$ as broad as the head; pronotum broader than long; mesonotum as long as broad, mesoëpinotal constriction deep. Epinotum with very convex basal surface, which forms a right angle with the posterior slope of the mesonotum, and passes over into the declivity through a rounded angle; declivity twice as long as the base, flattened above and somewhat concave below. Petiole almost without a trace of a node, elliptical from above, about twice as long as broad. Gaster rather narrow, pointed behind, with a slit-shaped anus.

Mandibles lustrous or shining, faintly and sparsely punctate. Head and thorax opaque, finely and densely punctate or reticulate, the declivity of the epinotum in some specimens more shining. Gaster smooth and shining. Legs and antennæ subopaque like the head and thorax.

Hairs yellowish, inconspicuous, absent except on the mandibles. Pubescence whitish, very short and sparse, most distinct on the gaster and appendages.

Dull yellowish brown, gaster somewhat darker, mandibles, antennæ and legs yellow; femora and scapes brownish.

Described from numerous specimens collected by Mr. Hans Sauter at Yamanaka, Suruga ("1100 ft., sifted in deciduous forests"); Kanagawa and Takakiyama.

This species which at first sight resembles a pale *Tapinoma erraticum* or *T. sessile* is closely related to *Technomyrmex albipes* It differs in its lighter color and the more gibbous structure of the epinotum as I find by comparison with specimens of that species from India and Madagascar. In these same characters and its smaller size *T. gibbosus* differs from *T. mayri* Forel of Madagascar. It differs from *T. grandis* Emery of Sumatra in lacking the erect hairs on the legs and antennal scapes and from *T. strenuus* Mayr of Borneo and Singapore in lacking the long hairs on the gaster, though it seems to resemble this species in the shape of the epinotum. Finally from *T. modigliani* Emery of Sumatra, the Japanese species may be readily distinguished by its much narrower head, feebler clypeal notch, shorter funicular joints, etc.

Subfamily CAMPONOTINÆ.

31. **Prenolepis flavipes** (*F. Smith*) *Mayr.*

Tapinoma flavipes F. SMITH, Trans. Ent. Soc. London, 1874, p. 404, ☿ ♀

Prenolepis flavipes MAYR, Verhandl. zool. bot. Ges. Wien, XXXVI, 1886, p. 363.

Prenolepis flavipes FOREL, Ann. Soc. Ent. Belg., XLV, 1901, p. 371.

Prenolepis flavipes FOREL, Bull. Soc. Ent. Suisse, X, 7, 1900, pp. 269, 270, ☿ ♀ ♂

Worker. Length 1.5–1.7 mm.

Mandibles 6-toothed. Head distinctly longer than broad, with rounded posterior angles. Clypeus convex, barely carinate, its anterior border deeply and rather broadly excised in the middle. Antennal scapes projecting for fully $\frac{2}{5}$ of their length beyond the posterior corners of the head; funicular joints all longer than broad. Pronotum broader than long; mesoëpinotal depression pronounced, flat at the bottom, longer than the transverse diameter between the two stigmata. Epinotum with a short convex basal surface, passing insensibly into the longer and flatter declivity. Petiole low, in profile with convex ventral border and node inclined forward, the latter with both its anterior and posterior slopes slightly convex; edge viewed from behind straight.

Whole body smooth and shining; mandibles finely striated.

Hairs yellow; long, erect and tapering on the body; shorter and suberect on the legs and antennal scapes. Pubescence grayish, distinct on the head, antennæ and legs, but almost imperceptible on the remainder of the body.

Body and appendages yellow; clypeus, upper surface of head and gaster dark brown. Mandibular teeth black.

Female. Length 4.5–5 mm.

Dark brown; mandibles, mouthparts, antennæ and legs yellow; mandibular teeth black. Wings uniformly brownish, with brown veins. Surface of body finely shagreened but shining, covered with long grayish pubescence, as are also the legs and antennæ. Hairs sparse, yellowish, erect, like those of the worker.

Male. Length 1.5–1.6 mm.

Resembling the worker in size and coloration, except that the thorax is dark brown like the head and gaster. Mandibles, legs, antennæ and genital valves slightly infuscated. Surface of the head, thorax and gaster very glabrous. Wings like those of the female. For the conformation of the genital valves see Fig. 1, *a–c*. Erect hairs on the body similar to those of the worker but shorter, absent on the antennal scapes and very sparse on the legs. Pubescence almost imperceptible except on the legs.

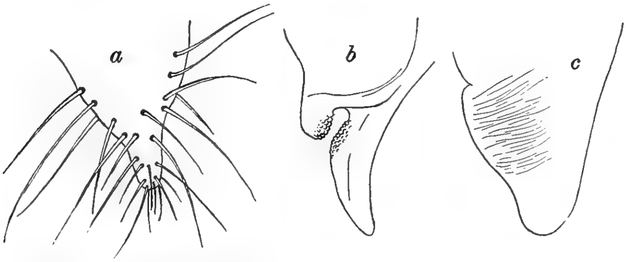


Fig. 1. *Prenolepis flavipes* (F. Smith), Mayr. Male. *a*, outer; *b*, median; and *c*, inner genital valve.

The types of this species are from Hiogo. Forel obtained workers from Osaka, and all three phases imported from Japan into Hamburg with plants. I have before me a large number of specimens of all three phases collected by Professor J. F. Abbott near the Marine Biological Laboratory at Misaki, and by Mr. Hans Sauter in the following localities: Kanagawa ("under bark at edge of pond"), Yamanaka ("sifted in deciduous and pine woods"), Negishi, Takakiyama and Okayama. There are several males from Okayama taken May 21, '05 and winged females from Kanagawa taken April 8, '05.

32. **Lasius niger** *Linn.*

F. Smith, Trans. Ent. Soc. London, 1874, p. 403.
Forel, Bull. Soc. Ent. Suisse, X, 7, 1900, p. 269, ☿
Forel, Mittheil. naturhist. Mus. Hamburg, XVIII, 1901, p. 66.

Numerous workers and a few deälated females of this well-known ant were collected by Professor J. F. Abbott near the Marine Biological Laboratory at Misaki, and by Mr. Hans Sauter in the following localities: Yamanaka, Suruga (1300, 1700 and 2000 ft.; "in rotten wood and under oak bark"), Kanagawa ("pine woods, on heaths, and along the edges of brooks") and Takakiyama. These specimens all closely resemble the typical European *niger*, in size, coloration and the hairiness of the legs and antennæ. Forel had specimens from Yezo and Osaka.

33. **Lasius niger** *Linn.* var. **alienus** *Förster.*

Ern. André, Bull. Mus. d' Hist. Nat. Paris, 1903, p. 128, ☿ ♀

A single worker of this variety was found among the material collected by Mr. Hans Sauter at Kanagawa.

34. **Lasius niger brunneus** *Latreille.*

Lasius brunneus Forel, Mitth. naturhist. Mus. Hamburg, XVIII, 1901, p. 66.

Recorded by Forel from Yokohama.

35. **Lasius umbratus** *Nylander.*

Forel, Bull. Soc. Ent. Suisse, X, 7, 1900, p. 269 ☿

Forel, Mittheil. naturhist. Mus. Hamburg, XVIII, 1901, p. 66.

A single winged female taken during July, 1901, by Mr. Hans Sauter at Okayama. The species is also recorded from Osaka by Forel.

36. **Lasius flavus myops** *Forel.*

A single worker taken by Mr. Hans Sauter at Kanagawa agrees very closely with typical specimens of this subspecies from Terni

37. **Lasius fuliginosus** *Latreille.*

F. Smith, Trans. Ent. Soc. London, 1874, p. 403.

A number of workers and males collected by Mr. Hans Sauter at Kanagawa (July 2, '05) "under the bark of an oak tree" are indistinguishable from European specimens.

38. **Formica sanguinea** *Latreille.*

Ern. André, Bull. Mus. d' Hist. Nat. Paris, 1903, p. 128, ♀

Possibly the female of the following variety, which was described from worker specimens only.

39. **Formica sanguinea** *Latreille* var. **fusciceps** *Emery.*

Emery, Zool. Jahrb., Abth. f. Syst., VIII, 1894, p. 335, *nota*, ☿

Emery's description of this variety, based on three workers from Yokohama, shows it to be closely related to the North American *F. sanguinea aserva* Forel, which is also characterized by the dark color of the head.

40. **Formica rufa pratensis** *DeGeer.*

Formica pratensis Forel, Ann. Mus. Zool. Acad. Impér. Sc. St. Pétersb. VIII, 1903, p. 18, ♀

Forel records a female of this palearctic subspecies of *F. rufa* L. from the island of Sakhalin. It will probably be found also in the northern portion of Japan or at high altitudes.

41. **Formica rufa truncicola** *Nylander.*

Formica truncicola Forel, Ann. Mus. Zool. Acad. Impér. Sc. St. Pétersb., VIII, 1903, p. 18, ♀

Formica rufa r. *truncicola* Ern. André, Bull. Mus. d' Hist. Nat. Paris, 1903, p. 128, ♀

Forel has also recorded a female of this subspecies from the Island of Sakhalin. Ern. André mentions a specimen of the same sex from Japan.

42. **Formica rufa truncicola** *Nylander* var. **yessensis** *Forel.*

Forel, Mittheil. naturhist. Mus. Hamburg, XVIII, 1901, p. 66, ☿

This variety, according to Forel, "is distinguished from the typical *truncicola* by its sparser erect hairs, which are very sparse on the antennal scapes and completely lacking on the extensor surface of the tibiæ; only on their lower surfaces are there any of the oblique, stouter hairs. The basal surface of the epinotum is also somewhat shorter and more convex." The types of this apparently northern form were collected in Serachi, province Ishikari, Yezo.

43. **Formica fusca** *Linn.* var. **nipponensis** *Forel.*

Forel, Bull. Soc. Ent. Suisse, X, 7, 1900, p. 270, ☿

Forel, Mitth. naturhist. Mus. Hamburg, XVIII, 1901, p. 66, ♀

Ern. André, Bull. Mus. d' Hist. Natur. Paris, 1903, p. 128.

Numerous workers collected by Professor J. F. Abbott near the Marine Biological Laboratory at Misaki and by Mr. Hans Sauter at Kanagawa (1700 ft.; "nest in ground on border of pond") and Takakiyama. Forel's specimens were from the island of Yezo and from Tokio.

The head and thorax of this variety resemble in their lustre the corresponding parts of the European *fusca* and the North American var. *subsericea*, but, as Forel has remarked, the gaster is much more opaque than in either of these forms. The legs and antennæ are redder than in the typical *subsericea*.

44. Camponotus herculeanus japonicus *Mayr.*

Camponotus japonicus MAYR, Verhandl. zool. bot. Ges. Wien, XVI, 1866, p. 885, ☿

Camponotus japonicus F. SMITH, Trans. Ent. Soc. London, 1874, p. 403, ☿

Camponotus herculeanus r. *pennsylvanicus* var. *japonicus* FOREL, Bull. Soc. Vaud. Sc. Nat., XVI, 1879, p. 56, ☿ ♀ ♂

Camponotus pennsylvanicus var. *japonicus* EMERY, Ann. Soc. Ent. France, 1893, p. 268.

Camponotus japonicus ERN. ANDRÉ, Bull. Mus. d' Hist. Nat. Paris, 1903, p. 128, ☿

Camponotus pennsylvanicus var. *japonicus* FOREL, Ann. Mus. Zool. Acad. Impér. Sc. St. Pétersb., VIII, 1903, p. 380, ☿ ♂

Camponotus japonicus BINGHAM, Fauna Brit. Ind., Hymenopt., II, 1903, p. 370, 371, fig. 117, ☿

This ant is represented in my collection by a number of workers, soldiers and females (one winged) collected by Mr. Hans Sauter at Kanagawa, Takakiyama and Bukenji near Yokohama; several soldiers and workers collected by Professor J. F. Abbott near the Marine Biological Laboratory at Misaki; one deälated female, two soldiers and two mediæ marked "Japan" (Coll. Am. Mus. Nat. Hist.) and a soldier and worker from Chemulpo, Corea (Coll. Phila. Acad. Sci.).

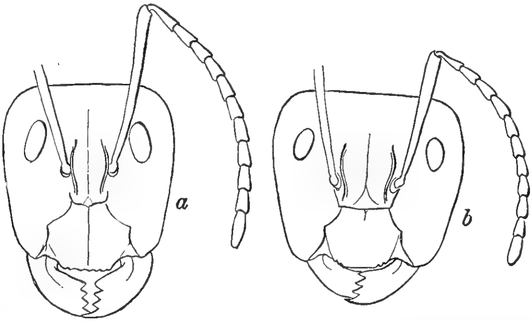


Fig. 2. *a*, Head of worker major of *Camponotus herculeanus japonicus* Mayr; *b*, head of worker major of *C. h. pennsylvanicus* De Geer.

Comparison of these specimens with a long series of our North American *C. herculeanus pennsylvanicus* convinces me that the Japanese form should rank as an independent subspecies. Not only is the clypeus of the soldier longer and more projecting, and the anterior border of the head red, as Forel has pointed out, but the head is narrower and has more flattened sides than in the American form (see Fig. 2*a* and *b*). The types of *japonicus* are in the Leyden Museum.

Forel has seen specimens from Osaka and also from southern Ussuri, Sidemi, Western China. Bingham has recorded it from the Karen and Shan Hills, Burma. Emery has noted its occurrence in the Philippines (Mindanao). He has also described two very similar Asiatic varieties of *herculeanus*, namely *punctatissimus* from Burma (Carin Cheba, 900–1100 m.) and *aterrimus* from Eastern Siberia. It may be admissible to attach these to the subspecies *japonicus*, which would then include all the East Asiatic *herculeanus*,—even the variety *sachalinensis* Forel (*vide infra*),—excepting the forms that are referable to the subspecies *ligniperdus*.

45. **Camponotus herculeanus** *Linn.* var. **sachalinensis** *Forel.*

FOREL, Ann. Mus. Zool. Acad. Impér. Sc. St. Pétersb., VIII, 1903, p. 14, ♀

Based on female specimens only, collected in Mongolia, Manchuria and Sakhalin. According to Forel, this variety "differs from the typical *herculeanus* in its entirely black color (mandibles included) and its feeble sculpture, which renders it smooth and more shining. The pubescence on the gaster is also shorter and sparser. These last characters ally this variety with *ligniperdus*, from which it differs however in color and the more thickset stature which is identical with that of *herculeanus*. The wings are exactly like those of the typical *herculeanus* and very different from those of *ligniperdus* and *vagus*. The sculpture and pilosity separate this variety completely from *pennsylvanicus* and *vagus*."

46. **Camponotus herculeanus ligniperdus** *Latreille* var. **obscuripes** *Mayr.*

Camponotus ligniperdus var. *obscuripes* MAYR, Verhandl. zool. bot. Ges. Wien, XXVIII, 1878, p. 645, ☿

Camponotus ligniperdus var. *obscuripes* FOREL, Bull. Soc. Ent. Suisse, X, 7, 1900, p. 270.

Camponotus ligniperdus var. *obscuripes* FOREL, Mittheil. naturhist. Mus. Hamburg, XVIII, 1901, p. 70.

Camponotus ligniperdus var. *obscuripes* ERN. ANDRÉ, Bull. Mus. d'Hist. Natur. Paris, 1903, p. 128, ♀ ♂

Of this variety, which is not represented in the material collected by Mr. Hans Sauter and Professor J. F. Abbott, Forel examined specimens from Osaka.

47. **Camponotus marginatus vitiosus** *F. Smith.*

Camponotus vitiosus F. SMITH, Trans. Ent. Soc. London, 1874, p. 403, ☿

Camponotus marginatus MAYR, Verhandl. zool. bot. Ges. Wien, 1878, pp. 645, 646.

Camponotus marginatus subsp. *vitiosus* Emery, Zool., Jahrb. Abth. f. Syst., VII, 1893, p. 675, *nota.*

Camponotus marginatus race *vitiosus* Forel, Bull. Soc. Ent. Suisse, X, 7, 1900, p. 270.

Worker major. Length 5–5.5 mm.

Mandibles, clypeus and anterior $\frac{2}{3}$ of head subopaque, finely and densely punctate and in addition with shallow, scattered foveolæ. Remainder of body shining, thorax sharply, occiput and gaster much more finely and indistinctly shagreened.

Hairs pale yellow, erect, obtuse and abundant on the mandibles, cheeks and front; longer on the thorax and edge of petiole; sparse and rather inconspicuous on the gaster.

Black; mandibles, anterior third of head, antennæ and legs deep red or brown; in some specimens the trochanters, tips of the coxæ and lower portion of the petiole are yellow; tips of antennæ infuscated.

Worker minor. Length 3.5–4.5 mm.

Resembling the worker major except that the anterior portion of the head is not foveolate, the legs are more yellow and the hairs on the cheeks are less numerous and mostly appressed.

Described from numerous workers taken by Mr. Hans Sauter at Kanagawa from a single colony nesting "in an old oak."

While the above described form is certainly a variety or subspecies of the well-known palearctic and nearctic *marginatus*, I am unable to state positively that it is the true *vitiosus* of F. Smith. None of the authors mentioned in the above synonymy has given a careful description of *vitiosus*, and it is not improbable that *marginatus* is represented in Japan by several undescribed varieties.

48. **Camponotus marginatus** *Latreille* var. **quadrinotatus** *Forel.*

Forel, Ann. Soc. Ent. Belg., XXX, 1886, p. 142, ☿ ♀

Forel, Bull. Soc. Ent. Suisse, X, 7, 1900, p. 270.

The types of this beautiful variety are in the Berlin Museum. I have examined a single worker media collected by Mr. Hans Sauter at Kanagawa, and a winged female, male, two major workers and a worker minor collected by Professor Mitsukuri, probably near Tokio, and kindly sent me by Dr. William H. Ashmead. As Forel has shown, the worker major differs from that of the typical European form in having a proportionally larger head. The two ivory yellow spots on the first gastric segment are sometimes confluent. The hitherto undescribed male is deep black, without a trace of spots on the gaster. At first sight one would be inclined to regard this form as more than a mere variety of *marginatus*, but closer examination shows that the only important character is the maculation of the gaster in the females and workers, and large series of specimens will undoubtedly show that this character is highly variable. Similar conditions are seen in the American *C. landolti* and in *C. quadrimaculatus* of Madagascar. Both of these species show all gradations between a beautiful development of gastric spots and their complete absence. A somewhat similar condition is seen also in the American *C. ruficeps.*

49. **Camponotus marginatus brunni** *Forel.*

FOREL, Mittheil. naturhist. Mus. Hamburg, XVIII, 1901, p. 70, ☿

Forel based this subspecies on the worker minor obtained from Hozuyama. It resembles the variety *quadrinotatus* but lacks the white spots on the gaster and has a blunt petiole.

50. **Camponotus (Colobopsis) rothneyi** *Forel.*

Camponotus (*Colobopsis*) *rothneyi* FOREL, Journ. Bombay Nat. Hist. Soc., VII, 1893, p. 435, ☿ ♀

Colobopsis rothneyi BINGHAM, Fauna. Brit. India, Hymenopt., II, 1903, p. 346.

A single soldier and deälated female, agreeing very closely with Forel's description of this species, were taken by Mr. Hans Sauter at Okayama. There are no pale spots on the gaster as in the European *C. truncatus*, of which it may be merely a subspecies. Forel has described from Singapore a form which he calls *C. rothneyi* r. *krafti.*

51. **Polyrhachis lamellidens** *F. Smith.*

F. SMITH, Trans. Ent. Soc. London, 1874, pp. 403, 404, ☿
MAYR, Verhandl. zool. bot. Ges. Wien, 1878, p. 652, ☿
FOREL, Bull. Soc. Ent. Suisse, X, 7, 1900, p. 270.
FOREL, Mittheil. naturhist. Mus. Hamburg, XVIII, 1901, p. 78.
BINGHAM, Fauna Brit. India, Hymenopt., II, 1903, p. 403, fig. 139, ☿

Worker. (Plate XLI, Fig. 2.) Length 6–6.5 mm.

Mandibles with 4 subequal teeth. Clypeus convex, anteriorly subcarinate. Head convex above, excluding the mandibles about as broad as long, with rounded sides and occipital border. Thorax with steep, flattened, lateral and concave dorsal surfaces, meeting on each side in a prominent ridge, which is sharply interrupted at the pronounced promesonotal and mesoëpinotal sutures. Pronotum about as broad as long, its lateral ridge continued anteriorly on each side into a long spine, which is directed outward and forward and curved downward at its tip. Mesonotum broader than long, bearing at the middle of each side a rapidly tapering spine about half as long as those of the pronotum, and curved upward, outward and especially backward. Basal surface of epinotum 1½ times as long as broad, terminating behind in a pair of very blunt flat spines, which are directed backward and somewhat outward and upward. The ridge along the side of the basal surface is sometimes crenate or serrate and is always continued down along the side of the declivity, which is very sloping and about as long as the basal surface. Petiole seen from above as long as broad, very thick above where it bears a pair of long, somewhat flattened, hook-shaped spines, which diverge laterally and somewhat posteriorly from their very insertions. Gaster spherical.

Head, legs and gaster shining, finely shagreened. Mandibles finely striated. Thorax and petiole opaque, punctate-rugulose, the dorsal surface of the former more uniformly punctate. Upper anterior surface of the petiole very finely and transversely rugulose.

Mandibles, legs and occiput with sparse, suberect grayish hairs. Pubescence pale, very sparse on the head, legs and gaster; more abundant, but by no means concealing the sculpture, on the pleuræ and base of the gaster.

Thorax and petiole dark red, tips of thoracic and petiolar spines and remainder of the body deep black.

Several workers taken by Mr. Hans Sauter at Okayama. Smith's types and the specimens studied by Forel were from Hiogo. Smith mentions the species as occurring also in Hong-Kong. Bingham has described a closely related species, *P. craddocki* from India. In this species the pronotal spines do not point downward, the mesonotal spines are nearly vertical and the petiole is "surmounted by two cylindrical spines which rise vertically and are close together and parallel for three-fourths of their length from the base." In *P. lamellidens* the petiolar spines diverge from their very bases.

EXPLANATION OF PLATE XLI.

Fig. 1. *Cremastogaster laboriosa* F. Smith var. *matsumurai* Forel. Worke,

Fig. 2. *Polyrhachis lamellidens* F. Smith. Worker.

Fig. 3. *Iridomyrmex itoi* Forel var. *abbotti* var. nov. Worker.

Fig. 4. *Technomyrmex gibbosus* sp. nov. Worker.

Fig. 5. *Sysphincta watasei* sp. nov. Worker.

Fig. 6. *Pachycondyla* (*Pseudoponera*) *sauteri* sp. nov. Worker. Fig. 6*a* antennal funiculus of same.

Fig. 7. *Pristomyrmex japonicus* Forel. Worker.

Fig. 8. *Pheidole nodus* F. Smith. Soldier.

Fig. 9. *Pheidole nodus* F. Smith. Worker.

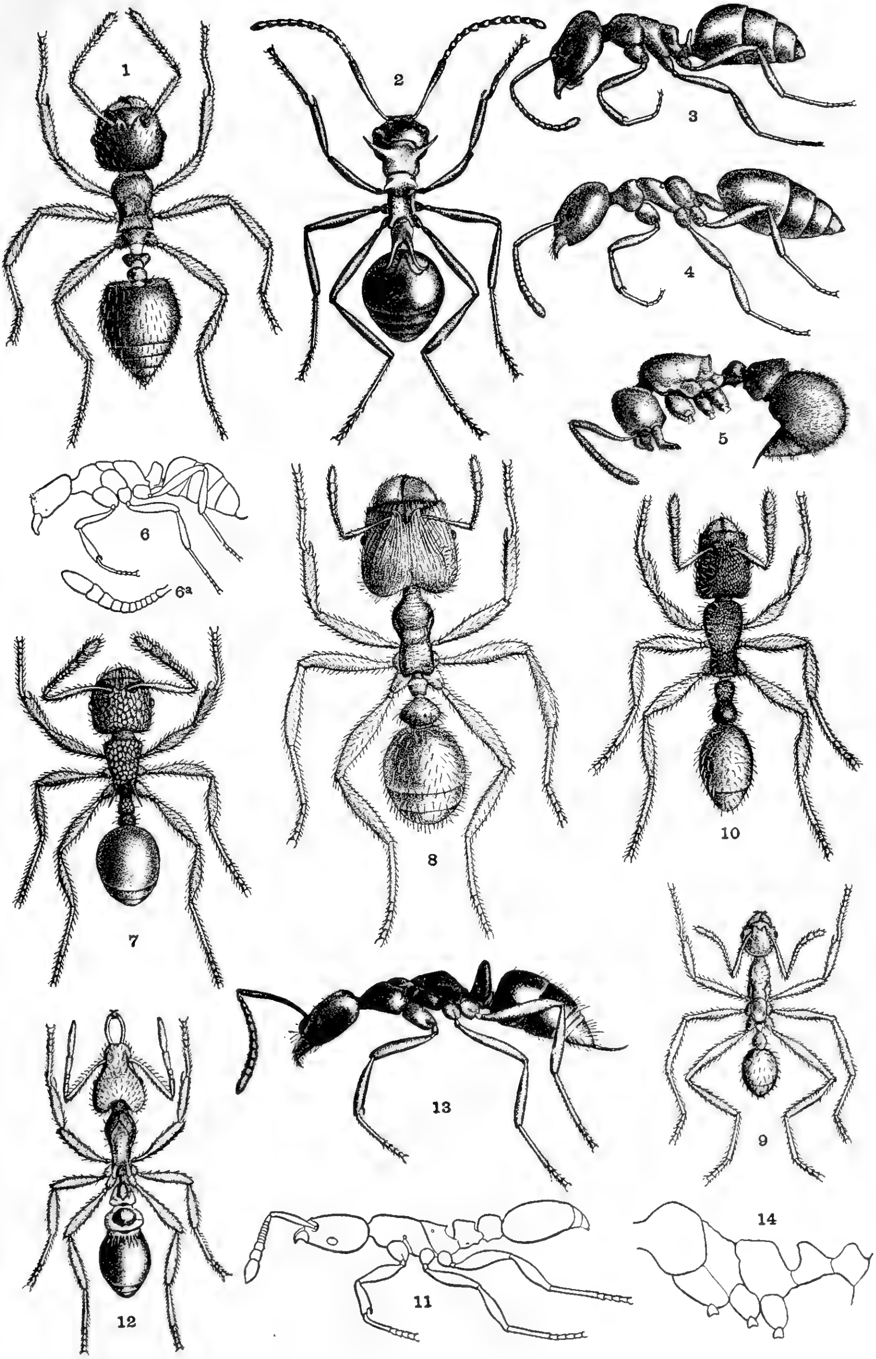
Fig. 10. *Vollenhovia emeryi* sp. nov. Worker.

Fig. 11. *Vollenhovia emeryi* sp. nov. Worker, in profile.

Fig. 12. *Strumigenys godeffroyi* Mayr var. *lewisi* Cameron. Worker.

Fig. 13. *Euponera* (*Brachyponera*) *solitaria* F. Smith. Worker.

Fig. 14. *Stenamma* (*Messor*) *aciculatum* F. Smith var. *brunneicorne* Forel. Thorax and pedicel of worker in profile.



R. B. Howe del.

JAPANESE ANTS.

The Ants of the Grand Cañon.

By William Morton Wheeler.

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Article XIX.—THE ANTS OF THE GRAND CAÑON.

By William Morton Wheeler.

During the spring of 1905 Dr. B. E. Dahlgren and myself visited several localities in New Mexico and Arizona for the purpose of collecting and studying the desert invertebrates and certain plants to be used in the construction of some of the large vertebrate groups in the American Museum of Natural History. While on this expedition we made an excursion to the Grand Cañon and spent three days (May 25 to 27) in a study of its fauna and flora, so far as these were accessible from the Bright Angel Trail. Special attention was given to the Formicidæ as a group of insects of more than ordinary interest from the standpoint of geographical distribution. I therefore collected all the species I could find from the Kohonino Forest on the rim of the cañon down to the bed of the Colorado River, 5000 feet below, noting the altitude and environment of each colony, so far as this was possible in the brief time at my disposal. The first day was spent in the great pine forest on the rim, the second was devoted to the Bright Angel Trail, and the third to the Indian Garden and the adjoining Angel Plateau.

Of the few naturalists who have visited the Grand Cañon for the purpose of studying the geographical distribution of its animals and plants, I may mention Merriam and Coville and McDougal. In his valuable paper on the biological survey of the San Francisco Mountains and the adjacent Desert of the Little Colorado[1] Merriam includes a brief but excellent account of the vertebrates and more conspicuous plants, with a list of 21 species of mammals and 57 species of birds taken on the southern wall from the rim to the bottom of the Grand Cañon. His conclusions are summed up in the following paragraph:

"In descending from the plateau level to the bottom of the cañon a succession of temperature zones is encountered equivalent to those stretching from the coniferous forests of northern Canada to the cactus plains of Mexico.[2] They result from the com-

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[1] Results of a Biological Survey of the San Francisco Mountain Region and Desert of the Little Colorado in Arizona. North American Funa. No. 3. U. S. Dept. Agricult., Divis. Ornith. and Mammal. Washington, 1890. 136 pp., 13 plates and 5 maps.

[2] "The extremes of temperature are well illustrated by the fact that the lowest temperature of the twenty-four hours at the bottom of the canon was 80° Fahr. at 4 A. M., September 13, while at the same time thick ice formed on a bucket of water at the top of the cañon.

bined effects of altitude and slope-exposure, the effects of the latter being here manifested in an unusual degree. Where the walls of the cañon face north or north east the uppermost tree-zone consists of Douglas and balsam firs (*Pseudotsuga douglasii* and *Abies concolor*)—northern species which do not occur elsewhere in the cañon. Below this is a belt of pines (*Pinus ponderosa*), succeeded in turn by a belt of junipers [*Juniperus occidentalis monosperma*] and piñon [*Pinus edulis*], usually more or less mingled with pines. Immediately below the piñon belt is a zone which corresponds in the main to the Desert of the Little Colorado; but since it has humid as well as arid areas, forms of vegetation unknown on the desert interrupt its stretches of cactuses, yuccas, and greasewoods. Still lower down another zone is encountered which may be recognized by the presence of huge cactuses, arborescent opuntias, agaves whose tall stems are conspicuous land-marks, and many of the plants characteristic of the Lower Colorado and Gila regions, together with subtropical humid forms and a certain percentage of species not found elsewhere. The complex and interacting effects of radiation and refraction, of aridity and humidity, of marked differences in temperature at places of equal altitude on opposite sides of the cañon, of every possible angle of slope-exposure, and of exposure to and protection from winds and storms, produce a diversity of climatic conditions the effect of which on the animal and vegetable life of the cañon has been to bring into close proximity species characteristic of widely separated regions, and to crowd the several life zones into narrow parallel bands along the sides of the cañon—bands which expand and contract in conforming with the ever-changing surface. The same conditions modify and alter the species there present in the manner in which the evolution of new species is brought about. In short, the Grand Cañon of the Colorado is a world in itself, and a great fund of knowledge is in store for the philosophic biologist whose privilege it is to study exhaustively the problems there presented."

Coville and McDougal give the following brief sketch of the flora of the Bright Angel Trail:[1] "A visit was made to the Grand Cañon of the Colorado with the expectation that its lower elevations would afford lodgment for many desert plants, and that a descent from the timbered rim at 6,866 feet, to the river at 2,436 feet, would permit the traveller to see in a brief trip a wide range of desert vegetation. Although the descent is full of botanical interest, and does carry one

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[1] Desert Botanical Laboratory of the Carnegie Institution. Washington, Carnegie Institution. November, 1903, 58 pp., 29 pll. and 4 text-figs.

down through several different belts of vegetation, the comparatively limited number of woody desert plants rendered the journey somewhat disappointing from the standpoint of the main object of our trip. For the first 2,600 feet of the descent the trees continue, but from that point to the river the slopes are treeless and the vegetation of a desert character. One of the most striking features is extensive fields of a rosaceous shrub, *Coleogyne ramosissima*, which extends in an almost pure growth over the canyon terraces at an elevation of about 3,600 feet in a soil seemingly well supplied with lime. There is a notable absence of many shrubs which would be present in the open desert at the elevations afforded by the lower parts of the canyon and which have a seemingly good route for extension up the canyon from the Mojave desert. The absence of these plants is presumably connected with the narrowness of the canyon, which besides producing abnormal air currents and temperature conditions is responsible for a rainfall greater than would occur at the same elevations in the open desert. A cloud sheet precipitating rain on the 7,000-foot plateau through which the canyon passes would presumably continue to precipitate as it drifted across the canyon, whereas if it should drift off the plateau over a desert of low elevation its precipitation would be greatly lessened or would cease altogether."

In walking down the Bright Angel Trail from the beautiful Kohonino Forest to the river, one can hardly fail to be impressed by the dryness of the walls of the vast chasm, the steadily increasing temperature, and the wonderful, omnipresent evidences of erosion caused by the torrential floods which at certain seasons must rush down the precipitous inclines. As steepness and dryness of slope are always unfavorable to ant-life, we are not surprised to find their colonies few and widely scattered, of small size and showing other evidences of adverse conditions, especially in unusual forms of nest architecture. At an altitude of 3670 feet on the trail, at a place called Indian Garden, there is a beautiful stream overgrown by low willows and hence known as Willow Creek, where the much less precipitous and more humid soil favors the development of colonies. On the adjoining Angel Plateau (3700 feet) which is covered with the *Coleogyne ramosissima* mentioned and figured by Coville and McDougal, the level is also more favorable, but here the soil is very dry and stony and actually much poorer in species than the deserts of the Lower Colorado. Finally, in the granite strata which extend to an elevation of 1000 or 1200 feet above the river and constitute the hard, sombre walls of the "inner cañon," there are no ants except where the sand

and pebbles have been washed into crevices or depressions or under rocks in the boulder beds of the streams.

As ants, with the exception of certain peculiarly modified desert species, are intimately dependent on moisture, we find that most of the species collected occur in the Kohonino Forest and about Willow Creek in the Indian Garden. But the species of these two localities, separated by an altitude of about 3400 feet, are almost entirely different: those on the Kohonino Plateau belonging to the general Rocky Mountain fauna of the same or similar altitudes (6000 to 8000 feet), whereas those of the Indian Garden are in large part identical with the species of the warmer and moister spots in Texas and New Mexico. The Kohonino fauna extends down sparingly on the walls of the cañon to the lower limit of coniferous trees at an altitude of about 4500 feet. The Formicidæ of the Angel Plateau and lower portions of the cañon to the river belong, like the flora, to well-known desert species widely distributed through western Texas, the southern portions of New Mexico, Arizona and California and the adjoining portions of Mexico at corresponding elevations. We may therefore distinguish the following four faunal zones in the distribution of the Formicidæ of the cañon:

1. The fauna of the rim and cañon walls from about 7000 feet down to an altitude of about 4000 feet. The most characteristic species of this zone is the "occident ant" of McCook (*Pogonomyrmex occidentalis*). The list of species comprises the following:

Monomorium minimum,
Cremastogaster lineolata,
Pheidole ceres,
Myrmica scabrinodis,
Pogonomyrmex occidentalis,
Leptothorax nitens,
Leptothorax neomexicanus,
Liometopum luctuosum,
Dorymyrmex pryamicus,
Tapinoma sessile,
Lasius americanus,
Formica moki,
Formica argentata,
Formica neorufibarbis,
Formica subpolita,
Camponotus nitidiventris,
Camponotus maccooki.

2. The Indian Garden fauna, which is in all probability representative of all the other humid spots in the cañon at the same elevation. This fauna comprises the following species:

Ponera opaciceps,
Myrmecina brevispinosa,
Monomorium minimum,
Pheidole vinelandica,
Aphænogaster texana,
Dorymyrmex pyramicus,
Iridomyrmex analis,
Nylanderia imparis,
Lasius americanus,
Formica gnava.

3. The fauna of the Angel Plateau and the adjacent dry boulder

beds is very meager and, so far as I have observed, represented only by the following, of which the second is the most common and characteristic:

Pheidole maricopa,
Pogonomyrmex rugosus,
Dorymyrmex pyramicus,
Iridomyrmex analis.

4. The warm desert zone, extending from the Angel Plateau to the river, comprises some half dozen species, of which the California harvester (*Pogonomyrmex californicus*) is the most abundant and characteristic:

Ponera opaciceps,
Solenopsis aurea,
Pogonomyrmex californicus,
Dorymyrmex pyramicus,
Prenolepis guatemalensis,
Myrmecocystus melliger.

A comparison of these lists shows that only a single species, *Dorymyrmex pyramicus*, ranges from the top to the bottom of the cañon. Of the other species only a few extend over more than one of the zones. Thus the Kohonino and Indian Garden zones have in common only the widely distributed *Lasius americanus* and *Monomorium minimum. Iridomyrmex analis* is common to the Indian Garden and Angel Plateau and *Ponera opaciceps* to the former and the desert zone of the cañon bottom. Excluding the humid zones and patches represented by the Indian Garden, we may say that each of the cañon zones is characterized by a species of *Pogonomyrmex*, the uppermost and coldest by *P. occidentalis*, the lowermost and warmest by *P. californicus*, and the intermediate zone by a form of the widely distributed *P. barbatus*. Each of these species occupies on the cañon walls a position which, with respect to altitude, moisture and temperature, corresponds very closely with its distribution over the vast stretches of country to the north and south of the cañon.

Whence came the species found in the different zones of the cañon? There can be no doubt that the colonies were founded by isolated queens that had drifted into the cañon while on their marriage flight. Although these insects are certainly carried long distances by the wind and must fall into the cañon in great numbers during the late spring and early summer months, it is equally certain that they can establish their colonies only under the most favorable conditions of soil, temperature and moisture. In this respect they resemble the wind-borne seeds of plants. Queens falling on inhospitable ground must either perish or run about till they find the proper sites for the establishment of their colonies. This is indicated very clearly in the sharp zonal demarcation of the various species on the walls of the cañon.

While it is equally clear that the ants of the rim can readily descend to the lower limit of the coniferous trees, it is not so easy to account for the origin of the fauna of the three lower zones. Spots like the Indian Garden, which are veritable oases, confined to springs and damp stream beds, probably derive their fauna from similar but more extensive areas in New Mexico, Arizona and Texas. I have taken all of the species of ants of the Indian Garden in similar locations in central Texas and the valley of the Rio Grande, with the exception of *Nylanderia imparis*. This ant, so common in our northern woods, occurs also in the mountains of Colorado and California and may have been overlooked among the species occurring on the Kohonino Plateau. One of the most abundant ants of the Indian Garden, *Formica gnava*, is very characteristic of the banks of streams in central and western Texas and parts of Colorado.

Two sources suggest themselves for the fauna of the Angel Plateau and the lower reaches of the cañon, namely, the Desert of the Little Colorado to the east and the more remote deserts about the Lower Colorado and Gila Rivers in southwestern Arizona. The ant-fauna of the latter region, as I can state from personal observation, comprises the very species found in the two arid zones of the cañon, in addition to several species which future collectors, working along other trails, will probably bring to light. The alternative sources above suggested are really reducible to one if we accept the view advanced by Merriam in regard to the origin of the fauna of the Desert of the Little Colorado, or Painted Desert, as it is sometimes called. He says: "The Desert of the Little Colorado, it will be remembered, is a deep basin on top of the Great Colorado Plateau. It is wholly disconnected from the desert region of Southern Arizona by the elevated and timber-covered highlands occupying the crest of the plateau escarpment. In fact the highest part of Arizona south of the Grand Cañon, except a few isolated mountains, is the edge of this plateau, which is nowhere below 2,130 meters (7,000 feet) and in places rises to the height of 2,740 meters (9,000 feet), as at the Mogollon Mesa. On the east the desert is separated from the valley of the Upper Rio Grande by a broad area covered with cedar and piñon, through which the continental divide passes, at an elevation of upwards of 2,130 meters (7,000 feet). Therefore the only possible channel through which the fauna and flora of the Painted Desert could have reached this desert during existing climatic conditions is by way of the Grand Cañon of the Colorado. At first thought it seems incredible that a fauna and flora should extend several hundred miles through a chasm of this character; but the evidence at hand indicates that it does. . . . The inference is that the life of the Painted Desert is derived from the deserts of western Arizona, and that it came by the roundabout way of the Grand Canoñ of the Colorado."

Merriam also calls attention to the occurrence near the bottom of the cañon of two lizards (*Sceloporus clarkii* and *Uta symmetrica*) "which belong to the torrid fauna of southern and western Arizona, and are not known to reach the Painted Desert." I believe that Merriam's interpretation will also hold good of the origin of the ant-fauna in the lower zones of the cañon; this fauna has simply advanced up the long, deep chasm from the deserts around the lowermost portion of the river. Further collections of the ants at different points in the cañon will undoubtedly add several desert species to my list. Among those which should occur at the lower elevations in the cañon are certain pale varieties of the honey ant (*Myrmecocystus melliger*) and of *Dorymyrmex pyramicus* (var. *bicolor*) which are common in the Mojave Desert, several species of *Pogonomyrmex* (*P. desertorum*, *dentatus* and varieties of *P. californicus* and *imberbiculus*), and above all the desert species of *Pheidole* and *Stenamma* (*S.* [*Ischnomyrmex*] *cockerelli* and *albisetosum* and *S.* [*Messor*] *pergandei*). One of the most interesting ants of the deserts of Arizona and California is *Messor pergandei*, which builds flat craters from a foot to 18 inches in diameter, with single or double entrances of very irregular outline, and garners great quantities of seeds. *Ischnomyrmex cockerelli* and *albisetosum* make similar but larger nests and have very similar habits. Owing to the limited supply of insect food obtainable in the desert during the greater part of the year, these ants, like the species of *Messor*, *Pogonomyrmex* and several species of *Pheidole*, are compelled to subsist on seeds.

Further details concerning the ants found in the Grand Cañon, together with descriptions of a few new forms, are included in the following systematic list:

Subfamily PONERINÆ.

1. **Ponera opaciceps** *Mayr*.—Several workers of this species were collected under stones beneath the willows of the Indian Garden. A single individual was taken in the bottom of a creek near the river.

Subfamily MYRMICINÆ.

2. **Myrmecina graminicola americana** *Emery* var. **brevispinosa** *Emery*.—Several workers which agree very closely with northern

specimens of this variety were taken under stones at the Indian Garden in the same places as the preceding. A similar variety of *M. americana* occurs also in the creek bottoms of Travis County, Texas.

3. **Cremastogaster lineolata** *Say.*—A single worker of this species, near the subspecies *coarctata* Emery var. *mormonum* Emery, was found running on the wall of the cañon at an elevation of about 5000 feet.

4. **Monomorium minutum** *Mayr* var. **minimum** *Buckley.*—Common under stones in the Kohonino Forest and near the Indian Garden. The colonies were in all respects like those found in Texas and New Jersey. This variety ranges as far north as Colorado and Massachusetts.

5. **Solenopsis geminata** *Fabr.* var. **aurea** var. nov.

Worker. Length 2–3.5 mm.

Deep yellow; mandibles and posterior margins of gastric segments brownish; mandibular teeth black.

Female. Length 5.–5.5 mm.

Deep yellow, like the worker; each gastric segment with a broad brown band, the one on the first segment sometimes nearly or quite interrupted in the middle. Wings whitish hyaline, with yellow stigma and veins. Each ocellus with a small brown spot near its inner margin.

Male. Length 5 mm.

Piceous brown; upper surface of head, thorax and gaster darker; mouthparts, antennæ, thoracic sutures and legs yellow; genitalia somewhat paler. Wings as in the female.

The types of this variety are from Mt. Bonnel near Austin, Texas. It is undoubtedly distinct from the typical form of the species, differing in its smaller size, much paler coloration, and in living in rather small colonies under stones in dry, stony situations. It appears to be nocturnal or hypogæic, unlike the typical *geminata*, which is found abroad at all hours of the day. I have taken the variety also at Fort Davis, Texas, on the dry summit of the Crouching Lion, and there are two specimens from Visalia, California, in my collection. A few workers were found under stones in the bottom of the Grand Cañon near the river.

6. **Pheidole vinelandica** *Forel.*—A few colonies of this species were seen along the Bright Angel Trail just above the Indian Garden at an elevation of about 3700 feet. It is common in central Texas and occurs near Colorado Springs, Colorado, at an altitude of 5000 to 6000 feet, extending north and east as far as New Jersey and

southern New York. It is a grain-storing species and seems to build indifferently under stones or in the open soil. In the latter case its shallow nests are surmounted by straggling craters scarcely more than an inch in diameter.

7. **Pheidole ceres** *Wheeler.*—A few colonies of this seed-storing species, which is common through the mountains of Colorado at an elevation of 6000 to 8000 feet, were found under stones near the Bright Angel Hotel on the rim of the cañon.

8. **Pheidole desertorum** sp. nov.

Soldier. Length 4.5–5 mm.

Head distinctly longer than broad; sides evenly arcuate, with the rather large convex eyes in front of the middle; posterior margin deeply excised, with a pronounced occipital groove. Mandibles convex, with two stout apical teeth. Clypeus short, flat, carinate in the middle, with a broad median excision in its anterior border. Frontal carinæ about $\frac{1}{3}$ as long as the head; frontal area subtriangular, somewhat truncated behind. Antennæ very slender, scapes slightly curved at the base, but not flattened, slightly thickened towards their tips which extend a little beyond the posterior corners of the head. Funiculus very slender, all the joints more than twice as long as broad; the 3-jointed club more than $\frac{2}{3}$ as long as the remainder of the funiculus, its joints subequal, nearly 4 times as long as broad. Thorax in front half as broad as the head, without distinct humeral angles; promesonotal depression shallow but distinct; mesoëpinotal depression deep. Basal surface of epinotum flat, longer than the declivity, which is sloping and longitudinally impressed in the middle. Epinotal spines small and erect, a little further apart at their bases than long. Petiole more than twice as long as broad; from above somewhat violin-shaped, with a rather high node, compressed anteroposteriorly and somewhat notched in the middle; its anterior slope long and concave, its posterior slope short and abrupt. Postpetiole short, about twice as broad as long, gradually narrowed anteriorly, truncated behind; in profile rounded above in front and abruptly concave behind. Lower surfaces of petiole and postpetiole rather flat. Gaster smaller than the head. Legs long and slender.

Shining; mandibles very sparsely and coarsely punctate; punctures elongated and parallel on the inner edges of the blades, outer basal surfaces very coarsely striated. Clypeus smooth in the middle, striated on the sides. Frontal area smooth. Anterior $\frac{3}{4}$ of head longitudinally and somewhat reticulately rugose, most distinctly on the cheeks and between the frontal carinæ; the spaces between the rugæ more or less punctate. Posterior corners smooth, without distinct punctures. Prothorax shining; meso- and metathorax with dense but shallow punctures. Petiole and postpetiole finely punctate, except the dorsal portion of the former, which is smooth. Gaster finely shagreened at the base.

Hairs abundant, suberect, pale yellow, covering the body and appendages throughout.

Body yellowish red or reddish brown; mandibles, clypeus and pedicel somewhat darker; gaster and edges of mandibles black, the base of the former yellowish or brownish. Legs and antennæ yellow.

Worker. Length 3–3.25 mm.

Head longer than broad, elliptical, narrowed but not conical behind the eyes; without posterior angles and with a constricted and marginate posterior border. Eyes a little in front of the middle of the head. Mandibles with two larger apical teeth and numerous smaller basal teeth. Anterior clypeal border sinuately excised in the middle. Antennæ very slender; scapes extending about ⅔ their length beyond the posterior corners of the head; funicular joints like those of the soldier. Thorax long and narrow, flattened above, with indistinct promesonotal depression; mesoëpinotal depression short and deep. Epinotal spines small and acute, directed upward and somewhat outward, nearly twice as far apart at their bases as long. Petiole slender, fully three times as long as broad, very little wider behind than in front, with subparallel sides; in profile with a short, rounded node near the posterior end. Postpetiole barely twice as broad as the petiole, as long as broad, subglobular. Gaster about the size of the head. Legs very long and slender.

Body smooth and shining. Mandibles indistinctly punctate. Epinotum and mesopleuræ subopaque, evenly punctate.

Pilosity like that of the soldier but less abundant.

Dark brown or piceous; mandibles and clypeus yellow; mandibular teeth black; legs somewhat paler than the body.

Female (deälated). Length 6.5–7 mm.

Head resembling that of the soldier, but the longitudinal rugæ and the punctation extend onto the posterior corners, so that these are subopaque. Clypeus depressed in the middle, sharply carinate and longitudinally rugose. Antennal scapes as long as those of the soldier but distinctly incrassated and slightly flattened at their bases. Epinotum with short, robust spines, its sides irregularly and longitudinally striated, the region between the spines with dense, shallow punctures. Mesonotum smooth and shining, with a finely, longitudinally and coarsely punctate area on either side of the middle line. Scutellum coarsely and sparsely punctate, with a few striæ running parallel with the posterior border. Petiole and postpetiole opaque, very finely punctate; the former twice as broad as long, semicircular in outline from above, in profile with an acute node, the posterior surface of which is strongly concave. Gaster shining, shagreened, especially at the base, and with scattered piligerous punctures. Color and pilosity similar to those of the soldier.

Male. Length 4.5–5.5 mm.

Head, excluding the eyes, longer than broad. Cheeks extremely short, ocellar region very prominent, with straight posterior border. Mandibles very small, with two larger apical and three or four minute basal teeth. Clypeus feebly emarginate in the middle. Antennæ filiform; scape somewhat longer and stouter than the subequal, cylindrical joints 2–12 of the funiculus; first joint subspherical, scarcely broader than the scape. Thorax very robust, nearly twice as broad as the head including the eyes; mesonotum flattened, a little broader than long, without Mayrian furrows. Epinotum short, sloping, with small protuberances in the place of the spines. Petiole 1½ times as long as broad, broadest behind; node rather sharp in profile, with longer, concave, anterior and shorter, concave posterior slopes. Postpetiole 1½ times as broad as the petiole, distinctly broader than long and much broader behind than in front, with subangular sides. Gaster somewhat flattened above, convex on the ventral side. Legs long and slender.

Smooth and shining; head finely granular except on the front; epinotum subopaque, finely punctate.

Hairs like those of the soldier but sparser; pubescence on the antennæ rather conspicuous.

Sordid yellow; head, with the exception of the clypeus and mandibles, black. Posterior $\frac{2}{3}$ of scutellum and upper surface of gaster dark brown, anterior portion of basal segment yellow. Wings grayish hyaline, with brown stigma and yellowish veins.

The types of this species, comprising several specimens of each of the above described phases, were taken at Fort Davis, Texas (5400 feet), during June, 1902. It forms rather populous colonies under stones or in rough crater nests, often in very dry spots in the desert, and like *Ph. dentata* is highly carnivorous. I have taken it also at Ash Fork, Prescott, Phoenix, and Tucson, Arizona (May, 1905). In Prescott one of the colonies was found nesting in a dry pine log. In both soldiers and workers from this locality the epinotal spines are very short, almost absent in the worker. The two following varieties may be distinguished among my specimens from other localities in the southwest:

Pheidole desertorum var. **comanche** var. nov.

Based on numerous soldiers and workers taken in the Paisano Pass near Alpine, Texas, (5079 feet, June, 1902) and at Terlingua in the Great Bend of the Rio Grande (Dec. 1901). These specimens are much darker than those of the typical form, the head, thorax, pedicel and gaster both in the soldier and worker being uniformly chestnut brown, the legs yellowish. The head of the soldier is somewhat more shining, especially behind. A single deälated female of this variety from the Paisano Pass differs from the female of the typical form in having the gaster black and the mesonotum darker in the middle.

Pheidole desertorum var. **maricopa** var. nov.

In this variety the soldiers and workers are yellow throughout, except the borders of the mandibles, frontal carinæ and anterior border of the clypeus, which are dark brown, and the antennal scapes and occipital groove, which are reddish. The head of the soldier is less shining than in the preceding variety and the mandibles have minute teeth along their basal border.

Described from several soldiers and workers taken from a single colony under a stone in the Grand Cañon just above the Indian Garden (3876 feet.)

Ph. desertorum is allied to *Ph. susannæ* Forel of the American tropics and *Ph. longipes* Pergande of Mexico. From *susannæ* it differs in its larger size, much longer antennæ in the soldier and much slighter constriction of the occiput in the worker. Comparison of my specimens of *desertorum* with Pergande's description of the soldier of *longipes*, with a type specimen of the worker of this species and another worker from San Jacinto, California, given me by Prof. Emery, shows a number of differences. Pergande describes the space between the frontal carinæ of the soldier as "quite smooth and faintly shagreened," the posterior half of the head as having "elongated shallow depressions", etc. The worker of *longipes*, like that of *susannæ*, has the head produced and much constricted in the occipital region and "forming a distinct neck", the long basal surface of the epinotum is distinctly convex, and the petiole is more campanulate than in *desertorum*.

9 **Myrmica rubra scabrinodis** *Nylander.*—A single colony of a small, dark-colored variety of this subspecies, with rather large, rounded, calyculate lobes on the base of the antennal scapes of the worker and female, was found under a stone in the Kohonino Forest on the rim of the cañon. This variety closely resembles a form not uncommon in the mountains of Colorado at a corresponding elevation, and others peculiar to the shady woods and tamarack bogs of the northern States.

10. **Pogonomyrmex occidentalis** *Cresson.*—The "occident ant" may be found nesting all the way from Ash Fork and Williams, Arizona, to the Grand Cañon, and from the rim of the latter to an altitude of 4000 feet, but not lower. The nests near Ash Fork and Williams are large and typical, with great bare areas, often 20 or 30 feet in diameter, surrounding their elegant gravel cones, but in the Kohonino Forest and especially on the walls of the cañon, they exhibit unmistakable effects of adverse conditions. The absence of horizontal surfaces and the washing of rains have induced the insects to nest under large stones or in crevices of the rock. They still heap the pebbles about the entrance, but the nests are merely caricatures of the fine structures in the plateau region. *P. occidentalis* is the ant *par excellence* of the Great Plains. A study of its distribution from Montana, Wyoming and Colorado to Arizona and New Mexico, shows that it is at its best only at an elevation of 6000 to 7000 feet and that it rarely descends below 4000 or 5000 feet.

11. **Pogonomyrmex barbatus rugosus** *Emery.*—Many workers of what I regard as a variety of this subspecies, were taken on the Angel Plateau (3700 feet) and down to an altitude of about 3000 feet, but not lower. The workers are somewhat smaller and smoother than the typical *rugosus*, which is common in the deserts about Tucson. The rugæ of the petiolar node are irregular and subreticulate. The base of the gaster has two large yellow or red spots. The nests, which, like those of the typical *rugosus*, are flat gravel discs 3 to 4 feet in diameter, were especially abundant in the *Coleogyne* zone. The ants were busily collecting the seeds of grasses and other herbaceous plants.

12. **Pogonomyrmex californicus** *Buckley.*—This ant occurs from just below the Angel Plateau to the river bottom, slightly overlapping the range of the preceding species. Its true home is in the torrid deserts of southwestern Arizona and southern California, where it prefers to nest in pure sand. I have also found it abundant at Albuquerque, New Mexico, and in a somewhat depauperate condition near Marfa in western Texas. Its nests are low, flat craters from 6 inches to a foot or more in diameter, with elegantly rounded slopes and slanting, usually somewhat excentric entrances. The workers can sting severely and those of large colonies actively resent any interference with their nests. They run rapidly with the gaster conspicuously elevated.

13. **Stenamma (Aphænogaster) fulvum** *Roger* var. **texanum** *Emery.*—Five workers taken under stones at the Indian Garden agree with specimens of this variety from Austin and New Braunfels, Texas, except that they are somewhat larger and have the head and thorax somewhat more coarsely sculptured. The body is slightly redder and the gaster is infuscated. In Texas the variety occurs in rather shady damp portions of the live-oak woods and mesquite thickets, and is never found in dry, open country.

14. **Leptothorax nitens** *Emery.*— A few colonies of a pure yellow form of this species were seen under stones in the Kohonino Forest on the rim of the cañon.

15. **Leptothorax neomexicanus** *Wheeler.*—A single small colony of this species was found under a stone in the same locality as the preceding.

Subfamily DOLICHODERINÆ.

16. **Liometopum apiculatum luctuosum** *Wheeler.*—This subspecies is common in the Kohonino Forest on the rim of the cañon and extends down the walls sparingly to an altitude of about 4000 feet.

As I have shown in a former paper[1] this ant occurs in populous colonies and moves about in files in search of insect foot and the sweet excretions of plant-lice. It appears to be more definitely associated with pine trees than the typical *apiculatum.*

17. **Dorymyrmex pyramicus** *Roger.*—This ant, the only species found over the whole cañon wall from the rim to the river, constructs crater nests somewhat larger than those of *Lasius niger.* It is common throughout Mexico, the West Indies and the southern and southwestern Stares, ranging as far north as New Jersey and Illinois. The form occurring in the Grand Cañon is somewhat smaller and paler than the var. *niger* Pergande and hence approaches very nearly the typical form of the species.

A clearly marked variety which may be called **bicolor** var. nov. has the head, thorax and petiole of the worker and female red, the gaster black. It occurs in pure sand from central Texas to the Mojave Desert of California and will probably be found in the lower reaches of the Grand Cañon. I have taken specimens of this variety at New Braunfels and Elgin, Texas, Phoenix, Tucson and Yucca, Arizona, and at Needles, California. It has also been taken at San Pedro, California, by Prof. T. D. A. Cockerell, and at Tuxpan, Jalisco, Mexico, by J. F. McClendon.

18. **Iridomyrmex analis** *André.*—Many populous colonies of this ant, teeming with larvæ and nude pupæ, were found under stones in the Indian Garden and down the cañon to a level of about 3000 feet, but the species was not seen on the rim or at the bottom.

19. **Tapinoma sessile** *Say.*—The common dark form of this widely distributed species is rather common under stones on the Kohonino Plateau. It occurs in similar localities at the same or even much greater elevations in Colorado and New Mexico. I have taken it at Cripple Creek, Colorado, at an altitude of 10,500 feet. In the northeastern States it descends to sea-level.

Subfamily CAMPONOTINÆ.

20. **Prenolepis guatemalensis** *Forel.*—A number of workers assignable to this species, were taken in the sand under stones in a creek bottom near the river along the lowermost portion of the Bright Angel Trail.

21. **Prenolepis (Nylanderia) imparis** *Say.*—A form of this species almost as light as var. *testacea* Emery, was common under stones in

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[1] The North American Ants of the Genus Liometopum. Bull. Am. Mus. Nat. Hist., XXI, 1905, pp. 321–333, 3 figs.

the Indian Garden. There I also found a solitary deälated female, with a cluster of small larvæ in the act of establishing her formicary. Many of the workers in these colonies were in a replete condition, indicating that they got their food from aphids or coccids. In the northern States I have seen hundreds of nests of this ant but on only two occasions have I found it nesting under stones. In fact, it seems to have as great an aversion as *Dorymyrmex pyramicus* to nesting in such places. In the Grand Cañon it is probably compelled to abandon its usual habits and to nest under stones for protection against the scouring rains.

22. **Lasius niger** *Linn.* var. **americanus** *Emery.*—A small yellowish form of this variety is common under stones in the Kohonino Forest on the rim of the cañon and occurs also but more sparingly at the Indian Garden. It is also common on the rocky hills about Prescott, Arizona, and Las Vegas, New Mexico, where the soil and elevation are like those on the rim of the cañon.

23. **Formica moki** sp. nov.

Worker. Length 4–5.5 mm.

Mandibles 8-toothed. Palpi long and slender. Head decidedly longer than broad, with rather straight sides, converging anteriorly, posterior margin straight, posterior corners rounded. Eyes large and convex. Clypeus with a very prominent keel, its anterior border entire, projecting in the middle. Antennæ slender, three basal funicular joints more elongated than joints 6 to 8; first and third joints equal, longer than the second joint; none of the joints less than twice as long as broad. Thorax long and narrow, in profile very low; pro- and mesonotum depressed, mesoëpinotal constriction shallow and very long at the bottom. Epinotum with flat basal surface, nearly twice as long as the very sloping declivity. Seen from above the pronotum is as long as broad, mesonotum nearly twice as long as broad. Petiole narrow, thick at the base, with sharp, horizontal upper border, and both the anterior and posterior surfaces, but especially the latter, distinctly flattened, so that the segment is cuneate in profile. Gaster small. Legs long and slender.

Subopaque; frontal area, sides of clypeus and bases of mandibles somewhat shining. Blades of mandibles rather coarsely striatopunctate. Head behind with a bronzy or glossy surface.

Body and appendages covered with fine grayish pubescence, which is densest and most conspicuous on the gaster and posterior portion of the head. sparser, but still readily discernible on the upper surface of the thorax and petiole and lower surface of the head. On the gaster a few of the hairs along the posterior borders of the segments are thick and obtuse. Legs with graduated, oblique, tapering hairs on the flexor surface of the tibiæ.

Dull reddish yellow; gaster dark brown or fuscous, as are also the posterior half of the head above, a large cloud on the pronotum, another on the mesonotum, the upper portion of the petiole, the coxæ, femora, and in some specimens also the apical half of each tibia. In some specimens the pleuræ also are more or less infuscated.

Described from 25 workers taken from a small colony under a stone on the wall of the Grand Cañon at an altitude of about 5500 feet and 2 workers taken on the rim in the Kohonino Forest (7000 feet) about three miles west of the Bright Angel Hotel.

This species seems to belong to the *Formica rufa* group although certain characters ally it with *F. fusca.* At first sight it resembles rather deeply colored specimens of the var. *neoclara* Emery of the latter species, but it differs from this and all the other North American *Formicæ* known to me in the very low and flat thorax and the length of the mesoëpinotal constriction. In these respects it approaches the forms of the *pallide-fulva* group, but the surface of the body is subopaque as in the smaller species allied to *F. rufa.* It will be impossible to assign *F. moki* to a precise position in the genus till the female is discovered.

24. **Formica fusca** *Linn.* var. **argentata** *Wheeler.*—Workers from one small colony of this subboreal variety were taken on the rim of the cañon at an elevation of a little over 7000 feet. No sharp line can be drawn between *argentata* and var. *subsericea* Say although it is easy to distinguish extreme specimens of the two varieties. *F. argentata* is more abundant in the western States at considerable elevations, *subsericea* in the eastern and middle States at lower altitudes.

25. **Formica fusca** *Linn.* var. **gnava** *Buckley.*—Numerous small colonies were found nesting in the grass and among the willows at the Indian Garden. The workers of this variety, which is quite distinct from the var. *neorufibarbis* Emery, in having the gaster much more pubescent and therefore more opaque, are indistinguishable from specimens taken from larger colonies in similar situations in other parts of Arizona (Ash Fork and Prescott and in Texas [Austin, New Braunfels, San Angelo, Fort Davis, Langtry, etc.]). This ant always prefers the moist shady banks of streams and is never found in the dry open country.

26. **Formica fusca** *Linn.* var. **neorufibarbis** *Emery.*—This variety, which is rare on the rim of the cañon at an elevation of 7000 feet, is similar in coloration and sculpture to *F. subpolita* Mayr, but lacks the erect hairs on the lower surface of the head. It belongs to the Canadian and Hudsonian zones and in the United States seems rarely to descend below 7000 or 8000 feet. In Colorado I have taken it only in the higher cañons and near timber-line on the mountains.

It is known to occur in Alaska, and in British America ranges as far east as Labrador and Nova Scotia.

27. **Formica fusca subpolita** *Mayr.*—Several colonies of this subspecies were seen nesting under stones in the Kohonino Forest on the rim of the cañon. It is common in similar situations throughout New Mexico, Colorado and California.

28. **Myrmecocystus melliger** *Forel.*—A single colony of a dark variety of the "honey ant", common in the deserts of southwestern Arizona, was seen between the upper limit of the granite and the *Coleogyne* zone, at an altitude of about 3000 feet.

29. **Camponotus maculatus vicinus** *Mayr* var. **nitidiventris** *Emery.*—Common in the Kohonino Forest on the rim of the cañon, where it forms populous colonies under large flat stones or even burrows in the open ground. In the latter case the nest-entrances are obscure and widely scattered craters. Winged females and males are common in the nests during May. Colonies extend down the cañon walls to an altitude of about 4000 feet. The variety is common at similar elevations in Arizona, New Mexico, and Colorado.

30. **Camponotus maculatus maccooki** *Forel.*—Several colonies of this ant were taken in the Kohonino Forest and down the walls of the cañon to an altitude of 5360 feet. Like the subspecies *vicinus* it nests under flat stones or in the open soil and resembles in its habits the var. *sansabeanus* Buckley of central Texas. I have taken it also on the rocky elevations about Prescott, Arizona, and in the vicinity of Manitou, Colorado.

The Ants of the Bermudas.

By William Morton Wheeler.

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Article XX.—THE ANTS OF THE BERMUDAS.

By William Morton Wheeler.

Professor Trevor Kincaid has recently sent me a small collection of ants, the study of which affords an opportunity of bringing together the little that is known concerning the ant-fauna of the Bermuda Islands. In this undertaking I have been materially aided by Professor A. E. Verrill's comprehensive work,[1] in which he has collected the scattered references to the Formicidæ. These references, together with the specimens taken by Professor Kincaid, indicate that the ant-fauna of the Bermudas is extremely meager. This is not surprising when we stop to consider the geological history of these isolated islands and the fact that their present terrestrial fauna and flora is very largely, if not exclusively, made up of species that have been introduced since glacial times by commerce or by purely accidental agencies. The ants certainly belong to widely distributed species, several of which have made their way as well-known tramps or stow-aways to many other islands besides the Bermudas. Even the single new species (*Prenolepis kincaidi*) described in the present paper is probably of West Indian origin.

There seem to have been times in the history of the Bermudas, however, when the ants made up in number of individuals for what they lacked in variety of species. This is shown by the extracts quoted by Professor Verrill from the works of Governor Butler[2] and Hurdis.[3]

In the following quaint passage Governor Butler mentions certain ants which were making the lives of the inhabitants uncomfortable as early as the beginning of the seventeenth century: "The moscitoes and flies also are somewhat over busie, with a certain Indian bugge called, by a Spanish appellation a caca-roche, the which, creepeinge into chestes and boxes, eate and defile with their dung (and thence their Spanish name) all they meet with; as doe likewise the little aunt, which are in summer time in infinite numbers; worms in the earth and mould also, ther are but too many (but of them we shall saye

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[1] The Bermuda Islands, an Account of their Scenery, Climate, Productions, Physiography, Natural History, and Geology, with Sketches of their Discovery and Early History, and the Changes in their Flora and Fauna due to Man, with 38 Plates and over 250 Cuts in the Text Reprinted from the Trans. Connecticut Acad. Sci., Vol. XI, with some changes. New Haven, Conn. 1902.

[2] Gov. Nathaniel Butler. Historye of the Bermudaes, 1609–22.

[3] John L. Hurdis. Rough Notes and Memoranda relating to the Natural History of the Bermudas. Edited by H. J. Hurdis from MS. notes mostly made from 1847–1855. London, 1897.

somewhat more by and by), as likewise the grass-hopper, and a certaine sommer-singinge great flie, the sure token of the established springe (and in that respect as the English nightingale and cukoe), whose loud note very much resemblinge the whirle of a spindle, hath caused herselfe thereby to be called the good-husewife." Hurdis mentions two species of Formicidæ, a house-ant and another ant of larger size which he supposed to be of West Indian origin: "Hill and dale and even the dwellings of men were equally alive with this insect pest. Dense columns of them might be seen travelling up and down every tree, and great was the havoc they occasioned among young pigeons and poultry, nor did the full-grown domestic rabbit escape their deadly attack, and pigs were sometimes destroyed by them." It is, of course, impossible to identify the species from these quotations. Hurdis's account may refer to the tropicopolitan fire-ant (*Solenopsis geminata*) or to *Monomorium destructor*, but whether he refers to one of these or to some other species, it is certainly of interest that no such species can be recognized among those enumerated by subsequent writers. He mentions the fact that the ant, after infesting Bermuda to a "fearful degree" for seven consecutive summers previous to 1848, was greatly reduced in numbers from some unknown cause. We must conclude that it has since become extinct or, at any rate, so rare as to have escaped the notice of subsequent collectors like Professor Verrill and Professor Kincaid. The supplanting of one species of ant by another is not unknown on other islands as I have shown in a recent paper.[1] In Madeira, for example, according to Stoll,[2] *Pheidole megacephala*, which was extremely abundant in the first half of the nineteenth century, as we learn from the careful work of Heer,[3] has been displaced by another tramp species, *Iridomyrmex humilis*. Stoll has also called attention to the extermination of the indigenous ant-fauna of the island of Reunion by *Plagiolepis longipes* of Cochin China.

If we omit the ants mentioned by Hurdis as unrecognizable, the following list comprises all the species known from the Bermudas:

Subfamily PONERINÆ.

1. **Ponera opaciceps** *Mayr.*—A deälated female and five workers collected by Professor Kincaid belong to the typical form of this species.

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[1] On Certain Tropical Ants Introduced into the United States. Entomol. News, Jan., 1906, pp. 23–26.

[2] Zur Kenntniss der geographischen Verbreitung der Ameisen. Mittheil. d. Schweiz. entomol. Gesell., X, 3, 1898, pp. 120–126.

[3] Ueber die Hausameise Madeiras. An die Züricher Jugend auf das Jahr 1852 v. d. naturforsch. Gesell. 54. Stuck, 1852, pp. 1–24, 1 Taf.

2. **Odontomachus hæmatodes insularis** *Guérin*.—This is evidently the form mentioned by Dahl[1] as *Odontomachus* sp. Among the material collected by Professor Kincaid during July, 1905, are a deälated female and several workers closely resembling in color, sculpture and pilosity the Bahaman variety of *insularis* which I have called *ruginodis*.

Subfamily MYRMICINÆ.

3. **Monomorium pharaonis** *Linn*.—I am inclined to believe that this cosmopolitan house-ant is the one mentioned by Professor Verrill as occurring in the Bermudas, and not *M. minutum*, of which he reproduces Marlatt's figure. The latter species is not a house-ant.

4. **Cardiocondyla emeryi** *Forel*.—A worker and two males collected by Professor Kincaid.

5. **Pheidole megacephala** *Fabr*.—This species was found in Bermuda by Dahl, who, like Professor Verrill, mentions it under the name of *Ph. pusilla* Heer. Professor Kincaid has sent me several males, winged and deälated females, soldiers and workers taken from at least four different colonies, and Prof. J. H. Comstock has sent me a soldier and worker. Professor Verrill mentions specimens from St. David's Island. It is probably very common throughout the Bermudas and may be responsible for the small number of species in the islands. It is not, however, a native of Madeira, as Professor Verrill states, but a well-known tropicopolitan ant, which, as above stated, overran that island in the first half of the nineteenth century. There can be little doubt that wherever it gains a foothold in tropical or subtropical countries it is able to propagate very rapidly, and to exterminate the indigenous ant-fauna. I have recently seen a good illustration of its habits in the Virgin Islands. During the past March I devoted ten days to a careful study of the aunt-fauna of the little island of Culebra off the eastern coast of Porto Rico without seeing a single specimen of *Ph. megacephala*. This island is, however, completely overrun with a dark variety of the vicious fire-ant (*Solenopsis geminata*). One day, on visiting the island of Culebrita, which is separated by a shallow channel hardly a mile in width from the eastern coast of Culebra, I was astonished to find it completely overrun with *Ph. megacephala*. This ant was nesting under every stone and log, from the shifting sand of the sea-beach to the walls of the lighthouse on the highest point of the island. The most careful search failed to reveal the presence of any other species of ant, though

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[1] Die Landfauna von Bermuda, in: Krummel, Reisebeschr. d. Plankton-Expedition. 1902, pp. 105-112, 1 Taf.

the flora and physical conditions are the same as those of Culebra! It is highly probable that *Ph. megacephala*, perhaps accidentally introduced from the island of St. Thomas a few miles to the east, had exterminated all the other ants which must have previously inhabited Culebrita. The absence of *megacephala* on Culebra is perhaps to be explained by the presence of the equally prolific and pugnacious fire-ant.

6. **Tetramorium cæspitum** *Linn.*—Professor Verrill says that he has recognized this species in the Bermudas. We should have expected the tropicopolitan *T. guineense* Fabr. instead, and venture to doubt the correctness of his identification. Although *T. cæspitum* has been introduced into the United States, I believe there is no record of its introduction into a subtropical country. *T. guineense*, however, is a well-known tramp species, occasionally found even in our northern hot-houses.

Subfamily CAMPONOTINÆ.

7. **Brachymyrmex heeri** *Forel.*—Numerous workers, winged females and males of the typical form of this diminutive ant were collected during July from two colonies by Professor Kincaid. This species together with the following variety has probably been introduced with plants from its original home in the West Indies.

8. **Brachymyrmex heeri** *Forel* var. **obscurior** *Forel.*—Three workers collected by Professor Kincaid.

9. **Prenolepis kincaidi** sp. nov.

Worker. Length 1.3–1.5 mm.

Head rectangular, a little longer than broad, as broad in front as behind. Eyes flattened. Clypeus very convex, subcarinate, its anterior border emarginate in the middle. Front with a transverse welt or swelling between the antennal insertions. Antennæ slender, scapes extending a little more than ⅓ their length beyond the posterior corners of the head. Thorax robust; pro- and mesonotum of about equal length; mesoëpinotal depression rather shallow and much shorter than the distance between the two stigmata. Epinotum rounded in front, flattened behind, without a distinct angle between the basal and declivous surfaces. Petiole small and narrow, with a blunt and rounded node. Gaster of the usual shape. Legs rather long.

Surface of body, especially the pleuræ, smooth and shining, without perceptible sculpture.

Hairs black, erect, obtuse and abundant on the head, thorax and gaster, more scattered on the legs. The antennal scapes have a few erect white hairs. Pubescence white, very sparse and visible only on the head and legs.

Body dark brown, head and gaster blackish above; antennæ, mouthparts, tibiæ and tarsi yellow.

Female. Length 3.5 mm.

Head about as long as broad, narrower in front than behind, with a straight posterior border. Clypeus convex, distinctly carinate, its anterior border very faintly emarginate in the middle. Antennal scapes extending about ⅓ their length beyond the posterior corners of the head. Front with a transverse ridge between the antennal insertions. Thorax robust, but little broader than the head, flattened above. Epinotum very sloping. Petiole much inclined forward, its posterior surface convex, its upper border sharp and feebly notched in the middle.

Subopaque; thorax, cheeks and posterior corners of the head smooth and shining.

Hairs like those of the worker but proportionally shorter. Pubescence gray, dense, especially on the gaster.

Dark brown; thorax paler, insertions of the wings, sutures and mouthparts yellow, as are also the tarsi and the articulations of the legs and antennæ. Wings grayish hyaline; veins brownish; stigma well-developed, dark brown.

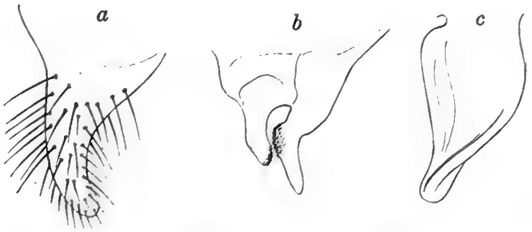

FIG. 1. *Prenolepis kincaidi* sp. nov. Male. *a*, outer; *b*, median, and *c*, inner genital valve.

Male. Length 2.3 mm.

Mandibles with an apical and a smaller subapical tooth. Thorax short, robust, with faintly rounded epinotum. Body shining. Pilosity and coloration as in the worker. Legs slender. Wings like those of the female but without a distinct stigma. Outer genital valves long, slender, and distinctly curved inward, with a blunt point and abundant but rather short hairs (Fig. 1, *a*). Outer process of median valve digitiform, somewhat bent in the middle and with the papillate surface at its tip; inner process nearly twice as long as the outer, slender and tapering, geniculate near its base and with the papillate surface on its basal half some distance from the slender tip (Fig. 1, *b*). Inner valve large, apparently twisted, and tapering to a blunt point like that of the outer valve (Fig. 1, *c*).

Described from four workers, two females and a single male taken from the same colony June 26, 1905, by Professor Kincaid.

I have described this species as new because I fail to find anything like it among the described American or Old World species of *Prenolepis*. In certain respects it resembles *P. anthracina* of Cuba, but

Roger's description of this species is too meager to admit of identification. *P. kincaidi* is evidently allied to *P. vividula* Nyl. and *P. bruesi* Wheeler, but the genital valves of the male are very different.

10. **Prenolepis** sp.—Seven workers, apparently all from the same colony, but varying much in size (from 2–3 mm.) They are very pilose and pubescent, with subopaque surface and finely punctate mesonotum. The species cannot be identified without the corresponding male, for, as Forel has shown, the only satisfactory diagnostic characters of the species in the difficult genus *Prenolepis* are to be found in the genital valves of that sex.

11. **Lasius niger** *Linn.*—This form is mentioned by Kirby[1] under its old name *Formica nigra* Linn. as occurring in the Bermudas. It was probably introduced, as he says, but whether from Europe or the United States it is impossible to ascertain.

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[1] On the Hymenoptera Collected during the Recent Expedition of H. M. S. "Challenger." Ann. Mag. Nat. Hist., ser. 5, XIII, 1884, pp. 403–413.

An Ethological Study of Certain Mal-Adjustments in the Relations of Ants to Plants.

By William Morton Wheeler.

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Article XXIV.—AN ETHOLOGICAL STUDY OF CERTAIN MALADJUSTMENTS IN THE RELATIONS OF ANTS TO PLANTS.

By William Morton Wheeler.

Plates LXIII–LXVIII.

Much has been written concerning the mutual helpfulness of certain species of ants and plants, but very little attention has been bestowed on the cases in which these organisms live together in a state of imperfect adaptation or antagonism. And yet such conditions may be expected to exist as the preliminary stage, if nothing more, in the course of development leading to such complete and harmonious adjustments as we witness in the symbiosis of certain ants, like the American Attii, with the fungi which they not only systematically cultivate but carefully transmit from mother to daughter colonies generation after generation. In the following article I have collected a few cases which seem to me clearly to prove the existence of a struggle between the ants and their plant environment, a struggle in which the ants, notwithstanding their notorious adroitness in surmounting obstacles to their welfare, seem always to succumb.

1. THE MOUND-BUILDING ANT AND THE HAIR-CAP MOSS.

Some months ago Mr. W. D. W. Miller of the American Museum of Natural History called my attention to a beautiful colony of the mound-building ant of the Alleghenies (*Formica exsectoides*) near Scotch Plains, New Jersey. This colony, which Mr. Miller visited with me during May and June, is situated in a wood on flat clayey soil, at an altitude of about 150 meters. The nests, forty to fifty in number, are scattered over an area of less than a square kilometer and are all built in open, sunny clearings among the trees. There are nests in all stages of growth, from their first inception to old extinct mounds covered with moss and other plants. The worker ants, in full possession of the surrounding woods, are everywhere to be seen, running about on the ground in search of dead and disabled insects, and climbing the trees and bushes for the purpose of collecting the honey-dew from the droves of aphids and membracids. Though less numerous, the nests near Scotch Plains compare very favorably in size with those of the famous colony near Hollidaysburg, Pennsylvania, described nearly thirty years ago by McCook.[1] With the aid of my assistant, Mr. Roy E. Miner, I measured eleven of the largest mounds and record their height, transverse diameter through the base and over the summit and the circumference in meters and in feet, in the following table:

No.	Height.			Basal Diameter			Diameter over Summit.			Circumference.		
	m.	ft.	in.	m.	ft.	in.	m.	ft.	in.	m.	ft.	in.
1.	.90	2	11.3	1.40	4	6.9	1.91	6	2.9	4.398	14	4.4
2.	.77	2	6.2	2.65	8	7.9	2.85	9	3.7	8.325	27	2.4
3.	.48	1	6.8	2.23	7	3.4	2.61	8	6.3	7.005	22	10.6
4.	.77	2	6.2	2.36	7	8.5	2.64	8	7.4	7.414	24	2.6
5.	.85	2	9.3	2.45	8	.04	2.92	9	6.5	7.696	25	1.6
6.	.95	3	1.2	3.61	11	9.5	4.00	13	.8	11.341	37	.6
7.	1.00	3	3.2	3.25	10	7.4	3.84	12	6.5	10.21	33	4.2
8.	.70	2	3.4	2.46	8	.4	2.61	8	6.3	7.728	25	3.
9.	.58	1	10.7	1.79	5	10.2	2.12	6	11.1	5.623	18	4.4
10.	.80	2	7.4	2.23	7	3.4	2.53	8	3.2	7.005	22	10.6
11.	.73	2	4.6	2.04	6	.10	2.43	7	11.3	6.408	20	11.2

The average height of these mounds is .78 m. (2 ft. 6.5 in.) with a basal diameter of 2.40 m. (7 ft. 10 in.), a convex diameter of 2.77 m. (9 ft. 5 in.) and a circumference of 7.55 m. (24 ft. 7.9 in.). They exhibit considerable differences in shape, some being more pointed or conical, others more depressed and rounded. Although unusually well developed, none of these hills reaches the dimensions of one measured by McCook (*l. c.*, p. 255). This, the largest on record, was 1.07 m. (3 ft. 6 in.) in height, 7.34 m. (24 ft.) in diameter over the summit, and 17.75 m. (58 ft.) in circumference.

The mounds of *F. exsectoides* undoubtedly answer the same purpose as those of *F. rufa* in Europe and certain of its varieties in this country. As Forel has shown, these accumulations of detritus serve as incubators for the brood, since their temperature during the day is, of course, much higher than that of the underground portions of the nests. Unlike the mounds of *F. rufa*, however, those of *F. exsectoides* consist very largely of earth and only to a very limited extent of vegetable detritus and pebbles. McCook is certainly in error when he writes (*l. c.*, p. 270) that "every hill furnishes a fair measure of the extent of the underground system of galleries connected therewith; for it is reasonably certain that the entire bulk of soil in each mound has been excavated and brought from the galleries beneath the sur-

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[1] Mound-building Ants of the Alleghenies. Trans. Am. Entom. Soc., VI, 1877, pp. 253–296, pll. ii–vi, 13 text-figs.

face." On the contrary, it is probable that much of the earthen material of the mounds, like all the vegetable detritus, is collected by the foraging workers from the surface of the area surrounding the nest. This material is brought together and built into the mound in the very same manner as the harvesting ants *Pogonomyrmex barbatus* and *P. occidentalis* collect their pebbles, and *F. rufa* its vegetable detritus. The interior of the mound of all these ants is riddled with galleries in which the larvæ and pupæ can be kept during the warm hours of the day for the purpose of accelerating their development.

It is not only an easy matter to observe any of our mound-making ants in the act of picking up and carrying materials to its nest, but the nature of the materials in certain localities is indisputable proof of such activity. Along the railroad tracks through Indiana, Ohio, and western New York, may be seen dozens of mounds of *F. fusca* var. *subsericea* covered with a thick layer of locomotive cinders that have been carefully collected by the worker ants. Even more striking is the same habit in *Pogonomyrmex barbatus* var. *molefaciens* along the railways of Texas, and in *P. occidentalis* in similar situations in Colorado and New Mexico. The large nest cones are often so black with cinders as to stand out in very sharp contrast with the pale surrounding soil. Along the Chicago, Burlington & Quincy R. R. for many miles east of Denver, Colorado, the nest cones of *occidentalis* close to the track are deep black, while those further away, to a distance of about thirty or forty meters, show a gradual fading in color, with the decrease in available cinders, to the light-colored nests of the open plains beyond. Recently, while collecting ants near Florissant, Colorado, I came upon a colony of three nests of *F. exsectoides* var. *opaciventris*. One of these, near the Colorado and Midland R. R. track, was heavily covered with cinders like the nest cones of *P. occidentalis* above described. Cinders in such situations are, of course, very suitable material for retaining the sun's heat, but it would be going too far to attribute to the ants any knowledge of their value in incubating the brood. Any particles of such a size and shape as to be conveniently carried to the nest, will be collected by these indefatigable insects. At Ash Fork, Arizona, I found some of the cones of *P. occidentalis* covered with the dung-pellets of spermophiles, and Wasmann has recently observed a similar habit on the part of the European *F. pratensis*, which, in certain localities, covers its nest with the dung-pellets of rabbits and the dried flower-heads of *Centaurea*.

Even more interesting than the dimensions and composition of the *exsectoides* nests is the fact that they show very clearly some of the conditions which lead to their ultimate decay and abandonment by the ants. Observations made near Scotch Plains, together with those I have collected in some other localities (Staten Island, Highland-on-Hudson, Colebrook, Conn.), show that these structures pass through the following evolutionary and involutionary stages:

1. The incipient nest. In a previous article[1] I maintained that nests of *F. exsectoides* may be established in two different ways: first by the association of a recently fertilized female with workers of her own species from the maternal or some neighboring colony, and the emigration of the company thus formed, followed by the construction of a new nest in a different locality, and second, by the association of a recently fertilized female with an effete or queenless colony of the common black ant (*F. fusca* var. *subsericea*). In the latter case the female remains with the host species until her first brood of workers matures and the host workers have perished. Then, the object of this temporary parasition having been accomplished, the pure *exsectoides* colony is able to multiply rapidly and without extraneous assistance. In this, the earliest stage in the development of the colony, the nest is, of course, that of *F. subsericea*, a low obscure mound overgrown with long grass and perforated with numerous entrances. Even when the colony is pure from the start, however, that is, when a young female associates herself with workers of her own species, the nest is of this same character as shown in my former paper (*antea*, Pl. XII, Fig. 1). Similar nests were seen in the Scotch Plains colony in close proximity to the large mounds.

2. As the ants keep enlarging their nest it takes on a somewhat different appearance. They deposit large quantities of earth and vegetable detritus on the summit of the mound and kill off the grass in this region, so that the mound comes to have a bare summit and is surrounded by a broad belt of tall grass This grass belt, to which the numerous openings of the nest are largely confined, is usually thinned out by the ants to admit the sun's light and warmth to the soil in which it grows. Two young nests of this description are represented in my former paper (*antea*, Pl. XIII, Figs. 1 and 2). The grass zone is occasionally retained until the nest reaches a large size. This is the case in the one figured on Pl. LXIII, which is No. 11 of the table on p. 404.

3. Most nests, however, that have attained a large size and are

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[1] On the Founding of Colonies by Queen Ants, with Special Reference to the Parasitic and Slave-making Species: Bull. Am. Mus. Nat. Hist., XXII, 1906, pp. 33–105, pll. viii–xiv.

inhabited by colonies or parts of colonies at the acme of their prosperity and development, are completely or almost completely free from grass. There can be no doubt that this vegetation usually succumbs to the sharp mandibles of the ants. A number of nests of this description, appearing as compact earthen mounds, covered only with a small quantity of vegetable detritus, were seen in a large clearing near Scotch Plains. Four of these are shown in Pl. LXIV. They were all smaller than any of those measured for the above table.

4. This stage is characterized by a growth of moss which first makes its appearance in a narrow band around the extreme base of the mound just above a shallow, moat-like depression about 20 cm. in diameter which often encircles the nest and separates it from the surrounding surface. This moss is *Ditrichum pallidum*,[1] a species which is too small and delicate to interfere with the activities of the ants. In the course of time it is partly or completely supplanted by a larger and more vigorous species (*Polytrichum commune*), which begins to form a densely tufted zone around the base of the mound. This moss is rarely found in the woods near Scotch Plains except on the ant-hills, and I was at a loss to account for its singular distribution till Mrs. Britton informed me that it is preëminently a bank-loving species. As the soil of the woods is very level, the plant naturally takes to the only bare elevations in the vicinity. It is not improbable that the *Ditrichum* may in some way prepare the soil for the growth of the *Polytrichum*. Pl. LXV represents the largest nest in the colony (No. 8 of the above table), which had a zone of *Ditrichum* 10-20 cm. broad around its base, but too delicate to show in the photograph. Plates LXVI, LXVII, and LXVIII show that the *Polytrichum* zone continually widens until only a small area at the summit of the mound, the umbilicus, is left uncovered. In Plate LXVII it has invaded a nest which retained a well developed grass zone, but this is evidently destined to disappear before the advancing moss. Nests over which the *Polytrichum* carpet is far advanced are invariably depauperate. The ants are few in number and seem to be rather inactive, a condition undoubtedly attributable to the growth of the moss. This plant has very hard, tough stems and roots, which the ants are unable to sever, so that they cannot dispose of it as they do of grass and other plants. It chokes up the basal zone of entrances, or at any rate grows so densely as to make them

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[1] For kindly identifying the mosses mentioned in this paper I am indebted to the well known bryologist Mrs. Elizabeth G. Britton.

inaccessible to the insects. The densely tufted moss is much like fur and seriously impedes the insects in going to and from the nest, so that in some nests invaded by the *Polytrichum*, a second zone of entrances had been constructed nearer the summit and along the inner edge of the moss zone. In one of the large twin nests (No. 6) shown in Pl. LXVI the ants constantly made a bridge of a fallen log running from the ground to the umbilicus. It is certain, moreover, that the moss, which absorbs and retains quantities of water and therefore reduces the temperature of its surroundings, must impair the usefulness of the mound as an incubator.

5. The *Polytrichum* carpet continues to grow at its upper edge until it envelops the summit of the mound and extinguishes the ant community. In one mound of this description, with an uncovered area only 20 cm. in diameter, a few lethargic ants still lingered in the earth of the summit; from other similar and older nests they had completely disappeared. While the dense carpet continues to expand,, herbaceous, and even woody plants of many species begin to settle on the mounds and eventually in great part completely replace the moss. The mound subsides somewhat, probably owing to the collapsing of its galleries and chambers, and becomes flatter and less conical. It may still be recognized, however, after the lapse of years as was shown by one mound which supported bushes with stems 5--6 cm. in diameter. On these advanced nests at least three other mosses (*Dicranella heteromalla*, *Catherinea angustata*, and *Hypnum recurvans*) may be seen growing singly or in company.

Do the ants emigrate and seek a new nesting site when the invasion of the *Polytrichum* becomes intolerable, or do they gradually die off without deserting the mound which they have reared with such diligent solicitude? This is a difficult question to answer, because a single *exsectoides* colony may extend over several mounds and these may be connected by subterranean galleries. The fact that the ants in mounds invaded by *Polytrichum* have all the appearance of relicts smitten with the weariness and dejection so characteristic of old and depauperate ant communities, certainly favors the view that the insects die off *in situ*.

It is equally difficult at present to answer the question as to the time required to bring about the changes described in the above stages. The age limit of the nest was considered by McCook (*l. c.*, pp. 265-267), who concluded that he had "good reason to believe that some of the hills are at least thirty years old." This estimate is probably as close as any that can be obtained until some one actually watches the growth of a mound from its inception to its decay.

It would be important to know whether the above stages may be detected in the development of the *exsectoides* nests throughout the range of the species. Incidental remarks in McCook's work seem to indicate that the nests in Pennsylvania present the same peculiarities which I have described. He mentions (p. 254) twenty nests near Warrior's Mark, in Blair County of that State, as " abandoned and covered with moss and grass." And on page 256 he says: " Many a romance of ant life lies hidden within those silent moss-covered mounds." "I have thought that some of these abandoned hills have been reoccupied as they carry a moss-grown and ancient appearance, although in full activity."

For any observations corresponding to those recorded for the Scotch Plains colony it is necessary to turn to the works of European writers. Europe possesses a species of Formica (*F. exsecta*) which is not only so like *exsectoides* in color and structure as to have suggested the name of the American species, but is also very similar in some of its habits. These have been studied by Forel,[1] Wasmann,[2] and more recently by Holmgren.[3]

F. exsecta lives in bogs and meadows, at lower altitudes in the north but in southern Europe on high hills or mountains. According to Wasmann, "The architecture of the nest is, generally speaking, a small edition of that of the fallow ant (*F. rufa*), both in regard to its dimensions and the materials employed. It consists of much finer substances, dried grass-blades, heather leaves, etc., and contains a much greater admixture of earth. The heaped-up vegetable detritus, so characteristic of all so-called 'ant-hills,' forms in this case only the top; beneath it lies a layer of densely felted grass-stems, grass-roots and soil, in which the true galleries and the chambers of the nest are excavated and whence they extend further down into the earth. The form of the nest is that of a strongly truncated cone. Almost never have I seen nests, either in Vorarlberg or in the Rhineland, with an arched dome like that of *F. rufa*, but almost invariably only such as had a flat top like that of *F. pratensis*. In mountain meadows the cone is sometimes 50 cm. or more in height, its circumference 1 or

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[1] Les Fourmis de la Suisse. Zürich, 1874, pp. 191, 192.

[2] Formica exsecta Nyl. und ihre Nestgenossen. Verhand. naturhist. Ver. Rheinl. Westf., 1894, I Heft.

[3] Ameisen (*Formica exsecta* Nyl.) als Hügelbildner in Sümpfen. Zool. Jahrb., Abth. f. Syst., XX, 1904, pp. 353-370, 14 text-figs.

even 1.5 m. The cone of the *exsecta* nest is, speaking more precisely a crater, consisting of soil and felted plant growth, filled in at the top with dry vegetable detritus. The nests therefore belong to Forel's 'combination nests,' in which an earthen substructure is combined with a superstructure of plant detritus. The *exsecta* nest is peculiar in having the earthen portion much more extensive than the top and enclosing it like a crater."

The development and decay of the nests of this ant have been studied near Aborrträsk in Gellivare, Lapland, with results that show a remarkable similarity to the conditions above recorded for the American *exsectoides*, if we make due allowance for the fact that the European ant nests in damp meadows or bogs whereas our American species prefers dryer soil or even hill-slopes covered with open woods.[1]

I here reproduce the summary of Holmgren's observations:

"1. The ant-hills in the willow zone are larger, but less numerous than those in the *Sphagnum* zone of the bogs. The greater size depends on the accessibility to more abundant building materials. Their smaller number is likewise attributable to the same conditions, since a greater number of ants are constrained to secure their food and building materials in a relatively small area. Migration for the purpose of founding new nesting sites is unnecessary on a large scale where food and especially building materials are abundant. Access to an abundance of the latter also explains the fact that in the willow zone the nests are not overgrown by *Polytrichum strictum*, for here the ants can inhibit the invasion of the moss by uninterrupted building.

"In the *Sphagnum* zone, however, building materials are scarce and on this account the ant colonies must be smaller and migration occurs on a larger scale. This accounts for the smaller size and greater number of ant-hills in this zone.

"In the damp bog, building materials are relatively very scarce. Here the hills are very much reduced in size and number. Owing to the moisture in this zone there are few spots that will permit the ants to build hills, for these insects require rather dry soil in which to establish themselves.

"2. The position of the hills in damp places prevents the ants

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[1] There are in America two other forms closely related to *F. exsectoides*, namely *F. exsectoides* var. *opaciventris* Emery and *F. ulkei* Emery. The former is known only from Colorado, where it nests in dry, open situations at an altitude of 6000–8000 ft. Its nest-cones resemble those of the typical *exsectoides* in shape but are covered with pebbles instead of vegetable detritus. *F. ulkei* which is unquestionably a boreal species, was originally described from South Dakota, but I have recently received worker and female specimens from Nova Scotia. Its nesting habits are unknown but probably resemble those of *exsecta* or *exsectoides*.

from establishing any large general trails when they go forth to forage. Where the base of the nest is completely surrounded by water, they are either completely isolated or must climb from leaf to leaf along the plants until they reach *terra firma*. In general, such hills undergo no further additions to their bulk.

"3. Plants are rather quick to gain a foothold on the ant-hills. The first and main vegetation of the nests is *Polytrichum strictum*, which forms a dense carpet. The condition which leads this moss to its invasion is the comparative dryness of the nest. The *Polytrichum* carpet gradually spreads until it completely covers the hill.

"4. The remaining plants that creep up onto the hills usually belong to species growing in the immediate neighborhood. Other plants are rarely found and these grow on the umbilicus or summit which they have reached as seeds and where they have found a place suitable for germination.

"5. The outer form of the ant-hill depends on the carpet of *Polytrichum*. If this moss advances onto the hill from the side, the substance of the nest flows over, so to speak, onto the opposite side. In other words, the ants continue to add to the mound on the uninvaded side. One observes, moreover, that the nest-substance always spreads in the directions where the moss carpet is least developed. In other words, the ants withdraw as the *Polytrichum* carpet advances.

"6. Owing to the conditions stated in the preceding paragraph, the basal portions of the ant-hill are abandoned by the ants *pari passu* with the advance of the carpet. This takes place step by step. The ants do not leave the basal portions till the carpet has risen too far. This explains why the inhabited portions of the nest extend down deepest into the hill where the diameter of the umbilicus is greatest.

"7. Another result of the invasion of the *Polytrichum* is the pronounced reduction in the number of ants in the hill due to emigration, since they are unable to add to the mound, while its habitable portion is continually growing smaller. These conditions account for the greater number of ant-hills in the zone of *Sphagnum* hummocks.

"8. When the *Polytrichum* carpet has reached a certain height the ants cease to build. This follows directly from the preceding paragraph.

"9. The *Polytrichum* carpet steadily advances till it displaces the ants completely.

"10. The apparent aversion shown by the ants for the inner portions of the hill already covered by the *Polytrichum* is due to the fact that the moss attracts and retains water, so that these portions become rather moist and therefore unsuitable as a dwelling for the insects.

"11. It follows as a general conclusion from paragraphs 5–10 that there must be between the *Polytrichum* and the ants a severe struggle in which the moss is always victorious.

"12. *Sphagnum* often gains a foothold on the hill before the *Polytrichum* has completely overgrown the summit, or umbilicus. *Sphagnum*, generally speaking, displaces *Polytrichum*. This is certainly the case wherever the *Polytrichum* hills have not been destroyed. From this follows:

"13. The *Polytrichum*-hummocks are converted into *Sphagnum*-hummocks through a displacement of the former by the latter moss; and this is the end-product of the ant-hills.

"The most general conclusion reached in the foregoing paragraphs is that the ants play an important rôle in the formation of hummocks in the bogs under consideration, since the hills serve as growth-foci for the moss and peat vegetation."

Holmgren has also observed that in Lapland the nests of another ant (*F. rufa*) are gradually overgrown by boreal plants (*Vaccinium vitis idæa, myrtillus* and *uliginosum* and *Rubus chamæmorus*). In this case also the plants creep upward from the base of the hill, gradually driving the ants to the summit and eventually extinguishing the colony.

According to a footnote in the excellent work of my friend Dr. K. Escherich of Strasburg[1] a struggle between ants and mosses like that recorded by Holmgren and myself seems to occur in certain parts of Germany. He says: "Dr. A. Ludwig brought me from a bog in Grunewåld near Berlin a number of dried masses of *Polytrichum strictum*, the basal half of which was perforated with chambers and galleries. The inhabitants of these, a species of *Myrmica*, are driven out by the increasing moisture due to the gradual intrusion of water-storing *Sphagna*." Escherich also mentions similar observations made by Kuhlgatz in the bogs of Western Prussia.[2]

Whether a similar displacement of ants by mosses occurs among such American bog-ants as *Myrmica rubra brevinodis*, which, as I have shown in a former paper,[3] nests in hummocks of *Polytrichum commune*, and *Formica cinerea* var. *neocinerea*, which I have found

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[1] Die Ameise. Schilderung ihrer Lebensweise. Braunschweig, 1906, 232 pp., 68 text-figs.

[2] Vorstudien über die Fauna des Betula nana-Hochmoores im Culmer Kreis in Westpreussen Nordd. Wochenschr., n. F. I, 1902, p. 613.

[3] Ethological Observations on an American Ant (Lepthorax Emersoni Wheeler), Arch. f. Psych. u. Neurol., II, 1903, pp. 1–31, 1 fig.

nesting in large grassy hummocks in meadows from Colorado to Illinois, must be determined by renewed observations.[1]

2. THE TENT-BUILDING ANT AND THE PITCHER PLANT.

While engaged in making the observations on the habits of the tent-building ant (*Cremastogaster lineolata*) recorded in a former article[2] I came upon another instance of maladaptation very different from that described in the preceding paragraphs. The tent-building ant is one of the most plastic and adaptable of our North American Formicidæ. This is shown both in its wide variability over an extensive geographical range and in its ability to construct, often at a considerable distance from its nest, beautiful carton or earthen tents over its herds of aphids and coccids. We should expect such an ant to be more than ordinarily skilful in evading or circumventing the wiles of inimical plants. This, however, seems not to be the case. While examining the pitcher-plants (*Sarracenia purpurea*) in the bogs about Lakehurst, New Jersey, I found the ascidia, or pitchers, in many cases partially filled with the dead remains of *Cremastogaster lineolata pilosa*, a subspecies which seems to be characteristic of boggy spots in the pine barrens. Undoubtedly thousands of workers of this ant are annually destroyed and consumed by these apparently passive insect-eating plants.

The extremely interesting devices whereby the plants of the North American genus *Sarracenia* are able to entrap great numbers of insects, have been described by several botanists, notably by Vogt,[3] Hooker,[4] Mellichamp,[5] Schimper,[6] Zipperer,[7] Macfarlane,[8] and Meehan.[9] Macfarlane, especially, has gone into the subject in considerable detail and has given many figures illustrating the development and structure of the pitchers in all the species of *Sarracenia* (*S. flava*,

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[1] The Occurrence of *Formica cinerea* Mayr and *Formica rufibarbis* Fabr. in America Amer. Natur., XXXVI, 1902, pp. 947–952.

[2] The Habits of the Tent-building Ant, *Cremastogaster lineolata* Say. Bull. Am. Mus. Nat. Hist., XXII, 1906, pp. 1–18, pl. i–vi.

[3] Phytohistologische. Beiträge, II, Die Blätter der *Sarracenia purpurea* Linn. Sitzber. K. K. Akad. Wien, 1865, I Bd. pp. 281–300, 2 Taf.

[4] Address to the department of Botany and Zoölogy. Report 44th Meet. Brit. Assoc. Adv. Sci. Belfast (1874) 1875, pp. 102–116

[5] *Sarracenia variolaris.* Amer. Natural., XI, 1877, pp. 432–433.

[6] Notizen über insectenfressende Pflanzen. Botan. Zeitg., 40 Jahrg., 1882, pp. 226–234, 242–248.

[7] Breitrag zur Kenntniss der Sarraceniaceen. Munich, 1885.

[8] Observations on Pitchered Insectivorous Plants. Part I, Ann. Botan., 1889–1890, pp. 253–266, pl. xvii; Part II, *ibid.*, 1893, pp. 403–458, pl. xix–xxi.

[9] *Sarracenia variolaris.* Meehan's Monthly, IV, 1894, p. 1, 2. pls.

drummondi, rubra, variolaris, purpurea, and *psittacina.*[1] While the general structure is the same in all of these, there are interesting differences in detail in the various species. In all the outer surface of the pitchers is furnished with scattered, honey-secreting cells, which Macfarlane appropriately calls "alluring glands," since they attract the insects, especially the ground-loving species, like the ants, and lead them to the orifice of the pitchers. In *S. purpurea* there are small upwardly directed hairs on the outside of the pitchers, while the inside presents a series of surfaces modified in such a way as to lead the insects to their death in the liquid contained in the bottom. For these surfaces Macfarlane has adopted the names proposed by Hooker. The uppermost portion of the pitcher lining, the so-called "attractive surface," is covered with short downwardly directed hairs. Below this there is a smooth slippery surface ("conductive surface") which is succeeded in turn by a densely "glandular surface" not represented in the other species of the genus. And finally the lowermost region presents a "retentive surface" furnished with long downwardly directed hairs. The hairs on the attractive and retentive surfaces prevent the insects from returning to the mouth of the pitcher, while the smooth conducting surface coöperates in offering a very insecure foothold, so that the insects fall into the liquid, usually present in the bottom, and are there eventually digested and in part absorbed by the plant tissues.

The prevalence of ants in the bottom of *Sarracenia* pitchers has been noticed by several observers. Mr. E. Daecke informs me that he has seen these organs of *S. purpurea* half full of dead *Cremastogaster* workers in the bogs near Bamber Station, New Jersey. Riley,[2] after describing the pitcher of *S. variolaris* of the Southern States, says: "The insects which meet their death in this pitcher comprise numerous species and of all orders; but as one might naturally infer, the ubiquitous, honey-loving ant is the principal victim." And Macfarlane makes a similar observation on our northern form: "I have had the opportunity of examining *S. purpurea* in the New Jersey swamps, and find that the ground-game, notably ants, are largely caught by the pitchers. Flying insects and slugs are not uncommon, and though bulk for bulk they may yield a considerable food supply for the plants, Hooker's supposition [that the pitchers

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[1] More recently he has published observations on another species (*S. catesbæi*) from the Southern States (The History, Structure and the Distribution of *Sarracenia catesbæi.* Contrib. Bot. Lab. Univ. Pa., II, 1904, pp. 426–434).

[2] Descriptions and Natural History of Two Insects which Brave the Dangers of *Sarracenia variolaris.* Trans. Acad. Sci. St. Louis, III, 1874, pp. 235–240, 2 figs.

are especially adapted for catching ground-game] appears correct for this species. In one specimen examined, a large nest of ants had been established in three of the older and rather dry brown leaves, just beneath the reddish green leaves that were actively catching prey."[1]

That these insects should actually inhabit the old leaves of a plant whose fresh leaves are so admirably adapted to their destruction, is a reflection on ant "intelligence," especially in view of the fact that some other animals have learned to turn the insect-eating habits of one of the species of *Sarracenia* to their own advantage. Meehan (*l. c.*) cites an observer who has seen birds hanging about the pitchers of *S. variolaris* and even splitting them for the sake of feeding on the entrapped insects, and Riley (*l. c.*) describes the larva of a moth which feeds on the leaves of the same *Sarracenia* and a carrion fly whose larvæ actually develop in the macerating insects at the bottom of the pitchers. The moth is *Exyra semicrocea.* "The egg is laid within the tube and the young larva covers the smooth surface with a fine gossamer-like web, generally closing up the mouth by webbing the lips together. As it increases in size it frets the leaf within, feeding on the parenchyma and leaving only the epidermis. The ochre-colored excrement falls in pellets to the bottom of the tube, where it gathers in a compact mass above the putrid remains of the insects which have been captured before the closing of the mouth. The transformations are undergone in a slight cocoon usually constructed just above the mass of excrement. There are at least two broods of the insect each year, the first larva appearing during the early part of May, the second toward the end of June."[2] The development of the fly (*Sarcophaga sarraceniæ*) is thus described by Riley: "The mother fly drops her living larvæ within the tube to the number of

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[1] On August 29, while the manuscript of this article was being copied for the printer, Miss Delia Marble had the kindness to send me several fine specimens of *Sarracenia purpurea* from a bog near Bedford, New York. The pitchers contained no specimens of *Cremastogaster* but instead species of two other genera, namely, several dead workers of a variety of *Formica fusca* near *subænescens*, two dead females of *Dolichoderus mariæ*, which does not nest in bogs, and in one of the old and somewhat withered pitchers, a fine living colony of *D. plagiatus pustulatus* var. *inornatus*, a rare ant of which I had never before seen the nest. This colony contained numerous pupæ and winged females. A search through the insect remains in the pitchers on the same and other plants failed to reveal any traces of *inornatus* workers. During September Mr. E. Daecke sent me from Toms River, New Jersey, a small, partially dried pitcher of *S. purpurea* in which he had found a living colony of another ant, *Tapinoma sessile.* Can it be that these ants have learned to exploit the *Sarracenia* without being entrapped?

[2] More recently Mr. F. M. Jones has published an interesting paper (Pitcher-Plant Insects, Entom. News, XV, 1904. pp. 14–17, pls. iii. and iv.) on the moths that breed in the pitchers of *S. flava.* He enumerates three species (*Exyra ridingsii*, *semicrocea* and *rolandiana*). He also finds that a solitary wasp (*Isodontia philadelphica*) builds its nest in the pitchers.

upward of a dozen, and these easily find their way to the bottom, where they feed on the softer parts of the macerating insects which have accumulated there. As a rule but one of the *Sarcophaga* larvæ matures, the others having fallen victims to its gluttony and superior strength. When full fed, or rather when it has appropriated all the nourishment at hand, this maggot works through the tube (by this time weakened and decayed at the base) and burrows in the ground, where it undergoes its transformations, and whence in a week or more, according to the season, the fly emerges."

A few years ago Dr. J. B. Smith discovered another dipterous insect, a mosquito (*Wyeomyia smithii*) whose larval and pupal stages develop in the liquid of the pitchers of *S. purpurea.*[1] Mr. Daecke writes me that he has found the *Wyeomyia* larvæ near Bamber Station, New Jersey, in pitchers in which so many *Cremastogasters* had been drowned, that he "wondered how they could exist, since the water must have been laden with formic acid." According to Dr. Smith these larvæ do not need to come to the surface of the liquid to breathe, like the larvæ of *Culex*, and even lived "for nearly two weeks under a film of oil which covered the surface of their breeding jar." He also finds that this insect winters in the *Sarracenia* pitchers "in the larval stage, freezing and thawing as often as need be during that season. It pupates late in May and becomes adult a week or ten days later. Eggs are laid in the leaves singly or in small groups; fastened to the sides or floating on the surface. The summer broods mature in about a month, and there are probably three if not four series; but the broods overlap so much that the breeding is practically continuous. Late in the season the adults select the new leaves for oviposition even if they are yet dry." [2]

It is evident that if the ants had sufficient intelligence to gnaw holes in the walls of the pitchers, they could not only enter and leave these organs at will, but also visit the nectaries and perhaps secure plenty of insect food with impunity. Although *Cremastogaster* has not yet developed this ability, there is no reason to suppose that it may not do so in the course of time. I am led to entertain this possi-

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[1] Ent. News, XXII, 1901, pp. 180, 254; Life History of Aëdes smithii Coq., Journ. N. Y. Ent. Soc., X, 1902, pp. 10–15; see also for a description of the larva: H. G. Dyar, Descriptions of the Larvæ of Three Mosquitoes. Journal of the N. Y. Ent. Soc., IX, 1901, pp. 177–179, pl. x, figs. 1–2.

[2] The above mentioned insects are by no means the only ones that can live in the *Sarracenia* pitchers. While examining the plants sent me by Miss Marble I found, in addition to the *Wyeomyia* two other fly larvæ that manage to thrive and develop in the digesting insect remains at the bottom of the pitchers. One of these was a *Chironomus* larva, present in considerable numbers in several of the pitchers, the other was apparently a Tipulid larva, of which only a single individual was seen.

bility because Vosseler[1] has recently seen some African ants which actually accomplish a similar feat. These insects were very fond of entering the immature flowers of *Cobæa scandens* and cutting away the woolly accumulation of hairs at the base of the bell-shaped corolla in order to reach the nectaries. When Vosseler plugged the opening of the corolla with cotton, the ants gnawed holes in the base of the flower and thus attained their end in the directest manner possible.

3. MYRMICA AND THE SUN-FLOWER.

Professor T. D. A. Cockerell has recently called my attention to a third case of maladjustment in the relations of ants to plants. In the neighborhood of Boulder, Colorado, he has repeatedly seen masses of ants (*Myrmica rubra brevinodis* var.) attracted and killed by the sap that exudes from broken stems and petioles of the sun-flower (*Helianthus annuus*). This plant is very abundant in the lower ground about Boulder, and its sap, as I can testify from personal observation, becomes excessively sticky on exposure to the air, so that an ant that has once touched it with its legs or antennæ is held fast until it perishes. In this case it is difficult to see how the plant can profit by destroying the insects, for the catastrophe is purely accidental, depending on an occasional injury to the plant. A typical specimen showing a number of dead ants partially embedded in the inspissated sap, was kindly forwarded to me by Professor Cockerell and is represented in the accompanying figure. It is interesting as showing on a small scale the way in which ants and other insects became embedded in such substances as amber and copal.

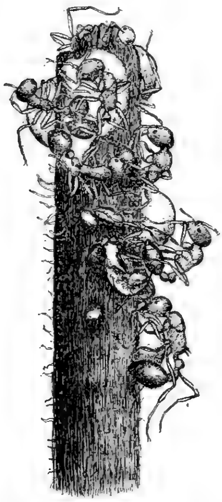

Fig. 1.—Broken twig of Sunflower, showing ants (*Myrmica brevinodis*) caught and killed by the exuding sap.

Professor Cockerell surmises that this fatal condition, in which, as in the preceding instances, the ants succumb, may be due to the meeting of two organisms originally belonging to widely separated biogeographical environments; the *Myrmica* being essentially a northern or subboreal species, while the sun-flower represents an austral element which has, during comparatively recent times, invaded the domain of the *Myrmica*. This view, which is certainly

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[1] Verhinderung des Fruchtansatzes bei Cobæa durch Ameisen. Zeitschr. f. wiss. Inseckt. Biol., II, 1906, pp. 204–206.

plausible in this instance, will not, however, apply to the preceding cases, for the *Polytrichum* and *Formica exsectoides* are both subboreal organisms, and the pitcher-plant and *Cremastogaster pilosa* are both of subtropical origin, and there is every reason to believe that these organisms have been associated with each other for long periods of time. It seems natural to suppose that in all the cases described in this article the havoc wrought by the plants is not sufficiently great seriously to impair the vitality of the respective species of ants. In other words, the drain of a heavy annual destruction of individuals or even colonies may be easily borne by organisms capable of reproducing so rapidly and abundantly as these insects.

EXPLANATION OF PLATES.

Photographs of *Formica exsectoides* mounds found near Scotch Plains, New Jersey. The dimensions of the nests are given on p. 404 under their respective numbers.

Plate LXIII. Nest No. 11, of unusually large size and still retaining the broad basal zone of sparse grass so characteristic of younger nests.

Plate LXIV. Four nests (not included in the table on p. 404) from a group of several in a clearing. These nests had been denuded of all grass by their ant inhabitants.

Plate LXV. Nest No. 7, the largest of the colony. It was surrounded by a zone of moss (*Ditrichum pallidum*) which, however, does not show in the photograph.

Plate LXVI. Twin nests invaded by moss (*Polytrichum commune*). The one in the foreground is No. 6 of the table on p. 404.

Plate LXVII. Nest No. 10, showing the zone of *Polytrichum* advancing and extinguishing the grass zone of an earlier stage (conf. Plate LXIII).

Plate LXVIII. Nest No. 8, showing the *Polytrichum* zone far advanced toward the summit, or umbilicus, which it will eventually cover.

LARGE NEST OF *Formica exsectoides* WITH GRASS-ZONE.

DENUDED NESTS OF *F. exsectoides.*

LARGE *F. exsectoides* NEST WITH ZONE OF *Ditrichum pallidum.*

TWIN NESTS OF *F. exsectoides* WITH ZONES OF *Polytrichum commune.*

NEST OF *F. exsectoides* WITH ZONES OF GRASS AND *Polytrichum*.

Nest of *F. exsectoides* with Advanced *Polytrichum* Zone.

The Polymorphism of Ants, with an Account of Some Singular Abnormalities Due to Parasitism.

BY WILLIAM MORTON WHEELER.

AUTHOR'S EDITION, extracted from BULLETIN
OF THE
American Museum of Natural History,
VOL. XXIII, ARTICLE I, pp. 1–93, pll. i–vi.
New York, January 15, 1907.

(Continued from 3rd page of cover.)

ETHNOGRAPHICAL ALBUM.

Jesup North Pacific Expedition.

Ethnographical Album of the North Pacific Coasts of America and Asia. Part 1, pp. 1–5, pll. 1–28. August, 1900. Sold by subscription, price, $6.00.

BULLETIN.

The matter in the 'Bulletin' consists of about twenty-four articles per volume, which relate about equally to Geology, Palæontology, Mammalogy, Ornithology, Entomology, and (in the recent volumes) Anthropology, except Vol. XI, which is restricted to a 'Catalogue of the Types and Figured Specimens in the Palæontological Collection of the Geological Department,' and Vols. XV, XVII, and XVIII, which relate wholly to Anthropology.

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BULLETIN

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VOLUME XXIII, 1907.

59. 57, 96: 11.51

Article I. — THE POLYMORPHISM OF ANTS, WITH AN ACCOUNT OF SOME SINGULAR ABNORMALITIES DUE TO PARASITISM.

BY WILLIAM MORTON WHEELER.

PLATES I–VI.

The study of sex determination among organisms — a subject obviously included under the greater problem of the origin of variation, since sexual dimorphism is the most striking and constant form of intraspecific variability both in animals and plants — and the related but much more restricted problem of polymorphism, have of late attracted the attention of many biologists. A perusal of some of the literature bearing on these subjects, however, has convinced me that the simplicity of the questions involved may have been overestimated. That this is especially true of polymorphism as manifested in the social insects, will, I believe, be evident from a consideration of the facts recorded in the following paper. At any rate, it will not be a difficult task to show that we are still very much in the dark concerning the fundamental causes of the differentiation of one sex into several distinct phases, and, while it may be urged that the problem of polymorphism as it is presented by the social insects, may be more complicated than that of sex, on purely *a priori* grounds the opposite view would seem to be the more probable, for polymorphism is undoubtedly not only a more restricted phenomenon but one of much more recent phylogenetic and ontogenetic development, and hence presumably dependent on conditions both more specialized and more amenable to observation and experimentation. While the observations recorded in this article suggest both the need of experiment and some of the points at which the problem is open to this method of investigation,

[January, 1907]

they indicate with equal force that the causes of polymorphism may be so recondite as to give little encouragement to the crude physiological methods at present available. In other words, much water will have to flow through the biological mill before we possess sufficient knowledge of the physiological chemistry of such small organisms as the insects, to enable us to determine the exact nature of the subtle influences that decide whether an ant or bee shall become a queen or a worker.

The following observations relate to some of the unusual or pathological individuals occasionally found in ant colonies, and referable, with more or less probability, to trophic disturbances induced by specific parasites. The inferences from these cases have a value approaching those derived from experiment, since the phenomena make their appearance only under very definite circumstances.

PART I. OBSERVATIONS.

1. The Parasitism of Orasema and other Chalcididæ on ants.

A. Orasema viridis Ashmead.

This beautiful Chalcidid is abundant in Texas in the nests of *Pheidole kingi* André subsp. *instabilis* Emery, but only from May to September. For this reason I failed to notice it till May 25, 1903, about six weeks before I moved from Austin to New York, although during my four years' residence in Texas I had examined hundreds of *instabilis* nests during the autumn, winter, and early spring months. I was so much impressed with the peculiar behavior of the *Orasema* and the ants that I devoted to the subject every available moment of the short remainder of my sojourn in Texas, but the necessary preparations for my departure, the intense heat, which sets in during the month of May, and a peculiar misunderstanding of the conditions under which the *Orasema* develops, seriously interfered with the progress of my work. It was only after I had left Texas that the study of preserved material led me to what I believe to be a correct interpretation of the life history of the insect.

Before describing the *Orasema* and its development it will be necessary to say something about the host. *Ph. instabilis* is a common ant in central Texas and certain parts of Mexico, at least as far south as the State of Morelos, where I have taken it near Cuernavaca. It forms populous colonies which prefer to nest under stones in sunny places. In central Texas it is often found in bottom lands and waste places where the soil is rich and supports an open growth of grasses and especially of Crotons (*Croton texensis* and *C. monanthogynus*). It is a harvesting species and stores the flat chambers of its nests with innumerable seeds collected from all the plants in the neighborhood. Like other harvesting ants, however, it does not confine itself to a vegetable diet, but eagerly seizes on any insect food that may fall in its way.

In common with other members of the great genus *Pheidole, instabilis* presents four phases known as the soldier, worker, female and male respectively. The soldier is 4–4.5 mm. long. The shape and extraordinary proportions of its head are shown in Plate I, Fig. 1, and Plate V, Fig. 63 *o*. Its gaster is black and shining, the mandibles and clypeus are dark brown, the remainder of the head, thorax and appendages reddish brown.

The head is subopaque and elaborately sculptured as shown in the figure. The worker (Pl. I, Fig. 7, and Pl. V, Fig. 63 *c*) is only 1.5–1.8 mm. long. It is shining throughout, and of a dark brown or black color with yellowish appendages. The female (Pl. I, Fig. 8 and Pl. V, Fig. 63 *a*), which measures 5.5–6 mm., is dull black, with the legs, antennæ, mandibles and anterior half of the head yellow. The wings (removed in the specimen figured) are yellowish hyaline with pale veins. The male (Pl. I, Fig. 9 and Pl. V, Fig. 63 *e*) is a much smaller and more graceful insect than the female, measuring only 4–4.3 mm. Its head and gaster are black, its thorax and appendages sordid yellow, the former with pale sutures. Its wings resemble those of the female.

While *instabilis* agrees with its congeners in having the four phases just described, it differs from all except a small group of North American species of *Pheidole* in presenting in every well-developed colony a series of individuals intermediate in size, structure, and sculpture between the soldier (Pl. I, Fig. 1) and the worker (Pl. I, Fig. 7). This series, which is very complete in large colonies, is represented in Plate I by a few selected individuals (Pl. I, Figs. 2–5 and Pl. V, 63 *r*). The occurrence of such intermediate forms, though well-known in some other genera of ants, like *Solenopsis* and *Camponotus,* is so unusual in the genus *Pheidole* as to call for the special explanation which I shall attempt to give in the sequel. It is also an interesting fact that the organs are not always reduced in size in strict correlative proportions as we descend the series of intermediate individuals from the soldier to the worker. As shown in Plate I, Figs. 5 and 6, for example, the antennal scape may be of the same length in two individuals which differ considerably in the size of the head. Or, again, as shown in figure 4, the scape may be longer in one individual than in others with larger (Pl. I, Fig. 3), or smaller heads (Pl. I, Figs. 5 and 6).

The acme of the colonial activities of *Ph. instabilis* is attained during the latter part of May and the first weeks of June. Then the nest is full of eggs, larvæ, pupæ, and callows of all the castes and presents a bewildering appearance, owing to the fact that the brood is not assorted according to ages, as in many ants, but lies jumbled together in the different chambers and galleries. The functions of the workers and soldiers are clearly distinct. The former are far and away the more numerous, and notwithstanding their diminutive size, may be said to manage the affairs of the colony. They collect the seeds and dead insects and drag them to the nest. They excavate the galleries, feed the brood and carry even the huge female larvæ and pupæ from chamber to chamber and assist the callows in escaping from their pupal envelopes. The soldiers act as carvers, or trenchers of the tough insects and hard seeds brought in by the workers. Their powerful mandibles admirably fit them for this office and for guarding the nest. They are often seen to form a stationary cordon about the brood and the callows in the chambers. They are never seen to eat the seeds or insects which they cut up for the other members of the colony but are fed on liquid food regurgitated by the workers. They are very stolid and inactive, very rarely leave the nest and never assist in carrying the larvæ and pupæ about. Their heads are so large in proportion to their bodies that, when dropped on their backs on a smooth surface like that of glass or polished wood, they are often unable to right themselves and may die standing on their heads. The intermediates are much more active and may be seen to leave the nest, collect food, carry larvæ and, in short, perform all the duties of the workers which they approach in their smaller size and smoother sculpture.

The larvæ of all the castes are provided with several pairs of flexuous, anchor-tipped dorsal hairs, by means of which they may be temporarily fixed to the earthern walls of the chambers or to the rough surfaces of the stone covering the nest. While in this position they are fed by the workers with bits of crushed seeds or insect fragments in the same way as the larvæ of the Ponerine ants. At least the younger larvæ of the males and females, however, appear to be fed largely, if not exclusively, with regurgitated liquid food.

Ph. instabilis is very common at Austin in the bottom and along the banks of a small limestone cañon, known as Shoal Creek. There, during May and June, 1903, I found a great number of colonies. Several of them were confined in artificial nests of the Fielde pattern and one was kept under observation till the latter part of September. I also preserved whole colonies in alcohol after killing them in water heated to 80° C.

Fully half of the colonies examined were found to contain the peculiar parasites which Dr. W. H. Ashmead has kindly identified for me as *Orasema* *viridis* Ashm., a Chalcidid fly originally described from specimens collected at large by Mr. E. A. Schwarz near San Diego, Texas.

The genus *Orasema,* which belongs to the subfamily Eucharinæ, was originally established by Cameron on *O. stramineipes* from Panama, in the 'Biologia Centrali-Americana'.[1] According to Ashmead,[2] this genus is characterized by the possession of 10-jointed antennæ in both sexes, and in having the right mandible two-toothed, the left with a single tooth, and both mandibles acute and falcate at their tips. The genus appears to be largely restricted to tropical and subtropical America but extends somewhat further north in the western than in the eastern portion of the United States.

The female *O. viridis* (Pl. I, Fig. 10, and Pl. V, 63 *m*) measures 2.5–3 mm. and is deep metallic green with the clypeus and thoracic dorsum more golden and the gaster blue or violet. The head, thorax and petiole are uniformly and densely punctate, the gaster very smooth and shining. The legs are honey-yellow, excepting the middle portions of the femora, which are metallic green, and the terminal tarsal joints, which are black. The antennæ are black, with the basal joints yellow, as are also the mandibles, tongue, and palpi. The wings are very clear and iridescent. The epinotum and scutellum together form a rounded cone through which the thorax reaches a greater vertical diameter than it does elsewhere. The male (Pl. I, Fig. 11, and Pl. V, Fig. 63 *n*) is distinctly smaller than the female (2.3–2.5 mm.) and differs in having a much longer petiole, a much shorter and smaller gaster, and longer and thicker antennæ, with the basal joints black instead of yellow.

On opening a large *instabilis* nest a dozen or more of these superb insects may be seen lying on their sides or creeping about among the ant-brood (Pl. V, Fig. 64). It is also easy to recognize their pupæ, white when young or nearly ready to hatch, of a dull blue-green color when mature, scattered among the larvæ and pupæ of their hosts. Such nests present a splendid appearance, reminding one of a jewel casket in which the sapphires and emeralds are represented by the *Orasema,* the pearls by the larvæ and pupæ, the opals by the iridescent wings of the parasites and of the male and female ants, the garnets and bits of jet by the glistening black and red seeds and the red heads and black bodies of the soldiers.

As soon as the nest is disturbed, the workers seize the *Orasemæ* and their pupæ and, even at the risk of neglecting their own brood and callows, carry them bodily to a place of safety. In artificial nests this great fondness for the *Orasema* may be witnessed at one's leisure. The adult parasites are not only carried about and continually licked and fondled, but are also fed

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[1] Vol. I, 1883–1900, pp. 104, 105, pl. v, fig. 20, pl. vi, fig. 18.

[2] Classification of the Chalcid Flies or the superfamily Chalcidoidea. Mem. Carnegie Museum, No. 4, 1904, pp. ix, 225–551, pll. xxxi-xxxix.

by regurgitation as if they were workers. They usually submit to these effusive attentions passively, but at times they may be seen to struggle and disengage themselves from the embraces of their hosts. When fully mature both sexes of the *Orasema* become highly phototropic and endeavor to escape from the dark nest to the open air and sunshine. The ants, however, redouble their attentions and carry them back to the dark chambers. Although usually aided by the workers in hatching from their pupæ, the *Orasemæ* themselves often remove the pupal envelopes from their antennæ by rubbing them with their fore legs, and, though fed by the ants, they sometimes visit and partake of the sugar in artificial nests. They spend much of their time in lying on their sides among the ant larvæ and pupæ. While the workers thus appear to be infatuated with their beautifully sculptured and brilliantly colored parasites, the latter are not sufficiently hypocritical to feign any interest in their hosts. They are, in fact, interested only in the ant brood and, as I shall show, only in a certain portion of the brood.

As several successive broods of *Orasema* pupæ appeared and hatched in my artificial nests, I was sure that the larval stages must also be present. These stages, it would seem, should be readily detected, but for a long time I was completely misled in my search for them, and even after I had found them, I was deceived by their appearance. This arose partly through certain prepossessions based on analogy with what I had read about other Chalcidids, and partly through the confusion produced by the high degree of polymorphism in the *Pheidole.* As nearly all Chalcidid larvæ are internal parasites in other larvæ, I was under the impression that the *Orasemæ* also start their life cycle within the larvæ of their hosts, and certain peculiarities in the *Orasema* larvæ merely tended to strengthen this prepossession. The great number of larval and pupal forms of the ant added to my confusion, especially as some of their larvæ differed in shape according to their feeding. Thus for a time I regarded certain small, spherical, sexual larvæ, fed with regurgitated liquids, as the young larvæ of *Orasema.* It was not till after I had left Texas and had nothing but preserved and stained material at my disposal that I succeeded in gaining a clear idea of the early larval stages of the parasite.

I have not seen the eggs of *O. viridis* after oviposition, but only the very young larvæ. Dissection of the female shows that, as we should expect in a parasite, the eggs are extremely numerous and minute. The mother insect, when she comes to oviposit, exercises a very careful selection among the ant brood. In the first place she has nothing to do with the *instabilis* larvæ but directs her attention to the pupæ. In the second place she selects, as a rule, only the pupæ of the soldiers, males, and females. The small worker pupæ would not furnish sufficient food for her larvæ. In the third place she selects only pupæ at the very critical moment when they have just been stripped of their larval skin by the workers and are, therefore, little more than semipupæ, for obviously at this moment the cuticle is thinner and will be more easily pierced by the young *Orasema* larva than during the preceding or succeeding stages. And in the fourth place, she does not lay her eggs at random anywhere on the body of the semipupa but carefully selects one of four regions near the head. Usually she places the egg on the sternal surface just beneath the still very short, incurving legs of the semipupa but occasionally it is placed on the back of the neck between the head and the prothoracic segment, or on the right or left side of the neck beneath the corresponding prothoracic leg. These regions would seem to be singularly appropriate, both because the cuticle of the semipupa is extremely thin and readily punctured by the parasitic larva at these points, and also because the egg or resulting larva, especially when it is covered with the overlapping appendages of the semipupa, is not so readily brushed or licked off by the *instabilis* workers. I believe that the danger of detaching the egg is very great and this, together with the other special requirements above enumerated, may account for the fact that comparatively few of the great number of *Orasema* eggs ever complete their development.

Further reflection shows still greater appropriateness in the time and place selected for oviposition by the mother *Orasema.* In the sexual semipupæ of *instabilis,* and especially in those of the soldiers, the small anterior end of the body is destined to grow very rapidly and to undergo extraordinary changes in structure. For this purpose carefully elaborated liquid substances of a very high nutritive value are suddenly propelled into the anterior portion of the body of the semipupa, which therefore appears tense, clear, and transparent in this region, while the abdominal region is full of opaque, nonmetabolized fat cells. The parasitic larva is thus situated from the first at a point where it has ready access to a rich food supply and is able to grow with surprising rapidity.

The instinct that leads the mother *Orasema* to oviposit with such precision is not, however, infallible. As the number of soldier and sexual pupæ in an *instabilis* colony is always very limited compared with the number of worker pupæ, the *Orasema,* impelled, apparently, by the need of getting rid of her eggs, sometimes oviposits on the latter, although even in such cases also, she chooses the cervical and sternal region. The interesting consequences of this instinct aberration will be considered in a later paragraph.

Several of the youngest *Orasema* larvæ seen are represented in Plate II, Figs. 30–35. They are extremely small — less than .1 mm. in length — and of a dark brown color. The head is distinct and furnished with short, acute mandibles; the body consists of a number of sharply marked segments, of which the anterior are longer and broader, the posterior smaller and often telescoped into one another so that it is difficult to ascertain their exact number. There are probably three thoracic and ten abdominal segments. The terminal segment bears a pair of hair-like cerci. Were it not for the absence of legs, these larvæ might be regarded as campodeiform and likened to the youngest stages of such parasites as the Stylopidæ and Meloidæ. Several of my preparations show these larvæ attached to the necks of worker semipupæ or pupæ, as represented in Plate II, Fig. 13. Twice I have seen a pair of these larvæ attached symmetrically on the sides of the same pupa. In other cases they were found on the nuchal or sternal surfaces.

So different are these minute, sharply segmented and dark brown larvæ from those of other Chalcidid larvæ, of which I have seen descriptions or figures, that I should never have regarded them as belonging to the life-cycle of *O. viridis*, had I not seen stages like those represented in Plate II, Figs. 14 and 15. These figures represent semipupæ of *instabilis* soldiers with undoubted *Orasema* larvæ .3 mm. in length attached, in the one case to the sternal surface between the pro- and mesothoracic segments, in the other to the nuchal surface. In Plate II, Fig. 14, the larva has its long axis at right angles to that of its host; in Fig. 15 the parasite and host are similarly oriented. The dark brown segments of the younger larva are represented in both cases by dark bands on a yellowish white background. The cerci have disappeared. The larvæ have plunged their mandibles into their host and have begun to absorb its juices, and this has led to a separation of the more heavily chitinized sclerites and great expansion of the intervening membranes.

Succeeding stages in the growth of these larvæ are shown in Plate II, Figs. 16, 17 and Plate V, Fig. 66. All of these represent female semipupæ of *instabilis*, and in each the *Orasema* larva, which is attached as in Fig. 14, has attained a length of .7–.9 mm. In Plate II, Fig. 17, which is drawn from a stained and mounted specimen, the parasite is somewhat shrunken through dehydration and clearing, but in Fig. 16, from an alcoholic specimen, the skin of the larva is smooth and tense. The fact that all traces of the dark bands have disappeared is probably due to the intervention of an ecdysis between this stage and the one represented in Figs. 14 and 15. It was stages like Figs. 16 and 17, which were first seen in my artificial nests and led me to an erroneous interpretation. The parasite in this stage was yellowish and semitransparent, while the semipupa to which it was attached was opaque, waxy white and more or less shriveled. The larva, moreover, seemed to make its appearance very suddenly, and this, coupled with the fact that the ants kept licking it till its surface glistened with saliva, led me to suppose that it had reached its full growth within the ant-larva and was just breaking through the integument on the nuchal or sternal side. I saw the workers, which evinced the greatest interest in this phenomenon, pull the larva away from the semipupa and throw aside the latter, now reduced to a sickly mass, though still retaining enough of the contents of the abdomen and of its original form to be recognizable as a pupa, notwithstanding the fact that the head, as shown in Fig. 16, was much smaller than in the corresponding stages of the nonparasitized soldiers and females.

Shutting my eyes to the correct interpretation of the above stages as indicating that the larva was ecto- instead of entoparasitic, I stained and mounted *in toto* whole series of soldier and female larvæ and young pupæ in the hope of finding the *Orasema* larvæ prior to their eruption. This search proved, of course, to be futile, and I was baffled until I accidentally found the crucial stages represented in Plate II, Figs. 13 to 15.

The growth of the parasite, after it has plunged its mouthparts into the integument of its host, must be extremely rapid. I doubt whether the stages above described require more than a couple of days for their completion. Such rapid growth, however, is not surprising when we consider the accessibility and high nutritive value of the food on which the larva subsists.

As soon as the full-grown *Orasema* larva has been separated from its prey, it begins to pupate. Occasionally the ants are either unable or neglect to detach the parasite. In such cases, two of which are shown in Plate II, Figs. 18 and 19, the larva begins to pupate *in situ*. It undergoes an ecdysis in which it is undoubtedly assisted by the workers, and then appears as a short, thick-set semipupa, slightly constricted just in front of the middle of its body. Another ecdysis seems to follow almost at once, leaving the semipupa covered with a peculiar envelope studded with large blisters, or pustules. These are arranged segmentally in regular rows along each side of the body but are absent in the middorsal and midventral regions. I am unable to assign any function to these singular organs, which in *O. viridis* disappear with the semipupa stage. On focussing through the pustulate envelope the semipupa is seen to present the appearance of Fig. 20 (Pl. II). The imaginal head, with its large eyes and antennæ, is embedded in a hood-like prothoracic mass; the legs and wings are clearly indicated. A little later the pustulate envelope is shed and the complete, pure white pupa of the *Orasema* is seen enclosed in a thick membrane (Pl. II, Fig. 22) which, in the intersegmental regions of the abdomen, is thrown into prominent transverse welts. The color, which now gradually deepens, becoming first blackish and then metallic green, is dimmed by the rather opaque, white pupal envelope (Pl. II, Fig. 23). Soon after this stage is reached, the insect hatches. The changes from the stage represented in Fig. 21 to that of Fig. 23 can hardly require more than three or four days. If this and my estimate concerning the rate of development in the earlier stages is correct, we must suppose that *O. viridis* completes its entire life-cycle, from the egg to the imago, in less than a week or ten days. Similarly rapid developments are known to occur in other Chalcidids, as I infer from the following statements in an interesting paper published some years ago by Howard[1]: "Ratzeburg has shown that in Europe *Pteromalus puparum* occupied on one occasion from June 11 to July 14 to undergo its entire transformation from egg to adult — thirty-seven days; but in this country Webster has recorded an instance (Insect Life, I, 225) in which the eggs of the same parasite were laid August 9, the adult insect developing August 27 — seventeen days later. Hubbard has noted (Fourth Report U. S. Ent. Com., p. 103) that the egg of *Aletia xylina* gives forth the adults of *Trichogramma pretiosa* on the seventh day after it was stung by its parents. *Euplectrus comstockii* has been shown by Schwarz to develop from egg to adult in Alabama in midsummer in seven days."

There can be little doubt that in a state of nature the male and female *Orasemæ* leave the nest very soon after hatching and mate in the open fields. This is indicated by their strong positive phototropism. The fertilized females then seek out fresh *Pheidole* nests in which to lay their eggs. In one of my artificial nests, however, which was kept from June 19 to September 20, three successive broods of *Orasema* were noted, the last disappearing about a week before the latter date. In this case, unless the offspring arose from parthenogenetic eggs, the males and females must have mated in the nest. Both in this and other cases it was found that the adult *Orasemæ*, after they had remained in the nest for several days, were killed and dismembered by the workers, as though the parasites had at last been recognized as predatory aliens. This slaughter, however, may have been due to other causes, since the workers also killed and dismembered their own females and ultimately reared only workers and intermediates, probably because these required less nourishment. Such conditions point to a deterioration of the colony and are frequently observed in artificial nests inadequately furnished with food. Similar behavior on the part of workers may be seen in other species of ants when the food supply becomes insufficient or is no longer palatable. Under these circumstances I have seen *Camponotus ferrugineus* workers kill and dismember their soldiers and *Myrmica brevinodis* workers do away with their males.

Before concluding this account of the relations of *O. viridis* to *Ph.*

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[1] The Biology of the Hymenopterous Insects of the Family Chalcididæ. Proceed. U. S. Nat. Mus., XIV, 1892, pp. 567–588.

instabilis, it will be necessary to return to the worker semipupæ on which the *Orasema* occasionally deposits her eggs. In such cases the young larvæ of the parasite must be very inadequately fed and probably soon die and fall off, leaving their hosts in a depleted condition but still able to pass on to the pupal stage. Now in all the nests infested with *Orasema,* and only in these, I have found a number of peculiar pupæ like those represented in Plate II, Figs. 24–26 and Plate V, Fig. 65 *s*, and differing from the normal worker pupæ (Fig. 27) in several important characters. They are smaller, of a waxy white color, with more decided intersegmental constrictions and are broad behind and very narrow anteriorly. The head is remarkable for the very small size of the brain and eyes and the situation of the latter on distinct stalks. The mandibles, too, are abortive. The resemblance of the head to depleted female pupæ, like the one represented in Fig. 16, is very striking. The thorax is extremely slender and the gaster has a high fold on each side, and in balsam preparations (Pl. II, Fig. 26 and Pl. V, Fig. 67 *i*) is seen to contain a number of large urate masses in the *corpus adiposum.* In many specimens the gaster is concave ventrally, with its tip turned upward and forward. Although these singular pupæ are carefully cleaned by the workers and kept with the normal individuals, they never succeed in hatching. After lying in the chambers for many days without even acquiring a deeper color of the body or pigment in the eyes, they are either carried to the refuse heap or eaten by the workers. I am convinced that these extraordinary pupæ, which may be called *phthisergates,* have arisen from worker semipupæ that have had part of their juices sucked out by *Orasema* larvæ, so that only enough formative material was left to produce pupæ with very defective head and thorax and hence quite unable to develop as far as the imaginal instar. It is interesting to note that these microcephalic, microphthalmic, and stenonotal characters represent merely greater diminution of the similar characters of the normal workers as compared with the more macrocephalic, macrophthalmic, and eurynotal soldiers and females. The theoretical bearings of these conditions will be considered in the latter part of this article. The depleted semipupæ of the *instabilis* females and males, which like the phthisergates are incapable of further development, may be called *phthisogynes* and *phthisanērs* respectively.

In this connection the question naturally suggests itself: are the intermediates between the *instabilis* workers and the soldiers due to similar depletion in their semipupal stages? In other words, do the intermediates arise from soldier semipupæ that have been partially exhausted by *Orasema* larvæ prematurely torn from their hosts by the workers? I am inclined to answer this question in the negative, for reasons to be given in the sequel.

After finding *O. viridis* so common in the nests of *Ph. instabilis* I was naturally led to look for it in the company of other Texan species of *Pheidole*. This search soon revealed the fact that the parasite can make its home also with other ants of this enormous genus. June 16, I found a single female *viridis* in a flourishing colony of *Ph. dentata* Mayr at Alice, Texas, which is only about ten miles east of San Diego where the types of the parasite were originally captured by Schwartz. *Ph. dentata,* it should be noted, is a carnivorous species with sharply separated soldier and worker castes, as represented in Plate III, Figs. 37 and 38. June 21, I again found at New Braunfels, Texas, a colony of this same *Pheidole* containing a few female pupæ of *O. viridis.* In this colony, which was kept for some weeks in an artificial nest, four phthisergates made their appearance. One of these is represented in Plate II, Fig. 28. They differed considerably in form from the *instabilis* phthisergates and had slightly pigmented eyes. These organs, however, as well as the head and thorax were notably reduced as compared with those of the normal worker pupa, which is essentially like that of *instabilis* (Pl. III, Fig. 27).

A little later in the month (June 24), I came upon a colony of a hitherto undescribed *Pheidole* (*Ph. sciophila* sp. nov.), containing a number of imagines and pupæ of *O. viridis.* This ant, like *Ph. dentata,* has no forms intermediate between the soldiers and workers. It is a rare species, nesting under stones in rather damp, shady places in the vicinity of Austin. These observations prove that *O. viridis* is not confined to a single host ant but has international relations with a number of species of the genus *Pheidole* in central and southern Texas. It may be expected to occur also in the nests of *Ph. crassicornis, Ph. hyatti, Ph. morrisi,* etc. Still another observation goes to show that the parasite is not confined to Texas, but is also probably widely distributed through Mexico. In my collection there is a female specimen of *O. viridis* taken August 4 at Tuxpan, in the state of Jalisco, by Mr. J. F. McClendon. As this specimen was found in a bottle containing a mixed lot of ants comprising three species of *Pheidole,* besides some species of other genera, I am unable to refer it to a particular host.

B. Orasema coloradensis Ashmead.

During August, 1903, while collecting ants in Colorado, I came upon a second species of *Orasema,* which Dr. Ashmead has identified for me as *O. coloradensis,* in the nests of two very different species of ants: One of these is a larger and usually darker form of a small *Solenopsis,* which I take to be *S. molesta validiuscula* Emery, the other *Pheidole vinelandica* Forel.

O. coloradensis (Pl. I, Fig. 12 and Pl. V, Fig. 68 *m*) is of about the same size as *O. viridis,* but is readily distinguished by its longer, lower, and smoother thorax, and less prominent scutellum and epinotum. In coloration it is like the Texan species, except that the thorax is less golden above and the mesopleuræ are more shining. In the male the petiole is shorter and the tibiæ are more or less infuscated. The mature pupæ of the two species are very readily distinguished by the character of the last pupal envelope. In *coloradensis* (Pl. IV, Figs. 53 and 54) this is pustulate like the semipupal envelope of *viridis*, the pustules appearing on the abdomen as dilatations in the transverse intersegmental welts above described for *viridis*. Then, too, the pupal skin of the Colorado species has a series of large pustules extending along the middorsal line of the epinotum and abdomen and about the front of the pronotum where they are completely absent in *viridis*.

O. coloradensis was first noticed August 3, in a colony of *S. validiuscula* (Pl. V, Fig. 68) at Manitou. The ants with their brood were confined in a bottle for the purpose of rearing some of their numerous male and female pupæ. The tiny workers were seen to spend much time shampooing an adult female *Orasema*. Later other females and a few males hatched in the nest and were cared for by the ants like members of their own species. In the course of a few days two of the *Orasemæ* were found dead on the refuse heap, one having been decapitated and shorn of its legs and wings. This led me to wonder whether the *Solenopsis* workers which are themselves parasitic and feed on the larvæ and pupæ of other much larger ants of the genera *Formica, Myrmica, Cremastogaster*, etc., are quicker than the species of *Pheidole* to recognize the *Orasemæ* as aliens after they have been reared. August 11, while collecting near Broadmoor, south of Colorado Springs, I found two more infested *Solenopsis* colonies. This *Solenopsis* was paler than the form taken at Manitou, and in this respect approached the typical *molesta*. In one of these colonies I counted twenty pupæ and adult *Orasemæ*. At the same time I noticed that there were very few male and female pupæ of the ant. The other colony, which contained nearly as many of the parasites, was living in cleptobiosis with a large colony of *Formica ciliata* Mayr. As *S. molesta* has only one form of worker, and this of minute size compared with the males and females and since, moreover, the males and females of *O. coloradensis* are of about the same size as the corresponding sexes of the ant, I infer that the larvæ of the parasite must feed exclusively on the sexual forms, while the tiny workers enjoy complete immunity from their attacks.

In the same locality in which I saw the *Solenopsis* nests above described, and on the same day, I found two colonies of *Pheidole vinelandica* containing the same species of *Orasema*. One of these colonies was taken alive and placed in a Fielde nest. A careful examination of the worker brood revealed the presence of a single phthisergate with somewhat pigmented eyes and very similar in shape to those of *Ph. dentata* above described. This phthisergate had neither hatched nor changed its appearance by August 29 — 15 days later. It eventually disappeared (eaten by the workers?). The colony was kept for several weeks but as no second brood of *Orasema* appeared, it was abandoned. August 20 I found near Beaver Ranch, southeast of Colorado Springs, a third infested *vinelandica* colony. This two was kept in an artificial nest, but the observations revealed nothing that has not been recorded for *Ph. instabilis* and *O. viridis.* According to Forel, *Ph. vinelandica* occasionally produces intermediates between the typical soldiers and workers, but although I have collected many colonies of this ant in different parts of the United States, I have seen only the typical soldiers and workers.

The foregoing observations prove that *O. coloradensis,* like *O. viridis,* does not confine its depredations to a single host ant. It may be said to be even more catholic in its habits, since it not only infests a species of *Pheidole* but also attacks ants belonging to the very different genus *Solenopsis.* The number of colonies observed was not sufficient to show which of these genera represents the original and more frequent host, but, judging from analogy with *O. viridis* and the next species to be considered, there can be little doubt that this is *Ph. vinelandica. O. coloradensis* probably occurs also in the nests of *Ph. pilifera* var. *coloradensis* and *Ph. ceres,* both common ants in the neighborhood of Colorado Springs and other localities of about the same altitude.

C. Orasema wheeleri Ashmead.

A third species of *Orasema,* which Dr. Ashmead will describe as *O. wheeleri,* was found July 14, 1902, on Keesy's Ranch at Fort Davis, Texas, in the nest of *Pheidole ceres* Wheeler. This ant is a small, dark colored species which makes obscure nests in the shade of the cotton-woods (*Populus fremonti*) and garners the woolly seeds of these trees. The *Orasema* was seen in only one of the nests, and though about a dozen pupæ were found among the ant brood, only a single mature specimen, which happened to be a female, could be secured. It measures 2.7 mm. and closely resembles *O. viridis,* especially in the shape of the scutellum and epinotum, but the thorax is broader and stouter. The last pupal envelope, like that of *viridis,* is without pustules, though it has strong intersegmental welts in the abdominal region.

I have examined many colonies of *Ph. ceres* near Fort Davis and in various Colorado localities without finding any intermediates between the soldiers and workers. In the single colony infested with *O. wheeleri,* however, there were several of these annectant forms. As this could hardly be a mere coincidence, we must assume that there is some connection between the existence of intermediates and the presence of the parasites.

D. Other Chalcidid Ant-Parasites.

From the observations recorded in the above paragraphs we may safely conclude that the remaining *Orasema* species, of which quite a number have been described by Cameron, Howard, and Ashmead, are parasitic on ants and have life-cycles analogous to that of *O. viridis.* Still other genera, however, of the enormous family Chalcididæ, contain ant-parasites and these, though very imperfectly known, may be passed in review before I proceed with an account of a very different type of parasitism. For the sake of convenience we may distinguish three groups of cases, first the ant-parasites of the sub-family Eucharinæ exclusive of *Orasema,* second those belonging to other subfamilies, and third, the cases too imperfectly known to be referred to any particular genera.

Among students of the Chalcididæ the opinion seems to have been gaining ground that the Eucharinæ, which according to Ashmead's recent synopsis (l. c. pp. 266–270) comprise some 25 genera, are largely, if not exclusively ant-parasites. Ashmead says that in this group "are found some of the most singular looking and wonderfully shaped Chalcids known, the structure of the thorax, and particularly of the scutellum, being most wonderfully and curiously modified and developed; and this development, in connection with the brilliant metallic green and blue colors of its members, makes the group the most striking and attractive of any in the subfamily. Some of the species are now known to be parasitic upon ants and probably the whole group attacks these insects. In temperate regions the family is poorly represented, but in tropical countries, where ants most abound and flourish in enormous colonies, these insects are not rare and seem to have reached a very highly specialized development." This extraordinary specialization, which at once reminds us of that obtaining in other highly myrmecophilous and termitophilous groups, like the Paussidæ among beetles and the Termitoxeniidæ among Diptera, etc., is clearly shown in the figures of some of the more striking Eucharine genera reproduced in this article (Pl. IV, Figs. 56–62).

The first to describe a Eucharine parasite on ants was Forel.[1] On opening the huge cocoons of one of the Australian bull-dog ants (*Myrmecia forficata*) he found several metallic green and coppery pupæ about a cm. long, which a year later were described and figured by Cameron[2] as those

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[1] Un parasite de la Myrmecia forficata Fabr. Extr. C. R. Soc. Ent. Belg., I Fev. 1890, 3 pp.

[2] Hymenopterological Notes. Mem. Lit. Phil. Soc. Manchester (4), IV, 1891, pp. 182–194, 1 pl.

of *Eucharis myrmeciæ.* These pupæ, according to Forel, were "couvertes d'aspérités et de boursoufflures," probably analogous to the pustules above described for the pupa of *Orasema.* He concluded that the *Eucharis* attacks the *Myrmecia* larvæ, but after what I have said of *Orasema* it is more probable that the Chalcidid attacks the semipupa or pupa of the ant after the cocoon is spun and encloses both host and parasite.

In the same paper in which the *Eucharis* is described, Cameron describes a member of another genus, *Chalcura bedeli,* which was taken in nests of the Algerian *Myrmecocystus viaticus.*

Wasmann in his 'Verzeichniss', published in 1894,[1] cites as the only Chalcidids known to occur with ants the two preceding species described by Cameron and a *Chalcura* sp. which was "bred from cocoons of *Formica rufa* at Prag (Polak)."

Another Chalcidid belonging to the subfamily Eucharinæ and closely related to the preceding, was accidentally detected in some alcoholic material of *Camponotus ligniperdus* var. *novæboracensis* Fitch, collected August 12, 1904, on a bare slope of the Porcupine Mountains in northern Michigan by Mr. Otto McCreary and sent me for identification by Dr. Charles C. Adams. Two of the worker cocoons, measuring respectively 6.5 and .7 mm., were found to contain pupal parasites, which Dr. Ashmead has identified for me as *Pseudochalcura gibbosa* Provancher. In one of the cocoons, represented in Plate II, Fig. 29, there were two pigmented and therefore nearly mature pupæ, lying face to face near the anterior pole, while the remains of the ant pupa, which they had consumed, were crowded against the black meconial spot at the posterior pole. The other cocoon contained four unpigmented pupæ. It would seem that the Chalcidid larva must attach itself to the *Camponotus* larva and wait till it has spun its cocoon, before devouring the host. As the ant is an unusually large species compared with the parasite, several of the latter can obtain sufficient nourishment even from a single worker and need not, like *Orasema,* attack the still larger intermediate, soldier, and female brood.

I have received with some miscellaneous ants (*Formica fusca* var. *neorufibarbis, Myrmica brevinodis,* etc.) collected by Mr. H. Viereck, on the summit (11,000 ft.) of the Las Vegas Range, New Mexico, a single male specimen of a *Eucharis* (Pl. IV, Fig. 62), which is in all probability an ant parasite, although I am unable to refer it to its precise host.

In the discussion following a paper read several years ago by Ashmead before the Entomological Society of Washington,[2] Howard called attention

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[1] Kritisches Verzeichniss der Myrmekophilen und Termitophilen Arthropoden. Berlin, 1894.

[2] Notes on the Eucharids found in the United States. Proc. Ent. Soc. Wash., II, 1890–92, pp. 354–358.

to the fact "that in the collection of St. Vincent Chalcids sent to Professor Riley from Cambridge University there is a specimen of *Kapala furcata* Fabr. which bears in its jaws a medium sized red ant." Events have shown that Howard was probably correct in supposing this peculiar Chalcidid to be an ant parasite. Dr. O. F. Cook informs me that he has bred a specimen of an allied genus, *Isomeralia coronata* Westwood (Pl. IV, Figs. 58 and 59), from a cocoon of the Guatemalan kelep (*Ectatomma tuberculatum* Oliv.), and Dr. Ashmead tells me that in his opinion *Kapala floridana* (Pl. IV, Figs. 56 and 57) is probably parasitic on the Florida harvester (*Pogonomyrmex badius* Latr). He also assures me that the type of *Pseudometagia schwarzi* was taken in an ant-nest near Washington, D. C.

To the foregoing observations on Eucharinæ I am able to add some notes on a parasite belonging to another subfamily of Chalcididæ. As stated on p. 2, I failed to find *Orasema* in nests of *Pheidole instabilis* except during the summer and late spring months. At other seasons I often took a species of the subfamily Asaphinæ, namely, *Pheidoloxenus wheeleri* Ashmead (Pl. III, Fig. 36), an exquisite little Chalcidid which runs about in the dense throng of *Pheidole* workers like one of their number. It is not easily detected, as it resembles the workers in its small size (1 mm.) and in being subapterous or practically wingless. Its head is very wide, with a concave occiput and 9-jointed antennæ inserted near the oral border. These appendages are very robust, and have a club-shaped funiculus terminating in a broad flat joint. The epinotum is very short, the wings are represented only by the tegulæ and minute vestiges of the alar membranes. The surface of the body is smooth and shining. The head is deep metallic blue, with green cheeks and yellow mandibles; the antennæ are yellow at the base, with the large apical and adjacent transverse joints black. The thorax is green with golden reflections, the epinotum more blue green, the tegulæ violet. The abdomen is metallic green with a broad violet band across the posterior portion of each of the basal segments. The legs are fuscous, with yellow knees, tarsi and trochanters.

I have not been able to learn anything concerning the development of this insect. According to Ashmead the vast majority of Asaphinæ are parasites "upon plant lice, Aphididæ, and upon the bark lice, Coccidæ," but this cannot be the case with *Pheidoloxenus* since this insect is a regular myrmecophile, and *Ph. instabilis* does not, like our northern species of *Lasius*, cultivate aphids and coccids in its nests. During the autumn and winter months I have occasionally seen the *instabilis* workers carrying small pink larvæ about in the chambers. These were certainly not a portion of the ant brood, but whether they were the larvæ of *Pheidoloxenus* or not, I have been unable to determine. On one or two occasions I have seen as many as six or eight of the little Chalcidids in a single nest. A careful search will probably show that they are even more abundant.

In the literature I find the following scattered references to Chalcidid ant-parasites:

Fritz Müller, according to Sharp,[1] mentions a South American Chalcidid which attacks the larvæ of *Azteca instabilis* in its nests in the Cecropia trees. When the parasite pupates it suspends itself, by its posterior end, from the walls of the chambers like a butterfly chrysalis.

Wasmann[2] cites an observation of Brauns who found a Chalcidid in one of the nests of a South African subspecies of *Pheidole megacephala*. When the nests were disturbed the workers were seen to carry the parasites, which probably devour the brood, to a place of safety.

A larva found by Rupertsberger attached to a large *Myrmica* larva, and mentioned by Wasmann in his 'Verzeichniss' (*l. c.*, p. 169) as possibly an Ichneumonid, was probably a Chalcidid.

Perhaps no single group of parasitic insects has greater surprises in store for the future investigator of habits and development than the Chalcididæ. This is indicated not only by the fragmentary materials collated in the preceding paragraphs, but more especially by the splendid researches of Bugnon,[3] Marchal,[4] and Silvestri,[5] on the extraordinary polyembryony of the Encyrtinæ. These and future researches in the same direction may be expected to bring about many radical changes in the present taxonomy of the enormous family Chalcididæ.

2. The Parasitism of Mermis in Ants.

Five years ago (June 3, 1901), I found at New Braunfels, Texas, on a shady hill that slopes to the lovely sources of the Comal River, two medium-sized colonies of *Pheidole dentata* var. *commutata* Mayr. They were under stones about sixty feet apart. One contained ants of the typical dark variety of the species, while both the soldiers and workers of the other colony were decidedly paler. On lifting the stones my attention was arrested by several very large and conspicuous individuals with huge gasters, moving about among the workers and soldiers of normal dimensions. Unfortunately I failed to preserve any living specimens at that time but collected instead a

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[1] Cambridge Natural History. Insects. Vol. I, 1895, p 550.

[2] Die Psychischen Fähigkeiten der Ameisen. Zoologica, Heft 26, 1899, pp. 1–132, Taf. i–iii.

[3] Recherches sur le Développement postembryonnaire, l'anatomie et les mœurs de l'Encyrtus fuscicollis. Recueil Zool. Suisse, V, 1891, pp. 435–534, pl. xx–xxv.

[4] Recherches sur la Biologie et le Développement des Hyménoptères Parasites. I, La Polyembryonie Spécifique ou Germinogonie. Arch. Zool. Expér. (4), II, 1904, pp. 257–335, pl. ix–xiii.

[5] Sviluppo dell' Ageniaspis fuscicollis (Dalm.) Thoms. Rendic. R. Accad. Lincei, XV, 1906, pp. 650–657.

number of specimens in alcohol. These were described in a paper published during the autumn of 1901.[1] In this paper the huge workers were called macroërgates, but for reasons presently to be given they may be more aptly designated as mermithergates.

Plate III, Figs. 37–40 represent, drawn to the same scale, the dorsal view of the soldier and worker, which in *Ph. commutata* are not connected by intermediates, and the dorsal and lateral views of a large mermithergate. The length of normal workers does not exceed 3 mm. Many of them are scarcely more than 2.5–2.8 mm., which was the length of Mayr's type specimens from Florida. The largest mermithergates, however, measured fully 5 mm., while the smaller ones varied from 4 to 4.5 mm. Thus the volumes of the normal workers and the extreme mermithergates, had they been of the same shape, would be in the ratio of 27 to 225, but the gasters of the latter were so enormously distended that the ratio must have been 27 to at least 300. In other words, the large mermithergates were some twelve times as large as the normal workers. They were even larger than the soldiers, which measure about 4 mm., though in this case, owing to the great size of the head in the latter caste, the difference is less conspicuous. The largest mermithergates differ from both soldiers and workers in usually possessing three ocelli, of which the anterior is the largest, and resemble the soldiers in the structure of the thorax (Pl. III, Fig. 39).

Examination of one of these extraordinary individuals, even with a good pocket lens, reveals the cause of the great enlargement of the gaster. Through its distended intersegmental membranes the coils of a parasitic worm may be distinctly seen. My friend Professor T. H. Montgomery, to whom I sent a few of the mermithergates, writes me that the parasite is a species of *Mermis*. Its exact location among the ant's viscera, *i. e.*, whether it occupies the lumen of the enormously distended ingluvies, or lies in the body cavity outside of the alimentary tract, is not easily determined. From careful dissection of a single large specimen (the one represented in Pl. II, Fig. 39) I concluded that the *Mermis* lies within the ingluvies, or crop. In this specimen the head of the parasite extended forward through the postpetiolar and into the petiolar segment, and thus occupied the attenuated neck of the crop and the most favorable position for securing the ingurgitated food of its host. The fat-body and reproductive organs seemed to have disappeared completely and the walls of the enormously distended crop were practically in contact with the walls of the gaster. The large mermithergate shown in Figs. 39 and 40 contained only a single closely convoluted *Mermis*, which was fully 50 mm. long, or ten times the length of the ant. One

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[1] The Parasitic Origin of Macroërgates among Ants. Amer. Naturalist, XXXV, Nov. 1901, pp. 877–866, 1 fig.

individual, dissected by Professor Montgomery, contained two somewhat smaller parasites, together with many of their eggs. I have seen specimens containing as many as six and eight parasites. The specimens dissected by Professor Montgomery were "either fully mature or in what von Linstow[1] calls the second larval stage, which is, however, really the immature stage."

While it is certainly somewhat singular that a species of *Mermis* should occur in ants, even greater interest attaches to the cases under discussion, on account of the manifest effects of the parasite on its host. The fact that all the mermithergates are of huge size as compared with the normal workers is remarkable, for, on first thought, one would certainly expect an animal infested with such large parasites to be stunted, or, at any rate, below the average stature of the species. This paradoxical condition of the mermithergates of *Ph. dentata* is easily understood, however, when we make due allowance for certain peculiarities in the behavior of ants. In the first place, it is obvious that the parasite must enter the body of the ant while she is still a larva. This was proved by the fact that two of the large mermithergates were callows, one of them still very soft and pale yellow, the other with harder integument but without the deep coloration of the mature workers. Such huge parasites could scarcely have made their appearance in ants so recently escaped from their pupal envelopes. But even if there had been no callows among the mermithergates, the truth of the above statement would still be patent, both because the mermithergates were all infested while none of the normal workers were found to contain parasites, and because the structure of an ant is, of course, fixed in the pupal stage and cannot be subsequently increased to the dimensions of the insects under consideration.

It is evident, furthermore, that the larger stature, which is very apparent not only in the distended gaster of the mermithergates, but also in all the other parts of the body, can have its origin only in an unusually large amount of food consumed during the growth period of larval life. Now *Ph. commutata* is exclusively carnivorous and feeds at least its older larvæ with pieces of insect food. The workers cannot, therefore, accurately regulate the amount of food consumed by each larva, and it must be possible for larvæ infested with parasites, and hence presumably endowed with a more voracious appetite, to consume a greater quantity and hence produce larger pupæ and imagines than unparasitized individuals. If this inference is correct we must suppose that the stimulus to the increased feeding, *i. e.* the appetite, which results in the larger stature of the mermithergate, resides

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[1] Das Genus Mermis. Arch. f. mikr. Anat., LIII, 1898, pp. 149–168, Taf. viii.

in the larva and cannot be accurately controlled by the worker ants. The theoretical bearings of these considerations will be postponed to a subsequent portion of this article.

Two years later (June 21, 1903), on revisiting New Braunfels I found on the very same hill slope two more colonies of *Ph. commutata* containing mermithergates. On this occasion every effort was made to secure the entire personnel of the colonies in a living condition. One colony, confined in too small a bottle, died before I reached my home, the other was successfully transferred to an artificial nest. On examining the asphyxiated colony I found it to consist of many female larvæ and pupæ, a few soldier and several worker larvæ and pupæ, and a dozen mermithergates which varied considerably in size from individuals but little larger than the workers and without ocelli, to huge individuals like those taken two years previously. These large mermithergates possessed ocelli, a thoracic structure like the soldiers and a rich red color like the females. Three pupal mermithergates were also found but their gasters were not distended. The earth of the nest contained two free *Mermithes*.

The personnel of the living colony comprised six adult and three pupal mermithergates, a winged and several pupal females, and a number of larval, pupal and adult workers and soldiers. All of the pupal mermithergates, like those in the asphyxiated colony, had the gaster in proper proportion to the remainder of the body, so that they appeared to be merely gigantic worker pupæ. One of these hatched June 24, the two others July 2. As soon as they had hatched, their gasters began to enlarge rapidly and in the course of a few days the coils of the *Mermis* became visible through the distended pellucid membranes between the widely separated segmental sclerites. Evidently the parasites were present but of very small size in the pupæ and grew very rapidly during the callow stages of their hosts while the chitinous investment of the gaster was still soft and distensible. This sudden growth of the parasite is probably due to the rich and abundant food with which the recently hatched callow is supplied by her sister workers.

This colony of *Ph. commutata* was kept under observation till August 12. Of the nine mermithergates which it contained, three had died by June 27, and three more by July 19, while the nest was being transported in my hand luggage from Texas to Colorado. Of the surviving three, two died July 25 and 30 and the last August 12. Hence, at least one of these parasitized ants must have lived fully six weeks in the imaginal stage. In all of these cases the *Mermis* died within its host and both were carried to the refuse heap by the workers. One of the dead mermithergates had burst and the loops of the parasite protruded. In a state of nature it probably escapes from its host at this or an earlier stage, and enters the soil for the purpose of laying its eggs. Or the eggs may, perhaps, be discharged into the alimentary tract of the ant and escape with its excrement. It is not difficult to conceive how they may find their way into the young larva. They may adhere to the body of the workers till gathered up by their strigils or tongues and transferred to the buccal pocket. Thence they could be fed inadvertently to the larvæ, either with the regurgitated liquid food or with pieces of insects that had been malaxated and distributed by the workers.

The living mermithergates were easily studied in my artificial nest and exhibited several interesting peculiarities in their behavior. On exposure to the sunlight they hurried, like the females, to the dark chamber, thereby evincing a much higher degree of negative phototropism than the workers and soldiers. They never carried the brood, although even the soldiers were seen to do this occasionally. They never fed the larvæ, workers or females, and, had earth been present in the nest, it is very probable that they would never have shown any inclination to excavate. They never visited the manger of the nest but were fed exclusively by regurgitation. As befitted animals containing such enormous parasites they were in a chronic state of hunger. It was impossible at any time to uncover the nest without finding one or more of them either being fed by a worker or eagerly begging for food. And as soon as one was offered food, three or four of them would rush up and put out their tongues for a share of it. Once I saw a single worker trying to feed five of her huge parasitized sisters simultaneously. While imbibing their food the mermithergates stridulated, either continuously or at regular intervals. Sometimes they were so impatient to be fed that they would hold down a worker's head with their large fore feet and compel the little creature to regurgitate. Under these circumstances the larvæ must have been poorly fed, for the insatiable mermithergates continually intercepted the workers on their way from the manger to the brood chamber. The mermithergates in my artificial nest may have been massacred or starved by the workers and did not die merely as a result of parasitism for when the food supply becomes insufficient the tiny *Ph. commutata* workers, like those of *Ph. instabilis,* probably rid the colony of voracious and nonproductive mendicants, even when these belong to their own species. Apart from their chronic hunger, the mermithergates exhibited no abnormal traits of behavior directly attributable to parasitism. They ran about with as much alacrity as the workers and soldiers. Their other peculiarities, such as their strong negative phototropism, their dependence on regurgitated food, and the absence of the foraging instinct, like their large size, their ocelli and rich red color, may be regarded as female or soldier traits.

Mermithergates occur also, I believe, in two other Texan ants belonging to the genus *Cremastogaster* (*C. minutissima* Mayr and *C. victima missouriensis* Pergande). Both are small honey-yellow species which nest under stones in shady places. From a colony of *minutissima* taken June 3, 1901, in the very same locality at New Braunfels as the parasitized colonies of *Ph. commutata,* I took three large workers which were described and figured by Miss Holliday as ergatoid females.[1] These measured 4.3–5 mm. whereas the normal workers of this species do not exceed 2 mm. They had small ocelli and greatly enlarged gasters, and though no parasites were found in them, it is not improbable that they contained young specimens of *Mermis* that may have been overlooked when Miss Holliday made her dissections for the purpose of ascertaining the condition of the ovaries.

In a lot of *C. victima missouriensis* collected by Miss Augusta Rucker at Paris, Texas, I have recently found four individuals resembling the *minutissima* mermithergates described by Miss Holliday. They measured 3.2 and 4.5 mm. respectively, although the normal workers measure only 2–2.5 mm. None of these mermithergates has ocelli. In the two largest specimens the gaster is very voluminous but seems to contain no parasites, and the mesonotum is unusually large and convex, so that the thorax resembles that of a pseudogynic *Formica.*

Recourse to the literature shows that Emery had seen mermithergates in certain Central American and South American ants as early as 1890. In his paper on a collection of these insects from Costa Rica he describes and figures two odd specimens of *Pheidole absurda* Forel from Alajuela.[2] They measured 7.25–7.75 mm., although the normal worker of this species measures only 2.75–3 mm. They had huge, elongated gasters, vestiges of ocelli, and a thorax similar to that of the soldier, but in the shape of the head they resembled the worker caste. He did not observe that they were parasitized but regarded them as "parthenogenetic females." In the same paper, and from the same locality, he also described three specimens of *Odontomachus hæmatodes* with a huge gaster and a minute ocellus, as possibly a new variety (var.? *microcephalus*).[3] In this connection he mentions three other similar cases: an *O. chelifer* (var.? *leptocephalus* Emery) from Rio Grande do Sul, a *Neoponera villosa inversa* from Venezuela, and another tropical American ant, *Ectatomma tuberculatum.* In all of these cases the great volume of the gaster was naturally attributed to an unusual development of the ovaries.

Since reading my paper Emery has reëxamined his specimens and finds

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[1] A Study of Some Ergatogynic Ants. Zool. Jahrb. Abth. f. Syst., XIX, 4, 1903, pp. 311, 312, 16 figs.

[2] Studii sulle Formiche della Fauna Neotropica. Boll. Soc. Ent. Ital. Ann., XXII, 1890, p. 49, pl. v, figs. 10 and 11.

[3] Emery calls attention to the fact that this form of *hæmatodes* had been previously seen by Roger.

that in all of them the enlargement of the gaster is due to *Mermis* parasites.[1] In addition to the above mentioned forms he also describes mermithergates in *Pachycondyla fuscoatra* from Bolivia, and in the well-known South American *Paraponera clavata.*

Both Emery (*l. c.*, p. 591) and Wasmann[2] object to my applying the name macroërgates to the *Pheidole* workers parasitized by *Mermis*. The latter author, who coined this term, applies it to "abnormally large workers with normal development of the gaster," and in another place,[3] to "individuals which approach the females abnormally in the size of the body, but in other respects (even in the development of the gaster) are normal workers." I am quite willing to be corrected, but it should be pointed out that the gaster in the adult pupæ of the mermithergates of *Ph. commutata,* and probably also of the other species, is normal in its proportions, the enlargement being confined to the imaginal instar. It is merely a mechanical dilatation such as is seen in the repletes, or plerergates of the honey ants (*Myrmecocystus*) and in Wasmann's "gynæcoid workers," which are merely workers whose ovaries contain mature eggs. Although the dilatation in these different cases is due to the difference in the contents of the gaster (liquid food, ovaries or parasites) the morphological results are the same. Even had the objection to the use of the term macroërgates been based on the presence of the ocelli, it would not have been greatly strengthened, for these may be absent in specimens to which the term would seem to be applicable. In my opinion it may be permissible to distinguish three classes of macroërgates, namely: macroërgates proper (as defined by Wasmann), mermithergates, and plerergates.

Emery adds to his observations an interesting hypothesis. He says (pp. 601–603): "I believe that the singular microcephaly of the worker ants infested with *Mermis* may be attributed to a general law of growth of the ant-body and perhaps also of the insect body in general.

"We must assume with Wheeler that the parasitic nematode enters the ant larva and has already attained a considerable size before its metamorphosis. As long as the larva retains its cylindrical, spindle, or clavate shape, the worm, no matter whether it is injurious to the growth and development of the larva or not, will have only a slight influence on the external form. But as soon as the constriction appears at the anterior end of the abdomen during the preparation for the pupal stage, and the whole worm is relegated to the latter region, the defective nutrition of the larva makes itself felt in

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[1] Zur Kenntniss des Polymorphismus der Ameisen. Zool. Jahrb. Suppl., VII, 1904, pp. 587–610, 9 figs.

[2] Ameisenarbeiterinnen als Ersatzköniginnen. Mittheil. d. schweiz. entomol. Ges., XI, 2, 1904, p. 67.

[3] Die ergatagynen Formen bei den Ameisen und ihre Erklärung. Biol. Centralbl., V, 1895, p. 606.

the anterior region, and especially in the head, while the abdomen is unduly expanded by the worm. Since the thorax of the normal worker, as a portion of the body already reduced to a minimum, is incapable of further diminution, it remains unchanged. In the head, however, the results of imperfect nutrition are more strongly felt; there is no longer sufficient substance to form the powerful muscles that go to move the mandibles, so they remain small, and with them the muscle-containing occipital portions of the head are unable to acquire their normal proportions. Hence the characteristic narrowing in the posterior region of the head.

"The explanation of the appearance of the ocelli and the greater development of the eyes in the parasitized microcephalæ seems to me to present more serious difficulties. It might be supposed that, owing to the small development of the occipital region of the cranium, a greater quantity of ectodermal substance had remained over and thereby established more favorable conditions of space and nutriment for the formation of the eyes and ocelli. Unfortunately, the preservation of the dry specimens did not permit an accurate anatomical study of the organs contained in the cranium. I feel certain, nevertheless, that we are here dealing with something like a general law.

"The effect of the parasite on the formation of the body, and especially of the head, is not always equally intense: the extent of this effect depends on the relations of the size of the worm to that of the ant. The larger the worm, and hence the greater the volume of the abdomen of the ant, the greater the aberration in the head. For this reason *Pheidole* shows the greatest alteration, then come the two species of *Odontomachus* and *Pachycondyla fuscoatra,* then *Neoponera inversa,* and finally *Paraponera*; in this gigantic ant the increase in the abdomen had no appreciable influence on the shape of the head."

This adaptation of Roux's 'Kampf der Teile in Organismus' to the mermithergates seems very plausible at first sight, but on closer examination it proves to be less satisfactory as an explanation of the phenomena. It would seem to be necessary to reach some definite conclusion, first, as to the morphological relations of the mermithergates to the normal castes of the species, and, second, as to which parts of the mermithergates are enlarged at the expense of other parts. In the case of *Pheidole* there are three possible answers to the first question: the mermithergates may represent small-headed, *i. e.,* defective soldiers; second, they may be very defective females, and third they may represent excess development of the worker caste. Emery rejects the third possibility, and while considering the two others, is inclined to regard the mermithergates as having arisen from soldier larvæ in which the gaster has appropriated the nutriment of the head region so that the latter is greatly reduced in size. This interpretation, which derives its plausibility from the soldier-like structure of the thorax in the parasitized *Pheidole absurda,* is equally applicable to *Ph. commutata.* Emery is, however, unable to account satisfactorily for the appearance of the ocelli and larger eyes. The case of *Pheidole* is certainly complicated by the existence of a soldier caste. Both in the Ponerine ants studied by Emery (*Odontomachus, Neoponera, Paraponera,* etc.), and in the species of the Myrmicine *Cremastogaster* above described, this caste does not exist, and hence the mermithergates may be only excess developments of the worker, or defective developments of the female. Although in these cases I believe that the former alternative is the more probable, at least in some of the species, the question can hardly be settled without much additional material.

Emery takes it for granted that the gaster is an excess development, because it is so greatly enlarged in the adult mermithergates. But I have shown that in the pupæ in *Ph. commutata,* at least, the gaster is proportionally no more developed than any other part of the body. Hence we cannot conclude that the head is small because the gaster is large. We must rather suppose that the whole body exhibits excessive and uniform growth, and this must, of course, mean a uniform distribution of the metabolized nutriment in the larva.[1] It would seem, therefore, that the mermithergates, if they really arise from soldier larvæ, retain small heads because the parasites and not the abdominal tissues appropriate the substances which in the normal soldier go to form the cephalic region. This is indicated by the fact that the head of the soldier does not develop till the semi-pupal stage, when the pellucid cephalic substances may be seen rapidly accumulating in the previously slender anterior region. This explanation, which resolves itself into a very obvious struggle between the larva and its parasite and not between the parts of the larva, will also account for the smaller heads in the Ponerine mermithergates. In all cases the pupa tends to become a well-proportioned whole. It is evident that this tendency is very different from an unequal struggle of the various body regions with one another, since it implies a uniform distribution of the available nutriment. It implies, moreover, defect developments in the head, in the case of the soldier larvæ. The failure to develop the huge head of the soldiers in *Pheidole* mermithergates is in all probability due to the suppression of a very recently acquired character by the parasite, since there is every reason to suppose that the soldier caste among these and other ants is of much less phylogenetic antiquity than the worker. This seems to be clearly indicated in the ontogene-

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[1] Dr. T. H. Montgomery informs me that crickets (*Gryllus abbreviatus*) infested with *Mermis* or with *Paragordius varius* are apt to be larger than uninfested individuals. The enlargement is not confined to the abdomen but also affects the other regions of the body as in mermithergates.

tic development of colonies of *Pheidole*, *Camponotus*, etc., for in these only small-headed workers are at first produced by the queens. Here scarcity of food produces almost the same results as parasitism — namely microcephaly. At the same time that the tendency to produce a well-proportioned pupa suppresses the recently acquired macrocephalic characters of the species, it may be conceived to encourage the development of certain ancient phylogenetic characters like the ocelli and larger eyes. This is especially the case in the *Pheidole* larva for two reasons: first, because the mermithergates of these ants probably approach more nearly the ancestral stature of the workers, since it is very probable that the *Pheidole* workers have undergone a reduction in size during the phylogeny of the genus, and second, because the larva, notwithstanding its parasites, nevertheless succeeds in accumulating more formative substance than is necessary for the production of a normal worker.[1]

On the basis of the above interpretation, which I would substitute for Professor Emery's, an interesting comparison may be instituted between the mermithergates of *Pheidole commutata* and *absurda* on the one hand, and the phthisergates of *Ph. instabilis* on the other. In the former cases the parasitic *Mermis*, situated in the abdomen of the larval ant, appropriates to its own growth the substances that will later be required to increase the volume of the pupal and imaginal head. In the latter case, the ectoparasitic *Orasema* larva, situated just behind the head of the semipupal ant, intercepts and extracts the head-producing substances as they flow forward from the abdominal region into the anterior end of the body. In both cases the result is a pathological microcephaly, extreme and peculiar in the moribund pupal phthisergates of *Ph. instabilis*, much less pronounced but persisting into the imaginal stage in the less seriously parasitized *Ph. absurda* and *commutata*.

Emery has called attention to the interesting fact that all the known mermithergates occur among American ants. They occur moreover in species peculiar to the tropical or subtropical portions of the New World. This would seem to indicate that the single or several species of *Mermis* which produce this anomaly in ants are of rather circumscribed distribution. The genus *Mermis*, however, seems to be cosmopolitan, judging from von Linstow's recent revision of the group (*l. c.*). He records species from Europe, Turkestan, Madagascar, Southwest Africa, New Zealand, United States, Costa Rica, and Brazil. Some of the species, like the European *M.*

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[1] The effects of the parasitic *Mermis* on the host are not confined to mere mechanical distortion and the withdrawal of nutriment. There is much evidence to show that both Nematodes and Cestodes secrete toxic substances that have a positive and far reaching effect on the tissues of their hosts. In this connection see: von Fürth, Vergleichende Chemische Physiologie der Niederen Tiere, Jena, 1903, pp. 308–310, and Faust, Die Tierischen Gifte, Braunschweig, 1906, pp. 223–228.

albicans von Siebold and *nigrescens* Duj., are well known parasites in several insect hosts, although no ants are recorded among the number.

3. THE PARASITISM OF THE LOMECHUSINI.

Our knowledge of the extraordinary myrmecophilous beetles of the Staphylinid tribe Lomechusini is largely due to the indefatigable researches of the Jesuit Father E. Wasmann. Beginning in 1886 and continuing to the present time, these researches comprise a series of more than thirty papers.[1] The work has been taken up more recently by Viehmeyer in Germany and by Father Muckermann in Wisconsin. My own observations, which are still very fragmentary but not without interest, will be recorded after reviewing the work of the authors just mentioned.

A. The European Lomechusa and Atemeles.

The ethology of the Lomechusini is succinctly summarized by Wasmann in the following paragraphs:[2]

"The *Lomechusa* group, embracing the palearctic genera *Lomechusa* and *Atemeles* and the nearctic genus *Xenodusa,* contains, from an ethological point of view, the most interesting and at the same time the largest of the true ant-guests (symphiles) of the arctic region. These Staphylinids, which belong to the subfamily Aleocharinæ, are treated by the ants like their own kith and kin, live in antennary communication with them, are cleaned and licked and occasionally also carried about; they are fed from the mouths of their hosts, although they are also able to eat independently and frequently devour the ant-brood. The ants are especially attracted to these beetles on account of the prominent tufts of yellow hairs on the sides of their abdomen which are licked by the host with evident satisfaction. Not only do these beetles themselves live as guests among the ants, but the same is also true of their larvæ. The larvæ of *Lomechusa* and *Atemeles* are reared by the ants like their own brood; they are licked, fed with regurgitated food and, before pupation, covered or embedded in cells like their own larvæ. When the nest is disturbed they are carried by the ants to a place of safety in preference to their own larvæ and pupæ. The predelection of the ants for these adopted larvæ is all the more remarkable because they are the worst enemies of the ant-brood and consume enormous numbers of the eggs and larvæ of their hosts. This brood parasitism, in fact, causes the development of abortive individuals intermediate between the female and worker castes, and these

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[1] Twenty-five of these papers, down to 1902, are cited by Wasmann himself at the end of a twenty-sixth contribution entitled: Neue Bestätigungen der Lomechusa-Pseudogynen-Theorie. Verhandl, deutsch. Zool. Ges., 1902, pp. 107–108; the remaining bibliography may be found among the cards of the Concilium Bibliographicum.

[2] Zur Biologie und Morphologie der Lomechusa-Gruppe. Zool. Anzeig., No. 546, 1897, pp. 463–465.

intermediates, which I have called pseudogynes, gradually bring about a degeneration of the parasitized colonies.

"Within the *Lomechusa* group an important ethological difference obtains between *Lomechusa* and *Atemeles*, inasmuch as the former is homœcious, *i. e.*, the species of this genus have each but a single host (a species of *Formica*), in whose company they complete their whole life-cycle; whereas the *Atemeles* are heterœcious, since as adult beetles they live with *Myrmica rubra* and a species of *Formica*, but have their larvæ reared only by the latter. The fact that *Lomechusa* has only a single host explains the more highly developed *passive* stage of its symphily. This is evident from the one fact among others that the beetle is more affectionately treated by its normal hosts and is fed, not like an ant, but more like an ant-larva. The heterœcious character of the *Atemeles*, which are compelled twice during their life time to change their normal hosts, once in the spring when they migrate for reproductive purposes from *Myrmica* to *Formica*, to have their larva reared by the latter, and once in the summer or autumn, when they migrate from *Formica* to *Myrmica* for the purpose of hibernating, enables us to explain the greater *active* perfection of their symphily, their greater initiative towards the ants, and the closer imitation of their behavior. The last peculiarity is especially apparent in that they do not, like *Lomechusa, Claviger*, and *Amphotis*, beg the ants for food merely by stroking them with their antennæ, but also raise their fore-feet after the manner of ants, and stroke the cheeks of the regurgitating hosts. On this account they are treated by their normal hosts like ants and not like ant-larvæ."

Five species of *Lomechusa* and a greater number of species and varieties of *Atemeles* have been described. Of these *L. strumosa* is the best known. It is exceedingly rare in England,[1] but appears to be more abundant in certain parts of the continent, especially in Holland and Luxemburg, where Wasmann has been carrying on his investigations. Its normal host is the blood-red slave-maker (*Formica sanguinea*), though very rarely it may be found in the nests of *F. rufa* and *pratensis*.

In the present article we are mainly concerned with the pseudogynes mentioned in the above quotation. Wasmann has subjected these individuals, which were well known to Forel[2] and Adlerz,[3] to a searching examination, and describes them as follows:[4]

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[1] According to Donisthorpe (Record of Capture of Lomechusa at Woking with Formica sanguinea. Entomologist, XXXIX, July, 1906, p. 163), only three specimens have been recorded from England. Besides the one referred to in his article, one was "taken by Sir Hans Sloane on Hampstead Heath in 1710, the other found by Dr. Leach in the mail-coach between Gloucester and Cheltenham."

[2] Les Fourmis de la Suisse. Zürich, 1874, p. 138.

[3] Myrmecologiska Studier. II Svenska Myror och deras Lefnadsförhållanden, Bihang. Svenska Vet. Akad. Handl., XI, No. 18, 1886, p. 76.

[4] Die ergatogynen Formen bei den Ameisen, *l. c.*, p. 612.

"Morphologically these pseudogynic workers may be characterized as an abortive combination of the thoracic structure of the female with the stature and gastric development of the worker; they impress one as frustrate workers, that have borrowed a female thorax. Their size, according to my observations, which extend over materials from a great number of colonies, is rarely greater than that of the average normal workers of the same colony, often considerably less. The head and gaster are small, the former, in its relatively small dimensions, more like that of the female than the worker. The ovaries are, if anything, more feebly developed than in the ordinary workers. The mesonotum is hunched, disproportionately large compared with the pro- and epinotum, and is usually relatively higher than in the female. In many specimens the scutellum is large and separated off by a transverse suture from the mesonotum. The postscutellum [metanotum], on the contrary, is barely indicated, although in some individuals it forms a distinct narrow strip, while the scutellum is not separated off in front, but instead divided into two halves by a longitudinal line which is lacking in the female." Wasmann has found the pseudogynes most frequently in the nests of *F. sanguinea*, more rarely with *F. rufa*, *pratensis* and *fusca*. When they occur they often make up from 5–7% of the personnel of the colony, more rarely as much as 20%. "The coloration of the pseudogynic workers is almost without exception paler than that of the normal workers. This is especially true of the thorax; the color of the head, however, is often darker than in the normal workers of the same colony, and corresponds to the darker head of the female. The slight color variation in the pseudogynic *sanguinea* is explained by the fact that in this species the female and worker are very similarly colored. Conditions are different in *F. rufa* and *pratensis*. Here the color of the pseudogyne, although generally more like the darker tint of the female, is much more variable. In some fully mature individuals it is paler than in the palest workers of the same colony....All pseudogynes are, as Forel observed, cowardly and indolent. Not one of them attempted to bite me while I was plundering their nests, though I often knelt near them for hours while sifting out the myrmecophiles. The very opposite was true of the normal workers, which defended themselves with fury. The pseudogynes act as if they regarded themselves as frustrate existences. In several of the observation nests of *F. sanguniea* kept in my room, they neither took part in excavating the earth nor in nursing the brood; they did more running about, however, than the females. Their vitality seems to be feebler than that of the normal workers, for none of them managed to survive a captivity of several months, although some were callows and the remainder of the colony was in a prosperous condition."

Transitions between the pseudogynes and the normal workers on the one hand, and normal females on the other, are of very rare occurrence. Wasmann[1] has, however, seen one colony in which "all possible transitions between normal workers and females were represented. The pseudogynes of this colony may be divided according to their stature into micropseudogynes, mesopseudogynes and macropseudogynes. Among the mesopseudogynes there are numerous transitions to the workers, but never with vestiges of wings; among the macropseudogynes there are ergatoid and gynæcoid forms, of which the former sometimes bear distinct vestiges of wings on the relatively short, narrow mesothorax, while the latter often possess perfectly developed but rather short wings on the exceedingly broad mesothorax, and in addition similar posterior wings on the metathorax. The latter forms may be designated as macronotal, brachypterous females, in contradistinction to the normal stenonotal, macropterous females."

As Wasmann's researches progressed he became more and more impressed with the fact that the parasitism of the Lomechusini and the occurrence of the pseudogynes stood in a causal relation to each other. A five years' statistical study of 410 colonies of *Formica sanguinea* near Exäten in Holland finally led him to maintain the following theses:[2]

"a. The regions in which pseudogynes occur always coincide with *Lomechusa* regions.

"b. The colonies containing pseudogynes are always the centers of *Lomechusa* regions.

"c. Pseudogynes are never found in *sanguinea* colonies outside the *Lomechusa* regions.

"d. In colonies in which *Lomechusa* lives merely as a beetle (*i. e.*, in the imaginal instar), pseudogynes are never developed, but only in such as have for years been rearing the larvæ of *Lomechusa*."

These results were found to hold good also for other European localities. He found, moreover, a similar causal connection between the occurrence of pseudogynes of *F. rufa* and the beetle *Atemeles pubicollis*, *F. rufibarbis* and *A. paradoxus*, *F. fusca* and *A. emarginatus*. In the case of *Atemeles*, of course, the pseudogynes are restricted to the ants among which its larvæ are reared and do not occur in the *Myrmica* colonies with which it merely hibernates. The *Formica* colony is therefore analogous to the definitive host of diœcious, non-social parasites like the tapeworm, while the *Myrmica* colony corresponds to the temporary host of this entozoon.

As early as 1895[3] Wasmann undertook to explain the origin of the

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[1] Ueber ergatoide Weibchen und Pseudogynen bei Ameisen. Zool. Anzeig., No. 536, 1897, p. 252.

[2] Neue Bestätigungen der Lomechusa-Pseudogynen-Theorie. Verhandl. deutsch. Zool. Gesell., 1902, p. 100.

[3] Die ergatogynen Formen, etc., *loc. cit.*

pseudogynes. Previous authors had been inclined to regard them as cases of atavism, *i. e.*, as reversions to the primitive female form (Adlerz) or as blastogenic anomalies, *i. e.*, as due to some peculiarity in the structure of the egg and hence referable to hereditary factors (Weismann, Forel). Wasmann, however, took the view that they "are probably due to a post-embryonic sistence in the development of the typical female form, and arise from larvæ which were originally destined to become females, but had already passed the stage of wing-formation and had then been converted into workers." He conceives this deflection in the normal development to take place in the following manner:[1]

"The normal mating period of *Lomechusa strumosa*, according to my observations, is from the middle of May to the middle of June. Usually the *Lomechusa* larvæ are to be found in the *sanguinea* nests only after this period. At the very time when the *Lomechusæ* begin to lay their eggs, *sanguinea* begins to lay a number of fertilized eggs which are to produce workers. Both among these and the young larvæ of the worker generation the *Lomechusa* larvæ, as I have observed, make terrific havoc. I have noticed that their food often consists almost exclusively of these eggs and young larvæ, and that in the course of a few days a single *Lomechusa* larva can devour a great number of them. I have seen some of the larger *Lomechusa* larvæ attack and devour several ant larvæ 4–5 mm. in length, one after another, although the *Lomechusa* larvæ in this stage are usually fed from the mouths of the ants. As there may be as many as several dozen *Lomechusa* larvæ in a single nest, the greater portion of the first annual worker generation may be destroyed in the course of a few weeks, for the parasites are extremely voracious and grow on the average almost a millimeter in length a day, and attain their definitive development (11 mm.) from the egg to the adult larva (and that at rather low temperatures in my observation nests) in 12 to 13 days. Hence there must arise a very perceptible and sudden falling off in the development of the worker generation and the ants endeavor to make good this deficiency by converting into workers all the available larvæ of the immediately preceding generation, that were originally destined to become females.

"Another factor, secondary in importance, however, compared with those above mentioned, confirms the tendency of the ants to transmute the female larvæ into workers, namely the extraordinarily rapid growth of the *Lomechusa* larvæ. On this account the workers lavish the care, which would otherwise be devoted to the female larvæ, on the *Lomechusæ* instead, for these impress the ants as being most admirable offspring. This in turn

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[1] Die ergatogynen Formen, etc., *loco cit.* p. 632.

leads to a neglect of the female larvæ. (It is the counterpart of the rearing of the young cuckoo in the nest of the white-throat!) As a matter of fact, the *Lomechusa* larvæ are the first to be rescued when the nest is disturbed. In general it may be said (according to my observations, in part previously published) that whenever I placed *Lomechusæ* in strange *sanguinea* nests, the presence of the beetles themselves often led to a neglect of the brood, and more especially of the large female larvæ."

It will be observed that Wasmann's view, which he styles a theory, rests on several inferences of very different degrees of probability. He may be said to have demonstrated that pseudogynes result from the parasitism of *Lomechusa* and *Atemeles* on various species of *Formica*. His further contention that the pseudogynes are not of blastogenic origin but arise from normal female larvæ that have developed under abnormal conditions, must also be granted; especially as it has recently received experimental confirmation from Viehmeyer.[1] This investigator removed an aged *sanguinea* queen from her colony which had for some years been producing pseudogynes, owing to the presence of *Lomechusa* larvæ, and caused her to be adopted by a new set of fifty unusually fine workers from an uninfested colony. Her eggs under the changed conditions developed into larvæ that gave rise to normal workers. This, of course, proves that the pathogenic conditions cannot have their origin in the queen or in her ova. Wasmann has since published a similar experiment.[2] Two *sanguinea* females belonging to a colony from Exäten and containing many pseudogynes were given slaves (*F. rufibarbis*) from Luxemburg colonies that had never been infested with *Lomechusa* and *Atemeles*. During four consecutive years the offspring of these females developed only into normal workers.

Up to this point Wasmann's hypothesis seems to rest on firm foundations, but as much cannot be said of his explanation of the pseudogynes as the abortive results of a belated attempt on the part of the workers to transmute female larvæ into workers. He here steps on debatable grounds. It seems to me that he has come nearer the truth in that portion of the quotation above cited where he calls attention to the neglect of the female larvæ by their nurses, for it is natural to suppose that these neglected larvæ would be able to pupate and produce pseudogynes without any active intervention on the part of the workers such as the administration of a particular kind or quantity of nourishment. The great variation in stature among normal *Formica* workers on the one hand, and among females on the other, shows that there must be wide limits of larval stature within which spontaneous pupation

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[1] Experimente zu Wasmann's Lomechusa-Pseudogynen-Theorie. Allgem. Zeitschr. f. Entom., IX, 1904, pp. 334–344.

[2] Ameisenarbeiterinnen als Ersatzköniginnen, etc., *loc. cit.* p. 69.

is easily possible; and there is no occasion to suppose that this may not occur among larvæ intermediate in size between those of the workers and females. The only apparent objection to this view is one which undoubtedly occurred to Wasmann himself and led him to suppose that the nurses actively transmute the female larvæ into workers, namely, the fact that the stature of the pseudogynes is usually below, and often considerably below, that of the largest workers. This, however, may be due to purely physiological causes resident in the larvæ themselves, for these would suffer starvation as a result of the ants' infatuation with the *Lomechusa* larvæ and hence lose much of their substance (water and fat) by oxygenation during the period previous to pupation and subsequent to the inhibited histogenetic changes that have already progressed beyond the worker stage. Under these circumstances pupation would wear the aspect of a regenerative or regulatory process analogous to that which leads the isolated blastomeres of the sea-urchin and other animal ova to develop into complete but more or less abortive and diminutive larvæ.

The chief advantage of such an explanation lies in the elimination of an appeal to special instincts such as would be implied by an endeavor on the part of the worker ants to restore one portion of the colony — the vanishing worker personnel, at the expense of another portion — the annual supply of virgin females. Such an endeavor, though itself of the nature of a colonial regeneration or regulation, is not improbable, but on the principle of *entia non sunt multiplicanda præter necessitatem,* does not seem to be necessary to an explanation of the phenomena. On general biological principles we should expect moribund ant colonies to take the opposite course and hasten the development of the sexual forms as the most appropriate method of insuring the survival of the species and thereby the production or rejuvenation of colonies. The explanation above suggested has, moreover, the advantage of being applicable to other cases besides the pseudogynes of *Formica.* While treating of *Pheidole instabilis* (p. 3) I called attention to the occurrence in that ant and in a few allied species belonging to the Sonoran province, of a series of intermediates, or *desmergates,* as they may be called, connecting the typical worker (*ergate*) and soldier (*dinergate*) castes. As these desmergates are perfectly normal I could not regard them as the result of *Orasema* parasitism like the phthisergates, phthisogynes, and phthisanērs. Moreover, similar intermediates are of regular occurrence in species of several other genera (*Eciton, Dorylus, Solenopsis, Azteca, Camponotus,* etc.) where parasitism as an explanation is out of the question. In all of these cases the desmergates probably arise from larvæ that have been neglected by the ants after having been enabled to grow and develop beyond the typical worker stage. That such neglect should often occur is not surprising when we stop to consider that much of the time and energy of the workers of an ant community are consumed in other duties besides feeding the brood, such as foraging, excavating, cleaning one another, etc. Then, too, the rate of reproduction is enormous and must often out-run the available food supply, which itself is by no means constant. The very slow development of ants in their larval stages is evidence of slow metabolism, and as this cannot be due to low temperatures, at least during the summer months, we must suppose that long periods of enforced fasting or positive starvation not infrequently intervene in the lives of larval ants. Still further conditions which may, perhaps, conduce to the same result may be found in the apparent absence of a very definite and well organized system of feeding the enormous brood, and the fact that this important function is frequently entrusted to the presumably more or less inexperienced callows.

B. The North American Xenodusa.

The Lomechusini are represented in North America by the single genus *Xenodusa*. Our best known species is *X. cava* Leconte (Pl. III, Fig. 41), a deep red beetle, 5–6 mm. in length, with slender legs and antennæ and tufts of golden hairs (trichomes) on the abdomen, which is concave above, like the thorax, and turned up at the tip. This species, which is so closely allied to the European forms that it has been placed successively in the genera *Atemeles* and *Lomechusa,* is stated by Wasmann to be "ziemlich häufig" in the United States, but it has certainly proved to be decidedly rare in my own experience and that of several coleopterists of my acquaintance. Messrs. W. Beutenmüller and C. Schäffer, who have given much attention to our beetles, tell me that they have never taken it, and there is only a single poorly preserved specimen in the large collection of the American Museum. There may, of course, be localities in which the insect is as common as *Lomechusa strumosa* in continental Europe, but if such exist, they have not yet been discovered or divulged.

Leconte, who in 1865 first described *X. cava* under the name of *Atemeles cavus,* stated that he had never taken the insect and did not know its host.[1] Some years later, according to McCook,[2] he succeeded in taking it in the mounds of *Formica exsectoides* in the Alleghenies of Pennsylvania and in the nests of *F. rufa* (?) in various localities. This latter datum, however, is negligible, since the species of the *exsecta* and *rufa* groups in this country had not at that time been clearly differentiated.

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[1] New Species of North American Coleoptera. I. Smiths. Miscell. Coll., No. 167, 1863, p. 30.

[2] Mound-making Ants of the Alleghenies, their Architecture and Habits. Trans. Am. Ent. Soc., VI, 1877, pp. 253–296, pl. i–vi.

Blanchard in 1879,[1] described in a brief note the capture of some 50 specimens of *X. cava* in a large colony of black ants, which could only be *Camponotus herculeanus pennsylvanicus* De G., in a white oak near Tyngsboro, Massachusetts. The word "recently" occurring in this note, which was dated May 1, shows that the *Xenodusæ* must have been taken during the winter or early spring and that they were hibernating with the *Camponotus*. Hamilton, who published a good list of American myrmecophilous beetles in 1888,[2] had apparently never taken *Xenodusa*, as he cites only the records of Leconte and Blanchard. Schwarz, in 1890,[3] mentions the insect as occurring with *C. pennsylvanicus* and *C. ligniperdus* var. *novæboracensis* (=*pictus* Forel) on his own authority and that of Leconte, Pergande, and Hubbard. Wickham,[4] also records it as occurring with *C. novæboracensis* at Iowa City, Iowa.

In a recent paper Muckermann,[5] has inaugurated a slight advance in our knowledge of the habits of *Xenodusa*. Aug. 23, 1900, he succeeded in finding it in the vicinity of Prairie du Chien, Wisconsin, in a nest of *novæboracensis*, and during October of the following year he found within a hundred feet of this nest a colony of *Formica sanguinea rubicunda* containing a number of pseudogynes. The circumstances indicated a causal connection between the occurrence of the pseudogynes and the parasites very similar to the connection established in Europe by Wasmann for the heterœcious *Atemeles*. It must be expressly stated, however, that Muckermann did not find *Xenodusæ*, either as adults or larvæ, in the *rubicunda* nest. And to my knowledge no one has yet taken the beetle in colonies of any of the Amercan forms of *sanguinea*.

Up to the present time I have been able to find *X. cava* only in two localities: Rockford, Illinois and Colebrook, Connecticut. These are, to be sure, the very localities in which I have collected ants most carefully. The following is the only observation made at Rockford: August 5, 1902, I took two fine specimens of *X. cava* from a large and flourishing colony of *C. novæboracensis* in an old log completely riddled with the galleries of the ants. Neither *Xenodusa* larvæ nor pseudogynes were seen. The nest was well stocked with *Camponotus* larvæ and pupæ in all stages and also contained several fine winged females. There were many *rubicunda* nests in the immediate vicinity but no pseudogynes were to be found among their inhabitants.

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[1] Bull. Brooklyn Ent. Soc., II, 1879, p. 4.

[2] Catalogue of the Myrmecophilous Coleoptera, with Bibliography and Notes. Canad. Entom., XX, 1888, No. 5, p. 164.

[3] Myrmecophilous Coleoptera Found in Temperate North America. Ent. Soc. Wash., I, No. 4, 1890, p. 243.

[4] Further Notes on Coleoptera found with Ants. Psyche, VII, 1894, p. 80.

[5] *Formica sanguinea* subsp. *rubicunda* Em. and *Xenodusa cava* Lec. Ent. News, Dec. 1904, pp. 339–341, pl. xx.

My observations in Colebrook were more extensive and were all made on nests occurring on the slopes of three adjacent hills, which, for present purposes, may be designated as the eastern, middle and western hill, covering a strip of territory about a mile and a half long and a quarter of a mile wide, or less than half a square mile. Late in August, 1900, I found a few *Xenodusæ* in two large *novæboracensis* colonies on the middle hill. These colonies were essentially like the one seen at Rockford, except that neither contained winged females. My remaining observations relate to a very different ant, *Formica schaufussi* var. *incerta* Emery, which forms many colonies on the Colebrook hills. This ant, as I have shown in former articles,[1] is the normal temporary host of *F. difficilis* var. *consocians* Wheeler. The following observations show that it is also the host of *X. cava.* I may mention incidentally that, although *F. rubicunda* and its var. *subintegra* are very common in the same territory, I have never been able to find the beetle in any of their nests.

F. incerta first impressed me as being a probable host of *Xenodusa* in 1904, when I began to notice pseudogynes in a number of the colonies. August 13 to 24 of that year I took pseudogynes from seven colonies on the eastern and middle hills. Five of these colonies each contained only a few of the abnormal insects, but two, which seemed to be incipient colonies, contained unusually small, pale workers together with numerous pseudogynes of the same dimensions. One of the latter colonies, taken August 25 also contained a diminutive but perfectly developed female (microgyne). This colony was kept in an artificial nest till September 16. The numerous pseudogynes behaved in all respects like normal workers. They fed one another, carried the cocoons away when the nest was illumined, etc. In another colony that was used for some experiments with *F. consocians,* two pseudogynes, which had hatched late in August, 1904, lived till April 9 of the following year, and this notwithstanding the fact that one of them had much crippled antennæ and had to be fed and cared for by the normal workers during the whole period.

A remarkable colony was found during the early morning of August 13. The preceding night had been unusually cold so that the ants were still very inactive and I was able to capture the entire personnel. It consisted of the following: a single deälated female, to all appearances the mother of the colony; 8 perfectly normal winged females; 46 normal workers; 2 larvæ; 193 pseudogynes, and 12 pseudogyne pupæ. In this colony, therefore, nearly 80% of the personnel were pseudogynes! In size these averaged like

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[1] A New Type of Social Parasitism among Ants. Bull. Am. Mus. Nat. Hist. XX, 1904, pp. 347–375; and On the Founding of Colonies by Queen Ants, with Special Reference to the Parasitic and Slave-making Species. *Ibid.*, XXII, 1906, pp. 33–105.

the workers, and were of the same color, except that a number of them had traces of the black antero-median and parapsidal blotches of the female on the mesonotum. They had a perfectly normal appearance, as the enlargement of the mesonotum led to less distortion and inelegance of profile than in pseudogynic *F. sanguinea* and *rufa*, since in *incerta*, which belongs to the *pallide-fulva* group, the thorax, even of the normal worker, is unusually long. Traces of the scutellum and metanotum were rarely present in any of the specimens, so that the only difference between these and normal workers was the greater prominence of the mesonotum. The extent of this modification may be clearly seen by comparing Plate III, Fig. 42, which represents a large typical worker, and Figs. 43 and 44, which represent pseudogynes from the same colony and drawn under the same magnification.

On finding these pseudogynes I was convinced that an examination of the *incerta* nests earlier in the season would reveal the presence of *Xenodusa*. Accordingly, on revisiting Colebrook during July of the following year (1905) I set to work to look for the beetle and its larva. July 1, I found under a stone on the middle hill a small colony of *incerta* containing about 75 normal workers, a few worker pupæ and larvæ, and 6 larvæ which, from their resemblance to Wasmann's figure of the *Lomechusa* larva[1] could at once be recognized as those of *X. cava*. The legs, however, seemed to be much longer and the body more slender and more concave above. They were clinging to the lower surface of the stone covering the nest. I transferred them to an artificial nest together with as many of the ants as I could capture. The larvæ associated themselves with the brood which the ants had collected in the cavities of the damp sponge in the dark chamber of the nest. They walked about but little and very clumsily as their legs seemed to be incapable of much movement at the strongly flexed articulation between the femora and tibiæ. They were frequently seen in the act of begging the ants and one another for food. At such times they raised their fore feet and stroked the head of the ant or fellow larva. Although the ants usually responded very willingly to this solicitation, the liquid food thus received seemed to be insufficient, for one morning I saw one of the *Xenodusa* larvæ seize and devour an ant larva about 3 mm. in length. On July 7 two of the *Xenodusa* larvæ had disappeared (eaten by the ants?) and the remaining four had become somewhat inactive after having grown appreciably during their week's confinement in the artificial nest. Fearing that the ants might devour the remaining parasites, and concluding from their size that they must be nearly ready to pupate, I removed them from the nest and embedded them in some earth. This proved to be disastrous as I had not taken the precau-

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[1] Die Moderne Biologie und die Entwicklungstheorie. 2 Aufl., Freiburg i. Br., 1904, p. 223, fig. 30.

tion to sterilize the earth which must have contained some predacious insect. At any rate, I could find no traces of the larvæ when I carefully examined the earth several days later.

This brief but interesting glimpse of the larval life of *Xenodusa* led me to examine all the *incerta* nests I could find in the hope of obtaining more of the parasites. Although I failed to secure any more of the larvæ, I was rewarded July 14 by finding a mature *Xenodusa* in a small colony on the western hill. This colony had a depauperate appearance and comprised only about 50 workers, two deälated females and a few worker pupæ. It contained no pseudogynes.

These observations, made, as I have stated, within an area of less than a square mile, prove that the larvæ of *X. cava* are reared by *F. incerta* during the latter part of June and the first weeks of July, and that the adult beetle may be found as early as the middle of the latter month. During August, however, the *Xenodusæ* are found only with *C. novæboracensis.* That they pass the winter with ants of this species is indicated by Blanchard's note cited above. It is probable therefore that *X. cava* is heterœcious like the European *Atemeles,* as Wasmann surmised,[1] but instead of a Myrmicine and a Camponotine host, both hosts in the American species are Camponotine ants.

The occurrence of pseudogynes late in the autumn in so many of the *incerta* nests agrees well with Wasmann's theory that these anomalous forms are the result of Lomechusine parasitism, but there are several facts connected with this occurrence which seem not to be in full accord with his theory. A colony like the one above described, which contained nearly 80% of pseudogynes together with several normal winged females, was not encountered by Wasmann in his study of the *sanguinea* colonies. He never found more than 20% and usually the number did not exceed 5%. He says, moreover:[2]

"According to this theory the pseudogynes arise from converted female larvæ; from which follows, first, one ought to find no recently hatched normal females, or at least very few of them, in the same colony with recently developed pseudogynes, since the female larvæ of the respective generation have been changed into workers as far as possible; second, the number of pseudogynes in a single colony must not surpass the number of normal females which they represent. I do not hesitate to subscribe to both of these conclusions. The former, at least according to my own observations, is actually substantiated, since I cannot remember ever to have found recently developed females associated with recently developed pseudogynes. At

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[1] Zur Biologie der Lomechusa-Gruppe. Deutsche ent. Zeitschr., 1897, Heft II, p. 275.
[2] Die Ergatogynen Formen, *loc. cit.*, p. 635.

first sight the second conclusion seems not to be justifiable. For how is it to be reconciled with the occurrence of as many as 20% of pseudogynes in a single nest? We must not, however, lose sight of the fact that the usual percentage of pseudogynes does not surpass that of the winged females, which may occur in a colony of *Formica sanguinea* or *rufa*, and that it certainly does not surpass the maximum which, according to my observations, may reach 5% in many *sanguinea* colonies. Now the pseudogynes do not leave the nest but remain in it, whereas the normal females escape at the time of the nuptial flight; hence it is only necessary that the conversion of larvæ into pseudogynes should be repeated for several generations and several years, to raise the number of these individuals to 20%." Wasmann also states that it is nearly always the same *Formica* colonies that are found to contain *Lomechusa* and *Atemeles* year after year. These considerations, however, fail to throw any light on the above described colony of *F. incerta* with its enormous number of pseudogynes associated with winged females and so small a number of workers. For if *X. cava* hibernates with *C. novæboracensis* it does not seem probable that it would return year after year to the same *incerta* nest, when there are hundreds of nests of this ant in the immediate neighborhood. Then, too, *incerta* colonies, unlike those of *sanguinea*, *rufa*, and *fusca* are very small, rarely comprising more than about 500 individuals, and could not even survive to raise *X. cava* year after year if the larvæ of this beetle are as destructive to the brood as the larvæ of *Lomechusa* and *Atemeles*. But this wholesale destruction would seem to be necessary, according to Wasmann's view, to bring about the conversion of female larvæ into pseudogynes. Moreover, if the pseudogynes are as short-lived as Wasmann supposes, how can they accumulate to any great extent in a single colony? And finally, how can a colony of *incerta* of the size of the one above described produce as many as 213 females in a single season? These considerations lend probability to the view that Wasmann's theory may require some emendation when we come to have a fuller knowledge of the habits of *Xenodusa*.

F. incerta and *rubicunda* are not the only North American ants that are able to produce pseudogynes. In going over my collection I find that I have mounted a number of these anomalous individuals with the normal workers from nests of the following ants:

1. *F. rufa integra* Nyl.

(a) A single pseudogyne taken several years ago by Mr. J. Angus at West Farms, now a part of New York City.

(b) A couple of callow pseudogynes collected July 8, at West Chester, Pennsylvania, by Mr. J. C. Bradley.

(c) Five pseudogynes which hatched in an artificial nest from cocoons taken August 1, 1905, from a very large colony at Colebrook, Connecticut. None of these is larger than a small or medium-sized worker of *integra*, but they all have the thorax clouded with black, although this subspecies differs from other forms of *rufa* in the absence of any infuscation of the head and thorax even in the smallest workers.

2. *F. rufa obscuriventris* Mayr. var. *melanotica* Emery.

During August, 1903, a number of cocoons of this ant were taken from a large and flourishing colony at Rockford, Illinois, and placed in an artificial nest containing *Polyergus rufescens breviceps* Emery with *F. cinerea* var. *neocinerea* Wheeler as slaves. The cocoons were at first neglected and finally carried by the workers to the refuse heap. On opening them I found in each a perfectly formed pseudogyne that must have died when very nearly ready to hatch. Some of these were as small as the smallest, but the majority were as large as the average *melanotica* workers. In two specimens, represented in Plate IV, Figs. 50–52, the thorax is seen to be more like that of the queen than in the pseudogynes of *F. incerta*.

3. *F. fusca* var. *neorufibarbis* Emery.

A single pseudogyne taken in Salt Lake County, Utah, by Mr. C. V. Chamberlin. In this specimen, which is smaller than the average worker, the dark thoracic blotches of the female are clearly indicated.

4. *F. sanguinea rubicunda* var. *subintegra* Emery.

(a) Two pseudogynes taken August 8, 1903, near Colorado Springs, Colorado, from a colony containing *F. fusca* var. *argentata* Wheeler as slaves.

(b) A single pseudogyne from a small colony taken August 13, 1903, in Cheyenne Cañon, Colorado. The slaves in this colony belonged to *F. argentata* and *F. subpolita* Mayr.

If we accept Wasmann's theory of the constant association of Lomechusini and pseudogynes, we must believe either that the single species, *X. cava*, breeds in the nests of several of our species of *Formica*, or that this name covers several closely allied species of *Xenodusa*, each with its normal host, but as yet undistinguished by coleopterists. Wasmann's description of different varieties of *X. cava*[1] may, perhaps, be regarded as supporting

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[1] Revision der Lomechusa-Gruppe. Deutsch. ent. Zeitschr., 1896, pp. 244–256.

the latter alternative. But there is still another possibility which I cannot regard as altogether precluded in the present state of our knowledge, namely, that Wasmann's theory may be too concisely formulated, and that pseudogynes may occasionally be produced even in colonies that have never been infested with Lomechusini. This would, indeed, be very probable if, as I have supposed, the pseudogynes arise from female larvæ that have been merely neglected by their nurses at a particular stage of development.

Even more fragmentary than our knowledge of *X. cava* is our knowledge of the other species of the genus. Wasmann recognizes three additional species from North America: *montana* Casey[1] from California, *caseyi* Wasm. from Colorado,[2] and *sharpi* Wasm. of Mexico.[3] Many years ago Walker described from Vancouver an *Atemeles reflexus*[4] which is probably the same as *X. cava,* and Fall[5] has recently described from southern California a *Lomechusa angusta,* which is a *Xenodusa* and may prove to be a synonym of Wasmann's *X. caseyi,* the smallest of our species.

The ethological notes accompanying the descriptions of these various species are very brief. According to Schwarz,[6] *X. montana* has been taken in the nests of *Camponotus lævigatus* F. Smith, an ant which hardly descends below 6,000 feet in the Rocky Mountains and Sierras, and P. M. Wirtner, O. S. B., according to Wasmann,[7] has taken this same beetle in the nests of *Formica subpolita* in Colorado. *X. montana* seems, therefore, to be heterœcious like *X. cava.* Father Wirtner also took the type of *X. caseyi* in the nest of *F. subpolita.* *X. sharpi* was found in a nest of *Camponotus auricomus.* One of the type specimens of *X. angusta* was taken by Dr. A. Fenyes "with ants in a large oak gall." It is probable that these ants belonged to some form of *Camponotus marginatus* as this is, according to my observations, the commonest and most widely distributed ant nesting in oak galls in the southwestern States. If this is the case, and if, as I suspect, *X. angusta* is the same as *X. caseyi,* this species would seem to be heterœcious like *X. cava* and *montana.*

Whether there are any *Xenodusæ* that are regularly or even occasionally monœcious with species of *Camponotus* cannot be decided at the present time. Wasmann entertains this possibility because pseudogynes of this genus have been described, and their existence would *ex hypothesi* require the rearing of *Xenodusa* larvæ by *Camponotus.* Emery has described a

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[1] Descriptions of North American Coleoptera, I. Bull. Calif. Acad. Sci., II, 1886–87. p. 202, 203.

[2] Eine neue Xenodusa aus Colorado mit einer Tabelle der Xenodusa-Arten. Deutsch. Ent. Zeitschr., 1897, II, p. 273, 274.

[3] Revision der Lomechusa-Gruppe, *l. c.*

[4] In Lord, The Naturalist in Vancouver Island and British Columbia, II, 1899, p. 317, 318.

[5] List of the Coleoptera of Southern California. Occas. Papers. Calif. Acad. Sci., VIII, 1901, pp. 219, 220.

[6] Myrmecophilous Coleoptera, etc., *loc. cit.*, p. 246.

[7] Zur Biologie der Lomechusa-Gruppe, *loc. cit.*, p. 275.

pseudogyne of a variety of *C. senex* Fabr. from Bolivia,[1] and Miss Holliday[2] has called attention to a couple of pseudogynes of *C. maculatus vicinus* Mayr. var. *nitidiventris* Emery collected by Professor Harold Heath at San Jose, California. Very recently Emery has discovered a pseudogyne of *C. igneus* (?) in the Baltic amber.[3] In another place[4] he has described what he regards as a pseudogyne of a Myrmicine ant, *Pheidologeton diversus*, of India. I figure some specimens of two different varieties of *Myrmica rubra* (*sulcinodoides* and *schencki*) which have a thoracic structure that may properly be called pseudogynic (Pl. IV, Figs. 45 and 46, 48 and 49) when compared with that of the normal worker (Fig. 47). The mesonotum is distinct and unusually convex, and there are clear traces of scutellar and metanotal sclerites. Some specimens (Fig. 45) bear vestiges of wings like those of the pterergates. As there is little probability that such forms are due to Lomechusini, it has been suggested that other parasites may be responsible for their production. I am inclined to believe that they arise occasionally even in uninfested colonies. If it be true that these anomalies as well as the above described pseudogynes of *Formica* arise from neglected immature female larvæ, it should be possible to produce them artificially by separating such larvæ from their nurses for several days. During the coming summer I hope to take up some experiments with this end in view.

4. The Commensalism of Metopina.

The parasitic insects considered in the preceding sections of this article are of more than usual interest because they produce certain effects noticeable both in the structure and behavior of their Formicid hosts. While all these effects are wrought through a withdrawal of nourishment from the developing larvæ, each natural group of parasites adopts a different method. Thus the ectoparasitic *Orasema* larva extracts important juices from the body of the *Pheidole* larva directly and with great rapidity, thereby reducing its host to a mere skin, which, though still able to pass on to the pupal stage, no longer possesses sufficient substance or vitality to reach the imaginal stage. The *Mermis* larva develops much more slowly within the alimentary tract of the ant larva and appropriates a portion of the food before it has been metabolized and converted into living compounds of high morphogenic potential. Finally, the presence of the Lomechusini within the *Formica*

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[1] Intorno al Torace delle Formiche. Boll. Soc. Ent. Ital., XXXII, 1900, p. 17 (of extract), fig. 14.

[2] Some Ergatogynic Ants, *loc. cit.*, pp. 313–315, fig. K.

[3] Deux Fourmis de l'Ambre de la Baltique. Bull. Soc. Ent. France, Année 1905, No. 13, p. 189, fig. 2.

[4] Zur Kenntniss des Polymorphismus, *loc. cit.*, p. 605–608, figs.

nest leads to a withholding of the necessary food from the larvæ, or, if Wasmann's view be adopted, at least to a withholding of the proper kind of food.

All of the above insects are ravenous parasites which ultimately destroy their hosts either individually or as communities. The insect to be described in the following paragraphs is much more benign, for if it surreptitiously appropriates some of the food that has been given to the larval ant, the amount it consumes seems to cause no serious inconvenience to its host. It is conceivable, however, that the presence of this commensal in great numbers might lead to very appreciable disturbances in the trophic status of a colony. The insect is a little Dipteron fly, whose larval and pupal stages I described in a paper published some years ago.[1] At that time I was unable to breed the imago and could only state that it was in all probability one of the Phoridæ. During the late autumn of 1901 Mr. C. T. Brues succeeded in rearing the adult insect from some larvæ which I gave him. He has since described it as *Metopina pachycondylæ*.[2] Much of my former account is here reproduced in a slightly altered form, together with an enlarged photograph (Pl. V, Fig. 69) of the larvæ and pupæ of both host and commensal.

On October 27, 1900, I made a short excursion to Mt. Barker, which is hardly more than an hour's walk from the university at Austin, Texas. The woods about the base and on the slopes of the elevation are favorite nesting grounds for the large black Ponerine ant, *Pachycondyla harpax* Fabr. In October this ant is rearing its second brood of larvæ and pupæ, having completed the education of its first brood during June and July.[3] Wishing to continue some observations on the babits of *Pachycondyla,* I dug up one of the largest colonies I could find and carried it home in a bag. On transferring it to a Lubbock nest I took the census of the colony and found it to comprise 25 worker ants, 13 cocoons, 8 mature larvæ, 7 immature larvæ, and a packet of eggs. While counting the larvæ, which are shaped like the well-known cucurbitaceous product known as the "crooked-necked squash," and covered with hairy tubercles, I noticed that six of the largest and one of the smallest presented an unusual appearance. Each of these seemed to wear about its neck a huge collar — a kind of Elizabethan ruff — consisting of a curled larva (Pl. V, Fig. 69 *x*). That this could not be another ant-larva was apparent from a moment's examination. In all cases it almost completely encircled the ant-larva in the region of the first abdominal, or in some cases the metathoracic, segment. The posterior end

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[1] An Extraordinary Ant-guest. Am. Naturalist, XXXV, 1901, pp. 1007–1016, 2 figs.

[2] A Monograph of the North American Phoridæ. Trans. Am. Ent. Soc., XXIX, No. 4, 1903, p. 384.

[3] For an account of the habits of this ant, see my paper, A Study of Some Texan Ponerinæ. Biol. Bull., Vol. II, No. 1 (Oct. 1900), pp. 1–31, figs. 1–10.

was provided with a kind of disk, which adhered so tightly that both larvæ could be killed in alcohol without separating. The collar-like larva was broad behind the middle, but tapered anteriorly to a very slender thoracic region and head provided with small jaws (Fig. 69 *z*). These were supported by a chitinous frame-work of such characteristic structure as to show that the adult form must be a true Dipteron. The very smooth and tense integument, which was armed with some short, hooked bristles, was very transparent, so that the peristaltic movements of the viscera were clearly visible.

As soon as the ants had been transferred to the Lubbock nest they were given a number of young larvæ of *Camponotus maccooki* var. *sansabeanus* Buckley. These they soon proceeded to malaxate with their mandibles, twirling the morsels about in the meantime with their fore legs and lapping up the exuding juices with their tongues. Finally they deposited the crumpled and pulpy remains of the *Camponoti* on the trough-like ventral surfaces of their larvæ, which had been previously placed on their backs in a rough chamber dug in the earth of the nest. This chamber was immediately under the glass roof-pane, so that further developments could be closely observed with a pocket lens. Each ant-larva at once stretched forth its head eagerly and began to devour the viands with which it had just been provided. At the same moment the Dipteron larva, too, as if sniffing the odor of the fresh food, unwound its tapering neck from the ventral surface of its host, and without shifting the attachment of its posterior end, at once plunged its mandibles into the food. Under the lens both larvæ could be seen greedily dining side by side till the last particle of *Camponotus* larva had been consumed or prematurely removed by the worker ants.

When the ant-larvæ were huddled close together, a collar-like larva was sometimes observed to reach over and help itself from the food supply of a neighbor; but even when thus compelled to crane its neck to the utmost, it never shifted the attachment of its caudal end. Sometimes when there was no food within reach it would tweak with its sharp little jaws the sensitive hide of a neighboring ant-larva, till the latter squirmed with pain. It would sometimes even tweak its own host, as if to make it wriggle and perhaps thereby incite the worker ants to bring a fresh supply of provisions.

The following day two living myriopods (*Lithobius*) were placed in the nest. During the morning hours they were killed by the *Pachycondyla* workers, shorn of their many legs, cut up into pieces of convenient length, malaxated, and fed to the larvæ as on the preceding day. And again I was able to witness the strange banquet — the dwarf reaching down from the shoulders of the ogre and helping himself from the charger formed by the trough-like belly of his host. The same observation was repeated on several consecutive days. Pieces of various ant-larvæ, beetle-larvæ, *Lithobius*, *Scutigera*, *Oniscus*,— all were served up to the ant-larvæ and partaken of with great relish by the Dipteron larvæ as well. There could be no doubt that the latter were true commensals,— perhaps the most perfect commensals, in the original meaning of the term, to be found in the whole animal kingdom!

As one of the smallest *Pachycondyla* larvæ, scarcely one-fourth grown, bore a very small Dipteron larva, it is, perhaps, safe to say that the ant-larva acquires its commensal at a very early age. The two then grow up together, so that there is always a certain relation between the two kinds of larvæ — large *Pachycondyla* larvæ bearing large commensals, and *vice versâ*. The worker ants lick and cleanse the commensals at the same time that they are caring for their own larvæ. This is usually done after meals. Since, during this operation of cleansing, the ants spend no more time over the commensals than they do on a similar area of the body surface of their own larvæ, it would seem that they are not even aware of the existence of the commensals. To these nearly blind ants, which must rely almost exclusively on their senses of smell and touch, the larvæ bearing commensals, if distinguished at all from individuals without these satellites, would probably be perceived merely as having unusually protruding necks. But there is nothing to indicate that these insects are really capable of perceiving such differences in their environment.

On the 5th of November I obtained satisfactory evidence that the *Metopina* larva is not obliged to remain always with the same *Pachycondyla* larva. During the night one of the large larvæ had moved and attached itself to the first abdominal segment of an ant larva which already bore a commensal around its metathoracic segment. The two larvæ were oriented in opposite directions, *i. e.*, with their heads reaching around opposite sides of their host. Subsequently one of these commensals moved to an unoccupied *Pachycondyla* larva. I was not present when the change occurred, nor was I able to determine whether it was the originally stationary or the adventitious larva that moved. Although this observation makes it certain that the *Metopina* larvæ can shift their position from one host to another, I am convinced, nevertheless, that they must do this with great reluctance and only under urgent circumstances, such as extreme hunger, the death of the larva to which they are attached, or, perhaps, when fully mature and about to pupate.

As the days passed, the mature ant-larvæ spun their brown cocoons (Pl. V, Fig. 69 *u*) one by one, and one by one the mature commensals disappeared. Did they also pupate and for this purpose conceal themselves in the soil of the nest? Or had the ants at last detected the villains and converted them into food for the larvæ which had not yet pupated? Or did they stick to their hosts and pupate within the cocoons? In order to ascertain, if possible, the true state of affairs, I transferred the whole colony to a fresh nest and examined the soil of the old nest with great care. There were no traces of the missing commensals. The only remaining resource was to open the cocoons. Several of the cocoons which had been taken with the nest October 27 had hatched, but by November 10 there were still thirteen cocoons in the nests, as several of the larvæ had pupated in the meantime. Five of these were opened, and in two, which contained semipupæ of *Pachycondyla* and were, therefore, of recent formation, commensals were found! Having shared the table of their host, they had come to share its bed as well. The *Metopina*, too, had pupated after the manner of its kind — forming a puparium; *i. e.*, instead of spinning a cocoon like the ant larva, the dead larval skin, somewhat shriveled and contracted, was used as an envelope, and within this the pupa proper was formed.

This puparium, represented in Plate V, Fig. 69 *v*, is from 2.25 to 2.5 mm. long and clearly of the cyclorhaph type. It is elliptical, much flattened dorso-ventrally, especially along the edges, which are thin and hyaline and almost alate. The brownish dorsal surface is thrown into delicate and irregular transverse wrinkles. Anteriorly, in the thoracic region, there is a pair of short black respiratory tubes. The ventral surface is very glabrous and distinctly paler than the dorsal surface.

Subsequently, several other cocoons were opened and two more were found to contain the puparia of commensals. In all four cases the puparium was invariably located in the caudal pole of the cocoon, just to one side of the black blotch of ejecta deposited by the ant-larva before becoming a semipupa. At this point the puparium was immovably stuck to the wall of the cocoon by means of its smooth ventral surface. Its anterior end was directed towards the cephalic pole. As there is always considerable space, especially at the posterior pole, between the walls of the cocoon and the enclosed ant-pupa, the much flattened fly puparium did not in the least crowd its host.

It would be interesting to know what the commensal larva is doing while the ant-larva is weaving its cocoon. Does it move about to avoid the swaying jaws of the spinning larva? Or does it take up its position from the first at the posterior end of the larval ant and there remain motionless while the posterior pole of the cocoon is being completed? It is very difficult to answer these questions. The fact that the posterior poles of all the cocoons containing puparia were somewhat distorted, being broader, more obtuse, and more irregular than the normal cocoons, would seem to indicate that the ant-larva may modify this end of its cocoon for the better accommodation of the commensal. I am inclined to believe, however, that the distortion may be produced by the *Metopina* larva while attaching itself just before pupating to the newly woven and still plastic cocoon.

Reflection shows that the position of the puparium in the posterior pole of the cocoon, though the reverse of the position of the larval commensal with respect to its larval host, is the only one which can be maintained by the commensal with perfect safety. Like other ants, the *Pachycondyla* leaves its cocoon through a rent in the anterior pole. This rent is certainly made by the mandibles of the hatching ant, and it is possible that the callow insect may succeed in making its way out of the cocoon without any assistance from the workers. I have hitherto failed, however, to surprise one of these ants in the act of hatching. But even if the obstetrical aid of the workers is necessary, as it is in the more highly specialized Camponotinæ, any position for the commensal puparium, except at the posterior pole of the cocoon, might be fatal, for the struggling jaws and legs of the emerging ant and the jaws of the assisting ants would certainly be very liable to cut into so delicate an object attached to the anterior or median walls of the cocoon.

At this point my first set of observations on the *Metopina* ended. The Phorid puparia were kept for several weeks in what I supposed to be the proper conditions of warmth and moisture, but to my intense disappointment they failed to hatch. During the autumn and winter frequent and diligent search was made for more of the commensals in all the *Pachycondyla* nests I could find, but in vain. Finally, during the latter part of May of the following year, I discovered in a very different locality two *Pachycondyla* nests which contained a few *Metopina* larvæ. This discovery proved that the Phorid is double-brooded like its host. But the larvæ were very small and attached to such very young ant-larvæ that I despaired of being able to raise them in my artificial nests as far as the imaginal stage. The search for *Pachycondyla* nests containing *Metopinæ* was again renewed in the fall. Two colonies were found, and from one of these Mr. Brues succeeded in rearing several of the imaginal flies. These measure 2 mm. in length, are black with yellowish brown legs and antennæ and clear, hyaline wings. As yet *M. pachycondylæ* is the only known North American species of the genus.

It is not difficult to imagine the circumstances under which the *Metopina* hatches and manages to lay its eggs in the same or other *Pachycondyla* nests. Undoubtedly the ant is the first to hatch and to leave the cocoon. Now very soon after this occurs, the useless cocoon is always carried by a worker and placed on the refuse heap, which in the natural nest is often almost entirely made up of the empty cocoons of from one to several broods of ants, and lies in a rather dry and well-ventilated spot immediately beneath the stone covering the nest. Along with the cocoon is carried the *Metopina* puparium still adhering to the wall at its unopened posterior end. Thus after a privileged existence as free pensioner and bedfellow to a generous host, it is unwittingly carried away in the worn-out bedclothes and consigned to the family rag pile. Here the small and very active Dipteron hatches, leaves by the wide-open front door of the cocoon, and, after mating, either returns to lay a few eggs in the galleries of its former host, or flies away to oviposit in some other *Pachycondyla* nest. Thus the simple fact that the *Metopina* hatches later than the ant renders it unnecessary for the fly to possess some peculiar means of perforating the tough wall of the cocoon, and also accounts for the position of the puparium in the posterior pole, where it would be completely concealed from the workers even after the escape of the callow ant.

In conclusion attention may be directed to certain particulars of special interest in connection with the life history of the *Pachycondyla* commensal: First, the peculiar habits of the Phorid show clearly that the Ponerine method of feeding the larvæ with comminuted insects is not only the typical but the only method employed by these ants, for such a commensal would certainly starve if the *Pachycondyla* larvæ were carefully fed like the larvæ of *Camponotus* and *Formica,* by regurgitation of liquid from the mouths of the workers. The Phorid profits by a peculiarity in the behavior of its host, and thereby demonstrates — by one of Nature's experiments — that *Pachycondyla harpax* does not feed its young by regurgitation. Second, in the peculiar symbiotic relationship existing between the Phorid and the ants, the adaptations are all on the side of the former, whereas the latter pursues its ancient and well-established mode of life uninfluenced by and apparently in complete ignorance of the very existence of its little guests. Even the distortion of the cocoon may be entirely due, as I have suggested, to the activity of the *Metopina.* These strikingly unilateral adaptations are probably to be explained on the ground that the Phorid is so careful and conservative of the life and welfare of its host. The small amount of food consumed by the little commensals can hardly be a serious drain on the provisioning instincts of the Ponerinæ, at least under ordinary conditions. The larvæ bearing the commensals were certainly as large and healthy as any others in the nest, and produced perfectly normal pupæ, which in the cases observed all lacked the imaginal disks for the wings and were therefore of the worker type.

PART II. CONCERNING THE POLYMORPHISM OF ANTS.

There is a sense in which the term polymorphism is applicable to all living organisms, since no two of these are ever exactly alike.[1] But when employed in this sense, the term is merely a synonym of 'variation', which is the more apt, since polymorphism has an essentially morphological tinge, whereas variation embraces also the psychological, physiological, and ethological differences between organisms. In zoölogy the term polymorphism is progressively restricted, first, to cases in which individuals of the same species may be recognized as constituting two or more groups, or castes, each of which has its own definite characters or complexion. Second, the term is applied only to animals in which these intraspecific groups coëxist in space and do not arise through metamorphosis or constitute successive generations. Cases of the latter description are referred to 'alternation of generations' and 'seasonal polymorphism.' And third, the intraspecific groups which coincide with the two groups of reproductive individuals existing in all gonochoristic, or separate-sexed Metazoa are placed in the category of 'sex' or 'sexual dimorphism.' There remain therefore as properly representing the phenomena of polymorphism only those animals in which characteristic intraspecific and intrasexual groups of individuals may be recognized, or, in simpler language, those species in which one or both of the sexes appear under two or more distinct forms.

As thus restricted polymorphism is of rare occurrence in the animal kingdom and may be said to occur only in colonial or social species, where its existence is commonly attributed to a physiological division of labor. It attains to its clearest expression in the social insects, in some of which, like the termites, we find both sexes equally polymorphic, while in the others like the ants, social bees, and wasps, the female alone, with rare exceptions, is differentiated into distinct castes. This restriction of polymorphism to the female in the social Hymenoptera, with which we are here especially concerned, is easily intelligible if it be traceable, as is usually supposed, to a physiological division of labor, for the colonies of ants, bees, and wasps are essentially more or less permanent families of females, the male representing merely a fertilizing agency temporarily intruding itself on the activities of the community at the moment it becomes necessary to start other colonies. We may say, therefore, that polymorphism among social Hymenoptera is a physical expression of the high degree of social plasticity and efficiency of the female sex among these insects. This is shown more specifically in two

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[1] The term is used in this sense by Waxweiler, for example, in his admirable 'Esquisse d'une Sociologie,' Brussels, 1906, pp. 141–143.

characteristics of the female, namely the extraordinary intricacy and amplitude of her instincts which are thoroughly representative of the species, and her ability to reproduce parthenogenetically. This, of course, means a considerable degree of autonomy even in the reproductive sphere. But parthenogenesis, while undoubtedly contributing to the social efficiency of the female, must be regarded and treated as an independent phenomenon, without closer connection with polymorphism, for the ability to develop from unfertilized eggs is an ancient characteristic of the Hymenoptera and many other insects, which made its appearance among the solitary species, like the Tenthredinidæ and Cynipidæ, long before the development of social life. Moreover, polymorphism may occur in male insects which, of course, are not parthenogenetic. That parthenogenesis is intimately connected with sexual dimorphism, at least among the social Hymenoptera, seems to be evident from the fact that the males usually if not always develop from unfertilized, the females from fertilized eggs.

While the bumble-bees and the wasps show us the incipient stages in the development of polymorphism, the ants as a group, with the exception of a few parasitic genera that have secondarily lost this character, are all completely polymorphic. It is conceivable that the development of different castes in the female may have arisen independently in each of the three groups of social Hymenoptera, although it is equally probable that they may have inherited a polymorphic tendency from a common extinct ancestry. On either hypothesis, however, we must admit that the ants have carried the development of female castes much further then the social bees and wasps, since they have not only produced a wingless form of the worker, in addition to the winged female, or queen, but in many cases also two distinct castes of workers known as the worker proper and the soldier. Some systematists have, therefore, appropriately separated them from all other Hymenoptera as 'Heterogyna.'

Different authors have framed very different conceptions of the phylogenetic beginnings of social life among the Hymenoptera and consequently also of the phylogenetic origin and development of polymorphism. Thus Herbert Spencer evidently conceived the colony as having arisen from a consociation of adult individuals. I infer this from his remarks on the origin of the amazon colony in his well-known reply to Weismann:[1] "Some variety of them [the amazon ants] led to swarm — probably at the sexual season — did not disperse again as soon as other varieties. Those which thus kept together derived advantages from making simultaneous attacks on prey and prospered accordingly. Of descendants the varieties which carried

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[1] A Rejoinder to Professor Weismann. Contemp. Review, Sept. 1893, p. 14.

on longest the associated state prospered the most; until, at length, the associated state became permanent. All of which social progress took place while there existed only perfect males and females." Although Spencer is particularly unfortunate in selecting a parasitic ant like the amazon (*Polyergus rufescens*) on which to hang his hypothesis, there are a few facts which would seem to make his view applicable to other social Hymenoptera. Fabre[1] once found some hundreds of a species of solitary wasp (*Ammophila hirsuta*) huddled together under a stone on the summit of Mt. Ventoux in the Provence at an altitude of about 5,500 feet, and Forel[2] found more than fifty deälated females of *Formica rufa* under similar conditions on the Simplon. I have myself seen collections of a large red and yellow *Ichneumon* under stones on Pike's Peak at an altitude of more than 13,000 feet, and a mass of about seventy deälated females of *Formica fusca* var. *gnava* Buckley apparently hibernating after the nuptial flight under a stone near Austin, Texas. I am convinced, however, that such congregations are either entirely fortuitous, especially where the insects of one species are very abundant and there are few available stones, or, that they are, as in the case of *F. rufa* and *gnava,* merely the result of highly developed social proclivities and not a manifestation of such proclivities in process of development.

A very different view from that of Spencer is adopted by most authors. They regard the insect society as having arisen, not from a chance concourse of adult individuals but from a natural affiliation of mother and offspring. This view which has been elaborated by Marshall[3] among others, presents many advantages over that of Spencer, not the least of which is its agreement with what actually occurs in the founding of the existing colonies of wasps, bumble-bees and ants. These colonies pass through an ontogenetic stage which has all the appearance of repeating the conditions under which colonial life first made its appearance in the phylogenetic history of the species — the solitary mother insect rearing and affiliating her offspring under conditions which would seem to arise naturally from the breeding habits of the nonsocial Hymenoptera. The exceptional methods of colony formation seen in the swarming of the honey bee and in the temporary and permanent parasitism of certain ants, are too obviously secondary and comparatively recent developments to require extensive comment. The bond which held mother and daughters together as a community was from the first no other than that which binds human societies together — the bond

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[1] Souvenirs Entomologiques. I, 3 ed., 1894, pp. 187, 188, 196 *et seq.*
[2] Fourmis de la Suisse, p. 257.
[3] Leben and Trieben der Ameisen. Leipzig, 1889, pp. 3–6.

of hunger and affection so beautifully described in the famous lines from Schiller's "Die Weltweisen":

> Einstweilen, bis den Bau der Welt
> Philosophie zusammenhält,
> Erhält sie [Natur] das Getriebe,
> Durch Hunger und durch Liebe.

The daughter insects in the primitive colony became dependent organisms as a result of two factors: inadequate nourishment and the ability to pupate very prematurely. But this very ability seems to have entailed an incompleteness of imaginal structure and instincts which in turn must have confirmed the division of labor and thus tended to perfect the social organization.

Before further discussing the problems suggested by this view of the origin of the colony and the general subject of polymorphism, it will be advisable to pass in review the series of different phases known to occur among ants. This review will be facilitated by consulting the diagram on Plate VI, in which I have endeavored to arrange the various phases so as to bring out their morphological relations to one another. The phases may be divided into two main groups, the normal and the pathological. In the diagram the names of the latter are printed in italics. The normal phases may again be divided into primary or typical, and secondary or atypical, the former comprising only the three original phases, male, female, and worker, the latter the remaining phases, which, however, are far from all having the same status or frequency. The three typical phases are placed at the angles of an isosceles triangle, the excess developments being placed to the right, the defect developments to the left, of a vertical line passing through the middle of the diagram. The arrows indicate the directions of the affinities of the secondary phases and suggest that those on the sides of the triangle are annectant, whereas those which radiate outward from its angles represent the new departures with excess and defect characters.

1. THE TYPICAL, ATYPICAL AND PATHOLOGICAL PHASES OF ANTS.

(1) The *male* (anēr) is far and away the most stable of the three typical phases which are found in all but a few monotypic and parasitic genera of ants. This is best shown in the general uniformity of structure and coloration which characterize this sex in genera whose female forms (workers and queens) are widely different; *e. g.*, in such a series of cases as *Myrmecia, Odontomachus, Cryptocerus, Formica, Pheidole,* etc. In all of these genera the males are very similar, at least superficially, whereas the workers and females are very diverse. The body of the male ant is graceful in form, one might almost say emaciated. Its sense-organs (especially the eyes and antennæ), wings and genitalia are highly developed; its mandibles are

more or less undeveloped and in correlation with them the head is portionally shorter, smaller and rounder than in the females and workers of the same species. Even when the latter phases have brilliant or metallic colors, as in certain species of *Macromischa* and *Ectatomma*, the males are uniformly red, yellow, brown or black. Yet notwithstanding this monotony of structure and coloration, the male type may present the following interesting modifications.

(2) The *macranēr* is an unusually large form of male which occasionally occurs in populous colonies.

(3) The *micranēr*, or dwarf male, differs from the typical form merely in its smaller stature. Such forms often arise in artificial nests.

(4) The *dorylanēr* is an unusually large male form peculiar to the driver and legionary ants of the subfamily Dorylinæ (*Dorylus* and *Eciton*). It is characterized by its large and peculiarly modified mandibles, long cylindrical gaster and singular genitalia. It may be regarded as an aberrant macranēr that has come to be the typical male of the Dorylinæ.

(5) The *ergatanēr*, ergatomorphic, or ergatoid male resembles the worker in having no wings and in the structure of the antennæ. It occurs in the genera *Ponera*, *Formicoxenus*, *Symmyrmica*, and *Cardiocondyla*. In certain species of *Ponera* (*P. punctatissima* and *ergatandria*) and in *Formicoxenus nitidulus* the head and thorax are surprisingly worker-like, in other forms like *Symmyrmica chamberlini* these parts are more like those of the ordinary male ant, while *P. eduardi* shows a more intermediate development of the head with a worker-like thorax. Forel,[1] has recently shown that the ergatanēr may coëxist with the anēr, at least in one species of *Ponera* (*P. eduardi* Forel). In other words, this ant has dimorphic males.

(6) The *gynæcanēr*, or gynæcomorphic male occurs in certain parasitic and workerless genera (*Anergates* and *Epœcus*) and resembles a female rather than a worker form. The male of *Anergates* is wingless, but has the same number of antennal joints as the female. In *Epœcus* both sexes are very much alike and both have 11–12-jointed antennæ.[2]

(7) The *phthisanēr* is a pupal male which in its late larval or semipupal state has its juices partially exhausted by an *Orasema* larva. This male is too much depleted to pass on to the imaginal stage. The wings are suppressed and the legs, head, thorax, and antennæ remain abortive.

(8) The *female* (gynē), or queen, is the more highly specialized sex among ants and is characterized, as a rule, by her large stature and the more uniform development of her organs. The head is well developed and

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[1] Dimorphisme du Mâle chez les Fourmis. Ann. Soc. Ent. Belg., XLVIII, 1904.

[2] For an account of the ergatandric and gynæcandric forms see Emery, 'Zur Kenntniss des Polymorphismus der Ameisen,' Biol. Centralbl., XXVI, 1906, pp. 624–630, 4 figs.

provided with moderately large eyes, ocelli, and mandibles; the thorax is large (macronotal) and presents all the sclerites of the typical female Hymenopteron; the gaster is voluminous and provided with well developed reproductive organs. The wings and legs are often relatively smaller than in the male.

(9) The *macrogyne* is a female of unusually large stature.

(10) The *microgyne*, or dwarf female, is an unusually small female which in certain ants, like *Formica microgyna* and its allies, is the only female of the species and may be actually smaller than the largest workers. In other ants, like certain species of *Leptothorax* and *Myrmica* microgynes may sometimes coëxist in the same nests with the typical females.

(11) The *β–female* is an aberrant form of female such as occurs in *Lasius latipes*, either as the only form or coëxisting with the normal female which is then called the *α*-female. In this case, therefore, the female is dimorphic. The *β*-female is characterized by excess developments in the legs and antennæ and in the pilosity of the body.

(12) The *ergatogyne*, ergatomorphic, or ergatoid female, is a worker-like form but with large eyes, ocelli, and a thorax more or less like that of the female, but without wings. Such females occur in a number of species of ants. They have been seen in *Myrmecia, Odontomachus, Anochetus, Ponera, Polyergus, Leptothorax, Monomorium*, and *Cremastogaster*. There is nothing to prove that they are pathological in origin. In fact, in *Monomorium floricola* and certain species of *Anochetus* they seem to be the only existing females. In other cases, like *Ponera eduardi*, as Forel has shown, they occur with more or less regularity in nests with normal workers. They occur also under similar conditions in colonies of the circumpolar *P. coarctata*, and probably also among other species of the genus.

(13) The *dichthadiigyne*, or dichthadiiform female is peculiar to the ants of the subfamily Dorylinæ. It is wingless and stenonotal, destitute of eyes and ocelli, or with these organs very feebly developed, and with a huge elongated gaster and extraordinary, voluminous ovaries.

(14) The *pseudogyne* has been sufficiently characterized in the preceding pages as a worker-like form with enlarged mesonotum and sometimes with traces of other thoracic sclerites of the female, but without wings or very rarely with wing vestiges.

(15) The *phthisogyne* arises from a female larva under the same conditions as the phthisanēr, and differs from the typical female in the same characters, namely absence of wings, stenonoty, microcephaly and microphthalmy. It is unable to attain to the imaginal instar.

(16) The *worker* (ergates) is characterized by the complete absence of wings and a very small (stenonotal) thorax, much simplified in the structure of its sclerites. The eyes are small and the ocelli are usually absent or,

when present, extremely small. The gaster is small, owing to the undeveloped condition of the ovaries. A receptaculum seminis is usually lacking, and the number of the ovarian tubules is greatly diminished.[1] The antennæ, legs and mandibles are well developed.

(17) The *gynæcoid* is an egg-laying worker. It is a physiological rather than a morphological phase, since it is probable that all worker ants when abundantly fed become able to lay eggs. Wasmann[2] observed in colonies of *Formica rufibarbis* that a few of the workers became gynæcoid and functioned as substitution queens. In colonies of the Ponerine genus *Leptogenys* (including the subgenus *Lobopelta*), and probably also in *Diacamma* and *Champsomyrmex,* the queen phase has disappeared and has been replaced by the gynæcoid worker.

(18) The *macrergate* is an unusally large worker form which in some species is produced only in populous or affluent colonies (*Formica, Lasius*).

(19) The *micrergate,* or dwarf worker, is a worker of unusually small stature. It appears as a normal or constant form in the first brood of all colonies that are founded by isolated females.

(20) The *dinergate,* or soldier is characterized by a huge head and mandibles, often adapted to particular functions (fighting and guarding the nest, crushing seeds or the hard parts of insects), and a thoracic structure sometimes approaching that of the female in size or in the development of its sclerites (*Pheidole*).

(21) The *desmergate* is a form intermediate between the typical worker and dinergate, such as we find in more or less isolated genera of all the subfamilies except the Ponerinæ, *e. g.*, in *Camponotus,* some species of *Pheidole, Solenopsis,* and *Pogonomyrmex, Azteca, Dorylus, Eciton,* etc. The term might also be employed to designate the intermediate forms between the small and large workers in such genera as *Monomorium, Formica,* etc.

(22) The *plerergate,* 'replete,' or 'rotund,' is a worker which in its callow stage has acquired the peculiar habit of distending its gaster with stored liquid food ('honey') till this portion of the body is a large spherical sac and locomotion becomes difficult or even impossible. This occurs in the honey ants (some North American species of *Myrmecocystus,* some Australian *Melophorus* and *Camponotus,* and to a less striking extent in certain species of *Prenolepis* and *Plagiolepis*).

(23) The *pterergate* is a worker or soldier with vestiges of wings on a thorax of the typical ergate or dinergate form, such as I have described in certain species of *Myrmica* and *Cryptocerus.*[3]

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[1] Adlerz's often-cited statement that the ovarian tubules are completely lacking in the workers of *Tetramorium cæspitum* seems to me to require confirmation. These organs may be easily overlooked in dissecting such small ants. The study of stained sections of adult pupal workers would probably yield more satisfactory results.

[2] Ameisenarbeiterinnen als Ersatzköniginnen, *loc. cit.*

[3] Worker Ants with Vestiges of Wings. Bull. Am. Mus. Nat. Hist., XXI, 1905, pp. 405–408, pl. xiv.

(24) The *mermithergate*, which has been described in detail in the preceding pages, is an enlarged worker, produced by *Mermis* parasitism and often presenting dinergate characters in the thorax and minute ocelli in the head.

(25) The *phthisergate*, which corresponds to the phthisogyne and phthisanēr, is a pupal worker which in its late larval or semipupal stage has been attacked and partially exhausted of its juices by an *Orasema* larva. It is characterized by extreme stenonoty, microcephaly and microphthalmy, and is unable to pass on to the imaginal stage. It is in reality an infraergatoid form.

(26) The *gynandromorph* is an anomalous form in which male and female characters are combined in a blended or more often in a mosaic manner.

(27) The *ergatandromorph* is an anomaly similar to the last but having worker instead of female characters combined with those of the male.[1]

2. The Views of Some Previous Authors on Polymorphism.

In their attempts to explain polymorphism authors have not, of course, taken all of the above enumerated phases into consideration, but have been content to include only the typical and perhaps a few of the atypical and pathological phases. And it is clear that if the main phases could be accounted for, the rarer and less important deviations would present few difficulties. I shall endeavor to show, however, that some of these singular forms may shed at least a few rays of light on the problem of polymorphism.

The social insects have held an important place in discussions of evolution and heredity ever since Darwin called particular attention to these animals in the eighth chapter of the 'Origin.' In later years they assumed even greater prominence in the controversies between the Neolamarckians and Neodarwinians concerning the efficacy of natural selection. This was unavoidable, for polymorphism would seem to be of such a nature as to afford a test of the validity of any hypothesis bearing on the inheritance or noninheritance of acquired characters as well as of any hypothesis concerning the rôle of preformation, or epigenesis, in the development of organisms. As it will be impossible in this place to present a detailed history of the subject or to dwell on all its wider implications, I shall confine myself mainly to the views which were championed by Weismann and Herbert Spencer respectively in their well-known controversy in the 'Contemporary Review',

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[1] For an account of the known cases of this and the preceding anomaly among ants see my paper: 'Some New Gynandomorphous Ants, with a Review of the Previously Described Cases.' Bull. Am. Mus. Nat. Hist., XIX, 1903, pp. 653–683, 11 figs.

and have been maintained with more or less modification by zoölogists down to the present time.[1]

In order to make his explanation of polymorphism conform with the remainder of his hypothesis of heredity, Weismann is compelled to assume, not only a set of germ-plasmic determinants for each of the sexes in ordinary sexual dimorphism, but a double set for the female in the social Hymenoptera and a double set for each sex in the termites. At least four sets must also be postulated for ants with differentiated worker and soldier castes. This is evident from the following quotation:[2]

"So when instead of dimorphism, there is polymorphism, when, for instance, the females of a species are similarly distinguished among themselves, and occur in two forms, this results, according to my idea, from the double determinants becoming triple determinants. If there were workers among the butterflies, and if these showed red color on the part of the wing that is blue in the male and brown in the female, there would always be three representative determinants present at a definite part of the extremely elaborate and highly complicated germ-plasm; but only one of these would become active during the development of the egg and sperm-cell concerned, and would produce the patch of brown or blue or red scales in the wing.

"According to this theoretical representation, every part of the body that is differently formed in the males, females and workers is represented in the germ-plasm by three corresponding determinants but in the development of the eggs, never more than one of these attains to value — *i. e.*, gives rise to the part of the body that is represented — and the others remain inactive.

"Thus, then, the metamorphosis of the body parts of the workers of ants and bees will have to be considered in connection with the fact that the males and females whose germ-plasm contains favorable variations of the determinants of the workers have a better prospect for the maintenance of their successors than others which showed less favorable variations of such determinants. The process of selection is the same as if the matter at issue were the attainment of favorable adaptations in the body of the sexual forms; for in both cases it is, as I have once before said, not really the body that is

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[1] The papers called forth by this controversy are here cited in the order of their publication: Spencer: 'The Inadequacy of "Natural Selection",' Contemp. Rev., Feb. and March, 1893, pp. 153–166, 439–456; 'Professor Weismann's Theories,' *ibid.*, May, 1893, pp. 743–760; Weismann: 'The All Sufficiency of Natural Selection,' *ibid.*, Sept., 1893, pp 309–338; Spencer: 'A Rejoinder to Professor Weismann,' *ibid.*, Dec. 1893, pp. 893–912; 'Weismannism Once More,' *ibid.*, Oct. 1894, pp. 592–608. Weismann has also repeated or elaborated his views on the polymorphism of the social insects in the following works: 'Das Keimplasma. Eine Theorie der Vererbung.' Jena, Gustav Fischer, 1892, pp. 494–498; 'The Effect of External Influences upon Development,' Romanes Lecture, London, Henry Frowde, 1894, pp. 29–48; and 'Vorträge über Descendenz-theorie,' Jena, Gustav Fischer. 2 Bd. pp. 101–118. For an aftermath of the Spencer-Weismann controversy see also the discussion of the subject in 'Natural Science,' IV, 1894, by Ball (Neuter Insects and Lamarckism, pp. 91–97), and Cunningham (Neuter Insects and Darwinism, pp. 281–289).

[2] The All-Sufficiency, etc., *loc. cit.*, pp. 326, 327.

selected, but the germ-plasm from which the body develops. The difference is this: in the one case the survival in the struggle for existence depends on characters and variations of the body of the individual; in the other, only on the character of a certain kind of descendant — the worker. If the ant state were composed of individuals connected together like a colony of polypes or *Siphonophoræ,* a process of selection by which only the workers were changed would be within easier reach of our imagination, as these would then, in a manner, be only *organs,* just like the snaring-threads, the swimming bells, and the gastric tubes of the *Siphonophoræ.* As these do not reproduce, and accordingly can only vary by selection of the egg or germ-plasm from which the whole colony is formed, so in the case of the ant-colony, or rather state, the barren individuals or organs are metamorphosed only by selection of the germ-plasm from which the whole state proceeds. In respect of selection the whole state behaves as a single animal; the state is selected, not the single individuals; and the various forms behave like the parts of one individual in the course of ordinary selection."

It must be admitted that this hypothesis is boldly and clearly conceived and its author's knowledge of myrmecology and melittology is only surpassed by the adroitness with which he compells the facts to tally with his assumptions. Nowhere in Weismann's work are both the strength and the weakness of his elaborate architectonics of the germ-plasm more apparent than in this attempt to explain the complicated and adaptively correlated organization of the sterile worker as the result of a single mechanical factor, natural selection, acting on constellations of fortuitous determinants in the germ-plasm of the fertile female.

Spencer, too, seeks a mechanical explanation of the purposeful adaptations of the worker, though this is utterly at variance with the fundamental teleological spirit of the Lamarckian view which he elsewhere advocates. He starts out with the social wasps (*Vespa*), some species of which present an uninterrupted series of transitional forms between the small sterile worker and the large fertile female, or queen. He calls attention to the abundant evidence to show that these arise progressively and in close dependence on the food supply of the colony, so that the sterility and dwarfing of the workers are manifestly caused by insufficiency of food during their larval stages. He then proceeds to extend this same explanation to the ants, although these insects differ from the wasps in presenting great morphological differences between the workers and females. After considering the African driver ants which have highly polymorphic workers, he goes on to say: "In contrast with this interpretation, consider now that of Professor Weismann. From whichever of the two possible suppositions he sets out, the result is equally fatal. If he is consistent, he must say that each of these intermediate forms of workers must have its special set of 'determinants,' causing its special set of modifications of organs; for he cannot assume that while perfect females and the extreme types of workers have their different sets of determinants, the intermediate types of workers have not. Hence, we are introduced to the strange conclusion that besides the markedly distinguished sets of determinants there must be to produce these intermediate forms, many other sets slightly distinguished from one another — a score or more kinds of germ-plasm in addition to the four chief kinds [namely for the male, female, soldier, and worker]. Next comes an introduction to the still stranger conclusion, that these numerous kinds of germ-plasm, producing these numerous intermediate forms, are not simply needless but injurious — produce forms not well fitted for either of the functions discharged by the extreme forms: the implication being that natural selection has originated these disadvantageous forms! If to escape from this necessity for suicide Professor Weismann accepts the inference that the differences among these numerous intermediate forms are caused by arrested feeding of the larvæ at different stages, then he is bound to admit that the differences between the extreme forms, and between these and perfect females, are similarly caused. But if he does this, what becomes of his hypothesis that the several castes are constitutionally distinct, and result from the operation of natural selection? Observe too that his theory does not even allow him to make this choice; for we have clear proof that unlikenesses among the forms of the same species cannot be determined this way or that way by differences of nutrition. English greyhounds and Scotch greyhounds do not differ from one another so much as do the Amazon-workers [soldiers] from the inferior workers, or the workers from the queens. But no matter how a pregnant Scotch greyhound is fed, or her pups after they are born, they cannot be changed into English greyhounds: the different germ-plasms assert themselves spite of all treatment. But in these social insects the different structures of queens and workers are determinable by differences of feeding. Therefore the production of their various castes does not result from the natural selection of varying germ-plasm."

If we omit the portion of Spencer's argument in which he postulates the dysteleological character of the intermediates, or desmergates, as I have called them — a probably erroneous assumption, since there is every reason to believe that individuals embodying varying combinations of the worker and soldier traits may be just as useful to the colony as the soldiers and workers themselves — the position taken in the above quotation seems to be unassailable. But when Spencer comes to deal with the crucial problem, namely the marvelous, purposeful coadaptation of organs in the sterile workers, he fails as signally as Weismann, for no one familiar with the habits and taxonomy of ants can regard his attempts to trace such specialized structures and instincts as those of the amazon slave-makers (*Polyergus*) to inherited presocial acquirements as seriously invalidating Weismann's argument. As I shall show in the sequel, however, Spencer presents a vague adumbration of facts which have since come to light and easily dispose of the portion of Weismann's argument relating to the amazons.

Weismann returns to the charge in his Romanes lecture and asserts that he cannot look upon Spencer's view "as a correct one in the sense implied. It is certainly true that bees have it in their power to cause a larva to become a queen or a worker according to the manner in which they feed it: it is equally true of all animals that they reproduce only feebly or not at all when badly and insufficiently nourished: and yet the poor feeding is not the *causa efficiens* of sterility among bees but is merely the stimulus which *not only results in the formation of rudimentary ovaries, but at the same time calls forth all the other distinctive characters of the workers.* It appears to me to be doubly incorrect to look upon the poor nourishment as the actual cause; for such a view not only confuses the stimulus with the real cause, but also fails to distinguish between an organ that becomes rudimentary and one that is imperfectly developed. Moreover the fact is overlooked that the ovaries of the workers are actually rudimentary organs: a great proportion of their really essential parts have disappeared, while only a small remnant is retained."

Weismann goes farther and maintains that he has disproved Spencer's view experimentally. He reared two lots of blow-fly larvæ (*Musca vomitoria*), one on poor the other on abundant food, and obtained imaginal flies differing greatly in size but with the reproductive as well as the other organs normally developed even in the smallest individuals. The latter on being well fed, mated and produced normal young. He concludes as follows from this experiment: "By comparing the result of this experiment with the known facts as to bees, the difference in the behavior of the two organisms is made clear. In the case of bees a distinct degeneration of the ovaries and various accessory organs of reproduction takes place in consequence of poor nourishment; while in flies the whole reproductive apparatus is formed quite as perfectly when the nourishment of the larva is deficient as when it is ample. There is even no delay in the maturing of the eggs, as shown by the fact that the first batch was laid at exactly the same time as in the case of the flies arising from normally fed larvæ.

"It might, however, be said that flies and bees are very different organisms, and therefore react differently to external influences. This is quite true, and is exactly what I wish to be acknowledged. My experiments with the flies were merely meant to show that all insects, even though they may resemble bees in some respects, do not react in a similar way to the bee to meagreness of nutrition, and that accordingly *this mode of reaction is a characteristic of bees*: — it is a new acquisition, and was not possessed by the ancestors of these insects."

The views of the more active European myrmecologists, Emery, Escherich, Forel and Wasmann, are in close accord with those of Weismann, but there are some significant departures, especially in Emery's view, which approaches that of Spencer. Emery gives this summary of his position in a paper on the origin and development of the worker among ants:[1] "The theory which I have attempted to carry out in hypothetical form, is based on the assumption, that the production of the worker depends on the instinctive art of breeding workers, and that the origin of the worker caste is to be attributed more to a difference in the quality, the differentiation of several kinds of workers more to the quantity of the food. From the latter process I would not, of course, exclude the possible play of qualitative factors; their intervention is, indeed, probable in specific cases, such as, *e. g.*, in the *Melissotarsus beccarii*, which I have described, and which has two kinds of workers of the same size but with heads of a different form.

"*The peculiarities in which the workers differ from the corresponding sexual forms are, therefore, not innate or blastogenic, but acquired, that is somatogenic.* Nor are they transmitted as such, but in the form of a peculiarity of the germ-plasm that enables this substance to take different developmental paths during the ontogeny. Such a peculiarity of the germ may be compared with the hereditary predisposition to certain diseases, which like hereditary myopia develop only under certain conditions. The eye of the congenitally myopic individual is blastogenetically predisposed to short-sightedness, but only becomes short-sighted when the accommodation apparatus of the eye has been overtaxed by continual exertion. Myopia arises, like the peculiarities of the worker ants, as a somatic affection on a blastogenic foundation.

"With this assumption the problem of the development of workers seems to me to become more intelligible and to be brought a step nearer its solution. The peculiarities of the Hymenoptera workers are laid down in every female egg; those of the termite workers in every egg of either sex, but they can only manifest themselves in the presence of specific vital conditions. In the phylogeny of the various species of ants the worker peculiarities are not transmitted but merely the faculty of all fertilized eggs to be reared as a single or several kinds of workers. The peculiar instinct of rearing workers

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[1] Die Entstehung und Ausbildung des Arbeiterstandes bei den Ameisen. Biol. Centralbl., XIV, 1894, pp. 58, 59.

is also transmitted, since it must be exercised by the fertile females in establishing their colonies."[1]

In other words, Emery supposes that the germ-plasm of the social insects is characterized by a peculiar sensitivity which makes it amenable to the different influences to which it is subjected in the fostering environment of the colony. This view, as I shall endeavor to show in the concluding paragraphs of this article, is worthy of more attention than it has received. It was rejected by Weismann in his Romanes lecture on the ground that typical organs like the wings, ovarian tubules, spermatheca, etc. could not disappear from the worker by any ontogenetic, but only by a phylogenetic process, but his argument is based on what is known to occur in other animals and necessarily fails to apply to animals which, like the social Hymenoptera, seem to be unique in presenting the very conditions Emery has been trying to explain.

Wasmann[2] accepts Weismann's view of the determinants and the function of nutrition as a mere stimulus, but he rejects his view that natural selection alone can account for the adaptive structures and instincts of worker ants.

Forel in his 'Fournis de la Suisse' (p. 440, 441, *nota*) accepts the Darwinian view of the origin of the worker caste by natural selection acting on a primitive differentiation of the female into fertile and sterile forms in the sphere of instinct before definite morphological differentiation sets in. In a recent paper[3] he is inclined to side with Weismann and to lay considerable stress on the effects of natural selection and the struggle for existence in producing variation and polymorphism as opposed to the internal factors.

Escherich,[4] has given a valuable review of the subject of polymorphism among ants, without, however, clearly defining the general issues. His own view is apparently in complete accord with that of Weismann.

Marchal, as the result of his splendid work on the habits of the social wasps,[5] has given the following suggestive discussion of polymorphism along the lines suggested by Spencer and Emery: "At the beginning of the social state the infertility of the first brood of progeny produced by the mother gradually became established. This infertility was the result of the necessarily insufficient nourishment distributed by the queen among her too numerous offspring, and the eggs in the ovaries of the young females could not mature, first, because the reserve substances (adipose tissue)

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[1] For a fuller account of Emery's views, see his article 'Le Polymorphisme des Fourmis et la Castration Alimentaire.' Compt. Rend., 3me. Congr. Internat. Zool., Leyde (Sept. 1895), 1896, pp. 395–407.

[2] Die ergatogynen Formen, etc., *loc. cit.*, p. 638.

[3] Ueber Polymorphismus und Variation bei den Ameisen. Zool. Jahrb., Suppl., VII, 1904, pp. 571–586.

[4] Die Ameise. Schilderung ihrer Lebensweise. Braunschweig, 1906, pp. 45–54.

[5] La Reproduction et l' Evolution des Guêpes Sociales. Arch. Zoöl. Expér. et Gén., 3. ser., IV, 1896, pp. 1–100, 8 figs.

stored up in the larva were insufficient, and second, because immediately after hatching, the young females had to devote themselves to the care of the numerous larval colony, and especially to the *function of nursing,* which, as we have shown experimentally, prevents the maturation of the eggs. The mother being relieved of the care of feeding the larvæ and having over the workers the advantage of ovaries swollen with eggs, while the other females at the time of hatching contained only immature germs, continued to lay to the exclusion of the other females, whose nutricial functions kept them in a condition of sterility.

"At the end of the year, however, owing to the greater length of the imaginal than of the larval period, and also on account of the diminution in the egg laying of the queen or owing to her disappearance, the adult colony came to surpass the larval colony sufficiently in numbers to permit the later broods to receive and store up the reserve food which is indispensable to the maturation of the eggs. Hence these later broods alone would be able to hibernate and reproduce the species during the following spring. Only these individuals, therefore, should be regarded as representing the stirp from which all the future individuals proceed, the others being naturally eliminated from the genealogical tree.

"This single fact, namely, that only the individuals reared at the end of the season participate in the direct lineage of the different generations, suffices to account for a modification in the germ-plasm of the species; for *without even adducing the specific instinctive dispositions* which would later be acquired by natural selection, the conditions of nurture, and in particular those of nourishment, which control the development of the animal till the end of the year, depart from the mean of the variable conditions of nurture to which the evolving presocial insect was submitted. Under the influence of this modification acting as *external conditions,* constantly and always in the same manner, a new physicochemical constitution of the germ-plasm must necessarily arise and a new direction of development be opened up, namely, that which leads to the queen type.

"If the preceding theory be granted, the realization of the worker type becomes equally comprehensible. As long as there is no perceptible variation in the constitution of the germ-plasm, the worker will differ from the queen only in slight quantitative morphological variations, depending essentially, as we have demonstrated, on the phenomena of nutrition. This is the case in *Polistes* and less obviously in certain species of wasps (*Vespa*) which present an uninterrupted series of forms connecting the worker and queen types.

"But as soon as a perceptible modification of the germ-plasm intervenes, matters cease to be the same. The egg laid by a queen in the spring, like all the eggs which she lays, contains, of course, this germ-plasm which has been modified by the autumnal régime and therefore presents all its modifications. Now the conditions under which it is called upon to pursue its development are not the same as those of the autumn, to which its germ-plasm has been exclusively habituated during a very long series of generations. This germ-plasm whose fixed constitution is adapted to a precise method of development in a given environment according to the queen type, and has been determined by the conditions to which it has been subjected for a great number of generations, finds itself in this particular egg suddenly emancipated from these modifying conditions and subjected to altogether new ones. What may we expect it to produce? If the modifications to which it finds itself submitted are too severe, it must perish; if, on the contrary, they are compatible with its evolution, it must proceed with its development as well as it can, like an animal constrained to develop under abnormal conditions. It is evident that the latter alternative alone is to be considered, since the former would lead to the extinction of the species. Now it is easy to see that this second alternative is nothing more nor less than a case of *experimental dichogeny*."

In a later paper Marchal[1] aptly designates the suppression of the functional activity of the ovaries through the nursing, or nutricial habits of the workers as *nutricial castration*. He has shown that by eliminating the queen from the *Vespa* colony as many as a third of the workers become fertile. A similar result is brought about by a suppression or merely by a temporary suspension of the egg-laying of the queen. This can be due, as he maintains, only to abolition of the nursing function and the appropriation by the workers of the food which under normal conditions they would feed to the larvæ.

Marchal's view differs from that of Weismann in postulating a homogeneous germ-plasm and in rejecting representative units like the ids, determinants, etc. He regards the "differentiation" of the queen as due to the direct action of external conditions, especially of nourishment, and the differentiation of the workers as belonging to a class of phenomena, "which, if not essentially understood, are nevertheless known in their manifestations, namely *teratogenesis* and *dichogeny*." Although this view is very similar to those of Spencer and Emery, the conception of nutricial castration seems to me to represent a valuable addition and I shall revert to it.[2]

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[1] La Castration Nutricial chez les Hymenopterès Sociaux. Compt. Rend. Sec. Biol., 5 Juin 1897, 2 pp.

[2] Nutricial castration (from *nutrix*, a nurse) must be distinguished from 'alimentary castration' (Emery, Le Polymorphisme, etc., *loc. cit.*), although both are responsible for the infertility of the worker. Through alimentary castration the development of the reproductive organs is inhibited in the larva and pupa, and this inhibition is maintained in the adult by the strong

The various extracts above quoted show very clearly that previous authors have been impressed by very different aspects of the complicated phenomena of polymorphism, and that each author has emphasized the aspect which seemed the most promising from the standpoint of the general evolutionary theory he happened to be defending. Escherich has recently called attention to two very different ways of envisaging the problem; one of these is physiological and ontogenetic, the other ethological and phylogenetic. As these furnish convenient captions under which to continue the discussion of the subject, I shall adopt them, and conclude with a third, the psychological aspect, which is certainly of sufficient importance to deserve consideration.

3. THE ONTOGENETIC AND PHYSIOLOGICAL ASPECTS OF POLYMORPHISM.

While the ontogeny of nearly all animals is a repetition or reproduction of the ontogeny of the parent, this is usually not the case in the social Hymenoptera, since the majority of the fertilized eggs do not give rise to queens but to more or less aberrant organisms, the workers. And as these do not, as a rule, reproduce, the whole phenomenon is calculated to arouse the interest of both the physiologist and the embryologist. The former, concentrating his attention on the reactions of the animal to the stimuli proceeding from its environment, is inclined to study its later stages as determined by the reactions to such stimuli, without regard to any internal or hereditary predetermination or disposition, while the embryologist seeks out the earliest moment at which the organism may be shown to deviate from the ontogenetic pattern of its parent. If this moment can be detected very early in the development he will be inclined to project the morphological differentiation back into the germ-plasm and to regard the efforts of the physiologist as relatively unimportant if not altogether futile. Now in his study of the social insects the embryologist is at a serious disadvantage, since he is unable to distinguish any prospective worker or queen characters in the eggs or even in the young larvæ. Compelled, therefore, to restrict his investigations to the older larvæ, whose development as mere processes of histogenesis and metamorphosis throws little or no light on the meaning of polymorphism, he is bound to abdicate and leave the physiologist in possession of the problem.

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nursing instincts which prevent the workers from appropriating much of the food supply of the colony to their individual use. In many of the higher animals also (birds, mammals) reproduction is inhibited by the exercise of the nutricial function. A third method of inhibiting or destroying the reproductive function is known to occur in the 'parasitic castration' of certain bees and wasps (*Andrena, Polistes*) by Strepsiptera (*Stylops, Xenos*, etc.). See Perez, Des Effets du Parasitisme des Stylops sur les Apiaires du Genre Andrena. Actes Soc. Linn. Bordeau., 1886, 40 pp. 2 pll. Westwood (Notice of the Occurrence of a Strepsipterous Insect Parasitic on Ants, discovered in Ceylon by J. Nietner, Trans. Ent. Soc. London (2), V, 1861, pp. 418–420) has also described a Strepsipteron (*Myrmecolax nietneri*) which in all probability produces this form of castration in certain Formicidæ.

The physiologist, in seeking to determine whether there is in the environment of the developing social Hymenopteron any normal stimulus that may account for the deviation towards the worker or queen type, can hardly overlook one of the most important of all stimuli, the food of the larva. At first sight this bids fair greatly to simplify the problem of polymorphism, for the mere size of the adult insect might seem to be attributable to the quantity, its morphological deviations to the quality of the food administered to it during its larval life. Closer examination of the subject, however, cannot fail to show that larval alimentation among such highly specialized animals as the social insects, and especially in the honey-bees and ants, where the differences between the queens and workers are most salient, is a subject of considerable complexity. In the first place it is evident that it is not the food administered that acts as a stimulus but the portion of it that is assimilated by the living tissues of the larva. In other words, the larva is not altogether a passive organism, compelled to utilize all the food that is forced upon it, but an active agent capable, at least to a certain extent, of determining its own development. And the physiologist might have difficulty in meeting the assertion, that the larva utilizes only those portions of the proffered food which are most conducive to the specific predetermined trend of its development. In the second place, while experiments on many organisms have shown that the quantity of assimilated food may produce great changes in size or stature, there is practically nothing to show that even very great differences in the quality of the food can bring about morphological differences of such magnitude as those which separate the queens and workers of many ants.[1]

These more general considerations are reinforced by the following inferences from the known facts of larval feeding:

1. There seems to be no valid reason for supposing that the morphogeny of the queens of the social Hymenoptera depends on a particular diet, since with the possible exception of the honey and stingless bees, to be considered presently, they differ in no essential respect from the corresponding sexual phase of the solitary species. In both cases they are the normal females of the species and bear the same morphological relations to their males quite irrespective of the nature of their larval food. Hence, with the above mentioned exception of the honey and stingless bees, the question of the morphogenic value of the larval food may be restricted to the worker forms.

2. Observation shows that although the food administered to the

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[1] Emery (Le Polymorphisme, etc., *loc. cit.*) has called attention to the importance of the assimilative powers of the ant larva itself, quite irrespective of the quantity and quality of the food administered by the nurses — a very obscure physiological phenomenon, but not without analogies in other animals and especially in plants, which may assume a dwarfed habitus under apparently very favorable trophic conditions. The production of 'high' and 'low' males in Scarabæid and Lucanid beetles seems to be of the same nature.

larvæ of the various social insects is often very different in its nature, even in closely related species, the structure of the workers may be extremely uniform and exhibit only slight specific differences. Among ants alone we find the larvæ fed with a great variety of substances. Thus the Attii feed their larvæ on fungus hyphæ, the harvesting species of *Pheidole, Pogonomyrmex,* etc., on seeds, the Ponerinæ and many Myrmicinæ on pieces of insects, and most Dolichoderinæ and Camponotinæ supply their young with regurgitated liquid food. According to Dahl,[1] the larvæ of at least one species (*Camponotus quadriceps*) feed on the pith of plants. The quality of the food itself cannot, therefore, be supposed to have a morphogenic value. And even if we admit what seems to be very probable, namely, that a salivary secretion — possibly containing an enzyme — may be administered by some of these ants at least to their younger larvæ, the case against the morphogenic effects of qualitative feeding is not materially altered, as we see from the following considerations:

3. In incipient ant-colonies the queen mother takes no food often for as long a period as eight or nine months, and during all this time is compelled to feed her first brood of larvæ exclusively on the secretions of her salivary glands. This diet, which is purely qualitative, though very limited in quantity, produces only workers and these of an extremely small size (micrergates).

4. In the honey-bees, on the other hand, qualitative feeding, namely with a secretion, the so-called "royal jelly," which according to some authors (Schiemenz) is derived from the salivary glands, according to others (Planta) from the clylific stomach of the nurses, does not produce workers but queens. In this case, however, the food is administered in considerable quantity, since it is not provided by a single starving mother, as in the case of the ants, but by a host of vigorous and well-fed nurses. Although it has been taken for granted that the fertilized egg of the honey-bee becomes a queen as the result of this peculiar diet, the matter appears in a different light when it is considered in connection with von Ihering's recent observations on the stingless bees (Meliponidæ) of South America.[2] He has shown that in the species of *Melipona* the cells in which the males, queens, and workers are reared are all of the same size. These cells are provisioned with the same kind of food (honey and pollen) and an egg is laid in each. Thereupon they are sealed up, and although the larvæ are not fed from day to day as in the honey-bees, but like those of the solitary bees subsist on stored provisions, this uniform treatment nevertheless results in the production of

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[1] Das Leben der Ameisen im Bismarck-Archipel, Friedländer u. Sohn, 1901, p. 31.

[2] Biologie der stachellosen Honigbienen Brasiliens. Zool. Jahrb., Abth. f. Syst., XIX, 1903, pp. 179–287, 13 pll., 8 text-figs.

three sharply differentiated castes. On hatching the queen *Melipona* has very small ovaries with immature eggs, but in the allied genus *Trigona*, the species of which differ from the *Meliponæ* in constructing large queen cells and in storing them with a greater quantity of honey and pollen, the queen hatches with her ovaries full of ripe eggs. These facts indicate that the large size of the queen cell and its greater store of provisions are merely adaptations for accelerating the development of the ovaries. Now on reverting to the honey-bee we may adopt a similar explanation for the feeding of the queen larva with a special secretion like the "royal jelly." As is well known, the queen honey-bee hatches in about sixteen days from the time the egg is laid, while the worker, though a smaller insect and possessing imperfect ovaries, requires four or five days longer to complete her development. That the special feeding of the queen larva is merely an adaptation for accelerating the development of the ovaries is also indicated by the fact that this insect is able to lay within ten days from the date of hatching.[1] If this interpretation is correct the qualitative feeding of the queen larva is not primarily a morphogenic but a growth stimulus.

5. The grossly mechanical withdrawal of food substances already assimilated by the larva, as in the case of the *Pheidole instabilis* parasitized by the *Orasema* described in the first part of this article, produces changes of the same kind as those which distinguish the worker ant from the queen, *i. e.*, microcephaly, microphthalmy, stenonoty, and aptery. This case is of unusual interest because the semipupa, after the detachment of the parasite, seems to undergo a kind of regeneration and produces a small but harmonious whole out of the depleted formative substances at its disposal. What is certainly a female or soldier semipupa takes on worker characters while the worker semipupa may be said to become infra-ergatoid as the result of the sudden loss of formative substances. These observations clearly indicate that the normal worker traits may be the result of starvation or withholding of food rather than the administration of a particular diet.

6. The pseudogynes of *Formica* admit of a similar interpretation if it be true, as I have maintained (p. 33) that they arise from starved female larvæ. Here, too, the organism undergoes a kind of regeneration or regulation and assumes the worker aspect owing to a dearth of sufficient formative substances with which to complete the development as originally planned.

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[1] Cheshire (Bees and Bee-keeping. Scientific and Practical, 2 vols.) gives a different interpretation of the rapid growth of the queens. On p. 244, Vol. I, he regards the acceleration as the result of selection, since the first queen to hatch destroys her unhatched sisters. Hence the more rapidly the insect develops the greater her chances of survival. In another place (Vol. II, pp. 320, 321), however, he regards this individual advantage as a social disadvantage, since the toleration of several queens would greatly increase the number of workers and thereby strengthen the colony. My view refers not so much to the acceleration of the development of the queen as to that of her ovaries. It is evident that this, too, may be expressed in terms of advantage to the colony, since it enables the queen to lay very soon after the marriage flight.

7. In the preceding cases, as I have shown in the first part of this article, the ants undergo a peculiar structural modification as the result of tolerating parasites that bring about unusual perturbations in the trophic status of the colony. When ants themselves become parasitic on other ants a similar perturbation results, but in these cases the morphological effects are confined to the parasitic species and do not extend to their hosts. This must be attributed to the fact that the parasitizing species live in affluence and are no longer required to take part in the arduous and exacting labors of the colony. Under such circumstances the inhibitory effects of nutricial castration on the development of the ovaries of the workers are removed and there is a tendency for this caste to be replaced by egg-laying, gynæcoid individuals or by ergatogynes, or for it to disappear completely. These effects are clearly visible in nearly all parasitic ants. In the European *Tomognathus sublævis*, for example, the only known females are gynæcoid workers. In the American *Leptothorax emersoni*, as I have shown,[1] gynæcoid workers and ergatogynes are unusually abundant while the true females seem to be on the verge of disappearing. Among the typical amazon ants (*Polyergus rufescens*) of Europe, ergatogynes are not uncommon. In *Strongylognathus testaceus* the worker caste seems to be dwindling, while in several permanently parasitic genera (*Anergates*, *Wheeleria*, *Epœcus*, *Epipheidole* and *Sympheidole*) it has completely disappeared. Only one cause can be assigned to these remarkable effects — the abundance of food with which the parasites are provided by their hosts.

8. In the Ponerinæ and certain Myrmicinæ, like *Pheidole*, *Pogonomyrmex*, and *Aphænogaster*, the larvæ are fed on pieces of insects or seeds, the exact assimilative value of which as food can neither be determined nor controlled by the nurses. And while they may perhaps regulate the quantity of food administered, it is more probable that this must fluctuate within limits so wide and indefinite as to fail altogether to account for the uniform and precise morphological results that we witness in the personnel of the various colonies. Moreover, accurate determination of the food supply by the workers must be quite impossible in cases like that of the *Pachycondyla* larva attended by the commensal *Metopina* which surreptitiously consumes a portion of the proferred food.

9. The intimate dependence of the appearance of the different castes of the social insects on the seasons may also be adduced as evidence of the direct effects of the food supply in producing workers and queens. The latter are reared only when the trophic condition of the colony is most favorable and this coincides with the summer months. In the great major-

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[1] Ethological Observations on an American Ant (Lepthorax Emersoni Wheeler), Arch. f. Psych. u. Neurol., II, 1903, p. 6.

ity of species only workers and males are produced at other seasons. Here, too, the cause is to be sought in the deficient quantity of food rather than in its quality, which is, in all probability, the same throughout the year, especially in such ants as the fungus-growing Attii and the seed storing Myrmicinæ.

While these considerations tend to invalidate the supposition that qualitative feeding is responsible for the morphological peculiarities of the worker type, they are less equivocal in regard to the morphogenic effects of quantitative feeding. Indeed, several of the observations above cited show very clearly that diminution in stature and, in pathological cases, even reversion to the worker form may be the direct effect of underfeeding. To the same cause we may confidently assign several of the atypical phases among ants, such as the micrergates, microgynes, and micranērs, just as we may regard the macrergates, macrogynes, and macranērs as due to overfeeding. These are, of course, cases of nanism and giantism, variations in stature, not in form. Similarly, all cases in which, as in certain species of *Formica, Camponotus, Pheidole,* etc., the workers or desmergates vary in size, must be regarded as the result of variable quantitative feeding in the larval stage. Here we are confronted with the same conditions as Weismann observed in the blow-flies and which entomologists have noticed in many other insects. Such variations are of the fluctuating type and are therefore attributable to the direct effects of the environment. The soldier and worker, however, differ from the queen in the absence of certain characters, like the wings, wing-muscles, spermatheca, some of the ovarian tubules, etc., and the presence of other characters, like the peculiar shape of the head and mandibles. In these respects the sterile castes may be regarded as mutants, and Weismann's contention that such characters cannot be produced by external conditions, such as feeding, is in full accord with de Vries's hypothesis. His further contention, however, that they must therefore be produced by natural selection need not detain us, since it is daily becoming more and more evident that this is not a creative but an eliminative principle. It is certain that the very plastic social insects, like the ants, have developed a type of ontogeny which enables them not only to pupate at an extremely early period of larval life, but also to hatch and survive as useful though highly specialized members of the colony. It is quite conceivable that this precocious pupation may be directly responsible for the complete suppression of certain organs that require for their formation more substance than the underfed larva has been able to accumulate. At the same time it must be admitted that a direct causal connection between underfeeding on the one hand and the ontogenetic loss or development of characters on the other, has not been satisfactorily established. The conditions in the termites, which are often cited as furnishing proof of this connection, are even more complicated and obscure than those of the social Hymenoptera. While Grassi and Sandias,[1] and Silvestri,[2] agree with Spencer in regarding the feeding as the direct cause of the production of the various castes, Herbst,[3] who has reviewed the work of the former authors, shows that their observations are by no means conclusive; and Heath[4] makes the following statement in regard to his experiments on Californian termites: "For months I have fed a large number of termite colonies of all ages, with or without royal pairs, on various kinds and amounts of food — proctodæal food dissected from workers or in other cases from royal forms, stomodæal food from the same sources, sawdust to which different nutritious ingredients had been added — but in spite of all I cannot feel perfectly sure that I have influenced in any unusual way the growth of a single individual."

This rather unsatisfactory answer to the question as to whether quantity or quality of food or both, have an ergatomorphic value, has led some investigators to seek a solution along more indirect lines. Thus O. Hertwig and Herbst suggest that the morphogenic stimulus may be furnished by some internal secretion of the reproductive organs. This, too, is possible, but owing to our very imperfect knowledge of the internal secretions, even in the higher animals, we are not in a position either to accept or reject this suggestion.

More tangible is Emery's attempt[5] to explain the worker characters as the result of a struggle among the parts of a prematurely metamorphosing insect. He has not been led into the invisible battle of the ids and determinants on which Weismann recently constructed his hypothesis of germinal selection,[6] but is content with a struggle between the larger regions of the body and between their various organs. This point of view was suggested by his study of the mermithergates. He is of the opinion that "the same law of growth which determines the proportions of the head and gaster in the *Mermis*-infested workers (see pp. 24, 25 *antea*) obtains also in normal ants. I designate it as the "law of opposition between head and gaster" and would state it as follows:

"While the imago is developing within the full-grown ant larva, what is needful for the structures essential to the life of the organism is first emphasized, especially for the digestive and reproductive organs contained in the gaster; the formation of the external shape of the head, and especially of

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[1] Costituzione e Sviluppo della Società dei Termitidi. Catania, 1893, 150 pp., 5 pll.

[2] Operai ginecoidi di Termes, con osservazioni intorno l' origine delle varie caste nei Termitidi, Real. Accad. Lincei, X, sér. 5, 1901, pp. 479–484.

[3] Formative Reize in der Tierischen Ontogenese, Leipzig, Arthur Georgi, 1901, pp. 20–24.

[4] The Habits of California Termites. Biol Bull. IV, Dec. 1902, pp. 62–23.

[5] Zur Kenntniss des Polymorphismus, etc., *loc. cit.*, p. 603.

[6] On Germinal Selection. Religion of Science Library. Open Court Publ. Co., Chicago, 1896.

the mandibles and of the muscles which are to move them, is regulated according to the amount of formative substance remaining. Perhaps phylogenetic factors also enter into this process and, with the absence of sufficient substance, also phenomena of atavism in the form of a certain stress on the phylogenetically older structures.

"As a result of these processes we find that when one of two metamorphosing larvæ has a large abdomen its head will be relatively smaller than that of the other, because there remains a relatively smaller amount of larval food substance."

Towards the end of his paper (pp. 608, 609) Emery still further elaborates this view and concludes with the following remarks: "The determination both of the relative size of the various regions of the body and of the individual organs to one another may be regarded as a struggle among the parts (Kampf der Theile) of the organism. In the metabolic insects, in particular, this struggle may be divided into two periods:

"During the first period, which may be of long duration, food supplies are accumulated in an indifferent manner as the larval fat-body while at the same time the rudiments of the imaginal organs arise and prepare themselves for the struggle.

"During the second period the struggle among the rudiments actually sets in and must be particularly acute in cases where the store of food is meager on account of underfeeding of the larva. The struggle will be decided in favor of the rudiments which are capable of most vigorously appropriating the nourishment.

"To this struggle is due the regular type of polymorphism as it is exhibited by worker ants in its definite relations to the volume of the body. But before this struggle takes place, the result is already decided, because the ability of the individual imaginal rudiments to attract the larval food reserves has been determined. We may therefore assume that during the first period, by a process still completely unknown, there is a determination of the growth energy of the individual imaginal rudiments which, in the second period, will struggle for the possession of the limited supply of larval food. We may further assume that during the first period, through the relations of the imaginal rudiments to one another and to the amount of larval food substances, the type of the individual, whether female, worker, pseudogyne, etc., as well as its size, is determined. These peculiarities, however, do not manifest themselves till the second period.

"As trophic polymorphism the polymorphism of the female sex in ants is a function of the distribution of the nutritive substances accumulated during larval life, a distribution which in turn is determined by the struggle among the imaginal rudiments."

In commenting on this hypothesis of a struggle of the parts in connection with the mermithergates, I have already shown (p. 26) that it is inapplicable to the cases which first suggested it. This does not, however, disqualify it as a possible explanation of the normal worker forms. It does, indeed, appear to give us an insight into the possible conditions of development in the starved larvæ from which the workers arise and suggests interesting problems for the experimentalist. Still it is incomplete and like the other views considered in the preceding paragraphs, fails to account for the highly adaptive structure of the worker.

There lurks, perhaps, in Emery's hypothesis a suggestion of a widespread notion that there is something monstrous, teratological or hypertelic, about the workers and especially about the soldiers of the social insects. This is more explicitly stated in the above-quoted passages from Spencer and Marchal (pp. 60, 65). The latter, in fact, regards the rearing of the sterile forms as a kind of experimental teratogeny. Such an impression is very natural, for the soldiers of many ants and termites certainly exhibit developments of the head and mandibles unlike anything found in other insects. And it is not impossible that these castes may have orginally made their appearance as teratological developments. But that they are such at the present time is very improbable, since we find that they are not only normal and all-important constituents of the colony, but have become exquisitely adapted to particular functions. Wherever the habits of the soldiers have been carefully studied it has been found that their singular and apparently hypertrophied structures have a very definite function. Thus it has been shown that the peculiarly truncated heads of the *Colobopsis* soldiers are used as "animated front-doors" in closing the circular entrances to the galleries of the nest, that the colossal crania of the *Pheidole* soldiers accommodate the huge muscle-masses of the jaws which in turn are used in cracking hard seeds and the tough integument of insects, and that the peculiar sickle-shaped mandibles of the soldiers of *Myrmecocystus bombycinus* are used for carrying the voluminous pupæ.[1] It is very probable that in termites the singular heads of the nasute and mandibulate soldiers will be found to be similarly adapted to special functions in the economy of the colony. At any rate we are not justified in regarding such structures as hypertelic or teratological till we know more about the habits of the species in which they occur.

We may conclude, therefore, that while the conception of the worker type as the result of imperfect nutrition is supported by a considerable volume of evidence, we are still unable to understand how this result can take

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[1] See Escherich, Die Ameise, *loc. cit.*, p. 46.

on so highly adaptive a character. Such a concise effect can hardly be due to manifold and fluctuating external causes like nutrition, but must proceed from some more deeply seated cause within the organism itself. Of course, the difficulty here encountered is by no means peculiar to polymorphism; it confronts us at every turn as the all-pervading enigma of living matter. Whether we shall fare better by approaching the subject from a different point of departure remains to be seen.

4. THE PHYLOGENETIC ASPECT OF POLYMORPHISM.

An intensive study of the structure and habits of ants must inevitably lead to a certain amount of speculation concerning the phylogenetic development of their colonies. That these insects have had communistic habits for ages is clearly indicated by the fact that all of the numerous existing species are eminently social. There can be little doubt, however, that they arose from forms with habits not unlike those we find today in some of the solitary wasps, such as the Bembecidæ, or in the remarkable South African bees of the genus *Allodape*.[1] Unlike other solitary wasps, the females of *Bembex* may be said to be incipiently social, since a number of them choose a nesting site in common and, though each has her own burrow, coöperate with one another in driving away intruders. *Bembex* has also taken an important step in the direction of the social wasps not only in surviving the hatching of her larvæ, but also in visiting them from day to day for the purpose of providing them with fresh insect food.[2]

At a very early period the ants and social wasps must have made a further advance when the mother insect succeeded in surviving till after her progeny had completed their development. This seems to have led naturally to a stage in which the young females remained with their mother and reared their progeny in the parental nest, thus constituting a colony of a number of similar fertile females with a common and indiscriminate interest in the brood. This colony, after growing to a certain size, became unstable in the same way as any aggregate of like units, and must soon have shown a differentiation of its members into two classes, one of individuals devoted to reproduction and another class devoted to alimentation and protection. In this division of labor only the latter class underwent important somatic modification and specialization, while the former retained its prim-

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[1] I infer this from a brief account (*in litteris*) of two species of these insects, recently received, together with specimens of their extraordinary larvæ, from Dr. Hans Brauns of Cape Colony.

[2] Interesting accounts of the habits of this insect have been published by Fabre (Souvenirs Entomologiques. Prem. Sér., Paris, Chas. Delagrave, 1 éd., 1879; 3 éd., 1894, pp. 221–234); Wesenberg-Lund (Bembex rostrata, dens Liv og Instinkter. Ent. Meddel. Kjöbenhavn, III, 1891, pp. 19–44; English résumé in Psyche, VII, p. 62); and Geo. W. and Elizabeth G. Peckham, On the Instincts and Habits of the Solitary Wasps. Wis. Geol. Nat. Hist. Surv., Bull. No. 2, 1898, pp. 58–72.

itive and more generalized characters. It is more than probable, as I shall attempt to show in the sequel, that this differentiation was manifested in the sphere of instinct long before it assumed morphological expression. The social wasps and bumble bees are practically still in this stage of sociogeny. The ants, however, have specialized and refined on these conditions till they not only have a single marked alimentative and protective caste without wings[1] and lacking many other female characters, but also in some species two distinct castes with a corresponding further division of labor. Both in the phylogeny and the ontogeny these characters appear as the result of nutricial castration.

If the foregoing considerations be granted the biogenetic law may be said to hold good in the sociogeny of the ants, for the actual ontogenetic development of their colonies conforms not only to the purely conjectural requirements of phylogeny but also with the stages represented by the various extant groups of social insects. It is clear that we cannot include the honey-bee among these groups, since this insect is demonstrably so aberrant that it is difficult to compare it with the other social insects.

Comparison of the different genera and subfamilies of ants among themselves shows that some of them have retained a very primitive social organization, and with it a relatively incomplete polymorphism, whereas others have a much more highly developed social life and a greater differentiation of the castes. Such a comparison coupled with a study of the natural relationships of the various genera as displayed in structure, shows very clearly that the advance from generalized to highly specialized societies did not follow a single upward course during the phylogeny, but occurred repeatedly and in different phyletic groups. And since the complications of polymorphism kept pace with those of social organization, we may say that the differentiation of the originally single worker caste into dinergates, or soldiers on the one hand and micrergates, or small workers, on the other,

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[1] Emery (Zur Kenntniss des Polymorphismus, etc., *loc. cit.*, pp. 628, 629) has recently restated his opinion that the females of the primitive ants were wingless, like the workers of existing species, and acquired wings during the phylogeny, an opinion to which he was led by deriving the ants from Mutillid-like ancestors. McClendon and I (Dimorphic Queens, etc., *loc. cit.*, p. 161, 162) dissented from this view on the ground that there is no known case among insects of a reacquisition after loss of these organs. Emery replies that they have not been lost but still exist in the germ-plasm of the female Mutillid, since she produces males with perfect wings. He believes that the wings of existing female ants are an inheritance from the male. The possibility of such an inheritance cannot, of course, be disputed, but when the matter is so largely conjectural, the simpler hypothesis maintained by McClendon and myself seems preferable. It is certainly easier to believe that both Mutillids and ants are derived from a common ancestor with both sexes winged, and that the wings were retained by the worker ants, as they are still in the social bees and wasps, till these castes had been definitely established, than to assume a loss followed by a reacquisition of these organs in the queens. Moreover, there is no known case in which an organ has been completely transferred to the opposite sex. Even cases like the vestigial mammæ of mammals and the antlers of the female reindeer are best explained as characters once equally developed and functional in both sexes. (See Lydekker, The Deer of all Lands, London, Rowland Ward, 1898, p. 10). The ergatoid and gynæcoid characters of male ants referred to by Emery, may indeed be inherited from the workers and females respectively, but they are modifications of well-developed and functional organs of the male. This case is therefore not strictly comparable with the transfer of whole organs like the wings with their complicated musculature, venation, etc., from one sex to the other.

has been repeated in remotely related genera. In some genera (*Stenamma* sens. str., *Leptothorax*) there are also indications of a lapsing of highly specialized into simpler conditions by a kind of social degeneration. In its extreme form this manifests itself as a suppression of castes and a consequent simplification of polymorphism. Beautiful illustrations of this statement are furnished by the parasitic species that have lost their worker caste. But there are also cases in which the queen caste has been suppressed and its functions usurped by workers.

Not only have these greater changes been effected and fixed during the phylogenetic history of the Formicidæ, but also many subtler differences such as those of stature, coloration, pilosity and sculpture. And although such differences belong to the class of fluctuating variations and are usually supposed to have a greater ontogenetic than phylogenetic significance, they are undoubtedly of great antiquity and must therefore be regarded as more important than many of the minor morphological traits.

Emery was the first to call attention to a number of peculiar phylogenetic stages in the development of stature among ants.[1] We find by comparison with the male, which may be regarded as a relatively stable and conservative form, that the cospecific females and workers may vary in stature independently of each other. The following are the stages recognized by Emery, with some additions of my own:

1. In the earliest phylogenetic condition which is still preserved in the ants of the subfamily Ponerinæ and in certain Myrmicinæ (*Pseudomyrma, Myrmecina,* etc.), the workers are monomorphic and of about the same size as the males and females.

2. The worker becomes highly variable in stature from large forms (dinergates, or maxima workers) resembling the female, through a series of intermediates (desmergates) to very small forms (minima workers, or micrergates). This condition obtains in the Dorylinæ, some Myrmicinæ, (some species of *Pheidole, Pheidologeton, Atta*), Camponotinæ (*Camponotus*) and Dolichoderinæ (*Azteca*).

3. The worker becomes dimorphic through the disappearance of the desmergates, so that the originally single, variable caste is now represented by two, the soldier (dinergate) and worker proper. We find this condition in certain Myrmicinæ and Camponotinæ (*Cryptocerus, Pheidole, Acanthomyrmex, Colobopsis,* etc.).

4. The soldier of the preceding stage disappears completely, so that the worker caste again becomes monomorphic but is represented by individuals very much smaller than the female. Such individuals are really micrergates.

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[1] Die Entstehung und Ausbildung der Arbeiter bei den Ameisen, *loc. cit.*, pp. 55, 56.

This condition is seen in certain Myrmicine genera, especially of the tribe Solenopsidii (*Carebara, Erebomyrma, Diplomorium,* most species of *Solenopsis,* etc.).

5. The worker form disappears completely, leaving only the males and females to represent the species, which thus returns to the condition of sexual dimorphism seen in the great majority of insects and other Metazoa. This occurs in the parasitic ants of the genera *Anergates, Wheeleria, Epæcus, Sympheidole* and *Epipheidole.*

6. In certain species the workers remain stationary while the female increases in size. This is indicated by the fact that the worker and male have approximately the same stature. Such a condition obtains in certain Myrmicinæ (*Cremastogaster*), Camponotinæ (*Lasius, Prenolepis, Brachymyrmex,* the North American species of *Myrmecocystus*), and Dolichoderinæ (*Iridomyrmex, Dorymyrmex, Liometopum*).

7. The worker caste remains stationary while the female diminishes in size till it may become even smaller than the large workers. This occurs in certain parasitic species of North America, like *Aphænogaster tennesseensis* among the Myrmicinæ, and among the Camponotinæ in the species of the *Formica microgyna* group (*F. difficilis, nevadensis, impexa, montigena, nepticula*).

8. The female phase disappears completely and is replaced by a fertile, or gynæcoid worker form. This occurs in the Myrmicine *Tomognathus sublævis,* in certain Ponerine genera like *Leptogenys* (including the subgenus *Lobopelta*), and probably also in *Diacamma* and *Champsomyrmex.* The conditions in *Acanthostichus* and certain Cerapachyi (*Parasyscia peringueyi*) indicate that the dichthadiigynes of the Dorylinæ may have arisen from such gynæcoid workers instead of from winged queens.

9. The female shows a differentiation into two forms (α- and β-females) characterized by differences in the structure of the legs and antennæ, in pilosity and coloration (*Lasius latipes*), or in the length of the wings (macropterous and micropterous females of *L. niger*). The macrocephalic and microcephalic females of *Camponotus abdominalis* and *confusus* described by Emery[1] may also be regarded as α- and β-forms. In this series of stages, one to five represent changes in the worker caste while the female remains relatively stationary, whereas stages six to nine represent the converse conditions. Stages one to four probably succeeded one another in the order given, but stage five may have arisen either from the first or fourth. The sixth to ninth stages must, of course, be supposed to have developed independently of one another.

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[1] Le Polymorphisme des Fourmis, etc., *loc. cit.*, pp. 400, 401.

The stature differences described in the above paragraphs are in most if not all cases, highly adaptive. This is clearly seen in such forms as the Indo-African *Carebara,* the huge, deeply colored females of which are more than a thousand times as large as the diminutive, yellow workers. This ant dwells in termite nests where it occupies chambers connected by means of tenuous galleries with the spacious apartments of its hosts. The termites constitute a supply of food so accessible and abundant that the workers are able to rear enormous males and females, while they themselves must preserve their diminutive stature in adaptation to their clandestine and thievish habits. Similar conditions are found in many species of the allied genus *Solenopsis,* which inhabit delicate galleries communicating with the nests of other ants on the larvæ and pupæ of which they feed. In one species of this genus (*S. geminata*) however, which leads an independent life and feeds on miscellaneous insects and seeds, the worker caste is still highly polymorphic.

Another interesting case of adaptation in stature is seen in the ants of the *Formica microgyna* group. The females of these species are temporarily parasitic in the nests of other *Formicæ* and are therefore relieved of the labor of digging nests for themselves and rearing their first brood of larvæ. On this account they need not store up large quantities of food, so that the nourishment which in nonparasitic species goes to produce a comparatively few large females may be applied to the production of a large number of small females. This latter condition is necessary in parasitic species which are decimated by many vicissitudes before they can establish themselves successfully among alien hosts. I have already emphasized the adaptive significance of the disappearance of the worker caste among permanently parasitic species like *Anergates, Wheeleria,* etc.

There are several cases in which the worker and female differ greatly in color, pilosity, or sculpture, and in such cases either caste may be conservative or aberrant according to ethological requirements. Thus in certain temporary parasites like *Formica ciliata, oreas, montigena, dakotensis,* and *difficilis,* the female is aberrant in one or more of the characters mentioned, while the cospecific worker retains the ancestral characters of the same caste in the closely allied forms of *F. rufa.* The same condition is seen in a very different ant, *Aphænogaster tennesseensis,* as the result of similar parasitic habits. In all of these species the females alone have developed myrmecophilous characters, like the long yellow hairs of *F. ciliata,* or the mimetic coloring of *F. difficilis,* which enable them to foist themselves on allied species and thus avoid the exhausting labor of excavating nests and rearing workers.

The foregoing observations indicate that in their morphological characters the worker and female of the same species have advanced or digressed in their phylogeny, remained stationary or retrograded, independently of each other. The same peculiarity is also observable in species with distinct worker and soldier castes. It thus becomes impossible even in closely related species of certain genera, like *Pheidole*, to predict the characters of the worker from a study of the cospecific soldier or *vice versâ*. And while adaptive characters in stature, sculpture, pilosity and color must depend for their ontogenetic development on the nourishment of the larvæ, it is equally certain that they have been acquired and fixed during the phylogeny of the species. In other words, nourishment, temperature, and other environmental factors merely furnish the conditions for the attainment of characters predetermined by heredity. We are therefore compelled to agree with Weismann that the characters that enable us to differentiate the castes must be represented in the egg. We may grant this, however, without accepting his conception of representative units, a conception which has been so often refuted that it is unnecessary to reconsider it in this connection. Far preferable appears to be the view of the constantly increasing number of biologists who conceive the adult characters to be represented in the germ as dynamic potencies or tensions rather than as morphological or chemical determinants.

Having touched upon this broader problem of heredity it will be necessary to say something about the inheritance or non-inheritance of acquired characters, especially as Weismann and his followers regard the social insects as demonstrating the non-transmissibility of somatogenic traits. In establishing this view and the all-sufficiency of natural selection to which it leads, Weismann seems to me to have slurred over the facts. While he admits that the workers may lay eggs, and that these may produce male offspring capable of fertilizing females, he nevertheless insists that this is altogether too infrequent to influence the germ-plasm of the species. I venture to maintain, on the contrary, that fertile workers occur much more frequently in all groups of social insects than has been generally supposed. As this fertility is merely a physiological state it has been often overlooked. Marchal (*vide ante*, p. 65), has shown how readily the workers of the social wasps assume this state, and the same is true of honey bees, especially of certain races like the Egyptians and Cyprians (*Apis mellifica-fasciata* and *cypria*). In the hives of these insects fertile workers are either always present or make their appearance within a few days after the removal of the queen. In the termites fertile soldiers have been observed by Grassi and Sandias (*l. c.*), and fertile workers by Silvestri (*l. c.*). Among ants fertile, or gynæcoid, workers occur so frequently as to lead to the belief that they must be present in all populous colonies. Their presence is also proved by the production of considerable numbers of males in old and queenless colonies. In artificial nests Wasmann,[1] Miss Fielde[2] and myself have found egg-laying workers in abundance.

As the males that develop from worker eggs are perfectly normal, and in all probability as capable of mating as those derived from the eggs of queens, we are bound to conclude, especially if we adopt the theory of heredity advocated by Weismann himself, that the characters of the mother (in this case the worker) may secure representation in the germ-plasm of the species. Weismann is hardly consistent in denying the probability of such representation, for when he is bent on elaborating the imaginary structure of the germ-plasm he makes this substance singularly retentive of alteration by amphimixis, but when he is looking for facts to support the all-sufficiency of natural selection the germ-plasm becomes remarkably difficult of modification by anything except this eliminative factor. Certainly the simplest and directest method of securing a representation of the worker characters in the germ-plasm would be to get them from the worker itself that has survived in the struggle for existence, rather than through the action of natural selection on fortuitous constellations of determinants in the germ-plasm of the queen.

If we grant the possibility of a periodical influx of worker germ-plasm into that of the species, the transmission of characters acquired by this caste is no more impossible than it is in other animals, and the social insects should no longer be cited as furnishing conclusive proof of Weismannism. Weismann undoubtedly deserves lasting credit for his accurate distinction of blastogenic and somatogenic characters, and for having rid biological science of a multitude of crude conceptions concerning the inheritance of the latter. Even the many investigators, who, like Boveri,[3] Delage,[4] Pauly,[5] Plate,[6] Rignano,[7] and Semon,[8] still believe in the transmissibility of acquired characters, show the effects of Weismann's clarifying and critical efforts.

Plate[9] attempts to overcome the difficulties presented by the normal sterility of the worker by supposing that the distinguishing characters of this caste arose prior to their inability to reproduce. He recognizes the following stages in the phylogeny of the social insects:

"1. The presocial stage with but a single kind of male and female.

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[1] Parthenogensis bei Ameisen durch Künstliche Temperaturverhältnisse. Biol. Centralbl., XI, 1891, pp. 21–23.

[2] Observations on the Progeny of Virgin Ants. Biol. Bull., IX, 1905, pp. 355–360; Temperature as a Factor in the development of Ants, *ibid.*, IX, 1905, pp. 361–367.

[3] Die Organismen als Historische Wesen. Wurzburg, 1906.

[4] L' Hérédité et les Grands Problèmes de la Biologie Génèrale. 2 ed., Paris, C. Reinwald, 1903.

[5] Darwinismus und Lamarckismus. München, Ernest Reinhardt, 1905.

[6] Ueber die Bedeutung des Darwin'schen Selectionsprincips und Probleme der Artbildung. 2 Aufl., Leipzig, Wilh Engelmann, 1903.

[7] Sur la Transmissibilité des Charactères Acquis. Paris, Felix Alcan, 1906.

[8] Die Mneme als Erhaltendes Prinzip im Wechsel des Organischen Geschehens. Leipzig, Wilh. Engelmann, 1904.

[9] Ueber die Bedeutung des Darwins'schen Selectionsprincips, etc., *loc. cit.*, p. 73–75.

"2. The social stage with but a single kind of male and female. The peculiarities in nesting, caring for the brood, and the other instincts were already developed during this stage.

"3. The social stage with one kind of male and two or several kinds of females, which were all fertile, but in consequence of the physiological division of labor became more and more different in the course of generations. The division of labor took place in such a manner that the sexual functions passed over primarily to a group A, while the construction of the nest, predatory expeditions and other duties devolved mainly on another group of individuals (B) which on that account used their reproductive organs less and less.

"4. The present stage with one kind of male, a fertile form of female, which arose from group A, and one or several kinds of sterile females, or workers (group B).

He thus assumes that the differentiation into sterile and fertile forms did not take place till stage 3, and, if I understand him correctly, not till after "the races had become differentiated morphologically." This view, as Plate admits, resembles Spencer's (p. 59). The two views, in fact, differ merely in degree, for the underlying contention is the same, namely that sterility is one of the most recently developed characters among the social insects. There can be little doubt, however, that the smaller adaptive characters, for example those of the females of certain *Formicæ* above mentioned, must have made their appearance in the fourth stage of Plate's scheme. The view which I have advocated differs from Plate's in admitting that even in this stage the workers are fertile with sufficient frequency to maintain a representation of their characters in the germ-plasm of the species. Conclusive evidence of the presence or absence of such representation can be secured only by experimental breeding and especially by hybridizing the male offspring of workers of one species (a), with females of another (b) that has workers of a different character. Under these conditions some of the characters of a should make their appearance in b. The most favorable genera for such experiments would probably be *Myrmica, Formica,* and *Lasius,* in all of which there are species, subspecies, and varieties with distinctly characterized workers while the corresponding males and females are sufficiently alike to make hybridization seem feasible.

5. The Ethological and Psychological Aspects of Polymorphism.

In the foregoing discussion attention has been repeatedly called to adaptation as the insurmountable obstacle to our every endeavor to explain polymorphism in current physiological terms. Of course, this is by no means a peculiarity of polymorphism, for the same difficulty confronts us in every biological inquiry. Adaptation, conceived as a phylogenetic process, and its ontogenetic counterpart, accommodation or regulation, are not only the central problems of all biology, but they constitute the proper field of ethology.[1] Emery,[2] and Waxweiler regard ethology as at bottom merely external physiology. The former defines it as treating of "the *ensemble* of phenomena whose physiological analysis has not yet been accomplished and is not even possible at the present time." This implies that when the analysis has been accomplished, ethology will be merged into physiology. Such a view is in my opinion open to discussion, since ethology also embraces the behavior, *i. e.*, the instinctive and intelligent actions by means of which organisms adapt or accommodate themselves to their environment and must be to that extent psychological. Hence there is opportunity for considerable difference of opinion in regard to the ultimate fate of ethology. Authors who believe that psychology will resolve itself into physiology will agree with Emery, whereas those who believe that biology will become increasingly psychological and metaphysical — and the number of these seems to be increasing — will predict that ethology will ally itself more closely with the mental sciences.

This dual possibility depends, of course, on two ways of envisaging the problem of adaptation. Those who view it from the physical (*i. e.*, mechanical), antiteleological and Neodarwinian standpoint, repudiate any attempt to substitute psychological terms in biological explanation, and assign as their reason for this course the existence of a psycho-physical parallelism. On the other hand, those who view the problem from the vitalistic, teleological and Lamarckian standpoint, turn to psychical manifestations like the will, with which we as acting subjects are perfectly familiar, as yielding a more adequate and satisfying insight into the phenomena. These different standpoints have been recently presented in violent contrast to each other in two works on adaptation by Detto[3] and Pauly.[4]

At first sight it may be difficult to understand why allusion should be made to these abstruse and very general matters in the discussion of a special subject like polymorphism. Reflection shows, however, that the social insects make a consideration of these matters necessary, since these organ-

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[1] An excellent discussion of the scope and problems of this science has been recently published by Waxweiler (Esquisse d'une Sociologie, *loc. cit.*, p. 29 *et seq.*). He has shown that Is. Geoffroy Saint Hilaire, in 1854, first introduced the term 'ethology' for the subject which Hæckel in 1866 designated as 'œcology' in his 'Generelle Morphologie.' The term 'bionomics' employed by Lankester, Baldwin, Gulick and others, is of course, of still more recent date. 'Ethology' therefore, not only has priority, but it is also more apt than the other terms that have been suggested. It will probably come into general use among English and American zoölogists, now that it has been adopted in such works as the 'Zoölogical Record.'

[2] Ethologie, Phylogénie et Classification. Comptes Rendus du 6 Congrès internat. Zool., Berne, 1904.

[3] Die Theorie der directen Anpassung und ihre Bedeutung für das Anpassungs-und Descendenzproblem. Jena, Gustav Fischer, 1904.

[4] Darwinismus und Lamarckismus, *loc. cit.*

isms are far and away the most plastic and adaptable and psychically the most richly endowed of all the lower animals. I use this term "psychically" advisedly, for, like Forel and Wasmann, I find myself utterly unable to accept the views of Bethe, Uexküll, and others, who regard the social insects as mere reflex machines. Nor have I the slightest hesitation in substituting psychological terms wherever physical terms are inadequate, as I am by no means convinced of the cogency of the hypothesis of psychophysical parallelism and the epistemological restrictions to which it is supposed to bind the investigator. If I am not greatly mistaken, psychophysical parallelism has of late received some pretty rough treatment at the hands of more than one eminent psychologist.[1]

As the type of polymorphism with which I have been dealing has been developed by psychically highly endowed social insects, it cannot be adequately understood as a mere morphological and physiological manifestation apart from the study of instinct. This has been more or less distinctly perceived by nearly all writers on the subject. However various their explanations, Spencer, Weismann, Emery, Forel, Marchal, and Plate all resort to instinct. Emery, especially, has seen very clearly that a worker type with its peculiar and aberrant characteristics could not have been developed except by means of a worker-producing instinct. In other words, this type is the result of a living environment consisting of the fostering queen and workers which instinctively control the development of the young in so far as this depends on external factors. Only under such conditions could a worker caste arise and repeat itself generation after generation. This caste may be regarded as a mutation, comparable with some of De Vries's *Œnothera* mutations, but able to repeat and maintain itself for an indefinite series of generations in perfect symbiosis with its parent form, the queen, because notwithstanding its relative infertility, it can be put to very important social use. Among ants this social use not only pervades the activities of the adult worker but extends even to the more inert larval stages. Thus the latter represent a rich and ever-fresh supply of food that can be devoured whenever a temporary famine overtakes the colony. In certain species, like the East Indian *Œcophylla smaragdina* and the South American *Camponotus senex,* the larvæ are put to a more humane use as spinning machines for constructing the silken nest inhabited by the colony. These examples also illustrate the purposive manner in which an organism can satisfy definite needs by taking advantage of ever-present opportunities.

In the lives of the social insects the threptic, or philoprogenitive instincts are of such transcendent importance that all the other instincts of the species,

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[1] See, *e. g.*, Busse, Geist und Körper. Leipzig, Dürr'sche Buchhandlung, 1903; and Binet, L'Âme et le Corps. Paris, Ernest Flammarion, 1905.

including, of course, those of alimentation and nest-building, become merely tributary or ancillary. In ants, especially, the instincts relating to the nurture of the young bear the aspect of a dominating obsession. The very strength and scope of such instincts, however, renders these insects more susceptible to the inroads of a host of guests, commensals and parasites. besides the parasitic larvæ of Chalcidids, Lomechusini and *Metopina* described in the first part of this article, there are many adult beetles and other insects on which the ants lavish as much or even more attention than they do on their own brood. And when the ants themselves become parasitic on other ants, it is always either for the sake of having their own brood nurtured, as in the temporarily and permanently parasitic forms, or for the purpose of securing the brood of another species, as in the slave-making, or dulotic species.

The philoprogenitive instincts arose and were highly developed among the solitary ancestral insects long before social life made its appearance. In fact, social life is itself merely an extension of these instincts to the adult offspring, and there can be no doubt that once developed it reacted rapidly and powerfully in perfecting these same instincts. It is not so much the fact that all the activities of the social insects converge towards and center in the reproduction of the species, for this is the case with all organisms, as the elaborate living environment developed for the nurture of the young, that gives these insects their unique position among the lower animals. A full analysis of the threptic activities would involve a study of the entire ethology of the social insects and cannot be undertaken at the present time. Nevertheless the bearing of these instincts on the subject of polymorphism can hardly be overestimated and deserves to be emphasized in this connection.

All writers agree in ascribing polymorphism to a physiological division of labor among orginally similar organisms. This is tantamount to the assumption that the phylogenetic differentiation of the castes arose in the sphere of function before it manifested itself in structural peculiarities. Although this view implies that the female, or queen, was the source from which both the instincts and structures of the worker were derived, it has been obscured by an improper emphasis on the instincts of the honey-bee, in which the female is clearly a degenerate organism, and on certain specialized instincts, supposed to belong exclusively to worker ants like the slave-makers (*Polyergus* and *Formica sanguinea*). We have therefore to consider, first, the instincts of the queen and, second, any evidence that may go to show that instinct-changes precede morphological differentiation in the phylogeny of the species.

It is evident that the social insects may be divided into two groups according to the instinct rôle of the queens. In one group, embracing the social wasps, bumble-bees, ants and termites, the female is the complete prototype of her sex. Even in the slave-making ants, as I have shown in a former article,[1] she manifests in the founding of her colonies all the threptic instincts once supposed to be the exclusive prerogative of the worker caste. These may be called the primary instincts. After the colony is established, however, and she no longer needs to manifest these instincts, she becomes a mere egg-laying machine and her instincts undergo a corresponding change. These may now be designated as secondary instincts. She thus passes through a gamut of instincts successively called into activity by a series of stimuli which in turn arise in a definite order from her changing social environment. The workers, however, are capable of repeating only a portion of the female gamut, the primary series. In gynæcoid individuals there is also a tendency to take up the secondary series, but in most workers this has been suppressed by countless generations of nutricial castration. The social insects of this type may be called *gynæcotelic,* to indicate that the female has preserved intact the full series of sexual attributes inherited from her solitary ancestors. In these the primary and secondary series were simultaneous or overlapped completely, in the gynæcotelic social insects they are extended over a longer period of time and overlap only in part, as social life permits the extension of the secondary long after the primary series has lapsed into desuetude. It will be seen that the division of labor which led to the spacial differentiation of like females into workers and queens is clearly foreshadowed in the consecutive differentiation of instincts in the individual queen.

The second group of social insects is represented by the honey-bees and probably also by the stingless bees (Meliponidæ). In these insects only the secondary instincts are manifested in the queen, while the worker retains the primary series in full vigor and thus more clearly represents the ancestral female of the species. This type may therefore be called *ergatotelic.*[2]

The suppression of the primary instincts in the queen honey-bee was undoubtedly brought about by a change in the method of colony formation. When the habit of swarming superseded the establishment of colonies by solitary queens, as still practiced by the gynæcotelic insects, the primary instincts of the female lapsed into abeyance or became latent. This change took place so long ago that it has had time to express itself in the structure of the queen honey-bee as compared with the worker (shorter tongue and wings, feebler sting, degenerate structure of hind legs, etc.).

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[1] On the Founding of Colonies by Queen Ants, etc., *loc. cit.*

[2] The distinction of gynæcotelic and ergatotelic types corresponds with Cook's "principles of matriarchy and ergatarchy" (The Social Organization and Breeding Habits of the Cotton-protecting Kelep of Guatemala. U. S. Depart. Agric., Bull. Entom., Tech. Series No. 10, 1905, p. 34). These terms are objectionable because they imply an erroneous, not to say anthropomorphic, conception of governing or ruling on the part of the queen or workers.

The first of the following examples, which seem to indicate the occurrence of instinctive prior to morphological differentiation, shows at the same time how the ergatotelic type of the honey-bee arose from the gynæcotelic type of the social wasps and bumble-bees.

1. The queens of certain species of *Formica* (*F. rufa, exsectoides,* etc.) are no longer able to establish colonies without the coöperation of workers. The common method of colony formation among these insects is by a process of swarming like that of the honey-bee: a certain portion of the colony emigrates and founds a new nest with one or more of the queens. When this method is impracticable the young queen seeks the assistance of an allied species of *Formica* (*F. fusca*), the workers of which are willing to perform the same function as those of her own species in rearing her brood. In *F. rufa* and *exsectoides* there is nothing in the stature or structure of the queen to indicate the presence of these parasitic instincts, but, in many of the allied species like *F. ciliata, montigena, microgyna,* etc., the colonies of which are smaller and no longer swarm, or do so only to a very limited extent, the queens have become more dependent on the workers of other species of *Formica* and have developed mimetic characters or a dwarf stature to enable them to enter and exploit the colonies of alien species.

2. In many ants the callows, or just-hatched workers, confine themselves to caring for the larvæ and pupæ and do not exhibit the foraging instincts till a later period. But even the adult workers may perform a single duty in the colony for long periods of time, if not indefinitely. Thus Lubbock,[1] and Viehmeyer,[2] have observed in certain nests of *Formica* that only certain individuals forage for the community. The latter has also noticed that certain other individuals, indistinguishable morphologically from their sister workers, stand guard at the nest entrances. In other genera, like *Camponotus, Atta, Pheidole,* etc., with species that have desmergates, the morphological differentiation between foragers and guardians is still unsettled. It becomes completely established, however, in certain genera and species with the suppression of the desmergates. A remarkable example of division of labor without corresponding structural differentiation is seen also in the above-mentioned *Œcophylla,* an ant which inhabits nests of leaves sewn together with fine silk. According to the observations of Dodd[3] and Doflein,[4] when the nests are torn apart the monomorphic workers separate into two companies, one of which stations itself on the outside of the nest, draws the separated leaves together and

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[1] Ants, Bees, and Wasps. Revised ed., New York, Appleton & Co., 1894, pp. 45–47.

[2] Experimentelle Untersuchungen, etc., *loc. cit.*, p. 336.

[3] Notes on the Queensland Green Tree Ant (*Œcophylla smaragdina* Fab.?). Victor. Natural., XVIII, 1902, pp. 136–140.

[4] Beobachtungen an den Weberameisen (*Œcophylla smaragdina*), Biol. Centralbl., XXV, 1905, pp. 497–507, 5 figs.

holds them in place with the claws and mandibles, while the other moves the spinning larvæ back and forth within the nest till the rent is repaired with silken tissue.

3. An interesting case is presented by the honey-ants (*Myrmecocystus melliger* and *mexicanus*). All the workers of these species, though variable in size, are structurally alike. Among the callows, however, and quite independently of their stature, certain individuals take to storing liquid food, as I have found in my artificial nests of the latter species, and gradually in the course of a month or six weeks become repletes, or plerergates. Except for this physiological peculiarity, which gradually takes on a morphological expression, the plerergates and ordinary workers are indistinguishable. We must assume, therefore, that the desire to store food represents an instinct specialization peculiar to a portion of the callow workers. There can be no doubt that as our knowledge of the habits of ants progresses many other cases like the foregoing will be brought to light.

It may be maintained that in these cases physiological states must precede the manifestation of the instincts, and that these states, however inscrutable they may be, are to be conceived as structural differentiations. There is undoubtedly much to justify this point of view. The elaborate sequence of instincts in the queen ant, for example, is accompanied by a series of physiological changes so profound as to be macroscopical. After the loss of her wings, the wing muscles degenerate and the fat-body melts away to furnish nourishment for the ovaries, which in the old queen become enormously distended with eggs as the breeding season approaches. Such changes would seem to be amply sufficient to account for the changing instincts. As I have shown,[1] mere artificial deälation at once alters the instincts of the queen, probably through a stimulus analogous to that which leads to the atrophy of a muscle when its nerve is severed, and in the case under consideration leads to the degeneration of the wing-muscles and to changes in the ovaries.

In the mermithergates and pseudogynes described in the first part of this paper, the aberrant instincts may be referred to peculiar physiological states. Similarly nutricial castration itself, considered as an instinct, may be said to be the result of the physiological state of hunger. There is indeed every reason to suppose that the worker, both in its ontogenetic and phylogenetic development, is through and through a hunger-form, inured to protracted fasting. Miss Fielde has shown,[2] that the workers of *Camponotus americanus* may live nearly nine months without food, which is as long

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[1] On the Founding of Colonies, etc., *loc. cit.*, p. 103.

[2] Tenacity of Life in Ants. Biol. Bull., VII, No. 6, Nov. 1904, p. 300; and *ibid.*, Temperature in the Development of Ants, *loc. cit.*, p. 366.

as the much larger and more vigorous queens are known to fast while establishing their colonies. The larvæ of ants, too, are known to remain alive in the nests for months without growing. And even when food is abundant the workers appropriate very little of it to their individual maintenance but distribute it freely among their sister workers, the brood and queen. It is not improbable, moreover, that the single instinct peculiar to workers, the instinct to leave the nest and forage, is the direct result of a chronic state of hunger.

Undoubtedly such physiological states are neither more nor less mysterious than those of man and the higher animals, in which they are universally recognized as leading to changes in the instinctive and emotional life of the individual. We may not only concede the existence of physiological states in the above and many other cases, but we may also admit that this concession is favorable to the hypothesis of psychophysical parallelism. On looking deeper into the matter, however, we find that our knowledge of the physiological states, and especially of their precise connection with the instincts, is extremely vague and unsatisfactory. Furthermore, we are compelled to confess that even the simplest physiological reaction, the simplest reflex depending on the simplest of physiological states, such as the general irritability of all living matter, still involves a non-mechanical or teleological and therefore a psychological factor, to the understanding of which the hypothesis of psychophysical parallelism contributes nothing. The interpretation of organic behavior as the result of "trial and error" seems to have a value in indicating that the teleological factor is a blind activity groping for the means with which to supply an organic need. But not only is this conception borrowed from psychology but it is thoroughly teleological, since the eventual selection and retention on the part of the organism of the particular mode of reaction best suited to supply its needs, is incapable of a mechanical explanation. Of course, 'teleology' as applied to biological phenomena must not be understood in the sense of an altruistic or external teleology like the 'design' of theologians but is, as Pauly has shown,[1] an immanent and egotistical principle capable of great simplification in the lower biological units like the cells, without losing its essentially purposive character.

Driesch,[2] in his attempt to establish the autonomy of the vital processes on the basis of regulatory phenomena in ontogeny, says: "A special problem which is calculated to lead to a parallelism between the instincts and ontogeny, may be briefly mentioned in conlcusion: the course of ontogeny may

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[1] Darwinismus and Lamarckismus, *loc. cit.*, pp. 15–22.
[2] Die "Seele" als Elementarer Naturfaktor, Leipzig, Wilhelm Engelmann, 1903, p. 26.

be interfered with, but it regulates itself; and from the study of just such regulations important insight has accrued to morphology. Will it also be possible to bring about regulations in instinctive processes? No definite answer can be given to this question at the present time." He goes on to say that if they should prove to be capable of such regulations, the instinctive reactions would present further evidence of the autonomy of living organisms.

It seems to me that there are, especially in the social insects, a few facts which point to such regulations in the sphere of instinct. When, for example, the firstling brood is removed from a queen ant that has just manifested her primary series of instincts, she will proceed to rear another brood, although under normal circumstances she would pass on to the purely secondary series of reactions. In this case the absence of a colony acts as a stimulus to produce a highly adaptive regulation, which is equivalent to a regeneration of the colony. If on the other hand the queen ant, wasp, or termite is removed from her colony, some of the remaining workers themselves become gynæcoid and function as substitutional queens, or in bees raise a new queen. A similar regulation of the personnel of the colony is also apparent in other cases, as when strange queens are adopted or the numerical proportions of the different castes are regulated. If we accept Wasmann's view of the production of pseudogynes in *Formica* nests infested with Lomechusini, the conversion of queen larvæ into workers would be a splendid example of regulation. Such facts point to instinct as offering evidence as important as that of ontogeny in support of a vitalistic conception. And even if my interpretation of the pseudogynes as the result of simple neglect and starvation be accepted, we still have an interesting case of regulation, for the pseudogynes of *Formica,* like the phthisergates of *Pheidole instabilis* and the mermithergates of *Ph. commutata,* are the result of a tendency to produce a symmetrical and adaptive whole out of formative materials that have been abnormally depleted, augmented, or disturbed in the course of their development through the action of parasites.

In concluding this rather long discussion of polymorphism it is hardly necessary to point out that I have added little of constructive value apart from a few suggestions and a clearer definition of some of the problems involved in an extremely intricate subject. If I have succeeded in showing that the underlying problem is the same as that of all other biological phenomena, and that the social insects cannot be used to support any of the current mechanical conceptions of development, my object will have been achieved.

EXPLANATION OF PLATES.

PLATE I.

FIG. 1. — *Pheidole kingi* André var. *instabilis* Emery. Soldier, Austin, Texas.

FIGS. 2–6. — Series of intermediate forms (desmergates) between the soldier and worker of *Ph. instabilis.*

FIG. 7. — Typical worker of same.

FIG. 8. — Deälated female of *Ph. instabilis.*

FIG. 9. — Male of same.

FIG. 10. — *Orasema viridis* Ashmead. Female. Austin, Texas.

FIG. 11. — *Orasema viridis.* Male.

FIG. 12. — *Orasema coloradensis* Ashmead. Female. Colorado Springs, Colorado.

PLATE II.

FIG. 13. — Phthisergate of *Ph. instabilis* with very young *Orasema viridis* larva attached to the right side of the prothorax beneath the fore leg.

FIG. 14. — Soldier semipupa of *Ph. instabilis* with *O. viridis* larva in second stage attached to the presternal region between the first and second pairs of legs.

FIG. 15. — Female semipupa of *Ph. instabilis* with *O. viridis* larva in the second stage attached to the pronotal region behind the head.

FIG. 16. — Female semipupa of *Ph. instabilis* with *O. viridis* larva in the third stage attached to the presternal region.

FIG. 17. — Female semipupa of *Ph. instabilis* with nearly mature *O. viridis* larva (shrunken by reagents) attached to the sternal surface between the middle and hind pairs of legs. From a specimen mounted in balsam.

FIG. 18. — Female pupa (phthisogyne) of *Ph. instabilis* with *O. viridis* semipupa in the pustulate stage, still attached in the position which it occupied as a larva. From a specimen mounted in balsam.

FIG. 19. — Female pupa (phthisogyne) with *O. viridis* semipupa in the pustulate stage, still attached to the sternal region. From an alcoholic specimen.

FIG. 20. — Semipupa of *O. viridis,* viewed as a transparent object, showing the head, wings, and legs developing beneath the hood-like prothoracic mass. From a specimen mounted in balsam.

FIG. 21. — Semipupa of *O. viridis* in a more advanced stage. From a specimen mounted in balsam.

FIG. 22. — Pupa of female *O. viridis* just before pigmentation, showing the prominent intersegmental abdominal welts.

FIG. 23. — Pigmented pupa of *O. viridis* nearly ready to hatch.

FIG. 24. — Phthisergate of *Ph. instabilis* viewed in profile as an opaque object. From an alcoholic specimen.

FIG. 25. — Phthisergate of *Ph. instabilis* in ventral view to show the greatly attenuated thorax, small projecting eyes, etc.

Fig. 26. — Phthisergate of *Ph. instabilis* viewed as a transparent object to show the urate masses in the gaster. From a specimen mounted in balsam.

Fig. 27. — Normal worker pupa of *Ph. instabilis* in profile. From an alcoholic specimen.

Fig. 28. — Phthisergate of *Ph. dentata* Mayr. From an alcoholic specimen.

Fig. 29. — Worker cocoon of *Camponotus herculeanus ligniperdus* var. *novæboracensis* Fitch, from northern Michigan, showing an enclosed pair of pupæ of *Pseudochalcura gibbosa* Provancher near the anterior pole, and the remains of the consumed *Camponotus* semipupa applied to the black meconial spot at the posterior pole.

Figs. 30–35.— Six larvæ of *Orasema viridis* in the youngest stage observed, corresponding with the one shown in Fig. 13.

Plate III.

Fig. 36. — *Pheidoloxenus wheeleri* Ashmead. Female, taken from a colony of *Ph. instabilis* at Austin, Texas.

Fig. 37. — *Pheidole dentata* var. *commutata* Mayr. Soldier. New Braunfels, Texas.

Fig. 38. — *Ph. commutata.* Worker.

Fig. 39. — Mermithergate of *Ph. commutata*, drawn to the same scale as Figs. 37 and 38; showing *Mermis* parasites in the distended gaster. The head of the ant bears occelli; the thorax is shaped like that of the soldier.

Fig. 40. — Lateral view of same mermithergate.

Fig. 41.— *Xenodusa cava* Leconte, taken from a colony of *Formica schaufussi* var. *incerta* Emery at Colebrook, Connecticut.

Fig. 42. — *Formica schaufussi* Mayr. var. *incerta* Emery. Normal worker. Colebrook Connecticut.

Fig. 43. — Pseudogyne of *F. incerta* drawn to the same scale as Fig. 42.

Fig. 44. — Pseudogyne from the same colony as Fig. 43, showing a somewhat different conformation of the thorax.

Plate IV.

Fig. 45. — Pseudogyne of *Myrmica rubra brevinodis* Emery var. *sulcinodoides* Emery, with vestige of left fore wing, from Isle Royale, Michigan.

Fig. 46. — Thorax of same in profile.

Fig. 47. — Thorax of normal worker of *M. sulcinodoides.*

Fig. 48. — Thorax of pseudogynic *M. rubra scabrinodis* Nyl. var. *schencki* Emery, from Jeanette, Pennsylvania. This specimen has minute vestiges of both fore wings.

Fig. 49. — Lateral view of same.

Fig. 50. — Pseudogyne of *Formica rufa obscuriventris* Mayr. var. *melanotica* Emery, with well-developed mesonotum, scutellum and metanotum, from Rockford, Illinois.

Fig. 51. — Dorsal view of thorax of same.

Fig. 52. — Pseudogyne of *F. melanotica* with more convex mesonotum, from the same colony as the specimen shown in Figs. 50 and 51.

Fig. 53. — Pupa of female *Orasema coloradensis* Ashm.; dorsal view showing the arrangement of the pustules.

FIG. 54. — Lateral view of same.

FIG. 55. — Pupa of female *Pseudochalcura gibbosa* Prov., from northern Michigan.

FIG. 56. — *Kapala floridana* Ashmead. Female, from eastern Florida. From a specimen in the United States National Museum.

FIG. 57. — *Kapala floridana.* Male, from eastern Florida. From a specimen in the United States National Museum.

FIG. 58. — *Isomeralia coronata* Westwood. Female, from Pernambuco, Brazil. From a specimen in the United States National Museum.

FIG. 59. — Lateral view of same.

FIG. 60. — *Dicœlothorax platycerus* Ashmead. Female. After Ashmead.

FIG. 61. — Scutellum of same, seen from above. After Ashmead.

FIG. 62.— *Eucharis* sp. Male, from the top of the Las Vegas Range, New Mexico (11,000 ft.).

PLATE V.

FIG. 63. — *Pheidole instabilis*; *a*, females (winged and deälated); *e*, male; *o*, soldier; *c*, workers; *r*, intermediates (desmergates); *m*, *Orasema viridis*, female; *n*, male. × 2.

FIG. 64. — Brood of *Ph. instabilis*; *a*, female larvæ and pupæ; *e*, male pupæ and semipupæ; *o*, soldier pupæ; *c*, worker larvæ and pupæ; *r*, pupæ of desmergates; *m*, *O. viridis*, adult female, *m′*, pupæ and semipupæ; *n*, male; *n′*, pupæ of same. × 3.

FIG. 65. — Brood of *Ph. instabilis.* Letters as in the preceding figure; *s*, phthisergates. × 3.

FIG. 66. — Three female semipupæ (phthisogynes) of *Ph. instabilis* bearing larvæ of *O. viridis* on their sternal surfaces. × 3.

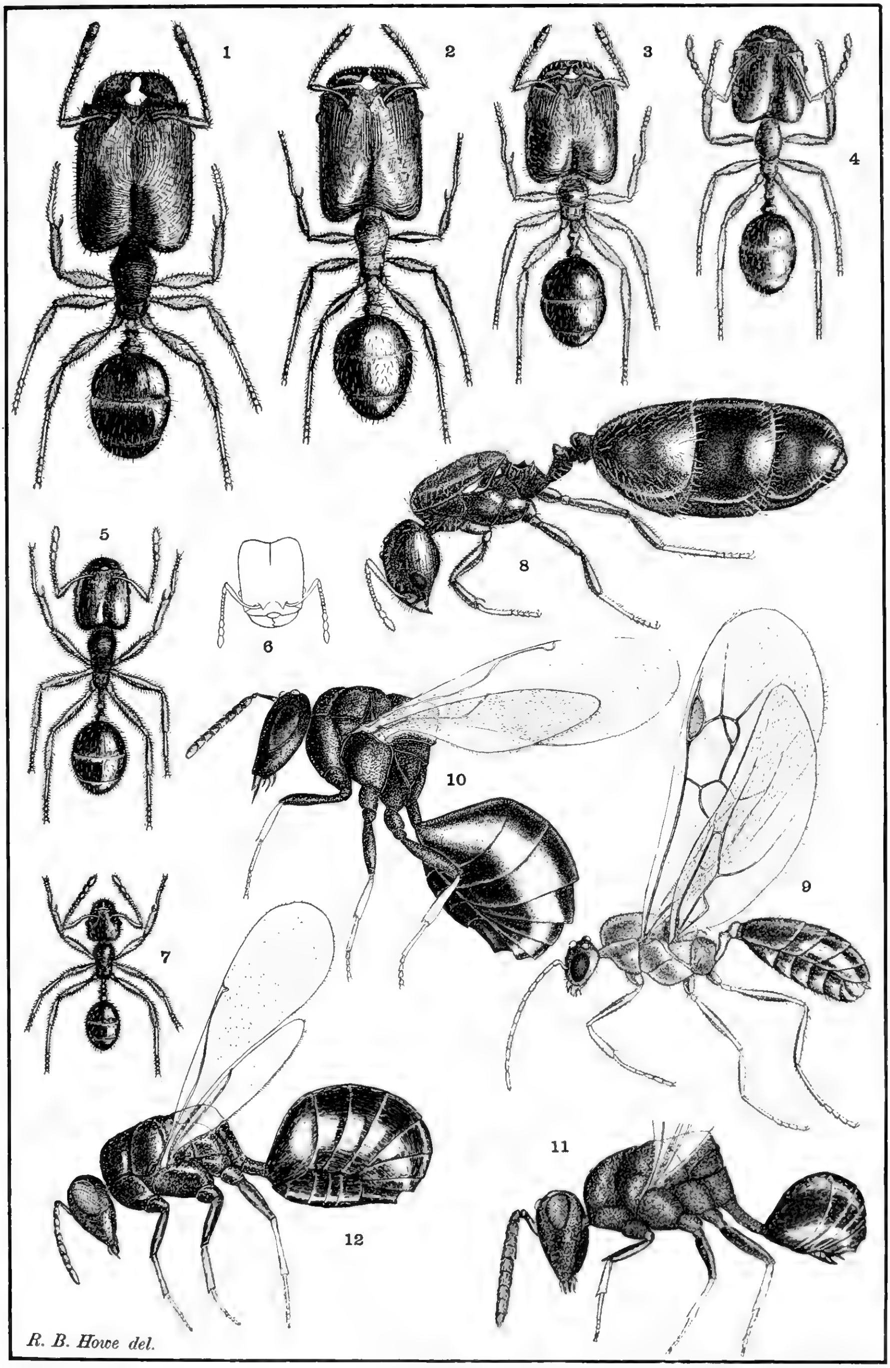
FIG. 67. — Worker brood of *Ph. instabilis*; *c*, normal worker pupæ and semipupæ; *i*, phthisergates; *r*, intermediate (desmergatic) phthisergate. From specimens mounted in balsam.

FIG. 68. — *Solenopsis molesta validiuscula* Emery; *a*, female; *e*, male; *c*, workers; *m*, *Orasema coloradensis*, female.

FIG. 69. — Brood of *Pachycondyla harpax* Fabricius. The larvæ marked *x* each bear a larva of *Metopina pachycondylæ* Brues; *z*, detached *Metopina* larva; *v*, puparium of *Metopina*; *u*, cocoon of *Pachycondyla.*

PLATE VI.

Diagram to illustrate the relationships of the typical and atypical phases of ants. The three typical phases are placed at the angles of an isosceles triangle, the excess developments to the right, the defect developments to the left of a vertical line passing through the middle of the diagram. The normal atypical phases are in ordinary, the pathological phases in italic type. The arrows indicate the direction of the affinities of the atypical phases. The phases arranged on the sides of the triangle are annectant, those radiating outward from its angles are new departures showing excess or defect characters. For definitions of the different phases see pp. 53 to 57.



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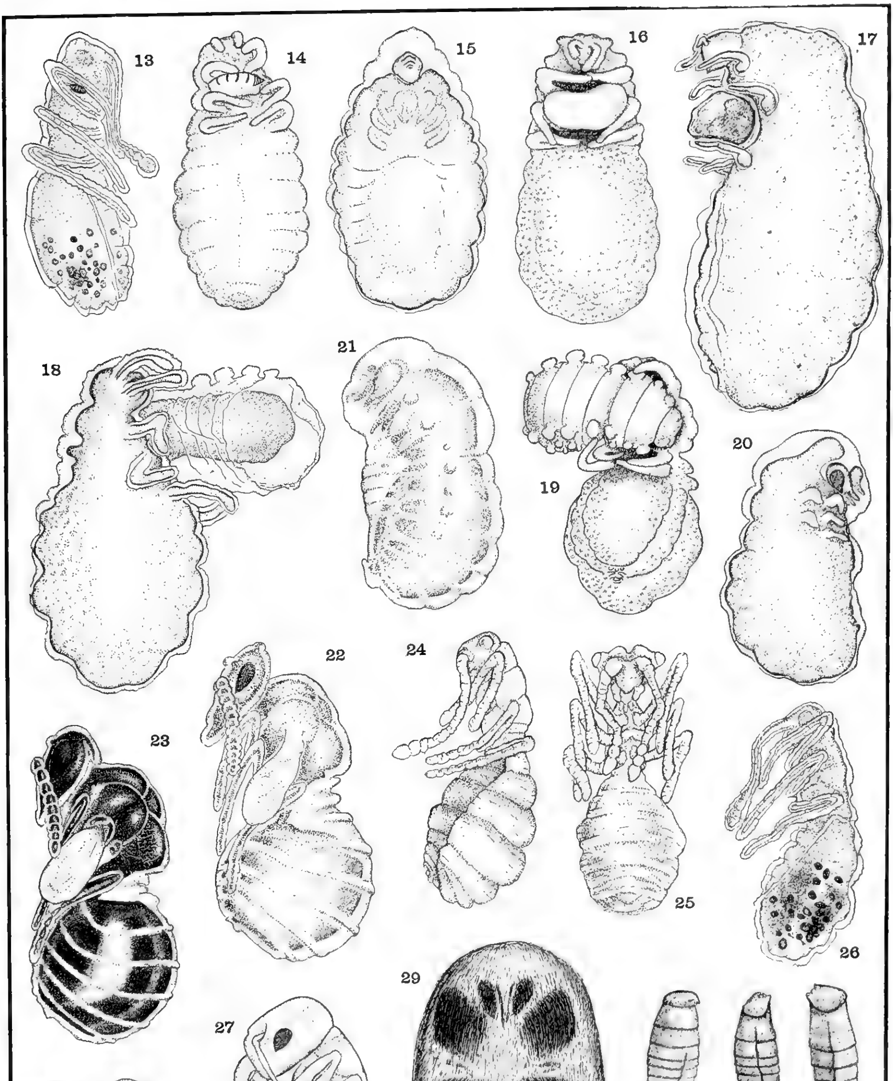
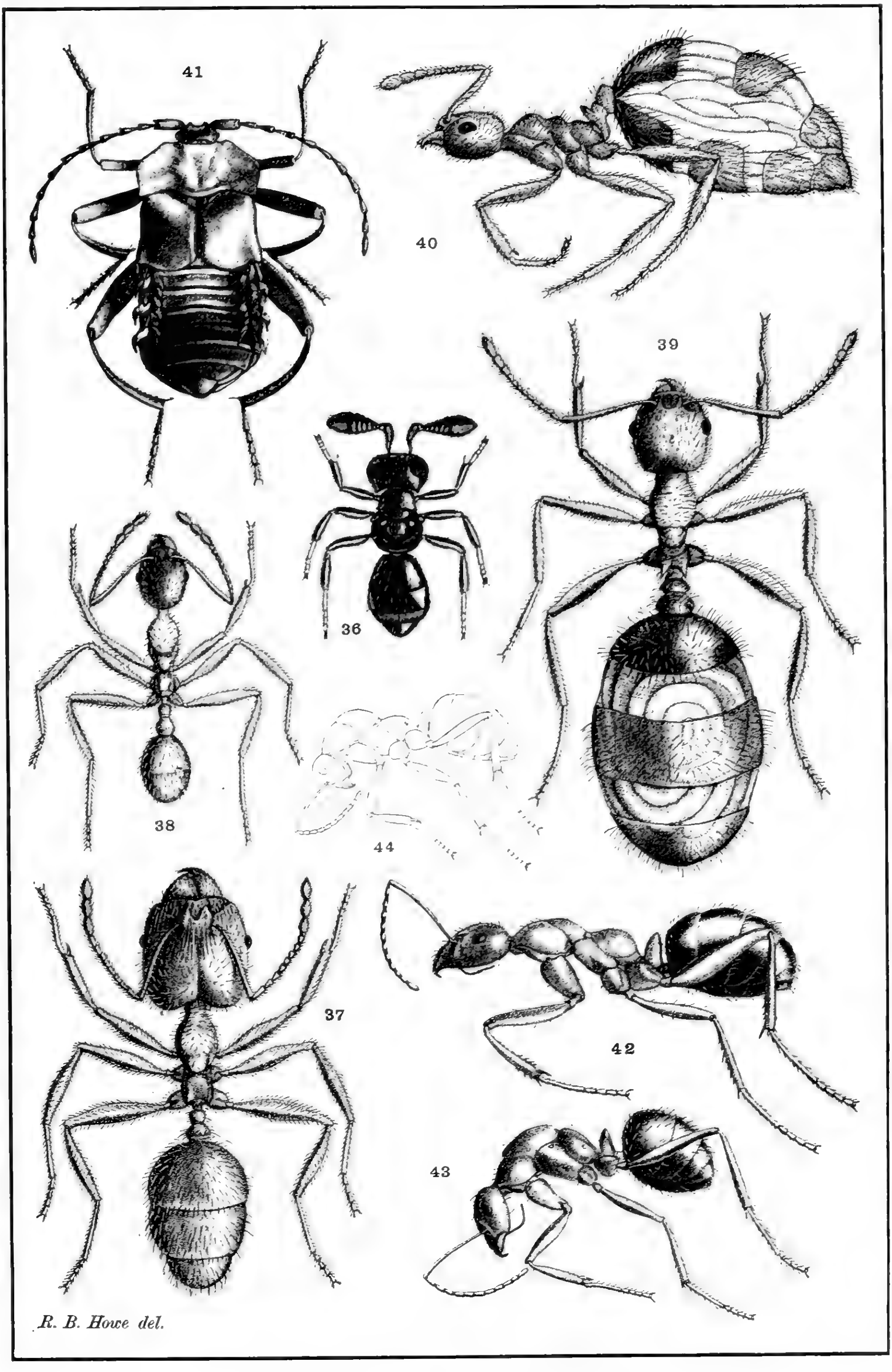
Pheidole instabilis and Orasema.



DEVELOPMENT OF ORASEMA



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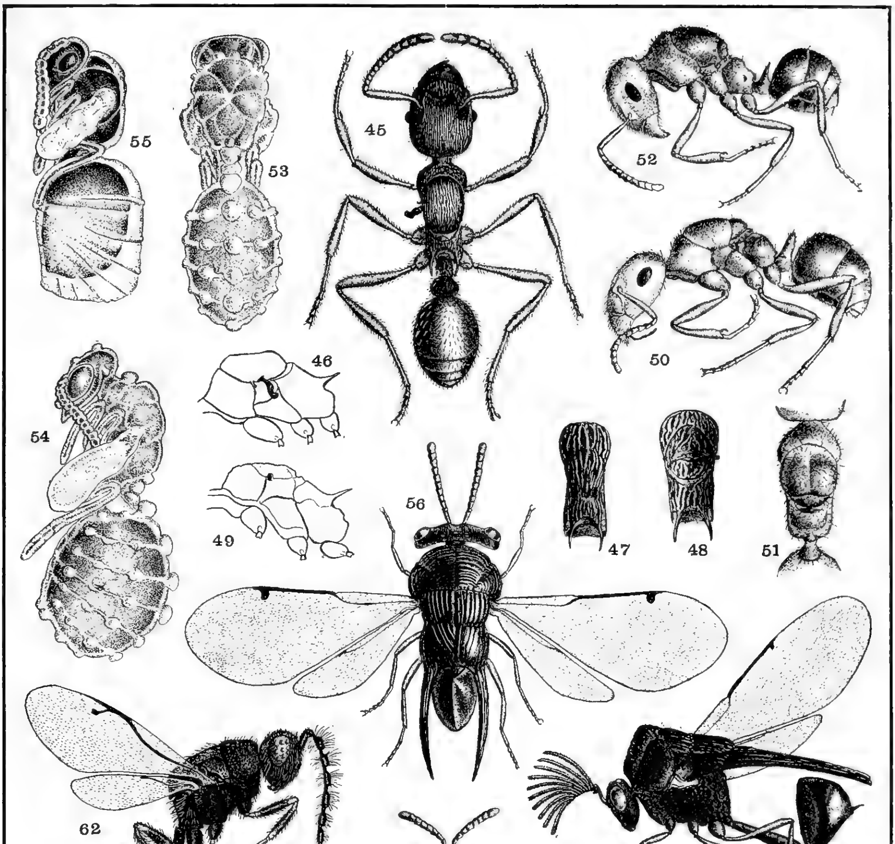
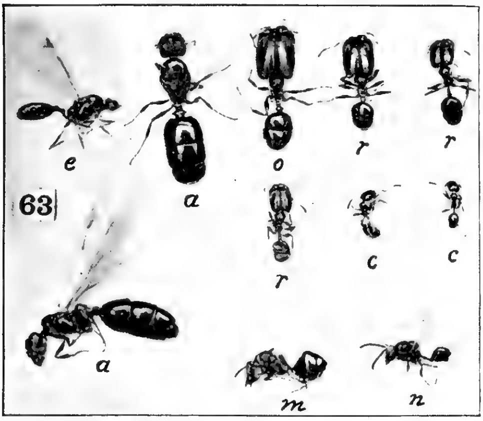
Parasites of Pheidole and Formica.



CHALCIDID PARASITES OF ANTS, ETC.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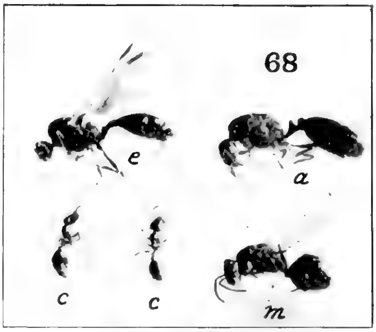
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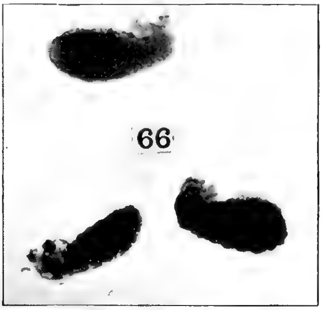
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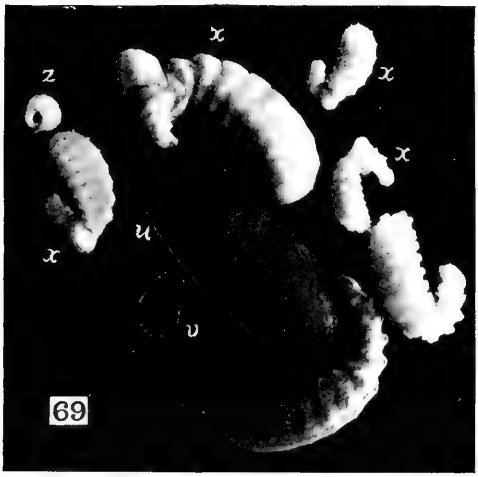
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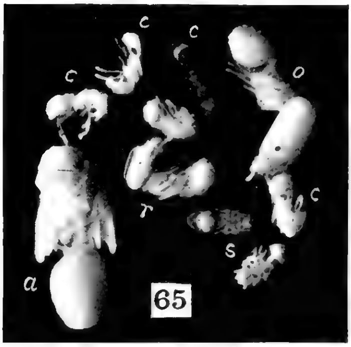
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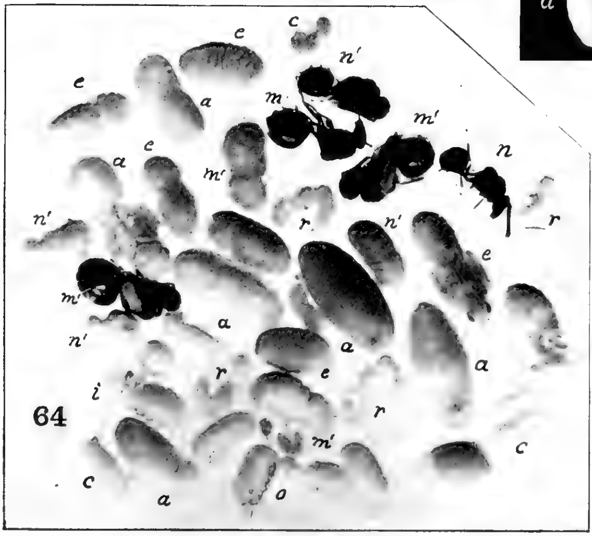
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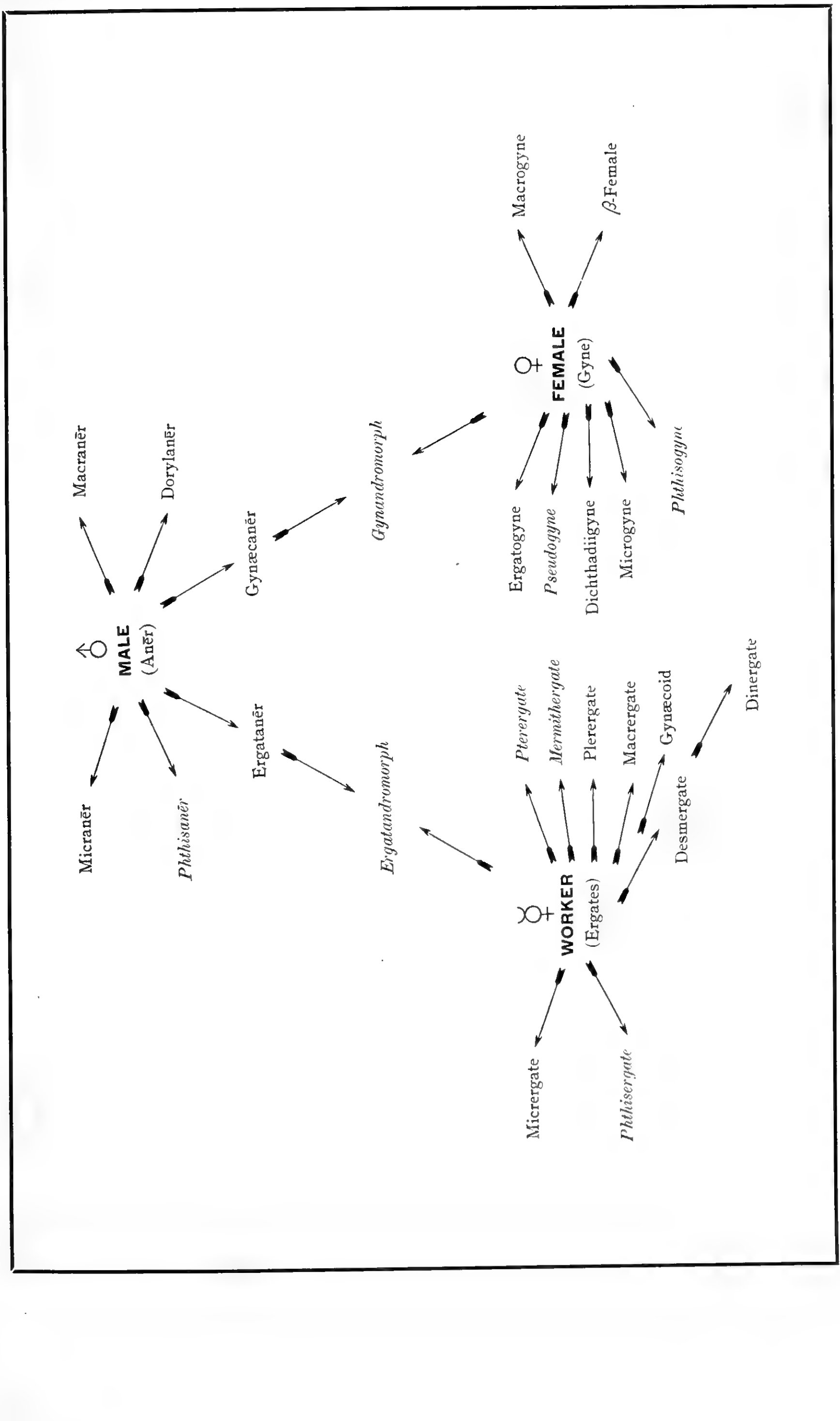
PARASITES OF PHEIDOLE, SOLENOPSIS AND PACHYCONDYLA.



THE TYPICAL, ATYPICAL AND PATHOLOGICAL PHASES OF ANTS.

A Collection of Ants from British Honduras.

BY WILLIAM MORTON WHEELER.

AUTHOR'S EDITION, extracted from BULLETIN

OF THE

American Museum of Natural History,

VOL. XXIII, ARTICLE XV, pp. 271–277.

New York, March 30, 1907.

(Continued from 3rd page of cover.)

ETHNOGRAPHICAL ALBUM.

Jesup North Pacific Expedition.

Ethnographical Album of the North Pacific Coasts of America and Asia. Part 1, pp. 1–5, pll. 1–28. August, 1900. Sold by subscription, price, $6.00.

BULLETIN.

The matter in the 'Bulletin' consists of about twenty-four articles per volume, which relate about equally to Geology, Palæontology, Mammalogy, Ornithology, Entomology, and (in the recent volumes) Anthropology, except Vol. XI, which is restricted to a 'Catalogue of the Types and Figured Specimens in the Palæontological Collection of the Geological Department,' and Vols. XV, XVII, and XVIII, which relate wholly to Anthropology.

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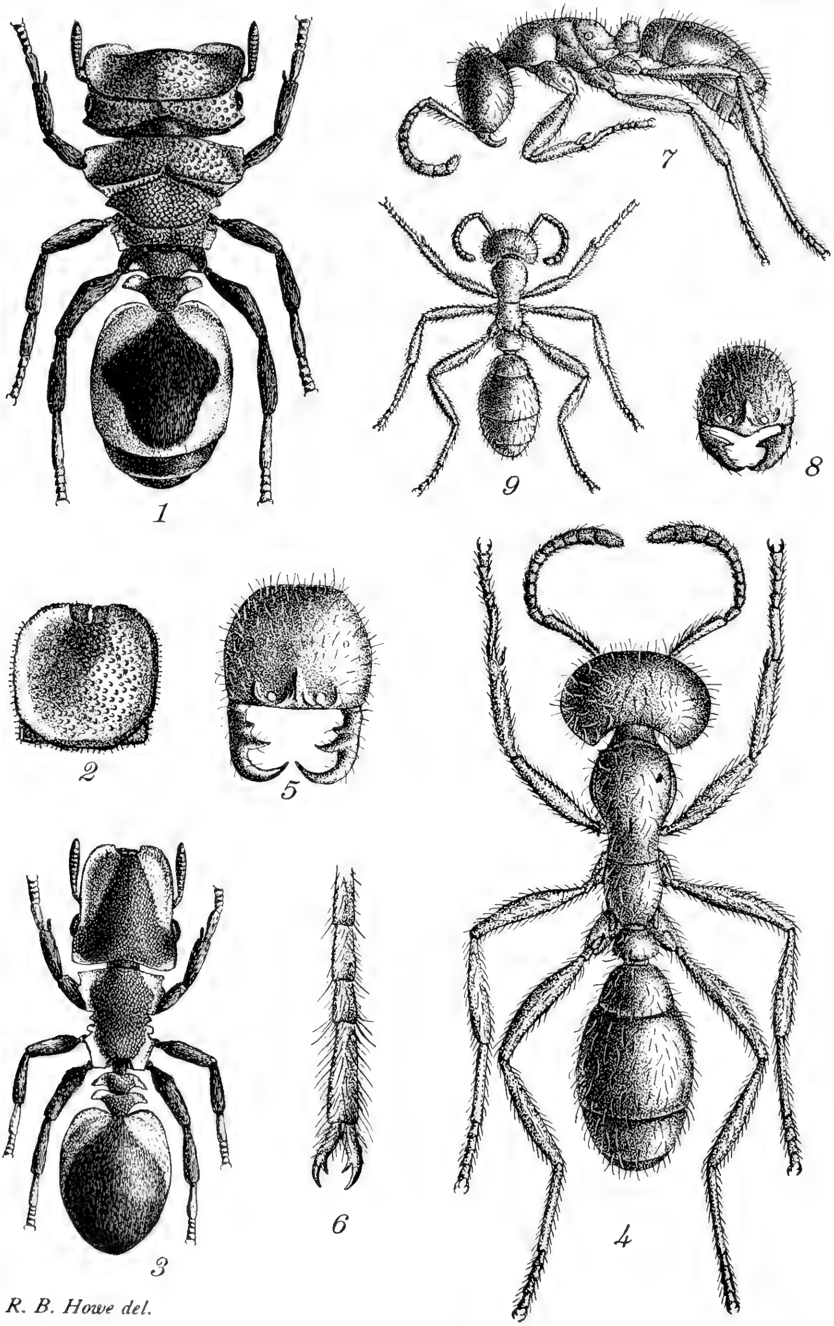
Printed by Edward W. Wheeler, Cambridge, Mass.



R. B. Howe del.

ANTS FROM BRITISH HONDURAS.

PENDANT CARTON NEST OF *Azteca schimperi* EMERY.

59.57, 96 (728)

Article XV.— A COLLECTION OF ANTS FROM BRITISH HONDURAS.

By William Morton Wheeler.

Plates XI and XII.

The collection of ants enumerated in the following pages was made during the autumn and winter of 1905–'06 by Mr. J. D. Johnson at Manatee, British Honduras. Although the specimens all belong to known species, they are interesting on account of the locality in which they were taken, as British Honduras is very rarely mentioned among the localities in Forel's admirable monograph of the Central American and Mexican ants in the 'Biologia Centrali-Americana.'

Ponerinæ.

1. **Pachycondyla harpax** *Fabr.*—Three workers indistinguishable from the typical form from Texas and Mexico.

2. **Pachycondyla (Pseudoponera) stigma** *Fabr.* — Numerous workers and a few males from several colonies.

3. **Anochetus (Stenomyrmex) emarginatus testaceus** *Forel.*— Numerous workers closely resembling in color the typical form of this subspecies from the West Indies and in having the anterior surface of the petiole smooth above and only moderately rugose near the base.

Dorylinæ.

4. **Eciton hamatum** *Fabr.*— Many soldiers and workers.

5. **Eciton vagans** *Oliv.*— Numerous workers.

6. **Eciton rogeri** *Dalla Torre.*— Numerous workers.

7. **Eciton prædator** *F. Smith.*— Numerous workers.

8. **Cheliomyrmex nortoni** *Mayr.* (Pl. XI, Figs. 4–9.)— Many workers measuring from 2.5 to 6 mm. in length, from two colonies. There can be no doubt that this ant forages in files like the species of *Eciton*. It is probably hypogæic like *E. cæcum* Latr. As Emery has shown, *C. nortoni* has dimorphic workers. The largest individuals (soldiers) have curved, falcate mandibles with a narrow, hooked apical and two large basal teeth (Pl. XI, Fig. 5) whereas the intermediates and small workers have short and proportionally broad mandibles, with only two large teeth separated by a series

of denticles. (Pl. XI, Fig. 8.) As in the genus *Dorylus* the clypeus is also more convex and projecting in the smaller than in the larger workers.

MYRMICINÆ.

9. **Pseudomyrma belti** *Emery* var. **fulvescens** *Emery.*— Many workers of the typical form of this variety.

10. **Pseudomyrma dolichopsis** *Forel.* — Several workers which agree perfectly with Forel's description except in size. They are only 3–3.3 mm. in length and may belong to an incipient colony.

11. **Pseudomyrma sericea** *Mayr.*— A single worker.

12. **Pseudomyrma caroli** *Forel.* — Numerous workers agreeing very closely with Forel's description of specimens from Costa Rica and with a type specimen of the var. *clapii* Forel from the Amazon.

13. **Pseudomyrma delicatula** *Forel.*— Four workers.

14. **Monomorium carbonarium ebeninum** *Forel.*— Many workers of the typical form of this subspecies.

15. **Monomorium floricola** *Jerdon.*— Numerous workers.

16. **Solenopsis geminata rufa** *Fabr.* — Many workers of the typical East Indian form of this common tropicopolitan ant. They are of a reddish yellow color, with a well developed spine on the mesosternum. The largest specimens measure only 3.5–4 mm.

17. **Pheidole anastasii** *Emery* var. **johnsoni** var. nov. — Numerous soldiers, workers and males taken from a single colony (Feb. 2). The soldiers and workers resemble the corresponding phases of *anastasii* except in having the whole head, thorax and pedicel opaque as in *punctatissima* Mayr. The color is that of *anastasii.*

18. **Pheidole megacephala** *Fabr.*— Several soldiers and workers of the typical form.

19. **Cremastogaster brevispinosa** *Mayr.* — Many workers from several colonies marked "small black house-ant." Among these are a number of pseudogynic individuals not exceeding the largest workers in size (2.3 mm.), with an enlarged mesonotum and sometimes with a small scutellum and minute nodular or strap-shaped vestiges of fore wings. These abnormal individuals are of exactly the same character as the pseudogynic specimens of *Myrmica* which I have described and figured in a former paper.[1]

20. **Cryptocerus cristatus** *Emery.*— A worker and two females. The wings of the latter are smoky brown, with heavy dark brown veins and stigma.

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[1] The Polymorphism of Ants, with an Account of Some Singular Abnormalities due to Parasitism. Bull. Am. Mus. Nat. Hist., Vol. XXIII, 1907, p. 43, pl. iv, figs. 45–49.

21. **Cryptocerus angulosus** *F. Smith.*

(Plate XI, Figs. 1–3.)

Cryptocerus angulosus F. Smith, Trans. Ent. Soc. London, 1867, p. 525, pl. xxvi, fig. 7. ☿.

Cryptocerus jucundus F. Smith, Trans. Ent. Soc. London, 1876, p. 606, pl. xi, Fig. 2, ☿.

Cryptocerus angulosus Emery, Bull. Soc. Ent. Ital., XXII, 1890, p. 39, tav. ix, fig. 9, ☿.

Soldier. (Pl. XI, Figs. 1 and 2.) Length: 4.6–5 mm.

Head surmounted by a disk, which is as long as broad, with straight, parallel sides and rounded anterior and posterior corners. The floor of the disk is convex in the middle and anteriorly, and very concave on the sides, with a thin, reflected and irregularly crenate border. Its anterior border is semicircularly excised in the middle, and encloses the mandibles, each of which has a long, acute apical. and a few indistinct basal teeth. Posterior corners of head projecting below and beyond the disk, rather acute, turned upwards and irregularly crenate. Thorax as broad as long, about twice as broad in front as behind. Promesonotal and mesoëpinotal sutures very distinct, the former subsemicircular, the latter but slightly curved. Pronotum with sharp, flattened anterior angles and a strong transverse, irregularly crenate, posterior crest, narrowly interrupted in the middle. Mesonotum somewhat more than half as broad as the pronotum, produced on each side into a short, sharp angle. Epinotum nearly as broad as the mesonotum, with thin, flat lateral borders, except in front where it is suddenly narrowed and produced into a small rounded lobe on each side. The lateral borders converge posteriorly and have blunt posterior angles. Petiole and postpetiole alike in shape and both with well-developed, recurved lateral spines, these on the petiole being, however, distinctly narrower, more acute and less flattened than those on the postpetiole. Grasor less than twice as long as broad, flattened, bluntly pointed behind, cordate in front, with thin, slightly upturned anterior borders. Legs robust.

Subopaque; upper surface of head shining. Head and thorax foveolate, the former more coarsely and much more sparsely, especially on the concave portions of the disk. Petiole, postpetiole, gaster and legs finely and densely foveolate-punctate.

Hairs glistening white, very short, scale-like and appressed, one to each of the foveolæ on the head and thorax; much smaller and denser on the remainder of the body. Edge of cephalic disc with a fringe of short, erect, clavate hairs.

Black; upper surface of head, pronotum, tibiæ, terminal tarsal joints, scapes and basal funicular joints of antennæ, brownish yellow. Lateral borders of epinotum, spines of postpetiole and all but a large lozenge-shaped area on the disc of the first gastric segment, sordid white, as are also the posterior borders of the remaining gastric segments.

Worker. (Pl. XI, Fig. 3.) Length: 3.5–4 mm.

Head not surmounted by a disk, longer than broad, narrower in front than behind, with sides straight and gradually converging in front, and with rounded, thin anterior lobes and distinct posterior angles. Anterior border with a semicircular excision for the mandibles. Thorax nearly 1½ times as long as broad, flattened above, without a pronotal crest; promesonotal suture obsolete, mesoëpinotal suture very indistinct. Pro- and epinotum each somewhat broader than long, with thin, dilated lateral borders, and each with a notch just behind its anterior angle. Mesonotum produced on each side into a short spine. Petiole and postpetiole similar to those of the soldier. Gaster cordate-elliptical, proportionally shorter than in the soldier.

Opaque; whole surface finely and densely granulate-foveolate, the head, thorax, petiole and postpetiole somewhat more coarsely than the gaster.

Hairs similar to those of the soldier but shorter; finer and denser on the gaster and legs than on the remainder of the body.

Black; anterolateral lobes and posterior corners of head, lateral borders of thorax, spines of petiole and postpetiole, anterolateral corners of first gastric segment, antennæ, knees and tibiæ, sordid or brownish white.

Male. Length: 4.5–5 mm.

Head, excluding eyes, broader than long, convex behind, with very short, concave cheeks. Mandibles with an acute apical and several small basal teeth. Antennæ short, not much incrassated towards their tips; scape much shorter than the second funicular joint, first funicular twice as broad as long, joints 2–11 subequal, less than twice as long as broad, rather robust, terminal joint somewhat shorter than the two preceding joints together. Thorax robust, somewhat broader through the wing insertions than the head through the eyes; Mayrian furrows of pronotum broadly impressed, shallow. Epinotum short, basal surface shorter than the abrupt declivity with which it forms nearly a right angle. Petiole and postpetiole subequal, rectangular from above, a little longer than broad.

Opaque; petiole, postpetiole and gaster shining. Head and thorax densely punctate or granular, the former with small, the latter with larger, shallow foveolæ. Mayrian and parapteral furrows coarsely longitudinally rugose. Petiole, postpetiole and gaster coarsely shagreened.

Hairs whitish, tapering, rather abundant, suberect; conspicuous on the body but much sparser on the legs.

Black; mandibles, antennæ and legs white; bases of mandibles, the scapes and bases of fore femora more or less infuscated. Posterior edges of gastric segments and genitalia yellowish. Wings whitish hyaline, with colorless veins and light brown stigma.

Described from numerous soldiers, workers and males, all taken from the same colony (Jan. 31).

22. **Atta cephalotes** *Linn.* — Numerous small and medium sized workers of this, "the wee-wee, or mound-builder," which is one of the few ants also cited by Forel from British Honduras.

23. **Atta** (**Trachymyrmex**) **saussurei** *Forel.* — Closely related, as Forel has shown, to *A.* (*T.*) *septentrionalis* of the United States. The numerous workers received from Mr. Johnson agree well with a typical specimen of *saussurei* given me by Mr. Pergande. They differ from *septentrionalis* in having a narrower head, much more convex and protruding eyes, longer antennal scapes, which surpass the posterior corners of the head by nearly $\frac{1}{3}$ their length, and more acute thoracic spines, of which four instead of three pairs may be seen on the profile of the pro- and mesonotum. The postpetiole is as long as broad instead of broader than long; the tubercles on

the gaster are larger and less numerous than in *septentrionalis* and the median black band is less distinct.

The hitherto undescribed female of *saussurei* differs from that of *septentrionalis* in the longer antennal scapes and postpetiole and the grosser tubercles, especially on the gaster. The first segment of the latter has a median and two lateral streaks of dark brown, and the ventral surface is also infuscated. The mesonotum has a large, triangular anteromedian and two lateral dark brown blotches and there is a similar blotch on the clypeus, one on the vertex and another on the scutellum. The wings are smoky brown, somewhat paler than those of *septentrionalis.*

In the hitherto undescribed male of *saussurei* the head is narrower behind and with blunter spines than in *septentrionalis*; the antennæ and legs are more slender, the postpetiole longer and with a pronounced transverse depression, and the tubercles on the petiole, postpetiole and gaster are much more prominent.

All the specimens received from Mr. Johnson were taken from the same nest (Feb. 9).

24. **Myrmicocrypta dilacerata** *Forel.*— Two males.

25. **Cyphomyrmex rimosus** *Spinola.*— Numerous workers of the typical form of this variable species.

DOLICHODERINÆ.

26. **Dolichoderus bispinosus** *Olivier.*— Numerous workers from two colonies, together with some Membracids which they were attending. This common and widely distributed neotropical species is cited by Forel from the Rio Hondo, British Honduras. Like several other species of the genus it constructs paper nests.

27. **Dolichoderus championi** *Forel.*— Numerous workers and a single deälated female. Forel has described all three phases of this insect from Mexico, Costa Rica and Panama, and also a subspecies and variety from Trinidad and Colombia.

28. **Tapinoma melanocephalum** *Fabr.*— Many workers from a single colony. This species appears to be widely distributed through the tropics of both hemispheres. It is common in the West Indies (Jamaica, Porto Rico, Bahamas) and has also been introduced into well-heated buildings in New York. During the past winter I have seen it visiting the sugar bowls on the tables of the Columbia University commons.

29. **Dorymyrmex pyramicus** *Roger.*— Numerous workers of the typical form of this species from two colonies.

30. **Azteca instabilis** *F. Smith.*— Many workers of all sizes and four-

teen winged females from four colonies (Nov. 1 and 14). The females are 9.10 mm. long. The head, excluding the mandibles, is very little longer than broad, convex and rounded on the sides behind the eyes, contracted and concave in the region of the cheeks and with a broad, shallow occipital excision. The tips of the antennal scapes reach to a little more than ⅔ the distance between the eyes and the posterior corners of the head. The body is dark brown, with the mandibles, clypeus, antennæ, head, pronotum, thoracic sutures, tarsi, venter, anterior and posterior borders of the gastric segments dull orange yellow. The front and a large portion of the upper posterior surface of the head dark brown. The wings have a pronounced yellow tinge, with dark brown stigma and scapular vein; the remaining veins being light brown. Pile and pubescence like those of the worker; antennal scapes and legs with prominent erect hairs.

31. **Azteca foreli** *Emery.*— Numerous workers of all sizes, agreeing perfectly with Emery's original description of this species.

32. **Azteca schimperi** *Emery.*— Numerous workers of all sizes taken from a paper nest which Mr. Johnson has forwarded to the American Museum. This nest, which is represented in Plate XII, was suspended from the branches of a tree. It is regularly egg-shaped, 15 cm. long and 9.5 cm. through its greatest diameter, and consists of dark brown, hard and friable carton. The outer surface is ornamented with broad flat carton scales of a paler and slightly reddish color. The numerous openings, scattered irregularly over the surface, are mostly elliptical and vary from 3 to 6 mm. in diameter.

CAMPONOTINÆ.

33. **Prenolepsis longicornis** *Fabr.*— Numerous workers.

34. **Prenolepsis guatemalensis** *Forel.*— Several workers and males which agree very closely with typical specimens of this species received from Prof. Forel.

35. **Prenolepsis sp.**— Three workers which I hesitate to refer to any of the described species, as they are not accompanied by males.

36. **Camponotus abdominalis ustulatus** *Forel.*— A number of soldiers and workers and two winged females taken Nov. 15, from "an empty hornet's nest."

37. **Camponotus abdominalis stercorarius** *Forel.*— Several soldiers and workers.

38. **Camponotus planatus** *Roger.*— Several soldiers and workers of a pale variety of this common neotropical species.

39. **Camponotus formicæformis** *Forel.*— A number of soldiers and workers.

40. **Camponotus lindigi** *Mayr.*— A few soldiers and several workers.

41. **Camponotus rectangularis** *Emery.*— Numerous soldiers and workers of the light-colored, typical form of this species.

42. **Camponotus claviscapus** *Forel.*— Two soldiers and fourteen workers agreeing perfectly with Forel's description. There are also in my collection two females and two males taken in Nicaragua by Mr. Wm. Fluck. None of these specimens has any trace of a carina on the clypeus so that I am unable to refer them to Forel's var. *carinata* of Guatemala. The female resembles the soldier very closely in the structure of the head and the distally incrassated antennal scapes. The thorax and gaster are long and narrow, the mesonotum being somewhat longer than broad and as broad as the head. The petiole is low and very thick, with blunt horizontal superior border when seen from behind. The gaster is nearly four times as long as broad, brown, with the anterior half of the first segment and a pair of large rectangular blotches on each of the succeeding segments, yellow. The wings are yellowish hyaline, with yellow veins and stigma.

43. **Camponotus sericeiventris** *Guérin.*— Two soldiers and a worker agreeing in all respects with specimens from various parts of Mexico.

EXPLANATION OF PLATES.

Plate XI.

Fig. 1.—*Cryptocerus angulosus* F. Smith. Soldier.
Fig. 2.—Head of same seen from above.
Fig. 3.—*Cryptocerus angulosus* F. Smith. Worker.
Fig. 4.—*Cheliomyrmex nortoni* Mayr. Soldier.
Fig. 5.—Head of same seen from the front.
Fig. 6.—Terminal tarsal joints of same.
Fig. 7.—*Cheliomyrmex nortoni* Mayr. Intermediate worker, in profile.
Fig. 8.—Head of same seen from the front.
Fig. 9.—*Cheliomyrmex nortoni* Mayr. Small worker, drawn to same scale as Figs. 4 and 7.

Plate XII.

Pendent carton nest of *Azteca schimperi* Emery.

The Fungus-Growing Ants of North America.

By William Morton Wheeler.

AUTHOR'S EDITION, extracted from BULLETIN
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(Continued from 3rd page of cover.)

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Ethnographical Album of the North Pacific Coasts of America and Asia. Part 1, pp. 1–5, pll. 1–28. August, 1900. Sold by subscription, price, $6.00.

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The matter in the 'Bulletin' consists of about twenty-four articles per volume, which relate about equally to Geology, Palæontology, Mammalogy, Ornithology, Entomology, and (in the recent volumes) Anthropology, except Vol. XI, which is restricted to a 'Catalogue of the Types and Figured Specimens in the Palæontological Collection of the Geological Department,' and Vols. XV, XVII, and XVIII, which relate wholly to Anthropology.

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Article XXXI.— THE FUNGUS-GROWING ANTS OF NORTH AMERICA.

By William Morton Wheeler.

Plates XLIX–LIII.

Introduction.

Among the multitudinous activities of insects, none are more marvellous than the fungus-growing and fungus-eating habits of the Attiine ants. Not only are these habits of interest as a most unusual specialization in diet — for all ants were originally and many are still exclusively entomophagous — but the successful cultivation of such delicate plants as fungi presupposes an astonishing range and complexity of adaptation even for these very plastic insects. This statement will be endorsed by those who have tried to obtain pure cultures of fungi either in the hot-house or the laboratory. Besides the selection of proper culture media and the accurate regulation of temperature and moisture, exquisite precautions have to be taken to exclude the germs of alien species. The Attii are able to achieve all this and, what is equally remarkable, at least two other groups of insects, namely, certain Old World termites and the "ambrosia beetles" (Tomicine Scolytidæ) of both hemispheres, have independently developed analogous habits.

The fungus-growing ants all belong to a single Myrmicine tribe, the Attii, and all the species of this tribe are fungus-growers. They are, moreover, confined almost exclusively to tropical and subtropical America, only a single species being known to range as far north as New Jersey. And since a few others occur as far south as Argentina, we may say that the geographical distribution of the tribe extends from 40° north to 40° south of the equator. About one hundred species, subspecies and varieties of Attii have been described and have been distributed among various genera and subgenera, as follows:

Genus *Atta* Fabricius.

Subgenus *Atta* sensu stricto, including: *A. cephalotes* L. with the vars. *lutea* Forel, *opaca* Forel, *polita* Emery and *integrior* Forel; *sexdens* L., with the subsp. *vollenweideri* Forel; *lævigata* F. Smith; *columbica* Guérin; *insularis* Guérin; *fervens* Drury; *texana* Buckley.

Subgenus *Mœllerius* Forel, including: *M. heyeri* Forel; *striata* Roger;

silvestrii Emery; *balzani* Emery; *landolti* Forel; *versicolor* Pergande with the subsp. *chisosensis* Wheeler.

Subgenus *Acromyrmex* Mayr, including: *A. subterranea* Forel; *lobicornis* Emery and its var. *ferruginea* Emery; *lundi* Guérin; *ambigua* Emery; *pubescens* Emery with the subsp. *bonariensis* Emery and *decolor* Emery; *emilii* Forel; *octospinosa* Reich with the var. *echinatior* Forel; *mœlleri* Forel with the vars. *panamensis* Forel and *meinerti* Forel, and the subsp. *modesta* Forel with the var. *andicola* Forel; *coronata* Forel; *mesonotalis* Emery; *discigera* Mayr; *muticinoda* Forel with the var. *homalops* Emery; *nigra* F. Smith; *aspersa* F. Smith with the var. *rugosa* F. Smith; *laticeps* Emery; *boliviensis* Emery; *iheringi* Emery.

Subgenus *Trachymyrmex* Forel, including: *T. urichi* Forel with the subsp. *fusca* Emery; *pruinosa* Emery; *septentrionalis* McCook with the var. *obscurior* Wheeler; *turrifex* Wheeler; *arizonensis* Wheeler; *jamaicensis* Ern. André; *saussurei* Forel; *squamulifera* Emery; *farinosa* Emery.

Subgenus *Mycetosoritis* Wheeler, including: *M. hartmanni* Wheeler; *aspera* Mayr.

Subgenus *Mycocepurus* Forel, including: *M. göldii* Forel, *smithi* Forel with the vars. *tolteca* Wheeler and *borinquenensis* Wheeler.

Genus *Cyphomyrmex* Mayr.

C. rimosus Spinola with the subsp. *minutus* Mayr, *salvini* Forel, *dentatus* Forel, *transversus* Emery and *olindanus* Forel, and the vars. *major* Forel, *fusca* Emery and *comalensis* Wheeler; *parallelus* Emery; *olitor* Forel; *auritus* Mayr; *morschi* Emery; *simplex* Emery; *strigatus* Mayr; *wheeleri* Forel; *kirbyi* Mayr; *flavidus* Pergande; *championi* Forel; *foxi* Ern. André; *bigibbosus* Emery.

Genus *Myrmicocrypta* F. Smith.

M. squamosa F. Smith; *dilacerta* Forel with the subsp. *cornuta* Forel; *subnitida* Forel; *godmani* Forel; *brittoni* Wheeler.

Genus *Sericomyrmex* Mayr.

S. opacus Mayr; *aztecus* Forel; *saussurei* Emery.

Genus *Apterostigma* Mayr.

A. pilosum Mayr; *scutellare* Forel; *mœlleri* Forel; *wasmanni* Forel; *urichi* Forel; *mayri* Forel; *collare* Emery; *robustum* Emery.

The various subgenera included under *Atta* sensu lato will probably be raised eventually to generic rank. The subgenus *Atta* comprises the leaf-cutting or parasol ants, the largest and most powerful species of the tribe, living in great colonies and inhabiting the territory between 30° north and 30° south of the equator. The workers are highly polymorphic and much smaller than the males and females. The colonies of the species of *Mœllerius* and *Acromyrmex* are much less populous, and the workers, though variable in size, do not exhibit such marked polymorphism as those of *Atta* s. str. In *Trachymyrmex* and the remaining subgenera the workers are monomorphic and but little smaller than the males and females, and the colonies are even feebler than those of *Acromyrmex*. *Mycetosoritis* and *Mycocepurus* are in certain respects transitional to the genera *Cyphomyrmex* and *Myrmicocrypta,* and species of the last show affinities with *Sericomyrmex*. *Apterostigma* is very aberrant, resembling in form certain Myrmicines of the subgenera *Aphænogaster* and *Ischnomyrmex*. The workers of *Atta* are covered with stiff, erect or suberect, hooked or curved hairs, and the surface of the body is tuberculate or spinose. In *Cyphomyrmex* the body is smoother and covered with short, appressed, scale-like hairs. In *Sericomyrmex* and *Apterostigma* the hairs are soft, flexuous and very abundant. With few exceptions all the Attii have the surface of the body opaque and of a ferruginous, brown or blackish color. All the species, moreover, though very powerful and able to make surprisingly extensive excavations in the soil, are very slow and stolid in their movements. The sting of the workers is vestigial, but in the larger species the sharp jaws may be used as most efficient organs of defence. The smaller species are extremely timid and when roughly handled "feign death" like Curculionid beetles. In all the species the hard, rough or spinose integument must afford efficient protection from alien ants and other enemies.

Owing to the labors of Forel, Emery and Mayr our knowledge of the taxonomy of the Attii is probably as satisfactory as that of any other groups of exotic ants. As much cannot, however, be said of our knowledge of the habits. Since all the Attii live in intimate symbiosis with fungi, a complete study of the habits of these insects requires the diligent coöperation of the entomologist and botanist. Hitherto the botanists, notably Alfred Mœller and Jakob Huber, have contributed the most accurate observations. As neither the botanists nor the entomologists of North America have shown any very serious interest in the Attii, I need not apologize for publishing the following pages. Though these contribute little towards a solution of many of the outstanding problems, they nevertheless contain a number of observations that may be of permanent interest and value. My attention was first attracted to these insects several years ago while I was sojourning in Texas. It was, in fact, the sight of a leaf-bearing file of *Atta texana,* moving along the bank of Barton Creek near Austin, one sultry afternoon in September, that first kindled my interest in the habits of ants. I postponed publishing my notes on this and other species, hoping to have an opportunity to study a greater number of forms in the heart of the tropics, but as there is no immediate prospect of my being able to continue the work in these regions, I have decided to publish my observations as they stand. The present article is divided into four parts, namely, a résumé of the writings of previous students of the Attii, a taxonomic revision of the known North American members of the group, including a few from Mexico and the West Indies, an account of my own observations on these same forms, and a general consideration of some of the main problems involved in the study of the fungus-growing instincts not only in the Attii but also in the termites and ambrosia beetles.

Part I. Historical.

The large leaf-cutting ants of the genus *Atta* s. str. are such conspicuous, widely distributed, and destructive insects in tropical America that they must have been only too familiar to the indigenes and the early settlers in those regions. That these ants figured prominently in the Indian mythologies is indicated by a passage in the Popul Vuh, a collection of Guatemalan traditions to which my friend Mr. F. Bandelier has called my attention.[1] This collection was made by Dominican friars, probably during the middle or latter half of the sixteenth century. The following myth refers to the larger species of *Atta* which are known to collect the petals and whole flowers as well as the leaves of plants. The mythical young men, Hunahpu and Xbalanqué, had been taken in ambush and required by their captors, Hun-Camé and Vukub-Camé to fetch four vases of certain flowers as a test, and to forfeit their lives in case of failure. "Thus they stayed in the House of the Lances during the night, when they called on all the ants: "Cutting ants and zampopos,[2] come and together fetch the flowers designated by the princes."

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[1] Popul Vuh. Livre Sacré et les Mythes de l' Antiquité Americaine avec les Livres Héroiques et Historiques des Quichés, par L' Abbé Brasseur de Bourbour. Paris, Aug. Durand, 1861.

[2] *Zanic* is the generic name of the ant. *Chequen-zanic* is a large ant which goes about at night cutting the stems of vegetables and tender flowers, as if with scissors. Its name among the Hispano-Guatemalan peoples is *zampopo.* (Commentator's note.)

"Very well," they replied. Then all the ants set out to fetch the flowers of the garden of Hun-Camé and Vukub-Camé. These had apprised the guardians of the flowers of Xibalba in advance: "As to you, give heed to our flowers; do not let these two young men, whom we have taken in ambush, carry off any of them. Where else could they go to get those we have designated? There are none elsewhere. Watch closely therefore throughout the night."— "It is well," they replied.

"But the sentinels of the garden heard nothing of what was going on. In vain they went about, walking on their legs, among the branches of the trees of the garden, and repeating the same song. "Xpurpurek, Xpurpurek! sang one.— "Puhuyu, puhuyu!" repeated the other.

"Puhuyu was the name of the two sentinels of the plantations of Hun-Camé and Vukub-Camé. But they did not notice the ants stealing away what had been committed to their charge, going and coming in innumerable hordes, cutting down the flower beds, moving along with the flowers which they bore away in their jaws above the trees, while under the trees the flowers exhaled a sweet odor.

"Meanwhile the sentinels kept shouting with all their might, without noticing the teeth that were sawing at their tails and wings.[1] There was a harvest of flowers mown down by their jaws and borne all odoriferous by their jaws into the House of the Lances.

"Very soon the four vases were filled with flowers, and they were quite full when the day dawned. Soon thereafter the messengers came to seek them. "Let them come," said the King, "and let them bring forthwith what we have demanded," said they to the young men.

"Very well," said they. Thereupon they proceeded to fetch the four vases of flowers. Then, having presented themselves before the king and the princes, these took the flowers whose sight it was a pleasure (to behold). Thus were those of Xibalba tricked.

"It was the ants alone who had been dispatched by the young men, and who in a single night had carried away all the flowers and placed them in the vases. At this sight all the (princes) of Xibalba changed color and their faces paled on account of the flowers.

"Then they sent the men to seek the guardians of the flowers: "Why did you permit our flowers to be stolen. Are these not our own flowers which we here behold?" said they to the guardians.— "We did not notice anything, my lord. They did not even spare our tails," they replied. Then they split the lips of the guardians, to punish them for having permitted the theft of that which was committed to their charge.

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[1] The commentator states that he is unable to understand this allusion. The guardians are evidently conceived as birds, as shown by the above reference to their "walking on their legs," although this is not clearly stated till the end of the passage.

"It was in this manner that Hun-Camé and Vukub-Camé were vanquished by Hunahpu and Xbalanqué, and this was the beginning of their labors. Thenceforth, too, the Purpueks had their mouths cleft, and cleft they are to this day." [1]

I am also indebted to Mr. Bandelier for the following extracts from the early historians of the Conquest. Gonzalo Fernandez de Oviedo y Valdes in his 'Historia de las Indias' (1535) gives an account of the pernicious ants and termites of Española (Santo Domingo). Among the former are certain species "which do very great damage throughout the island, in the plantations, destroying and burning up the cane and oranges and other useful plants." These ants must have been the large species of *Atta*, probably *A. insularis*, which does great damage to plantations also in the adjacent island of Cuba.

P. Bernabè Cobo, in his 'Historia de Neuvo Mundo' (1653) also describes a number of noxious ants in Santo Domingo. He says: "There is another kind of large ants which the Chiriquan Indians call Iczau, and it is these which eat the trees and whose young, when newly hatched, are called Icza, and are eaten by the Indians." These Iczau are evidently the virgin females of *Atta*. They are also eaten by the Brazilian Indians who call them Iças, according to von Ihering (1894). Cobo seems to be the first author to record the use of the heads of *Atta* soldiers by the Indians for surgical purposes: "They use a certain species of the said ants, because they bite severely, for closing wounds instead of stitching them with a needle. This is done in the following manner: they bring together the skin of the two sides of the wound and apply these ants, which bite and hold the two sides or lips together and then they cut off the insects' heads, which remain attached to the wound with their mouths or mandibles as firmly closed as they were in life."

Specimens of the large *Attæ* were, of course, taken to Europe by the early travelers. Seba (1734–35) gives a good figure of a soldier of *A. cephalotes* or *sexdens* which found its way into his collection. Linné described both of these species, and they were also known to Fabricius and Latreille. The latter authors, apparently misled by the accounts of Mlle. Merian (1771), confounded the habits of these ants with those of the "fourmis de visites," or *Ecitons*.

The first naturalist to publish observations on any of the North American Attii was Buckley (1860), who studied the habits of *Atta texana* at Austin, Texas. He was evidently under the impression that this ant eats the leaves, berries, etc., which it carries into its nests. He unearthed some of the

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[1] Here the guardians pass into the domain of fable; they become night birds, the one called Purpuek, the other Puhuy, which is a species of owl; at the present time the former is pronounced Parpuek. (Commentator's note.)

nests and describes the "soft grey spongy substance, apparently leaves, finely triturated and mixed with an animal secretion," found in the chambers. This "animal secretion" was undoubtedly the web of fungus hyphæ which binds the leaf particles together.

Bates (1863) in his classical 'Naturalist on the Amazon' gives an excellent account of *Atta cephalotes*, one of the ants called "Saubas" by the Brazilians. He described the extensive earthworks of this species, "large mounds of earth of a different color from the surrounding soil, which were thrown up in the plantations and woods. Some of these were very extensive, being forty yards in circumference, but not more than two feet in height..... The difference in color from the superficial soil of the vicinity is owing to their being formed of the subsoil, brought up from a considerable depth." He describes the manner in which the ants cut out pieces of leaves and the ensuing damage to cultivated trees and shrubs, and believes that "the leaves are used to thatch the domes which cover the entrances to their subterranean dwellings, thereby protecting from the deluging rains the young broods in the nests beneath." This erroneous inference was derived from seeing the workers "troop up" and cast their pieces of leaves on the hillocks of the nest where some of them are often covered by the earth brought up by the excavating workers. Bates also records the following observation to show the extent of the subterranean burrows of the Sauba: "The Rev. Hamlet Clark has related that the Saüba of Rio de Janeiro, a species closely allied to ours, has excavated a tunnel under the bed of the river Parahyba, at a place where it is as broad as the Thames at London Bridge. At the Magaory rice mills, near Para, these ants once pierced the embankment of a large reservoir: the great body of water which it contained escaped before the damage could be repaired. In the Botanic Gardens at Para, an enterprising French gardener tried all he could think of to extirpate the saüba. With this object he made fires over some of the main entrances to their colonies and blew the fumes of sulphur down the galleries by means of bellows. I saw the smoke issue from a great number of outlets, one of which was 70 yards distant from the place where the bellows were used." This ant not only does great damage to the foliage but also plunders stores of vegetable provisions such as farina or mandioca meal in houses at night. Bates observed the division of labor among the castes although he did not accurately define the soldier, or worker major. From the fact that the latter are often seen to be simply stalking about, he concluded that their "enormously large, hard and indestructible heads may be of use in protecting them against the attacks of insectivorous animals. They would be, in this view, a kind of 'pièces de resistance,' serving as a foil against onslaughts made on the main body of workers." Had Bates undertaken to excavate a large colony of these ants he would soon have discovered that these soldiers have a very important function to perform in the active defence of their fellow ants.

Lincecum in 1867 recorded a number of observations on *Atta texana* which, like his other publications on ants, are a strange jumble of truth and fiction. He states rather positively that this ant eats the vegetable substances which it collects. "In my observations on the habits of the cutting ants, I have not discovered them eating anything besides the foliage of various plants. Neither have I ever noticed them carrying anything else into their cities. Professor S. B. Buckley, who is a very close and accurate observer [sic!] states that he saw them carrying hackberries (*Celtis occidentalis*) and that they eat insects, tumble bugs, etc.... From the immense quantities of leaves collected by them during the autumnal months, which are carefully sun-dried and taken into the city, I should feel at a loss to say, if they are not intended for winter food, what other use they can put such quantities of leaves to; and furthermore, when it is known to be the kind of food upon which they subsist." It is interesting to note that while Lincecum overlooked the marvellous fungus-raising habits of *Atta texana* he nevertheless attributed to them certain horticultural interests: "The cutting-ants plant seeds of various trees, vines and other plants. When they locate a city in a bald prairie, which is often the case, where they cannot procure the seeds of trees, they cultivate the prickly poppy (*Argemone Mexicana*) the most appropriate plant for their purpose that grows in the prairie.... When the ants locate a city on some sunny point near the timbered lands, they do not plant the poppy, but appear to prefer certain trees and vines for shade. For this purpose they plant the seeds of the prairie dogwood (*Viburnum dentatum*), Yopon (*Ilex vomitoria*), Hackberry tree (*Celtis occidentalis*), Gum elastic tree (*Bumelia lycioides*), the mustang grape (*Vitis Texana*), *Cocculus Carolina* and occasionally the prickly ash (*Xanthoxylum fraxinum*)." While there can be little doubt that various herbs, shrubs, or even trees may spring up from the seeds collected and dropped by the ants on the soil of their nests, it is absurd to say that such seeds are actually planted with an awareness that they will ultimately grow and produce shade. Lincecum here repeats the error which he promulgated in regard to the harvesting ants of Texas (*Pogonomyrmex molefaciens*).

Norton (1868) gave a good general description of the Mexican *Atta fervens*, but made no observations on its fungus gardens.

In 1870 B. R. Townsend studied *A. texana* at Austin, Texas. Concerning the leaves collected by this ant he says: "These leaves are conveyed through these underground passages to their homes and deposited in one of their chambers, and, I presume, they secrete some substance that they put with the leaves, for if a handful of the leaves is taken in the hand and squeezed, a ball is made very much resembling coarse bees wax, and when dried is as hard as dry putty. I judge the leaves by their decay produce a gentle heat, or, at least, maintain a uniform temperature whereby the eggs are hatched. Formerly it was suggested that these leaves constituted a store of food, but such is not the case. Whether they feed upon vegetable or animal food I cannot say."

A new epoch in the study of the fungus growing ants was inaugurated by Belt in 1874 in his interesting volume, 'The Naturalist in Nicaragua.' He was the first to surmise the use to which the leaves, etc., are put by the species which he studied (probably *A. cephalotes*). As his work has become rather rare, I quote the pertinent passages in full: "Notwithstanding that these ants are so common throughout tropical America, and have excited the attention of nearly every traveller, there still remains much doubt as to the use to which the leaves are put. Some Naturalists have supposed that they use them directly as food; others, that they roof their underground nests with them. I believe the real use they make of them is as a manure, on which grows a minute species of fungus, on which they feed; — that they are, in reality, mushroom growers and eaters. This explanation is so extraordinary and unexpected, that I may be permitted to enter somewhat at length on the facts that led me to adopt it. When I first began my warfare against the ants that attacked my garden, I dug down deeply into some of their nests. In our mining operations we also, on two occasions, carried our excavations from below up through very large formicariums so that all their underground workings were exposed to observation. I found their nests below to consist of numerous rounded chambers, about as large as a man's head, connected together by tunnelled passages leading from one chamber to another. Notwithstanding that many columns of the ants were continually carrying in the cut leaves, I could never find any quantity of these in the burrows, and it was evident that they were used up in some way immediately they were brought in. The chambers were always about three parts filled with a speckled, brown, flocculent, spongy-looking mass of a light and loosely connected substance. Throughout these masses were numerous ants belonging to the smallest division of the workers, which do not engage in leaf-carrying. Along with them were pupæ and larvæ, not gathered together, but dispersed, apparently irregularly, throughout the flocculent mass. This mass, which I have called the ant-food, proved, on examination to be composed of minutely subdivided pieces of leaves, withered to a brown color, and overgrown and lightly connected together by a minute white fungus that ramified in every direction throughout it. I not only found this fungus in every chamber I opened, but also in the chambers of the nest of a distinct species that generally comes out only in the night-time, often entering houses and carrying off various farinaceous substances, and does not make mounds above its nests, but long winding passages, terminating in chambers similar to the common species and always, like them, three parts filled with flocculent masses of fungus-covered vegetable matter, amongst which are the ant-nurses and immature ants. When a nest is disturbed, and the masses of ant-food spread about, the ants are in great concern to carry away every morsel of it under shelter again; and sometimes, when I dug into a nest, I found the next day all the earth thrown out filled with little pits that the ants had dug into it to get out the covered up food. When they migrate from one part to another, they also carry with them all the ant-food from their old habitations. That they do not eat the leaves themselves I convinced myself, for I found near the tenanted chambers, deserted ones filled with the refuse particles of leaves that had been exhausted as manure for the fungus, and were now left, and served as food for larvæ of *Staphylinidæ* and other beetles.

"These ants do not confine themselves to leaves, but also carry off any vegetable substance that they find suitable for growing fungus on. They are very partial to the inside white rind of oranges, and I have also seen them cutting up and carrying off the flowers of certain shrubs, the leaves of which they have neglected. They are very particular about the ventilation of their underground chambers, and have numerous holes leading up to the surface from them. These they open out or close up, apparently to keep up a regular degree of temperature below. The great care they take that the pieces of leaves they carry into the nest should be neither too dry nor too damp, is also consistent with the idea that the object is the growth of a fungus that requires particular conditions of temperature and moisture to ensure its vigorous growth. If a sudden shower should come on, the ants do not carry the wet pieces into the burrows, but throw them down near the entrances. Should the weather clear up again, these pieces are picked up when nearly dried, and taken inside; should the rain, however, continue, they get sodden down into the ground, and are left there. On the contrary, in dry and hot weather, when the leaves would get dried up before they could be conveyed to the nest, the ants, when in exposed situations, do not go out at all during the hot hours, but bring in their leafy burdens in the cool of the day and during the night. As soon as the pieces of leaves are carried in they must be cut up by the small class of workers into little pieces. I have never seen the smallest class of ants carrying in leaves; their duties appear to be inside, cutting them into smaller fragments, and nursing the immature ants. I have, however, seen them running out along the paths with the others; but instead of helping to carry in the burdens, they climb on the top of the pieces which are being carried along by the middle-sized workers, and so get a ride home again. It is very probable that they take a run out merely for air and exercise. The largest class of what are called workers are, I believe, the directors and protectors of the others. They are never seen out of the nest, excepting on particular occasions, such as the migration of the ants, and when one of the working columns or nests is attacked; they then come stalking up, and attack the enemy with their strong jaws. Sometimes, when digging into the burrows, one of these giants has unperceived climbed up my dress, and the first intimation of his presence has been the burying of his jaws in my neck, from which he would not fail to draw the blood."

During his study of *Atta* in the province of Rio Grande de Sul, Brazil, Fritz Müller appears to have reached independently the same conclusion as Belt. A letter directed to Charles Darwin and published in 'Nature' during 1874 contains the following remarks: "As to the leaf-cutting ants I have always held the same view which is proposed by Mr. Belt, viz. that they feed upon the fungus growing on the leaves they carry into their nests, though I had not yet examined their stomachs. Now I find that the contents of the stomach are colorless showing under the microscope some minute globules, probably the spores of the fungus. I could find no trace of the vegetable tissue which might have been derived from the leaves they gather; and this I think, confirms Mr. Belt's hypothesis."

Although observations on the habits of the Attii continued to be published from time to time the suggestions of Belt and Müller were either overlooked or ignored for nearly twenty years. In his studies on *Atta texana*, which, like those of Buckley, Lincecum and Townsend, were carried on at Austin, Texas, McCook (1879*a*, 1879*b*, etc.) accurately described the formicaries and fungus gardens. He found the nests to consist of several chambers or pockets, sometimes as much as 2 ft. 10 inches long, 12 inches broad and 8 inches high. The fungus gardens within these chambers are correctly described as "masses of a very light, delicate leaf-paper wrought into what may be properly called 'combs.' Some of the masses were in a single hemisphere, filling the central part of the cave, others were arranged in columnar masses 2½ inches high, in contact along the floor. Some of these columns hung, like rude honeycomb or wasp nests from roots which interlaced the chambers. The material was in some cases of a gray tint, in others of a leaf-brown. It was all evidently composed of the fibre of leaves which had been reduced to this form within the nest, probably the joint action of the mandibles and salivary glands. On examination they proved to be composed of cells of various sizes, irregular in shape, but maintaining pretty constantly the hexagon. Some of the cells were one-half inch in diameter, many one-fourth inch, most of them one-eighth inch, and quite minute.

Large circular openings ran into the heart of the mass. Some of the cells were one inch deep; they usually narrowed into a funnel-like cylinder. Ants in great numbers, chiefly of the small castes, were found within these cells. In the first large cave opened were also great numbers of larvæ. The material was so fragile that it crumbled under even delicate handling, but a few specimens of parts of the ant's comb, with entire cells, were preserved and exhibited." Although McCook knew of Belt's opinion that these masses of triturated leaves serve merely as a culture medium for the growth of edible fungi, and even saw the film of hyphæ, he nevertheless preferred to interpret the latter as "only what might have been expected under such environment," and expressed the belief "that the ants feed upon the juices of leaves." He fully appreciated the extraordinary excavating powers of *A. texana.* "The ability of these emmet masons to excavate vast halls and subterranean avenues is remarkable. Several holes in the vicinity of Austin were visited, out of which 'beds' or nests of ants had been dug by an old man who used to follow the business of ant killing. These holes were nearly as large as the cellar for a small house. One such excavation, about three miles from Austin, was 12 feet in diameter and 15 feet deep. At the lowest point had been found the main cavity, quite as large as a flour barrel, in which were found many winged insects, males and females, and quantities of larvæ. This nest was situated 669 feet from a tree that stood in the front yard of a house which the ants had stripped." McCook examined and reconstructed the tunnel excavated by the ants in order to reach this point and found that although its course varied from 18 inches to 6 feet below the surface it deviated little from a direct line and gave off a couple of branch tunnels to a peach orchard 120 feet distant.

In 1880 Morris studied the habits of a small Attiine ant (*Trachymyrmex septentrionalis*) which he had discovered near the village of Tom's River on Barnegat Bay, New Jersey. During December of the same year McCook communicated this discovery to the Philadelphia Academy of Sciences and during the following year (1881) Morris published his own observations in the 'American Naturalist.' Both authors regarded the fungus-gardens as subterranean "combs" adapted for incubating the brood. Morris saw the ants carry in and incorporate into their fungus gardens the leaves of seedling pines, the flowers of cow wheat (*Melampyrum americanum*) and "the droppings of certain larvæ that feed on oak-leaves." The nest is described by both authors and figured by McCook as consisting of two spherical chambers, one above the other and connected by a short gallery. The entrance was oblique and about 2 inches in length. The upper chamber was 1½ inches in diameter, the lower 3 inches. The former was empty, the latter contained the "combs" suspended from rootlets that had been left intact while the ants were excavating the chamber. Morris's description of these "combs" is more accurate than McCook's.

Brent in 1886 described the nesting habits, etc., of the large *Atta cephalotes* of Trinidad: "A good sized mango tree, at least as large as an average apple tree, I saw stripped of every leaf in one night, and greater feats than this are recorded of these 'Fourmi Ciseaux,' as they are called by the Creoles." Brent gives a diagram of the nest and describes a tunnel leading from the lowermost fungus-chamber to a still lower level. He "invariably found this lower tunnel wherever the inclination permitted its construction" and has "no doubt that it is constructed as a drain, and that the ants know as much about the advantage of thorough drainage as they have been proved to know, by many eminent observers, of those of other sanitary matters." Some of the chambers of the nest are described as 3 feet in diameter. He mentions Amphisbænians as living in the nest and eating the ants. In regard to the use to which the leaves are put, Brent says: "A solution of arseniate of soda was next sprinkled upon orange leaves, which were strewn upon the mound. These were eventually cleared away, although at an immense sacrifice of life. This points, I think, to the true ant food, since unless the juices of the leaves as they were sawed up were swallowed, the poison would have no effect. This idea is strengthened by the fact that fiery and strongly aromatic plants as well as those with poisonous, milky juices are carefully avoided. No solid food is found in the crops of the insect at any time, but if these are examined after the insects have been engaged in leaf-cutting, they are found full of green leaf juice." Later he says: "The larvæ are embedded in a soft woolly matter which proved to be the finely masticated parenchyma of the leaves. Thus a use was found for the leaves, although it reflects seriously upon the supposed sagacity of the ants that they should procure so many more than are required for the purpose."

Emery (1890) appended a brief ethological note to his description of *Acromyrmex landolti* of Caracas, Venezuela. Simon wrote him that "this ant makes extensive formicaries with several entrances, each surmounted by a column or chimney of straws 10–15 cm. high, in which lives a large spider of the genus *Ctenus.* Simon never saw the ants carry in pieces of leaves like *Atta sexdens* and believes that they confine themselves to collecting pieces of dried grasses."

Observations on *A. cephalotes* in Trinidad were resumed in 1892 by Tanner in two important papers, which, owing to their publication in an obscure serial, have been overlooked by subsequent students. He was the first to study Attii in artificial nests and to prove that not only the adult ants but also the larvæ feed on fungus hyphæ. In his first paper (1892*a*) he describes the manner in which the workers triturate the leaves: "Each forager drops the portion of the leaf in the nest, which is taken up as required by the small workers, and carried to a clear space in the nest to be cleaned. This is done with their mandibles, and if considered too large it is cut into smaller pieces. It is then taken in hand by the large workers, who lick it with their tongues. Then comes the most important part, which almost always is done by the larger workers, who manipulate it between their mandibles, mostly standing on three legs. The portion of the leaf is turned round and round between the mandibles, the ant using her palpi, tongue, her three legs and her antennæ while doing so. It now becomes a small almost black ball, varying in size from a mustard seed to the finest dust shot, according to the size of the piece of the leaf that has been manipulated. The size of the piece of the leaf is from $\frac{1}{8}$ by $\frac{1}{8}$ of an inch, to $\frac{1}{4}$ by $\frac{1}{4}$ of an inch. I do not wish it to be understood that only one class of workers manipulate the leaf, for all seem to take to it very kindly on emergency. Even the smallest workers will bring their tiny ball to where the fungus bed is being prepared. These balls, really pulp, are built on to an edge of the fungus bed by the larger workers, and are slightly smoothed down as the work proceeds. The new surface is then planted by the smaller workers, by slips of the fungus brought from the older parts of the nest. Each plant is planted separately and they know exactly how far apart the plants should be. It sometimes looks as if the plants had been put in too scantily in places, yet in about 40 hours if the humidity has been properly regulated, it is all evenly covered with a mantle as of very fine snow. It is the fungus they eat, and with small portions of it the workers feed the larvæ."

In his second paper, published the same year (December, 1892), Tanner describes the eggs and larvæ of *A. cephalotes* and the method of feeding the latter, together with certain observations which go to show that workers lay eggs capable of developing into other workers or even queens. The eggs become enveloped in a "pearly white fluffy growth." The larvæ which hatch from these eggs "are usually placed on the top of the nest and are constantly attended by the smallest workers — the nurses — who separate them into divisions according to their size. At first it seemed a mystery, how these minute grubs could be fed so systematically, knowing that each individual larva was only one among so many, yet certain it was, that all were equally attended to. Further observations showed that nature had provided most efficiently for them to ask for food when they required it. This the larvæ do by pouting their lips; at this notification of their requirement the first nurse who happens to be passing stops and feeds them. The nurses are continually moving about among them with pieces of fungus in their mouths ready for a call for food. The nurses feed the minute larvæ by merely brushing the fungus across their lips showing that the spores alone are sufficient for its food at that period of its life. But it is not so when the larvæ have increased so much in size, that the pout can be seen without a glass, for then the whole piece after having been manipulated by the nurse's mandibles into a ball, in the same manner as the leaves are served, when they are first brought into the nest, is placed in its throat and if that is not sufficient the pout continues when the next one and even the next passing proceeds with the feeding, till the pout is withdrawn, showing that it is satisfied. No further notice is then taken of it by the feeders, until it agains asks for a meal by pouting later on in the day."

In 1893 a nephew of the celebrated Fritz Müller, Alfred Mœller, who was given a grant of 5,000 marks by the Berlin Academy of Sciences for the purpose of studying the habits of the Attii at Blumenau in the province of Rio Grande do Sul, published the most important of existing works on these insects and their relations to the fungi which they cultivate. He studied several species of *Atta* belonging to the subgenus *Acromyrmex* (*discigera, coronata, octospinosa, mœlleri*) and of the genera *Apterostigma* (*pilosum, mœlleri, wasmanni,* and an undetermined species) and *Cyphomyrmex* (*auritus, strigatus*). *A. octospinosa* and *discigera,* which nest in the woods, form truncated cones of dead leaves and twigs, beneath which they excavate a single chamber containing a large fungus garden sometimes 1½ meters long. *A. mœlleri* has similar habits, but *coronata* resembles the species of the subgenus *Atta* s. str. in forming several chambers, each with its own fungus garden. In all of these species the garden is built up on the floor of the chamber in the form of a loose sponge-work of triturated leaf-fragments permeated with fungus hyphæ which he describes as follows: "Over all portions of the surface of the garden are seen round, white corpuscles about ¼ mm. in diameter on an average, although some of them are fully ½ mm. and sometimes adjacent corpuscles fuse to form masses 1 mm. across and of irregular form. After a little experience one learns to detect these corpuscles with the naked eye as pale, white points which are everywhere abundant in all the nests. Under the lens they sometimes have a glistening appearance like drops of water. They are absent from the youngest, most recently established portions of the garden, but elsewhere uniformly distributed, so that it is impossible to remove with the fingers a particle too small to contain some of the white bodies. I call these the 'kohlrabi clusters' of the ants' nests. They constitute the principal, if not the only food of the species of *Atta.*" These clusters are made up of the "heads of Kohlrabi," which are small terminal dilatations of the hyphæ of a spherical or oval form. Mœller confirmed Belt's observations on the solicitude of the ants for their gardens, and showed that these insects in artificial nests will completely rebuild these structures within 12 hours after they have been disintegrated or scattered. He also saw the ants eating the fungus and was able to satisfy himself that the different species of *Atta* will eat the Kohlrabi from one another's colonies but not that of *Apterostigma* or *Cyphomyrmex.* He gives the following interesting description of the way in which the leaves are comminuted by the workers. "The manipulation of the pieces of leaves is the same in all the *Atta* species and the following description holds good uniformly for all of them. The ant first cuts the leaf it has brought in through the middle and then busies itself with only one of the halves, cutting off another piece, and so on. When the piece of leaf which it has retained is sufficiently small so that it can be turned round and round between its fore-feet with the aid of its jaws, it is felt of on all sides and turned in all directions as if the insect wished to get a clear idea of its form. Then an even smaller piece is cut off and this is repeated, till the piece that is retained is hardly longer than the ant's head. The rejected pieces are picked up by other workers and treated in the same manner. Then the ant holds the little piece between its fore-feet with the sharp edge directed towards its mouth and begins to pinch its edges at short intervals around the circumference without ever cutting through the substance. The piece thus manipulated shows fine, radial ridges under a good lens. The surface of the leaf is also abraded with the points of the mandibles, wounded, so to speak, so that it soon becomes soft. Then the ant kneads it with the feet and again inserts her jaws into the pellet thus formed in order to mould it thoroughly. Again and again the jaws close upon the pellet while the feet press it and place it in a new position, and again it is kneaded. This manipulation is carried on with great care and deliberation, and I have several times observed that an ant will spend a quarter of an hour in making such a pellet. When it has become a soft mass, the worker takes it in her jaws and seeks a suitable spot for it in the portion of the garden that is just being built. Once I saw an ant that had found such a spot, actually jab the pellet into the garden with a jerk of her head and a simultaneous opening of her jaws, and then carefully pat it down with her fore-feet. Another time a worker laid her pellet in a breach of a newly erected circular wall, and then shook and pushed it into the depression, like a mason setting the last brick in a fresh layer of mortar. During all of this work, the antennæ are continually moving and palpating the pellet just as they are while the ant is feeding." Into the new material thus added to the garden the fungus hyphæ grow very rapidly. By afternoon pellets built in during the morning hours have become permeated in all directions with mycelium. Belt supposed that the smallest workers or minims comminute the leaves and build up the fungus gardens. According to Mœller, however, this is the office of the mediæ, as the leaves are too thick to be manipulated by the smallest workers. The latter have another function, namely that of weeding the garden and keeping down the growth of spores belonging to alien fungi. Mœller emphasizes the remarkable fact that the gardens are pure cultures although the hairy, rough-bodied workers must be continually bringing into the nest all sorts of spores and bacteria. It is probable also, that the minims are instrumental in producing the "kohlrabi heads" as these are not developed when the mycelium is grown in artificial culture media apart from the influence of the ants. He summarizes the results of this portion of his studies in the following words: "All the fungus-gardens of the *Atta* species I have investigated, are pervaded with the same kind of mycelium, which produces the 'kohlrabi clusters' as long as the ants are cultivating the gardens. Under the influence of the ants neither free aërial hyphæ nor any form of fruit are ever developed. The mycelium proliferates through the garden to the complete exclusion of any alien fungus, and the fungus garden of a nest represents in its entirety a pure culture of a single fungus. The fungus has two different forms of conidia which arise in the garden when it is removed from the influence of the ants. The hyphæ have a very pronounced tendency to produce swellings or diverticula, which show several more or less peculiar and clearly differentiated variations. One of these which has presumably reached its present form through the influence of cultivation and selection on the part of the ants, is represented by the 'kohlrabi heads'."

A number of experiments were undertaken by Mœller for the purpose of ascertaining the behavior of the fungus in the absence of the ants. Under these conditions he found that the mycelium produces aërial hyphæ, the "kohlrabi clusters" and "heads" disappear and soon the fungus breaks up into masses of bead-like conidia. "As long as the ants are active in their garden, there is never either in it or in its immediate vicinity the slightest trace of an alien fungus, and, under these circumstances, the mycelium pervading the garden never produces aërial hyphæ or conidia." If, however, a few of the ants happen to be left in the garden, the development of aërial hyphæ is retarded, and though Mœller did not observe the process directly, he is certain that these hyphæ must be bitten off by the ants as soon as they make their appearance. "A relatively very small number of workers suffices to restrain the growth of the aërial hyphæ. But if the number is too small, the aërial filaments begin to appear sporadically. The ants are unable to move about in the dense growth of sprouting filaments and have to beat a retreat before the rapidly rising hyphal forest. This, however, as soon as it has acquired a little headway, proliferates mightily, and it is an amazing sight to behold the poor insects, tirelessly active till the last moment, fleeing before their own food-plant. If some of the larvæ and pupæ are still present, they are rescued. The last resort is the vertical wall of the glass, up which the insects creep and where they huddle together, while over the wide plain of the garden the fungus proceeds to the conidia-producing stage."

Mœller next undertook to determine the systematic position of the fungus. He naturally supposed that the discovery of the fruiting form would show it to be an asco- or basidiomycete. Although he failed to raise either of these forms from his mycelial cultures he succeeded on four occasions in finding an undescribed agaricine mushroom with wine-red stem and pileus growing on extinct or abandoned *Acromyrmex* nests. From the basidiospores of this plant which he called *Rozites gongylophora,* he succeeded in raising a mycelium resembling in all respects that of the ant gardens. Three of the species of *Acromyrmex* did not hesitate to eat portions both of this mycelium and of the pileus and stem of the *Rozites.* He believed therefore that he had definitively established the specific identity of the fungus cultivated by the ants.

The species of *Apterostigma* investigated by Mœller usually nest in cavities in rotten wood which is often also inhabited by other insects. The fine wood castings and excrement of these insects are used by the ants as material with which to construct their fungus-gardens. *A. wasmanni* constructs the largest nests, and it is only in the gardens of this species that the mycelium produces structures analogous to the "kohlrabi heads" and "clusters" of *Acromyrmex.* The heads, however, are club-shaped instead of spherical dilatations of the hyphæ. As it produces only irregular swellings on the hyphæ Mœller believes that *Apterostigma* represents a much lower stage in fungus-culture than the species of *Acromyrmex.* The *Apterostigma* are, however, very adaptable since they readily collect caterpillar excrement or even farina and incorporate these substances into their gardens. Mœller states that all the species of this genus cultivate the same fungus, which must be a distinct species as the ants will not eat the fungus grown by *Acromyrmex.* The gardens of *pilosum, mœlleri* and another undetermined *Apterostigma,* which live in small colonies of only 12 to 20 individuals, are suspended from the roofs of the small cavities, 3 to 4 cm. in diameter, in the rotten wood and exhibit a peculiar structure not seen in other *Attii.* "The garden is often completely, or at least nearly always in great part, enclosed in a white cob-web-like membrane. It was often possible to obtain a view of uninjured nests of *A. pilosum* that had been excavated in clefts of the rotten wood. In such cases the envelope enclosed the whole fungus garden like a bag with only a single orifice or entrance. The envelope is attached in a pendent position to the surrounding wood, roots or particles of earth by means of radiating fibres, and this explains why the gardens are so easily torn asunder while the nest is being uncovered." Even in captivity these ants persisted in hanging their gardens to the sides of the glass dishes in which they were kept. "Microscopical examination shows that the envelope consists of the same, loop-like hyphæ as the remainder of the garden. Such a structure cannot be produced by the fungus except under extraneous influences. We must assume that the ants bring about the development of the envelope, that they direct or coërce the growth of individual hyphæ with their antennæ or fore legs, spread them out into a layer and bite off the recalcitrant hyphæ that grow out from the surface." Mœller succeeded in cultivating the mycelium of the *Apterostigma* gardens in artificial media, but he failed to obtain the fruiting stage. He believes, however, that the fungus is a basidiomycete.

The two species of *Cyphomyrmex* observed by Mœller were found nesting under bark or in rotten wood like *Apterostigma.* The largest gardens of *C. strigatus* are only 8 cm. long, whereas those of *C. auritus* may attain a length of 15 cm. and a breadth and height of 5 cm. These gardens are never pendent and never enclosed in a mycelial envelope. In other respects they resemble those of *Apterostigma* and are grown on the same substrata. The heads are developed as long, irregular swellings in the hyphæ and therefore represent a more primitive and imperfect stage than those of *Acromyrmex.* Although he was unable to obtain the fruiting stage, Mœller nevertheless believed that the fungus of the species of *Cyphomyrmex* is different from that cultivated by the ants of other genera. He concludes his paper with a few interesting notes on the breeding habits of the Attii. The eggs of *Acromyrmex* are laid in masses and embedded in loosely woven hyphæ which enable the ants to carry them about in packets. The pupæ, too, are often enclosed in hyphæ, but this is not the case with the larvæ which are kept clean and shining.

In 1894 von Ihering, in an interesting paper on the ants of Rio Grande do Sul, records a number of observations on Attii (*Atta sexdens, Mœllerius striatus, Acromyrmex lundi, niger* and *Cyphomyrmex morschi*). His general account of the nests of *A. sexdens* agrees with that of preceding authors who have studied the large *Attæ* s. str., and comprises also an interesting observation quoted from a former paper (1882) on the importance of these insects in reversing the position of earth strata: "A piece of pasture land had been marked off by a recently excavated ditch several feet deep. The soil in this place, as generally in the surrounding country, consisted of sand. Beneath this in many portions of the region there was a stratum of heavy red clay at a depth of four feet or more. What attracted my attention in this ditch was the fact that here the clay lay uppermost in a layer about 1 dcm. thick. The explanation of this condition was not the result of geological but of zoölogical investigation, for closer inspection soon showed that the ants are responsible for the inversion of the normal position of the strata. It was the work of *Atta sexdens.* It is very doubtful whether such an enormous task can be accomplished by any insects except the large species of *Atta.*" Von Ihering observed the marriage flight of *A. sexdens* and the digging of the nests by the recently fertilized females, an instinct manifested even by individuals whose gasters have been bitten off by birds. *A. sexdens* extends southward in Brazil only to the Cebus-line (latitude 30°) The nests of *Acromyrmex lundi* are excavated to a depth of 50–60 cm. and consist of a single chamber with a cubic capacity of $\frac{1}{2}$ to 1 litre, in older nests 5 to 10 times as great. This cavity contains a single fungus garden and is connected with the surface by means of a large horizontal or tortuous gallery 1–2 m. long. From the nest-entrance, branching, well-worn roads lead off over the surface often to a distance of 40 m. and further, and it is along these that the ants travel to and from the grasses which they cut down together with their green seeds. This ant carries the exhausted portions of the fungus garden out of the nest and deposits them on a refuse heap. The same is true of *Mollerius striatus.* This species clears the ground of vegetation around its nest entrance which is surmounted by a crater. Like *A. lundi* it collects pieces of grass, flowers, leaves, etc. *A. niger* nests in thickets between the roots, where it excavates its nest at some distance from the entrance. It does not confine its cutting operations largely to grasses like *lundi* and *striatus* but attacks many other plants and is therefore of greater economic importance.

Cyphomyrmex morschi nests in the soil, where it excavates a chamber about the size of an orange and containing a fungus garden of leaf detritus covered with mycelium. The entrance is surmounted by a circular crater.

Von Ihering is one of the few who have considered the question of the origin of the fungus-raising instincts of the Attii. His remarks on this subject will be considered in the concluding portion of this article.

Urich, in two papers published during the same year (1895*a*, 1895*b*) records a number of observations on several of the Attii of Trinidad (*Atta sexdens, A. cephalotes, Acromyrmex octospinosus, Trachymyrmex urichi, Sericomyrmex opacus, Apterostigma urichi, A. mayri* and *Cyphomyrmex rimosus*). His account of the large species of *Atta* adds little of interest to that of previous authors. On two occasions he found the deälated females of *Acromyrmex octospinosus* "working just as hard and engaged in the same occupation as the neuters, viz: cutting leaves and carrying them to the nest. They all issued from the same nest and therefore could not have been mothers of new colonies." He "also noticed that several females lost their wings in the nest without any marital flight, although a few weeks later the winged ones swarmed out in the usual way on a damp evening."

The nest of *Trachymyrmex urichi* is "excavated in clayey soils and never anywhere else. It consists of one chamber at about the depth of a foot and is never directly under the entrance hole, but always on one side at right angles and about 9 inches away from it. It has a habit of carrying the particles of earth which result from its mining operations a little way from the entrance hole, say about a foot, and deposits them in a small conical heap.... These ants also cultivate a fungus and if it is not *Rozites gongylophora* it is very much like it.... Any roots of plants going through the ants' chamber are not cut away, but are made to suspend their mushroom gardens which are in their case regular hanging gardens.... They are nocturnal in habits and when disturbed sham death." They "seem to like small fallen flowers and the fruit of various kinds of plants to be found in gardens, but at the same time they do not despise rose plants, especially the young and tender shoots. They are not at all energetic and are very slow in their movements."

The habits of *Apterostigma urichi* are described as follows: "Unlike *Atta* this species does not excavate its nests but builds them in rotten trunks of trees.... They are built in hanging position, *i. e.*, the ants start working from the top, but never let the nest touch the bottom of the cavity. Unless the garden is quite recent and small it is always enclosed in a delicate white covering, which at first sight looks like fine cobweb, with an exit hole at the bottom. The nests therefore look like a more or less rounded ball and are never larger than an apple. On breaking away this delicate covering a small mushroom garden is found consisting of irregular cells in which the ants, larvæ and pupæ are scattered." The fungus is similar to that described by Mœller for the Brazilian species of *Apterostigma*. "The gardens are always found under rotten wood and the ants invariably use the excrementa of wood-boring insects as a medium for growing their fungus on..... The colonies of these ants are small, not numbering more than 20 or 30 dark brown workers, all of about the same size, viz. 6–6½ mm. and with abnormally long legs which measure 7–7½ mm. without the hip. They are of nocturnal habits." The smaller *A. mayri* constructs similar gardens in dark cavities, not only under rotten wood but also under large stones. It, too, collects the excrement of wood-boring insects, but is also fond of fruits or even parts of flowers. The mycelium has the kohlrabi aggregated into regular clusters and according to Urich represents a more advanced condition than that of *A. urichi.* The ants are nocturnal and sham death for many seconds.

Urich has also given us the only existing account of the habits of a *Sericomyrmex* (*S. opacus*). "The nests of these ants are found commonly about Port of Spain, in gardens, in the grass as a rule, but sometimes in the flower beds, and from their peculiar raised entrance can be readily recognized.

They are always excavated in clayey soil, and the raised entrances, which are more or less cylindrical, are constructed with the particles of earth resulting from their mining operations and are about an inch in height. In young colonies this entrance leads into a small chamber, about six inches below the surface of the ground, situated not at the end of the gallery but either to the left or right of it. As the colony increases the ants do not enlarge this original chamber, but, piercing its side, form another chamber near it with a small entrance hole. In large colonies, which never consist of more than about 200 individuals, a nest consists of two or three chambers which open on the original excavation. This is no longer used for growing the fungus in, but forms a sort of ante-chamber which generally contains material brought in by the ants to grow their mushrooms on, which is deposited here and gradually made use of. The chambers adjoining are more or less round, with a diameter of about 2–3 inches, and any small roots of plants growing through them are not cut away but used by the ants to hang their mushroom gardens on. These fill the interior of the chamber and consist of a gray spongy mass consisting of a great number of little irregular cells and resembling a coarse sponge, amongst which are scattered larvæ, pupæ and ants. The walls of the cells consist of small round pellets resembling dust shot and are penetrated by and enveloped in white fungus hyphæ, which hold the mass together. Strewn thickly upon the surface of the garden are to be seen round white bodies about a quarter of a millimeter in diameter. These are what Mœller terms "Kohlrabi" clumps, and consist of an aggregation of hyphæ with special swellings at their ends. It is on this that the ants feed. The fungus found by Mœller in the nests of the Brazilian fungus growers (*Acromyrmex*) is the *Rozites gongylophora*, Mœller, and if it is not the same species cultivated by *S. opacus* it is, at any rate, very nearly related to it. As material to grow their mushrooms on the ants make use of particles of fruit, flowers, and leaves, but prefer fruit. They do well in artificial nests, constructed on Sir John Lubbock's plan, and are easy to watch. I have tried them with all kinds of vegetable products; they have taken orange, banana, rose petals and leaves and once they even made use of the dried glue from the back of an old book lying near their nest, but that day they had nothing else; if the choice be left to them they invariably take fruit and seem to prefer the orange amongst these. Very small particles of the white skin of the oranges are torn off, and after undergoing a slight kneading process in the ants' mandibles, are planted in the nest. The neuters are all of the same size, varying but slightly and never exceed 4 mm. in length. They are more diurnal in their habits than other species of fungus growers,—but also work a little at night. I have found winged forms in the nests in the month of July."

Urich is responsible for the erroneous statement that *Cyphomyrmex rimosus* "does not cultivate any fungus," a statement which has been repeated by subsequent writers (Forel, Emery).

In 1896 Swingle read a paper on *Trachymyrmex septentrionalis* (= *tardigrada* auct.) before the American Association for the Advancement of Science. He says: "In July of this year I examined some colonies of *Atta tardigrada,* which Mr. Pergande had found in the vicinity of Washington. The nests are small subterranean cavities, 6–10 cm. in diameter, situated from 2 to 15 or 20 cm. below the surface. Some nests have one cavity, others two. Almost the whole cavity is filled with a grayish material loosely and irregularly connected together. By watching the ants, it was determined that they carried into their nests the excrements of some leaf-eating insect, lying on the ground under neighboring oak-trees. The same material was found to constitute at least a large part of the substance filling the nest. Even with a low magnifying lens, tufts of minute sparkling bodies could be seen on the fragments of the fungus garden, while the whole mass was interpenetrated by the white mycelium of a fungus. Examination with higher magnification showed that the glistening tufts were really composed of 'Kohlrabi' even more perfectly spherical than figured by M. Mœller. The mature 'Kohlrabi' were very much larger than the mycelium below, being 22 to 52 μ wide and 30 to 56 μ long, while the supporting mycelial threads were only 4 to 8 μ in diameter. There are no septa dividing the 'Kohlrabis' from the mycelial threads. The whole appearance of the fungus is strikingly similar to that found by Mœller, and it is by no means impossible that it will prove to be the same species though the Kohlrabis are nearly twice as large as what he reports."

Forel (1896*a–c*, 1897, 1899–1900*b*) has recorded a number of observations on the *Attii* of Colombia (*A. sexdens, cephalotes* and *lævigata*; *Acromyrmex octospinosus,* and species of *Trachymyrmex, Sericomyrmex, Mycocepurus,* and *Apterostigma*). He excavated one of the huge nests of *A. sexdens* belonging to an extensive colony at Rio Frio (1896*b*). "This nest looked like an immature volcano and consisted of a mass of 12 to 20 fused craters. The whole nest was 5 or 6 m. in diameter and about 1 m. high. The largest (median) crater was about 60 cm. in diameter, 28 cm. high, and had an opening below of about 3½ cm. The smaller accessory nests in the neighborhood (100 to 200 steps distant) had only 2–3 craters and were much smaller. There are two kinds of craters; one consisting of sand or soil of a gray color and consisting of the excavated earth, the others are brown and consist of the rejected and useless remains of the gardens, *i. e.*, the portions that have been exhausted by the fungi, thrown out in this manner in the form of brown pellets. The medium-sized workers are seen continually coming out of the latter craters laden with brown pellets which they cast aside, while into the gray craters a stream of the same kind of workers is entering in an almost continuous procession laden with green leaves. Some small workers also stand around the openings. On disturbing the nest one is severely attacked by the largest workers. With their sharp jaws, worked by enormous muscles, they can bite so severely as to bring the blood; in fact, a small artery in my little finger was severed by one of these workers. The wounds were as much as 4 mm. in length. Nevertheless Mr. Bradbury, a native and myself attacked the nest with a shovel and dug into it deeply. Thousands of the large workers rushed out at us. The half-naked Indian ran away and I had to retreat from time to time with bleeding hands. But the interior of the nest was laid bare. This consisted of a number of great cavities, 15 to 20 cm. long and 8–12 cm. high and each was nearly always filled with a fungus garden, which looks very much like the single garden of the *Acromyrmex* species. In the labyrinth of this gray to brown garden live thousands of the smallest and medium sized workers, together with the whole ant brood. Colossal female larvæ are there found covered with a regular envelope of larvæ of all sizes, so that they have the appearance of hedge hogs. The workers held fast to the larvæ so tenaciously that I could take them in my hands and even kill them in alcohol without their losing their hold....The large species of *Atta* therefore have not only one but hundreds of fungus gardens. The fungus chambers communicate with one another by means of broad galleries 2–3 cm. in diameter. The lower portion of the garden is uniformly light rust-red with white fungus patches, whereas the upper portions are more gray. The dark brown portions seem to represent the residuum. The fungus garden is so friable that it is impossible to remove it without destroying its form. How the old myth, or nonsense, that these *Atta* species line their nests with leaves could have originated and could even be revamped by McCook is incomprehensible to me....All the pupæ are naked, that is, not enclosed in cocoons. The workers have the habit of carrying their straying sisters exactly like our species of *Formica* (the carried ant is rolled under the head of the carrier)." In another place (1899, 1900*b*) Forel says that *Acromyrmex octospinosus* carries its sister workers in the reverse position, *i. e.*, like *Myrmica*. He also describes (1896*b*) very briefly the nests and distribution of *A. cephalotes* and *lævigata*. The latter also has very large but deeply subterranean nests. It lives more in the mountains at and above an altitude of 1,000 m. and so far down in the ground that Forel could not reach the fungus gardens. *Cephalotes* is intermediate; its nests are nearly as large as those of *sexdens* and the fungus-gardens have a very similar structure and arrangement. The colonies of *cephalotes* and especially of *lævigata*, are less populous than those of *sexdens*. The nests of *cephalotes* occur from sea-level to an altitude of more than 1,000 m., those of *sexdens* only in the low-lying regions.

According to von Ihering (1898) the nest of the Brazilian *Atta sexdens* differs from that of the Colombian form described by Forel. It consists of from one to two dozen chambers, each 25–30 cm. in diameter and 12 to 15 cm. high, with a flat floor and arched ceiling. Each of these chambers, *panellas* (pots) or *pratos* (plates) as they are called by the Brazilians, has one or more, rarely two, galleries entering it at the side and connecting it with the other cavities and the vertical shafts leading to the surface of the nest. The chambers are ½ to 1 m. apart and are excavated at a depth of 4 to 6 m. below the surface or even lower. The fungus gardens are built up on the flat floors of the chambers. Von Ihering found that when the nests are inundated the ants at once remove portions of their fungus gardens to higher ground. When this is impracticable or the inundation is very great, the population of the nest forms a ball held together by the closed jaws of the workers and enclosing in its interior a portion of the fungus garden and probably also the queen. This ball then floats on the water till carried ashore, when the ants land and start a new nest out of reach of the flood. Von Ihering says that his neighbor took advantage of this habit, which by the way is also exhibited by several other tropical ants (*Anomma, Solenopsis geminata*, etc.), to free his premises from the leaf-cutting *Attæ*, by rowing about in his canoe, catching up the floating balls and throwing them into a bucket of boiling water. Von Ihering also gives an interesting account of the *iças*, or virgin queens of *Atta sexdens*. At the time of swarming these are captured in great numbers by the Brazilians. The iça hunter stations himself at the entrance of the nest with his feet in a tub of water in order to protect himself from the savage soldiers and workers, and collects the females while they are issuing from the galleries. A successful catch may yield as many as 12 to 20 litres. The gasters of these iças, removed from the thoraces, legs and heads and roasted with salt, garlic and mandioca meal are eaten as a delicacy ("*passoca*") in many parts of Brazil.

Forel (1899–1900*a*, 1901) has also recorded a few notes on the fungus-gardens of a colony of *Trachymyrmex septentrionalis* which he observed at Black Mountain, North Carolina, but he adds little to the above cited descriptions of Morris, McCook and Swingle. Forel (1905) later published some notes of Gœldi on the nests of *Acromyrmex octospinosus*, the fungus gardens of which are built over the stems of plants and fully exposed to the air in the damp forests of Para. Two photographs accompanying the article show that this fungus garden consists of a number of separate portions unlike the single garden which Urich and Forel describe this ant as making when nesting in the ground.

In 1900 Moreno published some observations on the Mexican *Atta* (probably *fervens*) but these add nothing of value to what was previously known.

In 1901 I recorded a few notes on *Atta fervens* and *Cyphomyrmex rimosus dentatus* which I observed in Mexico. I was able to convince myself that the statements of Urich, Forel and Emery to the effect that the latter species makes no fungus-garden, are erroneous. This ant constructs a fungus garden with caterpillar excrement and cultivates a peculiar fungus consisting of small yellow nodules, which have been overlooked by previous investigators. More recently (1905*a*) I have found that other varieties and subspecies of *C. rimosus* in Texas, Florida, the Bahamas, Porto Rico and Culebra have the same habit. In this same paper I also described briefly the habits of *Trachymyrmex jamaicensis*, and in a subsequent paper (1905*b*) also those of *T. septentrionalis*. A fuller account of these various species will be found in the third part of the present article.

M. T. Cook (1906) has very recently studied the habits of *Atta insularis* and has published a few notes on the ravages of this ant in the plantations of Cuba.

The preceding paragraphs deal almost exclusively with observations on adult colonies of the *Attii* and the constitution and care of their fungus gardens. As soon as these habits had been demonstrated, the question naturally arose as to how the ants first come into possession of the fungi which they cultivate with such marvellous skill and assiduity. The labors of the South American naturalists Sampaio, von Ihering, Gœldi and Jakob Huber have supplied the answer to this interesting question.

Sampaio (1894) on digging up an *Atta* female ten days after the nuptial flight, found her in a cavity with two small white masses, one consisting of 50–60 eggs, the other of a filamentous substance which was the young fungus garden, though not recognized as such. Three and one half months after the nuptial flight he excavated another nest which had an opening to the surface of the soil. He found numerous workers of three different sizes but all smaller than the corresponding castes in adult colonies. They were already cutting leaves and had a fungus garden about 30 cubic centimeters in volume. He estimated the number of workers at 150 to 170, that of the larvæ and pupæ at about 150 and the eggs at 50.

The much more important observations of von Ihering (1898), including his brilliant discovery of the method of transfer of the fungus culture from the maternal to the daughter colony, deserve fuller consideration. According to this observer there are repeated nuptial flights of the Brazilian *Atta sexdens* from the end of October to the middle of December. These flights are essentially like those of other ants. On descending to the earth the fertilized female "rids herself of her easily detached wings by quick motions of her legs and then begins to dig her burrow in some spot more or less free from vegetation. This canal is nearly or quite vertical and measures about 12–15 mm. in diameter. It is so narrow that the 'Iça' cannot turn around in it, but is compelled to walk backwards whenever she returns to the surface. She bites off lumps of earth with her powerful jaws, makes them into a pellet by means of loose threads of saliva, brings them up and deposits them a short distance from the entrance to the burrow. The earth thus brought up forms a circular wall, thickened in front and interrupted behind, about 4–5 cm. broad in front and at that point 3 cm. from the entrance. The burrow varies from 20–30 cm. in length according to circumstances and ends in a small laterally placed chamber about 6 cm. long and somewhat less in height. As soon as the chamber is completed, the ant closes the upper portion of the burrow to a distance of 8–10 cm. from the entrance with pellets of earth and this closure becomes more and more compact in the course of weeks, probably through the action of the rain. If the nest be opened in one or two days, the female will be found in the empty chamber unchanged, only more lethargic, as if exhausted. A few days later one finds near the ant a little packet of 20–30 eggs undergoing segmentation. Beside them lies a flat heap of loose white substance, only 1–2 mm. in diameter. This is the earliest rudiment of the fungus garden. Microscopical examination shows that it consists of compact masses of the well-known fungus-hyphæ, but without traces of "kohlrabi" corpuscles. As time goes on the fungus garden grows rapidly and becomes more voluminous till it reaches a diameter of about 20 cm. It seems to consist of closely aggregated spherules about 1 mm. in diameter. As soon as it has attained this size the transparent pyriform globules bud out, which Mœller called 'kohlrabi' and the ant is seen to eat them frequently, She always keeps close to the fungus garden and in it embeds her eggs. The larger of these soon become larvæ. The eggs are not spun over with fungus hyphæ but have the chorion smooth and shining. Eggs are also found in the interior of the fungus mass, which the ant keeps rearranging and redistributing from time to time. It was easy, for purposes of observation, to transfer the ant to a terrarium. Without excavating anew she remained with her garden on the fresh layer of earth. The garden did not grow, but rather diminished in volume, for it is difficult to imitate the conditions, especially the precise degree of moisture, in which it grows and develops in its cavity. I failed therefore to keep the ant and her garden till the first workers appeared. The time required to accomplish this must be between two and three months. Presumably the last phase of this first brood period is very precarious, since leaves must be brought in to serve as a substratum for the further growth of the fungus garden.

In any event, the development of the garden is in need of further elucidation. According to my investigations, which need fuller confirmation, the organic substratum is provided in the form of malaxated eggs, but perhaps the soil, which is rich in vegetable mould, may itself contain nutrient substances .... As soon as the first workers appear, the colony may be regarded as established and the opening up of the burrow, the enlarging of the first chamber, carrying in of leaves, etc., lead to the well-known conditions of the adult colony....The preceding description is hardly complete without an answer to the question: Whence come the fungus germs for the establishment of the new garden?" After searching the queen for fungus spores concealed about her person, von Ihering made the important discovery that "every *Atta* queen, on leaving the parental nest, carries in the posterior portion of her oral chamber a loose pellet, .6 mm. in diameter, consisting of hyphæ of *Rozites gongylophora*, small fragments of bleached *i. e.*, chlorophylless leaves, and chitinous bristles. The last are undoubtedly derived from the larvæ undergoing ecdysis in the parental nest." Von Ihering is of the opinion that the female keeps the pellet of hyphæ, etc., in her mouth till she has excavated her chamber and then spits it out where it will serve to kindle the fungus garden of the new colony.

The observations of Gœldi, (Forel 1905, Gœldi 1905 *a* and *b*) are little more than a confirmation of those of von Ihering. He maintains that the fungus is actually grown on some of the malaxated eggs of the *Atta* queen, who would thus be sacrificing a part of her offspring as a culture medium for the fungus that goes to nourish both herself and her workers in their larval and adult stages.

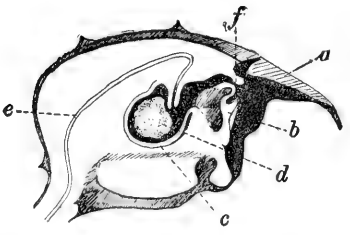

Fig. 1. Head of recently fertilized queen of *Atta sexdens* longitudinally bisected.
a. Mandible; *b*, labium retracted; *c*, buccal pocket containing *d*, the pellet of fungus hyphæ carried from the parental nest; *e*, œsophagus; *f*, oral orifice. (After J. Huber.)

None of these investigators succeeded in rearing an *Atta* colony from its very inception till the hatching of the firstling workers and the bringing in of the leaves for the purpose of keeping up the fungus culture. This has been accomplished very recently by Jakob Huber (1905) who besides correcting a few errors in the work of his predecessors, has added a number of new and important observations. His paper, from which the following abstract is taken, also contains several interesting figures from photographs of the *Atta* female, her progeny, and fungus garden. The female expels the pellet from her buccal pocket (Fig. 1, *c*) the day following the nuptial flight. It is a little mass .5 mm. in diameter, white, yellowish or even black in color, and consists of fungus hyphæ imbedded in the substances collected from the ant's body by means of the strigils on her fore feet and thence deposited in her mouth. By the third day 6 to 10 eggs are laid (Fig. 2). At this time also the pellet begins to send out hyphæ in all directions. The female separates the pellet into two masses on this or the following day (Fig. 3). For the next 10 to 12 days she lays about 10 eggs daily, while the fungus flocculi grow larger and more numerous. At first the eggs and flocculi are kept separate, but they are soon brought together and at least a part of the eggs are placed on or among the flocculi. Eight or ten days later the flocculi have become so numerous that they form when brought together a round or elliptical disc about 1 cm. in diameter. This disc is converted into a dish-like mass with central depression in which the eggs and larvæ are thenceforth kept. The first larvæ appear about 14 to 16 days after the *Atta* female has completed her burrow, and the first pupæ appear about a month after the inception of the colony. By this time the fungus garden has a diameter of about 2 cm. There are no "kohlrabi" corpuscles in the earlier stages, and when first seen they are at the periphery of the disc. A week later the pupæ begin to turn brown and in a few days the first workers hatch. Hence the time required for the establishment of a colony under the most favorable conditions is about 40 days. After this rapid survey of the matter, Huber asks the important question: How does the *Atta* female manage to keep the fungus alive? Obviously the small amount of substance in the original pellet must soon be exhausted and the growing hyphæ must be supplied with nutriment from some other source. His interesting answer to this question may be given in his own words: "After carefully watching the ant for hours she will be seen suddenly to tear a little piece of the fungus from the garden with her mandibles and hold it against the tip of her gaster, which is bent forward for this purpose (Fig. 4). At the same time she emits from her vent a clear yellowish or brownish droplet which is at once absorbed by the tuft of hyphæ. Hereupon the tuft is again inserted, amid much feeling about with the antennæ, in the garden, but usually not in the same spot from which it was taken, and is then patted in place by means of the fore feet (Fig. 5). The fungus then sucks up the drop more or less quickly.

Fig. 2. Eggs and fungus garden in cell of queen *Atta sexdens*, forty-eight hours after the nuptial flight. (After J. Huber.)

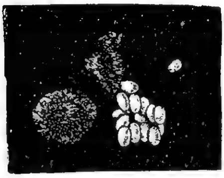

Fig. 3. Eggs and fungus garden in cell of queen *Atta sexdens* seventy-two hours after the nuptial flight. (After J. Huber.)

Often several of these drops may be clearly seen scattered over the young fungus garden [Fig. 6]. According to my observations this performance is repeated usually once or twice an hour, and sometimes, indeed, even more frequently. It can almost always be observed a number of times in succession when a mother ant that has no fungus, as sometimes happens in the cultures, is given a piece of fungus belonging to another *Atta* female or from an older colony. The mother ant is visibly excited while she explores the gift with her antennæ, and usually in a few minutes begins to divide it up and rebuild it. At such times she first applies each piece to her vent in the manner above described and drenches it with a fecal droplet." From these observations Huber concludes that the droplet must be liquid excrement and that the fungus owes its growth to this method of manuring. A direct use of malaxated eggs for this purpose was never observed and could not be detected by microscopical examination, although a number of observations show that the same result may be accomplished indirectly, namely by the female eating her own eggs. This habit is so common and apparently so normal that Huber estimates that 9 out of every 10 eggs are devoured by the mother, often as soon as they are laid. The life of the *Atta* female in her little cell during all this time is very rhythmical. At regular intervals she conscientiously examines the walls of the cavity, flattens out the earth, etc. She devotes more time to licking and manuring the fungus garden and, of course, lavishes most care on the brood. As soon as the larvæ appear they are fed directly with eggs thrust into their mouths by their mother. Huber concludes that this is their normal diet till the first workers hatch. He never saw the female either eating the fungus mycelium herself or feeding it to the young. As proof of his contention he cites the case of one of his *Atta* queens who brought up a brood without a fungus garden. With the appearance of the firstling workers, which are minims, that is members of the smallest worker caste, a change comes over the colony. They begin to

Fig. 4. Silhouette of a queen *Atta sexdens* in the act of manuring her fungus garden. (From an instantaneous photograph after J. Huber.)

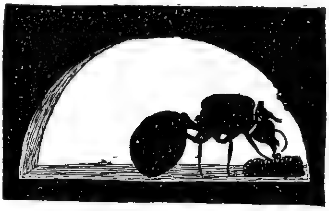

Fig. 5. Silhouette of a queen *Atta sexdens* replacing in the fungus garden tuft of mycelium saturated with fecal liquid. (From an instantaneous photograph after J. Huber.)

usurp the functions of the mother ant. They manure the garden, which at the time of their appearance measures hardly more than 2.5 cm. in diameter, and feed the larvæ with their mothers' eggs. The workers themselves, however, feed on the "kohlrabi" which has been developing on the hyphæ in the meantime. After about a week some of the workers begin to dig in the earth, and ten days after the appearance of the first worker and seven weeks after the inception of the colony, they break through to the surface of the soil and surround the entrance of the nest with a tiny crater of earthen pellets. They now begin to bring in pieces of leaves, knead them up into minute wads, and insert them in the fungus garden. The method of manuring the garden with fecal droplets seems now to be abandoned. The mother *Atta* henceforth pays no attention to the development of the garden or to the brood, but degenerates into a sluggish egg-laying machine, while the multifarious labors of the colony devolve on the workers. In the meantime the "kohlrabi" has become so abundant that it can be fed to the larvæ. In concluding his paper Huber makes the important observation that fertile females of *Atta sexdens* are readily adopted by strange workers of their own species. Such adoptions may be frequently resorted to in a state of nature and would perhaps account for the enormous size and great age of some of the formicaries of the larger species of *Atta*, which in this respect resemble the colonies of *Formica rufa* and *F. exsectoides* in the north temperate zone.

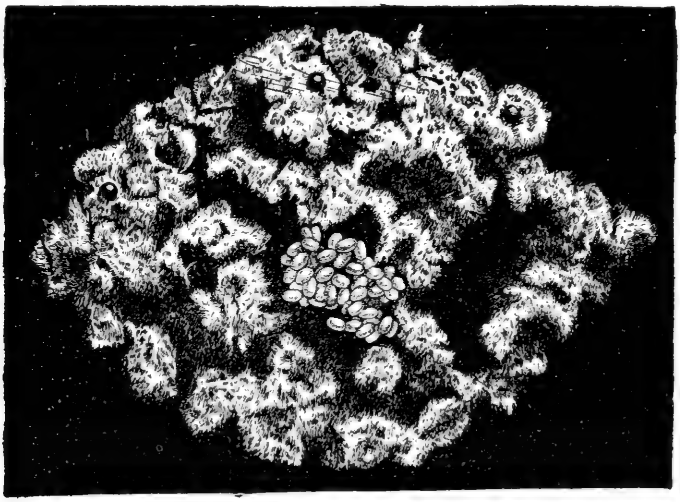

Fig. 6. Fungus garden of *Atta sexdens* fourteen days after the nuptial flight. There are about 100 eggs which the queen has placed in a depression in the middle of the garden. Near the periphery there are three drops of the fecal liquid with which the queen manures her garden. (After J. Huber.)

PART II. DESCRIPTIONS OF NORTH AMERICAN ATTII.

1. **Atta texana** *Buckley.*

Myrmica (*Atta*) *texana* BUCKLEY, Proc. Acad. Nat. Sci. Phila., 1860, p. 233, ☿ ♀ ♂.
Myrmica texana BUCKLEY, Proc. Acad. Nat. Sci. Phila., 1861, pp. 9–10.
Œcodoma texana LINCECUM, Proc. Acad. Nat. Sci. Phila., 1867, pp. 24–31.
Œcodoma texana BUCKLEY, Proc. Ent. Soc. Phila., VI, 1867, p. 347, no. 62, ☿ ♀ ♂.
Atta fervens TOWNSEND, Amer. Entom. and Botan., II, 1870, pp. 324–325, figs. 202 and 203, ☿ ♀.
Atta fervens MCCOOK, Ann. Mag. Nat. Hist., (5) III, 1879, pp. 442–449.
Atta fervens MCCOOK, Nature, XX, 1879, p. 583.
Atta fervens MCCOOK, Proc. Acad. Nat. Sci. Phila., 1879, pp. 33–40.
Œcodoma texana NEHRLING, Zool. Garten, XXV, 1884, p. 265.
Atta fervens DALLA TORRE, Catalog. Hymen., VII, 1893, pp. 152, 153 (in part).
Atta fervens EMERY, Zool. Jahrb., Abth. f. Syst., VIII, 1894, p. 329.
Atta fervens FOREL, Biol. Centr. Amer., Hymen., III, 1899-1900, p. 33 (in part).
Atta fervens WHEELER, Amer. Natur., XXXV, 1900, pp. 851–862, 2 figs.
Atta fervens WHEELER, Trans. Texas Acad. Sci., IV, no. 2, 1902, p. 13.

Soldier. (Fig. 7 and Pl. XLIX, Fig. 11.) Length 10–12 mm.

Head cordate; without the mandibles broader than long, with rounded posterior corners and shallow obtuse occipital excision. Mandibles long, flattened, with a large acute apical and 9 or 10 blunt, subequal basal teeth. Clypeus short and broad, with bidentate and arcuately excised anterior border. Frontal carinæ continued as distinct, diverging ridges as far back as the middle of the head; their lobes with a prominent tooth above the insertion of each antennal scape. Frontal area large, triangular, indistinct. Antennæ slender. Eyes convex, hemispherical, about ¼ the distance from the anterior to the posterior corners of the head. Ocelli absent. There is a tooth on the lateral carina between the eye and the clypeus, two small spines or teeth on the ventrolateral surface of the head, one or two similar teeth on each occipital lobe and behind them a large prominent spine. Thorax with four pairs of spines: one small acute pair on the inferior corners of the pronotum, a large robust, acute and erect pair, sometimes reduced to conical projections, above on the sides of the pronotum; a much shorter, often more slender and less tapering pair on the mesonotum, and a long, acute, backwardly directed pair on the epinotum. The last are prolonged forward at their bases in the form of a pair of anteriorly converging ridges. Petiole about 1½ times as long as broad, pentagonal from above, broadest in the middle; node concave in the middle with a ridge on each side. Postpetiole nearly twice as broad as the petiole, about as broad as long, narrowed in front, flattened above, with a pair of more pronounced and uneven mesial and a pair of shorter and feebler lateral ridges. Gaster oval, broadest at the middle, with somewhat angular anterior corners and abruptly conical tip. Legs very long and slender.

Mandibles and clypeus shining; the former coarsely striatopunctate, the latter finely and unevenly punctate. Remainder of body opaque, very finely punctate or granular.

Hairs long, erect or reclinate, curved, golden yellow or fulvous, covering the body and appendages. Pubescence abundant on the body and rather long, of the same color as the hairs; absent on the appendages, with the exception of the antennal funiculi.

Ferruginous brown; borders of mandibles black.

Media. (Fig. 7 and Pl. XLIX, Fig. 13). Length: 3–9 mm.

Resembling the soldier but with proportionally smaller head and all the cephalic and thoracic spines longer and more acute, especially the posterior occipital and the superior pronotal pairs. The latter are often much longer than the epinotal spines and curved forward at their tips.

Minima. (Fig. 7 and Pl. XLIX, Fig. 14.) Length: 1.5–2.5 mm.

Head proportionally smaller than in the soldier and media; mandibular teeth more acute; lobes of frontal carinæ, lateral carinæ and ventro-lateral surfaces of head without teeth. Anterior and posterior occipital spines much reduced. On the thorax the superior are not longer than the inferior pronotal spines and much shorter than those on the epinotum. Pubescence and hairs much sparser and more inconspicuous than in the soldier and media.

Female. (Fig. 7.) Length: 17–18 mm.

Head without the mandibles, much broader than long, arcuately excised behind, with rather straight, anteriorly converging sides. Mandibles and clypeus similar to those of the soldier, but the former with at least 12 basal teeth, the latter with the two teeth of its anterior border blunter and more prominent. Frontal and lateral carinæ with prominent teeth. Spines of anterior occipital and ventro-lateral surface of head reduced to low projections. Posterior occipital spines small but acute. Thorax robust, distinctly longer than the first gastric segment; twice as broad as the head. Inferior pronotal spines small and acute; superior pair lacking. Scutellum rounded, convex, without a median longitudinal impression. Epinotum with a pair of small, acute, backwardly directed spines, each of which has a prominent, elongate swelling in front of its base. Petiole more than twice as broad as long; broadest in the middle and produced on each side into a long, slender spine or process. Postpetiole less than twice as broad as the petiole and fully twice as broad as long, widest behind with two pairs of truncated lateral projections, of which the posterior is the longer. Lower surface with a prominent transverse ridge. Gaster nearly as broad as long, but little broader in the middle than at its straight anterior border. Anterior corners of first segment rectangular. Legs slender and weak.

Mandibles, anterior border of clypeus, scapes and legs shining; clypeus and mandibles punctate, the latter also very coarsely striated. Remainder of body opaque, granular-rugulose. Mesopleuræ coarsely rugose.

Hairs and pubescence tawny, the former dense and erect on the body and appendages, the latter sparse, somewhat reclinate and hooked, most conspicuous on the head and gaster.

Deep maroon brown, legs more reddish; borders of mandibles black. Wings with ferruginous brown veins and a strong suffusion of the same color in the membranes, especially along their anterior borders.

Male. (Fig. 7, and Pl. XLIX, Fig. 24.) Length: 13–14 mm.

Head small, without the mandibles but little broader than long, flattened behind but not excised, with large and very prominent eyes and ocelli. Mandibles well-developed, with pointed tips and about a dozen blunt basal teeth. Anterior border of clypeus with two broad blunt teeth and a median excision. Space between frontal and lateral carinæ concave, elliptical. Antennæ slender. Cephalic spines obsolete, except those of the posterior occipital region, which are short, acute and sometimes bent downwards at their tips. Thorax through the wing insertions more than twice as broad as the head. Mesonotum as broad as long, projecting in front over the small pronotum, which has a short, broad tooth at its inferior corner on each side. Scutellum convex, with a faint longitudinal impression in the middle. Epinotum unarmed. Petiole and postpetiole similar to those of the female, but each side of the former sometimes with two spines of unequal length, and the postpetiole is less angular on the sides. Gaster as broad as long, elliptical, convex above and below. Hypopygium broader than long, fenestrate, with its free edge faintly bidentate and not excised but instead slightly produced in the middle. Outer genital appendages slender, strap-shaped with subparallel borders and obliquely truncated tips. Median pair long with infolded edges and geniculate towards the apex, which is flattened and provided with a strong basal and two feebler terminal teeth. Wings 22 mm. long.

Mandibles somewhat shining, finely striate and coarsely punctate. Head and thorax opaque, pedicel and gaster slightly shining. Clypeus, frontal area and facial concavities uniformly granular, remainder of head coarsely reticulate-rugose. Thorax rather coarsely granular and punctate. Mesonotum with undulating transverse rugulæ. Pedicel and gaster densely and finely punctate, with more scattered, larger piligerous punctures. Legs and genitalia shining.

Hairs fulvous brown, long, dense, and erect on the head and upper portions of thorax and pedicel, sparser on the pleuræ and legs; on the gaster much shorter and sparser and hardly more than a dilute, suberect pubescence. Outer genital valves and free edge of hypopygium with numerous hairs.

Ferruginous brown; gaster, genitalia, legs and antennæ somewhat paler. Wings like those of the female.

Texas: Chapel Hill, Brenham, La Grange, Ye Gua Creek (Lincecum); Austin (Buckley, Lincecum, Townsend, McCook, Wheeler); Alice, New Braunfels, Elgin, Granite Mountain (Wheeler).

There exists some confusion in the literature in regard to this species. The European myrmecologists, Mayr, Forel and Emery, have confounded it with a closely related, but in my opinion, perfectly distinct Mexican species, *A. mexicana* F. Smith (*A. fervens* Say). The soldiers and mediæ of the latter, of which I possess specimens from Guadalajara (J. F. McClendon), Irapuato (C. H. T. Townsend), Esquinapa (J. H. Batty), Cuernavaca and Queretaro (Wheeler), differ from the corresponding phases of *texana* in having the head smooth, shining and hairless above. In the male the hypopygium (Pl. L, Fig. 25) is shorter, distinctly excised in the middle with the blunt teeth further apart, and without a median fenestra. The outer genital appendages are slender and taper to a sharp point; the middle pair are more slender and flattened, less geniculate and more uniformly curved. In Pl. L, Figs. 21–25 are given camera drawings of the male hypopygia of all the species of *Atta* s. str. except *columbica* (which is probably a variety of *cephalotes*), because, as Mayr has shown in his work on the Formicidæ of the Novara Expedition, this scelerite and the genital appendages furnish excellent characters for distinguishing the species.

2. **Atta mexicana** (*F. Smith*).

The name of this species, which is not known to occur in Texas, though it is widely distributed in Mexico at an altitude of 5,000 to 7,000 feet, must either be attributed to Drury, and not, as has usually been done, to Say, or if, as Dalla Torre maintains, the *Formica fervens* of Drury is merely a synonym of *A. cephalotes,* we must adopt *A. mexicana* F. Smith as the name of the Mexican form. As it seems to me to be impossible to determine the species to which Drury's female specimen belonged, I believe that the name *mexicana* should be adopted. The synonymy disentangled from that of *A. texana* would then read as follows:

?*Formica fervens* Drury, Illustr. Nat. Hist., III, 1782, p. 58, pl. 42, fig. 3. ♀.
Atta fervens Say, Boston Journ. Nat. Hist., I, 3, 1836, p. 290, ♀.
Œcodoma mexicana F. Smith, Catalog. Hymen. Brit. Mus., VI, 1858, p. 185, no. 9 ♀. Pl. X, fig. 20.
Œcodoma Mexicana Norton, Amer. Natur., II, 1868, p. 66, pl. I, figs. 9 and 10. ☿ ♀.
Œcodoma mexicana Norton, Proc. Essex Inst., VI, 1868, Comm. p. 9, fig. ☿ ♀.
?*Œcodoma mexicana* Moreno, Naturaleza, III, 1876, pp. 189–190.
Atta fervens Leconte, Writings of Th. Say., Entom., II, 1859, p. 734.
Atta fervens Mayr, Reise der Novara, II, 1. Formicidæ, 1865, p. 81, ☿ ♀ ♂.
Atta fervens Forel, Bull. Soc. Vaud. Sc. Nat., XX, 1884, p. 47 (in part).
Atta fervens Dalla Torre, Catalog. Hymen., VII, 1893, pp. 152, 153 (in part).
Atta lævigata Pergande, Proc. Calif. Acad. Nat. Sci. (2), V, 1895, p. 896, ☿.
Atta fervens Forel, Biol. Centr.-Am., Hymen., III, 1899–1900, p. 33 (in part).
Atta fervens Forel, Ann. Soc. Ent. Belg., XLV, 1901, p. 124, ☿.
Atta fervens Wheeler, Ann. Soc. Ent. Belg., XLV, 1901, p. 200, ☿.

3. **Atta (Mœllerius) versicolor** *Pergande.*

Atta versicolor Pergande, Proc. Calif. Acad. Sci. (2), IV, 1893, pp. 31, 32, ☿.
Atta (Acromyrmex) versicolor Emery, Zool. Jahrb., Abth. f. Syst., VIII, 1894, p. 330, ☿.
Atta versicolor Fenner, Entom. News, VI, 1895, p. 215.
Atta (Acromyrmex) versicolor Forel, Biol. Centr.-Am., Hymen., III, 1899–1900, p. 36, ☿.
Atta (Mœllerius) versicolor Emery. R. Accad. Sci. Ist. Bologna, April 1905, pp. 108, 111, ☿.

Worker, (Pl. XLIX, Fig. 5.) Length: 2.3–6 mm.

Head without the mandibles broader than long, in larger specimens somewhat narrowed in front, broadly and obtusely excised behind, with rounded posterior corners and slightly convex sides. Eyes convex, less than $\frac{1}{3}$ the distance from the anterior to the posterior corners. Mandibles rather convex, with several blunt teeth. Clypeus concave in the middle, with two very short, blunt teeth on the anterior margin. Frontal carinæ with expanded, toothed lobes in front. Frontal area obsolete. Antennal scapes reaching to the posterior corners of the head, somewhat incrassated towards their tips. Lateral carinæ with a short, acute tooth. Postocular spines absent; anterior and superior occipital regions with a number of short teeth or spines; posterior occipital region with a longer acute spine on each side. Pronotum with a pair of short, downwardly directed inferior and a pair of long, robust and acute superior spines directed forward and outward. Mesonotum with two pairs of spines, the anterior about half as long as the superior pronotal pair, but more rapidly tapering and directed upward and backward; the posterior pair smaller and closer together. Epinotum with two spines which are nearly as long as the superior pronotal pair but more slender and directed backward, upward and slightly outward. Petiole longer than broad, its node subrectangular, with four equidistant, subequal teeth in a transverse row. Postpetiole nearly twice as broad as the petiole, broader than long, concave above, with six short bidentate spines, four in a transverse anterior row and two behind and more widely separated at their bases. Gaster broadly elliptical, broadest behind the middle; basal segment with a median longitudinal depression, on each side of which there are several acute tubercles, longest near the anterior and lateral margins.

Mandibles shining, coarsely punctate and striate; remainder of body, including the legs and scapes, opaque, densely punctate. Head, thorax, pedicel and anterior border of gaster vermiculately or reticulately rugulose. Basal gastric segment with scattered, shallow foveolæ.

Hairs brown or tawny, suberect, not very abundant, rather short, curved or hooked on the body, straighter on the scapes and legs.

Ferruginous brown; borders of mandibles and anterior border of clypeus black.

Female. Length: 8 mm.

Head resembling that of the worker, but the posterior corners are more acute and the antennal scapes are longer. Pronotum with two broad and rather blunt inferior and two acute superior spines, which are directed forward and outward. Scutellum trapezoidal with bidentate posterior edge. Epinotal spines long, curved and diverging, of nearly uniform thickness up to their rapidly tapering tips which are bent downwards. Petiole and postpetiole similar to those of the worker, but the median pair of teeth in the former longer than the lateral pair and the spines on the postpetiole reduced to small teeth. Gaster pyriform, with the first segment flattened above and without the pointed tubercles.

Mandibles and legs shining; remainder of body opaque. Head coarsely, densely and crenately rugose, the rugæ being longitudinal on the sides but diverging from the front and median line on the upper surface. Thorax covered with rugæ similar to those on the head, transverse on the pronotum, longitudinal on the mesonotum and pleuræ, and irregular on the scutellum. Pedicel and gaster densely and irregularly rugulose; on the middle of the first segment of the latter the rugulæ are more regular and longitudinal. Antennal scapes and legs coarsely punctate and more or less roughened.

Pilosity like that of the worker.

Ferruginous brown; upper surface of head, mesonotum and gaster blackish, the mesonotum with a V-shaped red spot on the middle and the gaster with a pair of elliptical ferruginous spots on the basal segment. Wings opaque yellowish brown, with dull yellow veins.

Male. (Pl. L, Fig. 26.) Length: 8 mm.

Head, without the mandibles and eyes, as long as broad, subrectangular, with nearly straight posterior border. Eyes large, protruding, hemispherical, with their posterior orbits at the middle of the head. Mandibles well-developed, acute, flattened and multidentate. Clypeus very faintly and sinuately excised in the middle. Frontal and lateral carinæ without teeth. Antennal scapes extending fully ⅓ their length beyond the posterior corners of the head. The latter with a small, acute superior and a broad flattened inferior tooth on each side. Pronotum with a larger inferior and much smaller superior tooth on each side. Mesonotum with distinct Mayrian furrows. Scutellum with a median longitudinal depression and a pair of blunt posterior teeth. Epinotum with short, convex base and longer straight declivity; spines like those of the female but more slender and tapering more gradually. Petiole and postpetiole like those of the female, the former with small acute teeth above and three lateral teeth, the latter with four teeth on each side. Gaster broadly elliptical, with the basal segment flattened above and without tubercles. Genital appendages convex, curved inward, with broad, rounded, subtruncate tips. Legs slender.

Body including the mandibles and legs, opaque; gaster slightly shining. Mandibles finely striated and coarsely punctate. Head, thorax and pedicel densely rugulose, the rugulæ being longitudinal on the head, mesonotum, scutellum, pleuræ and epinotum, and transverse on the pronotum, petiole and postpetiole. Gaster and legs densely punctate. Genital appendages with a few scattered foveolæ.

Pilosity like that of the worker and female.

Black; mandibles, border of clypeus, frontal carinæ, neck, antennæ, coxæ, tibiæ, tarsi and gaster ferruginous brown, posterior borders of gastric segments and genitalia somewhat paler. Wings like those of the female.

Arizona: Tucson (Fenner, Wheeler); Yucca (Wheeler).

Mexico: Calamujuet, Lower California (Eisen and Haines); Sonora (Coll. Am. Mus. Nat. Hist.).

The types are from Calamujuet; the above description is drawn from Tucson specimens.

4. **Atta (Mœllerius) versicolor chisosensis** subsp. nov.

A number of workers taken by Judge O. W. Williams in the Chisos Mountains of southwestern Texas, and a few workers taken by myself at Terlingua in the same region, represent a distinct subspecies.

They differ from the typical *versicolor* in their distinctly lighter and more yellowish color, much less pronounced sculpture and in having only a few (about 12) pointed tubercles on each side of the median gastric depression, whereas in the typical form there are two or three times as many. Owing to their feebler sculpture the workers of *chisosensis* are throughout much more shining than the typical form.

5. **Atta (Trachymyrmex) septentrionalis** *McCook.*

? *Œcodoma virginiana* Buckley, Proc. Ent. Soc. Phila., VI, 1867, p. 346, no. 61, ☿.
? *Œcodoma tardigrada* Buckley, Proc. Ent. Soc. Phila., VI, 1867, p. 349, no. 65, ☿. ♀ ♂.
Atta septentrionalis McCook, Proc. Acad. Nat. Sci. Phila., 1880, pp. 359–363, Fig. ☿.
Atta (Acromyrmex) tardigrada Forel, Bull. Soc. Vaud. Sci. Nat. (2) XX, p. 91, 1884, p. 358, ☿ ♀ ♂.
Atta tardigrada Mayr, Verh. zool. bot. Ges. Wien, XXXVI, 1886, p. 442.
Atta (Trachymyrmex) tardigrada Forel, Ann. Soc. Ent. Belg., XXXVII, 1893, p. 601.
Atta tardigrada Dalla Torre, Catalog. Hymen., VII, 1893, p. 154.
Atta tardigrada var. *septentrionalis*, Catalog. Hymen., VII, 1893, p. 154.
Atta (Trachymyrmex) tardigrada Emery, Zool. Jahrb., Abth. f. Syst., VIII, 1894, p. 329.
Atta (Trachymyrmex) tardigrada Forel, Rivista Sci. Biol., II, 1900, p. 9.
Atta (Trachymyrmex) tardigrada Forel, Ann. Soc. Ent. Belg., XLV, pp. 396, 397.
Atta (Trachymyrmex) septentrionalis Wheeler, Trans. Tex. Acad. Sci., IV, Pt. II, no. 2, 1902, pp. 13, 14.
Atta (Trachymyrmex) septentrionalis Wheeler, Psyche, June, 1903, p. 101, Fig. 6b.
Atta (Trachymyrmex) septentrionalis Wheeler, Bull. Am. Mus. Nat. Hist., XXI, 1905, pp. 386, 387.

Worker. (Pl. XLIX, Fig. 4.) Length: 2.5–3 mm.

Head, without the mandibles, about as broad as long, a little broader behind than in front, with obtusely excised posterior border, somewhat rounded posterior angles and rather straight sides. Eyes not very prominent, more than ⅓ the distance from the anterior to the posterior corners of the head. Mandibles with two larger acute apical and 7 or 8 small basal teeth. Anterior border of clypeus sinuately excised in the middle. Frontal area triangular, obsolescent. Frontal carinæ with flattened, rounded lobes in front, continued back as a pair of diverging ridges beyond the middle of the head as far as but not meeting the lateral carinæ. Antennal scapes extending about ¼ their length beyond the posterior corners of the head, somewhat thickened towards their tips. Region between the frontal carinæ and posterior corners of the head covered with small acute tubercles, one pair of which on the posterior corners is longer and bidentate. Pronotum with a pair of blunt, downwardly directed inferior spines, two long acute superior spines and between these in the middle a pair of short bidentate spines or tubercles, which are closer to each other than to the lateral tubercles. Mesonotum with two pairs of blunt spines. Mesoëpinotal constriction pronounced. Epinotum with four longitudinal rows of tubercles, the inner continued back into the bases of a pair of acute spines which are directed upward, backward and outward and are from ⅓ to ½ as long as the slightly convex base of the epinotum. Declivity sloping, forming in profile an obtuse angle with the base. The upper surface of the thorax and all the spines, with the exception of the inferior pronotal pair are covered with small tubercles. Petiolar node from above nearly square, a little broader than long; in profile its anterior surface is flattened, its summit acute and furnished with a pair of teeth. On each side of these there is also a small blunt tooth. Postpetiole about as broad as the epinotum, somewhat more than twice as broad as the petiole, and distinctly broader than long, subpentagonal from above, concave in the middle behind and covered with small tubercles. Gaster pyriform, broadest behind the middle; first segment with a faint, longitudinal, median depression and a short ridge on each lateral border. The dorsal surface is covered rather uniformly with small, acute tubercles, as are also the antennal scapes.

Mandibles and anterior border of clypeus faintly shining or glossy, the former finely and densely striated. Remainder of body and appendages opaque and indistinctly granular.

Hairs brownish yellow, short, hooked, more or less erect and not very abundant, usually arising from the small tubercles and covering the body and appendages rather uniformly.

Body ferruginous brown, legs slightly paler, mandibular teeth black, front and vertex dark brown; gaster in many specimens with a broad longitudinal fuscous or blackish stripe on the middle of the first segment.

Female. Length: 3.8–4 mm.

Head resembling that of the worker. Pronotum besides the blunt, downwardly directed inferior spines, with a pair of strong, somewhat flattened, acute superior spines directed outward and somewhat forward. Scutellum semicircularly excised and bidentate behind. Epinotal spines long, of rather uniform thickness to within a short distance of their acute, rapidly tapering tips. Pedicel and gaster as in the worker, but the lateral teeth of the petiole are smaller and blunter and the posterior margin of the postpetiole is excised. Wings 4 mm. long.

Sculpture similar to that of the worker; mesonotum and scutellum covered with rows of small elongated tubercles.

Like the worker also in pilosity and coloration. Head with a large black spot on the ocellar region and the gastric stripe is deeper and more distinct, but not reaching the anterior border of the basal segment. Wings blackish with veins of the same color; costal cell yellowish.

Male. Length: 3–3.5 mm.

Head but little broader behind than in front, broadest in the region of the eyes, with slightly convex posterior border. Eyes convex, posterior orbits at the middle of the head. Mandibles like those of the worker but smaller. Clypeus with broad, entire anterior margin. Frontal carinæ lobed in front, uniting behind with the lateral carinæ, which are furnished with a small tooth in the middle. Posterior corners of head with several small, acute spines or teeth. Antennæ slender; scapes somewhat thickened distally and surpassing the posterior corners by about ⅓ of their length. Pronotum with small acute superior and inferior teeth. Mesonotum with well-developed Mayrian furrows. Scutellum similar to that of the female. Epinotum with subequal base and declivity; spines slender, acute, diverging, bent downward at their tips, their bases continued forward as a pair of crenated ridges on to the base of the epinotum. Petiole and postpetiole like those of the worker, but the latter segment without distinct tubercles. Gaster elliptical, convex above, the first segment with smaller and more scattered tubercles than in the worker and female, and without a median longitudinal impression. Outer genital appendages broad and short, with rounded edges; median pair with straight, slender, pointed tips. Hypopygium entire, with a broad, rounded point in the middle. Legs long and slender; terminal tarsal joint not enlarged.

Opaque, mandibles and clypeus granular; head and thoracic dorsum coarsely, pleuræ, petiole and postpetiole more finely reticulate-rugose. Epinotum and gaster finely reticulate or granular. Legs smoother and somewhat shining.

Pilosity similar to that of the worker and female.

Ferruginous brown; upper surface of head, thorax, pedicel and first gastric segment more or less blackened; legs and posterior borders of gastric segments yellowish; antennal scapes dark brown. Wings as in the female.

Texas: Austin, Montopolis, Milano (Wheeler); Denton (W. H. Long); Paris (Miss A. Rucker, C. T. Brues).

Florida: (Mrs. Mary Treat, T. Pergande), Miami and Jacksonville (Wheeler).

District of Columbia: Washington (Pergande, Swingle).

North Carolina: Black Mountain (Forel).

New Jersey: Vineland (Mrs. Treat); Toms River (Morris, McCook); Lakehurst (Wheeler, W. T. Davis); Lucaston (E. Daecke); Miltown and Manusquam (Davis).

I believe that Buckley's name *tardigrada,* which has been very generally applied to this species, should be rejected and replaced by McCook's *septentrionalis,* first, because Buckley's description will apply equally well to this or the following species or even to *Mycetosoritis hartmanni,* although his account of the nests applies to none of these but rather to a small colony of *Atta texana*; and second, although Forel wrote in 1884 that Mayr had in his possession a type specimen of Buckley's *tardigrada* which made it possible to refer Florida specimens received from Mrs. Treat to this species, Dr. Mayr writes me (March 24, 1902); "Ich besitze von *Atta* (*Trachymyrmex*) *tardigrada* keinen Buckley'schen Typus." There is no possible means of ascertaining just what species Buckley described. McCook's description is equally worthless, but his specimens were redescribed by Forel, so that the name *septentrionalis* must stand. The above description is drawn from specimens taken early in May from a single colony at Montopolis, near Austin, Texas. Forel regarded McCook's specimens as representing a variety of the southern form, but Emery failed to distinguish any varietal differences between southern and northern specimens. A number of workers taken by me at Lakehurst, New Jersey are larger (3.4–3.6 mm.) than specimens from Texas and Florida and are of a paler, more yellowish color with a darker and more distinct gastric stripe. A deälated female from Lakehurst and a winged individual from Lucaston, New Jersey agree in having a dark spot on the middle of the pronotum, one on the postpetiole and in having the infuscation of the head and middle of the gaster more extensive. If we regard the New Jersey specimens as representing the typical form of the species it will be necessary to distinguish the darker southern form as a variety, for which I would suggest the name *obscurior* var. nov.

6. **Atta (Trachymyrmex) turrifex** *Wheeler.*

WHEELER, Psyche, June, 1903, pp. 100–102, fig. 6a, ☿ ♀.

Worker. (Pl. XLIX, Fig. 3.) Length: 3–3.75 mm.

Head without the mandibles a little longer than broad, slightly broader behind than in front, with obtusely excised posterior border, rather straight sides and prominent posterior angles. Eyes convex, in front of the middle of the head. Mandibles pointed, 7–8-toothed. Clypeus sinuately and rather deeply excised in the middle. Frontal area triangular, indistinct. Frontal carinæ with large round anterior lobes, somewhat concave in the middle, and continued back as a pair of diverging ridges nearly as far as the posterior corners of the head, but not meeting the almost equally long lateral carinæ. Antennæ robust; scapes reaching only to the posterior corners and fitting into deep grooves between the frontal and lateral carinæ. Upper surface of head, with the exception of these grooves, covered with tubercles, two pairs of which on the superior and inferior portions of the occipital corners are larger than the others and bidentate. Scapes covered with similar but smaller tubercles. Pronotum on each side with an acute downwardly directed inferior spine; above with a pair of rather long, acute lateral spines and a shorter bifurcated median spine. Mesonotum with two pairs of thick blunt spines. Mesoëpinotal constriction very pronounced. Epinotum with subequal base and declivity at right angles to each other in profile; the former convex, the latter concave; spines acute, nearly as long as the base, directed upward, backward and outward and prolonged forward at their bases as a pair of subparallel, crenated ridges lying between a shorter pair of similar lateral ridges. All the thoracic spines, with the exception of the inferior pronotal pair, are covered with small tubercles. Similar tubercles are also scattered over the dorsal surface of the thorax between the spines. Petiole from above as broad as long, nearly square, with a transverse row of four equidistant tubercles across its middle and connected with the median pair by longitudinal ridges. There is another pair near the posterior edge of the segment. Postpetiole twice as broad as the petiole and nearly twice as broad as long, impressed in the middle behind and covered with small tubercles. Gaster suboblong, with straight anterior border and subparallel sides, a little broader behind than in front, convex above and below; first segment with longitudinal ridges half way down its sides, a faint median and two lateral depressions. Its whole surface is covered with small tubercles which are connected with one another by a net-work of indistinct ridges. Legs stout, and as far as the second tarsal joint, covered with tubercles which are somewhat smaller than those on the body.

Mandibles with shining, coarsely striatopunctate tips, and opaque, finely striated bases. Remainder of body opaque, obscurely granular and more or less rugulose.

Hairs brown, hooked, suberect, covering the body and appendages, except the antennal funiculi which are clothed with a very fine whitish pubescence.

Ferruginous brown; front and vertex dark brown, legs somewhat paler than the body. In old specimens the body is darker in color and the roughened portions are overlaid with a bluish bloom.

Female. Length: 4–4.5 mm.

Head resembling that of the worker. Pronotum with short, acute inferior and superior spines, the latter not flattened. Scutellum with two long, blunt teeth and a deep median excision in its posterior border. Base of epinotum barely half as long as the declivity, which is concave; spines long, stout and rather blunt. Pedicel and gaster similar to those of the worker; posterior border of the postpetiole entire. Wings 6 mm. long.

Sculpture similar to that of the worker. Mesonotum and scutellum with indistinct longitudinal rows of small tubercles; remainder of thorax granular, with minute, scattered tubercles.

Pilosity and color like those of the worker. Wings opaque brown, with darker veins.

Texas: Austin, Montopolis, Marble Falls, Fort Stockton, Paisano Pass, Marfa, Del Rio, Langtry (Wheeler).

The worker of this species may be readily distinguished from that of *septentrionalis* by the more pointed posterior corners of the head, the much shorter antennal scapes which do not extend beyond the posterior corners, the unpaired pronotal spine, and the rougher legs and gaster. The female *turrifex* is distinguished by several of these characters and also by the much longer and paler wings.

7. **Atta (Trachymyrmex) arizonensis** sp. nov.

Female (deälated). (Pl. XLIX, Figs. 9 and 10.) Length: 4.75 mm.

Head, without the mandibles, as broad as long, somewhat broader behind than in front, with straight sides, obtusely excised posterior margin and rather pointed posterior corners. Eyes moderately convex, in front of the middle of the sides. Mandibles with two larger apical and several smaller basal teeth. Anterior border of clypeus sinuately notched in the middle. Frontal area triangular, indistinct. Frontal carinæ with large reflected and rather angular lobes, without rounded impressions in their surfaces, continued back as diverging ridges nearly to the posterior corners of the head, but not meeting the much shorter lateral carinæ. Antennal scapes distally enlarged, extending about $\frac{1}{4}$ their length beyond the posterior corners of the head. The latter with numerous conical tubercles, two of which on the inferior occipital angles are somewhat larger than the others and double. Pronotum with two small, flat, lappet-like inferior spines and a pair of long, but not compressed superior spines, directed outward and slightly forward. Posterior border of scutellum with a broad median excision and a pair of blunt teeth. Base of epinotum sloping, about half as long as the concave declivity. Spines short, acute, a little longer than broad at the base, directed backward and outward. All the spines of the thorax, excepting the inferior pronotal pair, covered with tubercles. Petiole from above oblong, slightly longer than broad, with bidentate anterior angles, and a pair of longitudinal dorsal ridges elevated into short spines or teeth at their anterior ends. Postpetiole more than twice as broad as the petiole, somewhat broader than long, transversely elliptical, with the sides produced in the middle in the form of short double spines; posterior margin semicircularly excised and somewhat reflected; upper surface with a pair of irregular elevations and numerous small tubercles. Gaster subspherical, but little longer than broad, anterior border straight, first segment obtusely ridged on the sides anteriorly, without a median depression and uniformly covered with small tubercles which are somewhat larger on the dorsal than on the ventral side. Legs well-developed and, like the antennal scapes, covered with small tubercles.

Mandibles somewhat shining, finely striated at their bases, more coarsely towards the inner edges of the blades. Remainder of body opaque, granulate-rugulose; rugulæ on the sides of the head and between the lateral and frontal carinæ longitudinal and minutely and irregularly tuberculate, on the front converging from each side towards the median line. On the thorax the rugulæ are irregularly longitudinal, more regularly on the mesonotum and scutellum where they are interrupted by low tubercles. Postpetiole and first gastric segment, especially at its base, obscurely and longitudinally rugulose.

Hairs dark brown, short, hooked or curved, suberect, uniformly covering the body and appendages. Antennal funiculi with very fine whitish pubescence.

Ferruginous brown, front and vertex darker, mandibular teeth black. Whole surface of body bluish pruinose.

Male. Length: 4.5 mm.

Head, without the eyes, somewhat longer than broad, a little broader behind than in front, with straight posterior border. Posterior orbits at the middle of the head. Mandibles well-developed, with two larger, acute apical and several small basal teeth. Clypeus with entire, broadly rounded anterior border. Frontal carinæ with well-developed anterior lobes and short posterior ridges which bend around laterally and pass over into the lateral carinæ, thus enclosing two elliptical facial cavities. Antennæ slender, scapes slightly thickened distally and reaching more than ⅓ their length beyond the posterior corners of the head. Posterior corners with short, acute spines, those on the superior and inferior angles being somewhat larger than the others. Inferior and superior pronotal spines very small and acute. Mayrian furrows of mesonotum distinct but shallow. Scutellum like that of the female. Epinotum with base somewhat shorter than the oblique declivity; spines rather short, somewhat longer than broad at the base, as long as the base of the epinotum, acute, directed backward and slightly outward, covered with small tubercles. Petiole similar to that of the female but concave in the middle and traversed by four longitudinal tuberculate ridges. Postpetiole less than twice as broad as the petiole, and nearly twice as broad as long, subpentagonal, with broadly excised posterior border and covered with tubercles. Gaster elliptical, convex above, covered uniformly with small acute tubercles except in the middle line near the base. Outer genital valves short and broad, with rounded tips; median pair terminating in a straight, attenuate point. Hypopygium entire, very bluntly pointed in the middle. Legs long and slender, covered with very small and rather indistinct tubercles. Last tarsal joints enlarged.

Mandibles subopaque, very finely and indistinctly striated. Body and appendages opaque. Facial cavities granular; dorsal portions of head, mesonotum, paraptera and scutellum coarsely and reticulately rugose. Remainder of body coarsely granular, the pronotum, pleuræ and epinotum also more or less irregularly rugulose.

Hairs fulvous, similar to those of the female.

Black or dark brown; mandibles, clypeus, anterior corners of head, funiculi, thoracic sutures, tarsi, knees and tips of tibiæ, genitalia and posterior and lateral borders of the gastric segments fulvous. Wings blackish, with yellowish costal cell and brown veins.

Arizona: Palmerlee, Cochise County, Aug. 24 (C. Schaeffer).

Described from a single female and six males.

This species is clearly distinct though in certain respects it is intermediate between *T. septentrionalis* and *turrifex*. The female differs from that of *turrifex* in the longer antennal scapes, which surpass the posterior corners of the head, and the posteriorly excised postpetiole, and from both this and *septentrionalis* in its much heavier sculpture, the greater size of the pronotal spines and the shape of the gaster, which is not oblong and impressed in the middle.

8. **Atta (Trachymyrmex) jamaicensis** *Ern. André.*

Atta (Acromyrmex) jamaicensis Ern. André, Rev. d'Entom., Juillet, 1893, p. 149, ☿.

Trachymyrmex sharpii Forel, Trans. Ent. Soc. London, 1893, Pt. IV, Dec. pp. 372, 373, ☿.

Atta (Trachymyrmex) maritima Wheeler, Bull. Am. Mus. Nat. Hist., XXI, 1905, pp. 107–109, pl. vii, figs. 7 and 8, ☿.

Worker. Length: 3.5–4.5 mm.

Head, without the mandibles, as broad as long, somewhat broader behind than in front, with obtusely excised posterior border, rather acute posterior angles and slightly convex sides. Eyes somewhat flattened, in front of the middle of the head. Clypeus with a small sinuate notch in the middle of its anterior border. Frontal area triangular, indistinct. Frontal carinæ with broad subtriangular lobes in front, their surfaces not impressed in the middle, continued back as a pair of diverging ridges to the posterior corners where they meet the postorbital ridges thus enclosing elongated grooves for the antennal scapes. Vertex with a pair of blunt projections and short rows of small tubercles. Each posterior corner of the head with three short blunt spines at the angles of an equilateral triangle. Antennæ slender, scapes somewhat enlarged towards their tips which surpass by less than $\frac{1}{5}$ their length the posterior corners. Pronotum with a blunt, lappet-shaped inferior and a long pointed superior spine on each side. In the middle between the two spines is a small double tubercle. Mesonotum with a pair of robust and rather blunt anterior and a pair of small acute posterior spines. Mesoëpinotal constriction long and rather shallow. Epinotum with subequal base and declivity meeting almost at a right angle, the former convex in profile, the latter straight; spines long, acute and rather slender, distinctly shorter than the base of the epinotum, directed obliquely upward, backward and outward and continued forward as a pair of blunt, subparallel ridges on the base of the epinotum. All the thoracic spines, except the inferior pronotal pair, covered with small tubercles. Petiole from above oblong, slightly longer than broad, abruptly narrowed anteriorly into a short peduncle; node with four equidistant acute teeth. Postpetiole trapezoidal, more than twice as broad as the petiole, as long as the petiole, as long as broad, semicircularly impressed in the middle behind but with straight, entire posterior border. The border of the impressed region and the sides beset with small tubercles. Gaster suboblong, slightly broadest behind the middle, narrowed in front; first segment with prominent lateral ridges and three broad longitudinal depressions on the dorsal surface. Tubercles small and acute, absent in the median depression and on the ventral surface. Legs long and like the antennal scapes covered with small tubercles.

Mandibles with shining, coarsely punctate blades, more opaque and finely striated at the base. Remainder of body and appendages opaque, granular.

Hairs brownish, very short and curved, longer on the anterior and inferior portions of the head and legs than on the body. Pubescence whitish, very fine and dilute, confined to the antennal funiculi.

Black; mandibles, except the teeth, thorax, petiole, and postpetiole ferruginous or yellowish; pleuræ more or less clouded with black or fuscous; antennæ, legs and apex of gaster dark brown, middle portions of femora and tibiæ often blackish.

Female. Length: 4.5–5 mm.

Head similar to that of the worker. Pronotum with rather blunt inferior and long and pointed superior spines, which are directed outward and forward and slightly upward. Scutellum convex, its posterior edge excised in the middle and with a pair of acute, laterally compressed teeth. Epinotum with short convex base and longer flattened declivity; spines long, slender and acute, directed backward and somewhat outward. Petiole, postpetiole and gaster like those of the worker, but the first broadest in the middle and constricted behind and the second without tubercles on its upper surface. Wings 6 mm. long.

Surface of body coarsely granular; front and vertex rugulose; mesonotum with longitudinal rows of small tubercles.

Pilosity like that of the worker, but longer on the thorax and gaster.

Head and gaster very dark brown; thorax, pedicel, mandibles, antennæ and legs paler, ferruginous. Pleuræ, two triangular spots on the anterior border of the mesonotum, an oblong blotch on the middle of the same region behind, the paraptera and anterior corners of the scutellum, black or dark brown. Wings smoky brown with darker veins and yellowish costal cell.

Male. Length: 3.5–4.2 mm.

Head small, without the eyes and mandibles nearly as broad as long, with rounded and constricted posterior and very prominent ocellar region. Eyes large and convex, their posterior orbits at the middle of the head. Mandibles acute, denticulate, but rather feeble. Clypeus with straight, entire anterior border. Antennæ very slender; scapes surpassing the posterior corners of the head by about ½ their length. Pronotum with very small, acute superior spines and the inferior spines reduced to angles on the lower border of the segment. Mesonotum and scutellum convex, the former with distinct but shallow Mayrian furrows, the latter with a pair of small acute teeth on the posterior border. Epinotum with short, convex base and longer sloping and concave declivity; spines short, acute, not longer than the base and hardly longer than broad at their insertions. Petiole and postpetiole like those of the worker, but the former narrowed behind the middle and the latter with more obscure tubercles. Gaster elliptical, broadest in the middle tapering behind, without depressions and ridges on the first segment and with very minute piligerous tubercles on both the dorsal and ventral surfaces. Genitalia small and retracted. Legs very slender, without tubercles; terminal tarsal joint slightly enlarged. Wings large, 5.5 mm. long.

Whole body and appendages opaque, minutely granular; head finely and longitudinally rugulose behind. Mesonotum with longitudinal rows of shallow oblong depressions or foveolæ. Mesopleuræ feebly rugulose.

Hairs like those of the worker and female, but finer, straighter and more appressed on the legs and antennæ.

Dull, rather light ferruginous; posterior portion of head, Mayrian furrows, lateral borders and a large oblong spot on the posteromedian portion of the mesonotum, paraptera and sides of the scutellum black. Wings like those of the female.

West Indies: Jamaica (T. D. A. Cockerell); St. Vincent (H. Smith); Andros and New Providence Is., Bahamas (Wheeler); Culebra (Wheeler).

I believe there can be no doubt that Forel's *T. sharpi*, André's *jamaicensis* and my *maritima* are all the same species. I have recently found in the collection of the Philadelphia Academy of Sciences a few workers from Jamaica, which agree very closely with André's description and with my specimens of *maritima* from the Bahamas. These, in turn, are almost identical with specimens collected from a greater number of colonies in the island of Culebra. Prof. Forel, to whom specimens from the latter locality were sent, pronounces them to be "indistinguishable from small specimens of *sharpi*." André's name *jamaicensis* must stand, however, as his description was published some six months earlier than Forel's. So far as known, therefore, there is only a single widely distributed species of *Trachymyrmex* in the West Indies, although there is an allied form (*T. urichi* Forel) in Trinidad and a subspecies of this (*fuscatus* Emery) and several distinct species of the subgenus on the adjacent South American continent.

T. jamaicensis is readily distinguished from all of our North American species by the peculiar coloration of the worker and female, the structure of the frontal and postorbital carinæ, the shape of the petiole and postpetiole, etc. The male is peculiar in coloration, the shape of the head, and in having very small, concealed genitalia.

9. **Atta (Mycetosoritis) hartmanni** subgen. et sp. nov.

Worker. (Pl. XLIX, Figs. 6 and 7.) Length: 1.8–2 mm.

Head, without the mandibles, longer than broad, but little broader behind than in front, with broadly and obtusely excised posterior margin, subparallel sides and rather acute posterior corners. Eyes moderately convex, just in front of the middle of the head. Mandibles convex, with two large, acute apical and several small and indistinct basal teeth. Clypeus moderately convex, with entire, broadly rounded anterior margin. Frontal area large, triangular, distinct. Frontal carinæ with very large, broad, flattened lobes anteriorly overlapping the insertions of the antennæ. These lobes have acute anterolateral corners and are separated by distinct reëntrant angles from the posterior ridges which are straight, diverging and continued back to the posterior corners of the head. Lateral carinæ continued back only a little behind the eyes where they turn in but fail to meet the frontal carinæ, though leaving a marked groove for the accommodation of the scape and extending to the posterior corner. Antennæ robust, scapes somewhat thickened distally, reaching with their tips to the posterior corners. Thorax long and stout, especially in front, though decidedly narrower than the head. Pronotum without inferior spines, with a pair of obtuse spines at the humeral angles and a pair of tubercles in the middle almost as far apart as each is from a lateral spine. Mesonotum with a blunt ridge on each side, somewhat higher in front and behind than in the middle. These ridges converge rapidly behind and just in front of the deep mesoëpinotal constriction. Epinotum in profile with subequal base and declivity, the former convex, especially in front, with a pair of ridges diverging posteriorly and continued into the small rather blunt spines, which are but little longer than broad at their bases, and directed upward, backward and outward. Epinotal declivity sloping, concave. Petiole from above suboblong, broader than long, a little broader behind than in front where it is suddenly constricted into a short peduncle; node above with a pair of rather acute teeth. Postpetiole 1½ times as broad as the petiole, broader behind than in front, sides slightly rounded, posterior border angularly excised in the middle. Gaster suboblong, broader behind than in front, not impressed in the middle above, anterior and lateral borders straight, the latter with indistinct longitudinal ridges. Legs rather long and stout.

Opaque throughout; mandibles very finely striated, especially at the base. Body very finely granular; front and vertex longitudinally rugulose; first gastric segment covered uniformly with minute tubercles.

Hairs whitish, suberect, curved and short on the body and appendages, longer and more conspicuous on the clypeus and mandibles.

Ferruginous brown; upper surface of head more or less blackish.

Female. Length: 2.5–2.7 mm.

Head resembling that of the worker, anterolateral corners of frontal carinæ more acute; ocelli very small and indistinct. Pronotum large, with a pair of stout, acuminate superior spines directed forward, outward and upward. Mesonotum small, elliptical, flattened, somewhat narrowed in front, with distinct but shallow Mayrian furrows. Scutellum as long as broad, with excised posterior border and acute posterior angles. Epinotum with short, convex base, long concave and vertical declivity and short spines directed backward and outward. Petiole, postpetiole and gaster resembling those of the worker. Wings short (2 mm.) and rounded; venation like that of *Trachymyrmex* and *Cyphomyrmex* but with the inner branch of the cubital and the distal segment of the externomedian veins very faint or obsolete.

Like the worker in sculpture, pilosity and coloration, but with the mesonotum longitudinally rugulose. Scutellum and paraptera darker than the remainder of the thorax. Wings opaque, fuscous; yellowish towards the base and costal margin.

Male. (Pl. XLIX, Fig. 8.) Length: 2 mm.

Head, without the eyes and mandibles, but little longer than broad, broader behind than in front, with flattened occipital region and a longitudinal ridge on each side of the rather acute posterior corners. Eyes large and convex, the posterior orbits a little behind the middle of the head. Mandibles like those of the worker in shape but smaller and feebler. Clypeus with entire, rounded anterior margin. Lobes of frontal carinæ similar to those of the worker but erect; their posterior ridges short and meeting the lateral carinæ. Scapes very short, extending only a little distance beyond the posterior corners of the head; funicular joints cylindrical, joints 1–7 less than twice as long as broad, terminal joints somewhat longer. Pronotum with short, acute superior spines; inferior spines absent. Mesonotum with distinct Mayrian furrows. Paraptera produced posteriorly as short teeth. Scutellum like that of the female. Epinotum with subequal base and declivity, the former convex, the latter concave; spines about half as long as the base, blunt, somewhat curved, directed upward and outward. Petiole and postpetiole like those of the worker, but the former proportionally longer, the latter broader. Gaster elliptical, median genital appendages digitiform, with blunt tips. Hypopygium with entire rounded posterior margin. Legs rather stout; terminal tarsal joints not enlarged.

Opaque; mandibles and gaster faintly shining; the former very finely, the body more coarsely and densely punctate. Head, thorax and postpetiole also irregularly reticulate-rugulose; first gastric segment above with minute, acute and uniformly distributed tubercles.

Hairs like those of the worker; more distinct and scattered on the gaster.

Head, thorax and pedicel black; first gastric segment very dark brown; remaining gastric segments, mandibles, antennæ and legs light brown or yellowish, antennal scapes, coxæ, and middle portions of the femora infuscated. Wings like those of the female.

Texas: Montopolis and Delvalle, near Austin (Wheeler).

This species which I take pleasure in dedicating to my former pupil, Mr. C. G. Hartmann, who aided me in excavating the nests of this and other Texan Attii, may be regarded either as a degenerate and simplified *Trachymyrmex* or as an aberrant *Cyphomyrmex.* It resembles the species of *Trachymyrmex* in its form and pilosity, while it approaches the species of *Cyphomyrmex* in its small size, the very large lobes of the frontal carinæ, the reduction of the cephalic and thoracic spines and the absence of tubercles on the greater portion of the body. In 1887 (Verh. zool. bot. Ges. Wien, XXXVII pp. 561, 562) Mayr described an aberrant female Attiine ant from Brazil as *Cyphomyrmex asper,* which, though considerably larger than the above described species, would seem nevertheless to belong to the same subgenus. More recently Emery (Bull. Soc. Ent. Ital., XXXVI, 1905, pp. 162, 163) has described and figured a single worker specimen from Chubut, Argentina, as dubiously referable to Mayr's species. This specimen measures 3 mm. in length and has no reëntrant notch between the anterior lobular and posterior ridge-like portions of the frontal carinæ, and the shape of the thorax appears to differ considerably from that of *hartmanni.* Emery, to whom I sent some workers of this latter form, says, however, that both species "connetano tra loro i generi *Atta* e *Cyphomyrmex;* é dubbio a quale dei due convenga meglio assegnarli." As I shall show in the latter part of this paper, the habits of *hartmanni* are much more like those of *Trachymyrmex* than *Cyphomyrmex,* so that the subgenus *Mycetosoritis,* which I have erected for this species and *aspera* Mayr, belongs rather with *Atta* s. lat. *M. hartmanni* should be regarded as the type of this subgenus as Mayr's species is so imperfectly known.

10. **Atta (Mycocepurus) smithi** *Forel.*

Atta (*Mycocepurus*) *smithii* Forel, Trans. Ent. Soc. London. 1893, p. 370. ☿.

Worker. (Pl. XLIX, Figs. 15 and 16.) Length: 2.2–2.5 mm.

Head, without the mandibles, slightly longer than broad, a little broader in front than behind, with obtusely excised posterior border, pointed posterior corners and rather convex sides. There is a distinct though shallow occipital groove. Eyes moderately convex, just behind the middle of the head. Mandibles narrow, acute, with oblique, 5-toothed blades. Clypeus short and broad, with entire, nearly straight anterior border. Frontal carinæ with small rounded lobes, very close together and separated only by a narrow, cuneate groove; they are continued behind as low diverging ridges which fade away before reaching the posterior corners. Postorbital carinæ indistinct, reaching the posterior corners but not including with the frontal ridges distinct grooves for the accommodation of the antennal scapes. Scapes much shorter than the funiculi, slightly thickened towards their tips, which barely surpass the posterior corners of the head. Thorax long, in front about ⅔ as broad as the head, with deep mesoëpinotal constriction. Pronotum without inferior spines, above with four upwardly directed spines arranged in an arc with its convexity directed forward; the two outer spines longest and each with a small acute tooth in front of its base; the inner pair of spines small. Mesonotum also with an arc of four spines but with its convexity directed backward, so that the spines on both segments form a broad ellipse. The anterior mesothoracic spines are longer than the posterior pair. There is also a pair of small projections close together near the anterior borders of the mesonotum and in the middle of the ellipse. Epinotum with the base fully twice as long as the declivity, the former with four successive pairs of spines, the first and third very short and acute, the second longer and the fourth, representing the typical epinotal spines of other Attii, fully as long as the declivity, slender, pointed, directed upward and slightly backward and outward, curved inward at their tips. Metasternum with a small blunt tooth on each side. Petiole from above narrow, fully twice as long as broad, somewhat violin-shaped, broader behind than in front, constricted just in front of the node which is cuboidal, with a concave surface and each of the four upper corners produced into a small spine. In profile its upper surface is horizontal, its anterior slope long and concave. Postpetiole nearly four times as broad as the petiole and nearly as broad as long, campanulate, with four longitudinal ridges of which the median pair are blunter and separated by a longitudinal groove deepening suddenly at the posterior margin of the segment to form a somewhat circular pit. Gaster much smaller than the head, fully ⅓ longer than broad, widest posteriorly, with straight sides and anterior border and acute anterior angles. The first segment has a sharp longitudinal ridge on each side but no median depression. Legs long and rather stout.

Opaque throughout; mandibles very finely striated; head above irregularly reticulate-rugose, more coarsely behind than in front. Remainder of body and appendages very finely and obscurely punctate-granular and faintly reticulate, except the gaster which is more distinctly and evenly punctate and slightly roughened on its upper surface. Legs and scapes also slightly scabrous.

Hairs yellowish; very short, curved and sparse, subreclinate, most distinct on the gaster and appendages. Pubescence very fine, whitish, confined to the antennal funiculi.

Yellowish ferruginous; upper surface of head and gaster and the ridges and tips of the spines darker. Mandibular teeth black.

St. Vincent: Bellisle (H. H. Smith).
Cuba.

I have redescribed this species from a type specimen kindly sent me by Professor Forel who has also described a closely related species, *M. gœldii*, from Brazil. The subgenus *Mycocepurus*, as Forel has shown, is related to the other subgenera of *Atta* on the one hand and to *Cyphomyrmex* and *Myrmicocrypta* on the other. It is peculiar and aberrant, however, in its small size, its small, closely approximated frontal lobes and spinulation. Hitherto *M. smithi* has been known only from St. Vincent. I have received specimens from Cuba. Among the materials in my collection I find also a number of workers from two other localities and representing the following varieties:

11. **Atta (Mycocepurus) smithi** var. **borinquenensis** var. nov.

Porto Rico: Vega Baja, Arecibo, Utuado, Monte Mandios (Wheeler).

The workers of this form resemble the type very closely in size, coloration and sculpture but have on each side of the occipital furrow at the posteromedian border of the head, a distinct tooth which is nearly as large as the teeth which form the posterior corners. The posterior epinotal spines are curved inward at their tips as in the type.

12. **Atta (Mycocepurus) smithi** var. **tolteca** var. nov.

Mexico: Tuxpan, Jalisco (J. F. McClendon).

Closely resembling the type, but of a yellow color and with straight, more acute and more erect posterior epinotal spines and feebler cephalic sculpture. The two median occipital teeth of *borinquenensis* are represented by low, pointed ridges.

13. **Cyphomyrmex rimosus** *Spinola.*

Cryptocerus ? rimosus SPINOLA, Mem. Accad. Sci. Torino (2), XIII, 1851, p. 65 no. 49, ☿ ♂.
Cryptocerus rimosus F. SMITH, Trans. Ent. Soc. London (2), II, 7, 1854, p. 223, no. 28.
Meranoplus difformis F. SMITH, Catalog. Hymen. Brit. Mus., VI, 1858, p. 195, no. 7, ☿.
Cryptocerus rimosus F. SMITH, Trans. Ent. Soc. London (3), I, 4, 1862, p. 409, no. 11, ☿.
Meranoplus difformis F. SMITH, Trans. Ent. Soc. London (3), I, 4, 1862, p. 413, no. 7, ☿.
Cyphomyrmex deformis MAYR, Verh. zool. bot. Ges. Wien, XXXVII, 1887, p. 558, ☿ ♀ ♂ (in part).
Cyphomyrmex rimosus DALLA TORRE, Catalog. Hymen., VII, 1893, p. 150 (in part).
Cyphomyrmex rimosus EMERY, Bull. Soc. Ent. Ital., XXVI, 1894, pp. 88, 89.
Cyphomyrmex rimosus URICH, Trinidad Field Nat. Club, II, no. 7, 1895, p. 181.
Cyphomyrmex rimosus FOREL, Biol. Centr.-Am., Hymen., III, 1899–1900, p. 40.

The typical form of this widely distributed and variable species appears to be confined to northern South America and the adjacent mainland of Central America and Mexico. It is represented in my collection by a few worker and female specimens from Grenada, Nicaragua (C. T. Baker) and a number of workers from Manatee, British Honduras (J. D. Johnson). In these specimens the postpetiole of the worker is less than twice as broad as long and the color is of a rich yellowish brown, with the head and posterior portion of the gaster clouded with dark brown. In the female the postpetiole is scarcely broader in proportion to its length and has a perfectly straight posterior border. According to Emery the male has a relatively narrow head, with very acute posterior angles and the postpetiole is less than 1½ times as broad as long. A single worker in my possession from Hayti (P. J. Schmitt) approaches the typical *rimosus* more closely than the Central American specimens, as its thoracic protuberances are longer and more acute and the postpetiole is only 1½ times as broad as long. The following variety, according to Emery (*in litteris*), approaches the typical *rimosus* very closely except in its darker color.

14. **Cyphomyrmex rimosus** var. **comalensis** var. nov.

Worker. (Pl. XLIX, Fig. 1.) Length: 1.8–2 mm.

Head, without the mandibles, longer than broad, much narrower in front than behind, with obtusely excised posterior margin and rather sharply angular posterior corners. Eyes moderately convex, near the middle of the head. Mandibles small, 5-toothed. Clypeus short on the sides, with a triangular median portion which has a rounded, raised and entire anterior border. Behind it is wedged in between the frontal carinæ which are dilated in front to form two large horizontal lobes impressed in the middle, rounded on the sides, bluntly angular in front and separated at the level of the eye by a reëntrant angle from the posterior ridges. These diverge and extend to the posterior corners of the head where they meet the postorbital ridges and form with them rounded ear-like lobes. Each postorbital ridge is furnished with a blunt but distinct tooth just behind the eye. The frontal and postorbital ridges enclose a deep groove for the accommodation of the antennal scape. Vertex of head with a pair of low, rounded elevations. Antennal scapes robust, thickened towards their tips which extend a little beyond the posterior corners of the head; funiculi slender at the base; joints 2–8 slightly broader than long. Pronotum with four blunt protuberances above in a transverse row, the lateral pair larger and more angular, the inner pair small and closer together than to the lateral pair. Mesonotum a little longer than broad, broader in front than behind, on each side with a blunt ridge, nearly interrupted in the middle so that in certain lights the mesonotum seems to bear two pairs of blunt, elongated elevations. Mesoëpinotal constriction very short and rather deep. Epinotum with a convex base, which is considerably shorter than the sloping, flattened declivity, and with a pair of anteriorly converging ridges. The spines are represented by very small, blunt elevations at the posterior ends of these ridges. Petiole somewhat more than twice as broad as long, flattened above, with rounded sides, only $\frac{2}{3}$ as broad as the postpetiole, which is twice as broad as long, convex in front and with a feeble excision in its posterior border. In front of this excision there is a distinct elongate median depression. Gaster suboblong, somewhat longer than broad, with a very short and indistinct median depression at the anterior border. Legs long and stout; hind femora bent and angularly dilated near the base on the flexor side.

Opaque throughout; mandibles very finely and densely striated; remainder of body minutely granular.

Hairs white, short, scale-like, appressed and uniformly distributed, more slender on the legs than on the body. Pubescence very fine, whitish, confined to the mandibles and funiculi.

Very dark brown, upper surface of head and gaster black, anterior portions of the frontal lobes, antennal scapes and tibiæ dark brown; remainder of legs, funiculi and mandibles light brown.

Female. Length: 2.2–2.4 mm.

Head very similar to that of the worker. Pronotum with pointed inferior angles at the coxal insertions, and above with a pair of blunt angular projections which are as broad at their bases as long. Mesonotum anteriorly with a longitudinal median depression and distinct Mayrian furrows, so that its surface is separated into four slightly convex, elongated areas, two anterior and two posterolateral. Epinotum with very short, convex base and long, abrupt and concave declivity; spines blunt, laterally compressed, shorter than broad at their bases. Scutellum flattened, broader than long; its posterior margin excised in the middle and produced as a broad tooth on each side. Pedicel, gaster and legs similar to those of the worker, but the postpetiole nearly three times as broad as long, with nearly straight posterior border.

Like the worker in sculpture and pilosity.

Head, postpetiole, gaster and appendages colored as in the worker. Thorax dark brown, mesonotum and scutellum blackish, each of the convex areas of the former with a reddish brown spot. Wings opaque, smoky brown, with pale veins.

Male. Length: 2.3 mm.

Head, including the eyes, about as broad as long, with straight posterior border and acute posterior angles. Eyes large and convex, in front of the middle of the head. Ocelli projecting. Mandibles rather slender, with two apical and no basal teeth. Clypeus convex, with very faintly notched anterior border. Lobes of frontal carinæ like those of the worker but erect; posterior ridges obsolete. Antennæ slender; scapes suddenly thickened towards their tips and surpassing the posterior corners of the head by nearly ½ their length; funicular joints cylindrical, less than twice as long as broad except the four terminal joints which are longer; first funicular joint thicker than the others. Thorax similar to that of the female but much more slender; basal surface of epinotum longer; spines short and rather acute. Petiole and postpetiole like those of the worker, but the former segment is proportionally longer and the latter has the median depression further forward. Gaster elliptical, slightly flattened; first segment in front with a narrow, faintly impressed line. Genitalia retracted. Legs slender; hind femora without a triangular projection on the flexor side.

Opaque; gaster finely shagreened and distinctly shining.

Appressed white hairs less scale-like and conspicuous than in the worker and female, especially on the gaster; very short on the legs and antennal scapes.

Coloration similar to that of the worker; terminal gastric segments, legs and antennæ dull yellowish brown. Wings as in the female.

Texas: Sources of the Comal River at New Braunfels (Wheeler).

15. **Cyphomyrmex rimosus** var. **fuscus** *Emery.*

EMERY, Bull. Soc. Ent. Ital., XXVI, 1894, p. 89, ☿ ♀ ♂.

In this variety, described from Santa Catharina, Brazil, all three phases are "entirely brown; mandibles, funiculi and articulations reddish; stature a little more robust" than the typical form.

16. **Cyphomyrmex rimosus** var. **major** *Forel.*

FOREL, Ann. Soc. Ent. Belg. XLV, 1901, p. 125. ☿.

In the worker of this variety from Guatemala the stature is somewhat larger (2.7–2.8 mm.) than that of the typical form, the ear-like corners of the head longer and the thoracic ridges and projections more prominent.

17. **Cyphomyrmex rimosus minutus** *Mayr.*

Cyphomyrmex minutus Mayr, Verh. zool. bot. Ges. Wien, XII, 1862, p. 691 no. 1 ☿.
Cataulacus deformis Roger, Berl. entom. Zeitschr., VII, 1863, p. 210, no. 104, ♀ ♂.
Cyphomyrmex steinheili Forel, Bull. Soc. Vaud. Sc. Nat. (2) XX, 91, 1884, p. 368, ☿,
Cyphomyrmex deformis Mayr, Verh. zool. bot. Ges. Wien, XXXVIII, 1887, p. 558, ☿ ♀ ♂ (in part).
Cyphomyrmex rimosus Dalla Torre, Catalog. Hymen., VII, 1893, p. 150 (in part).
Cyphomyrmex rimosus Forel, Trans. Ent. Soc. London, 1893, Pt. IV, p. 374.
Cyphomyrmex rimosus subsp. *minutus* Emery, Bull. Soc. Ent. Ital., XXVI, 1894, p. 89, ☿ ♂.
Cyphomyrmex rimosus Forel, Biol. Centr.-Am., Hymen., III, 1899–1900, p. 40 (in part).
Cyphomyrmex rimosus subsp. *minutus* Wheeler, Bull. Am. Mus. Nat. Hist., XXI, 1905, p. 106, figs. N. and O.

Venezuela: Cayenne (Emery).

West Indies: Cuba (Mayr); St. Vincent (H. H. Smith); New Providence, Bahamas (Wheeler); Culebra and Porto Rico (Wheeler).

Florida: Planter, Key Largo (Wheeler).

This subspecies which is confined to the West Indies and adjacent shores of North and South America, appears to differ very slightly from the typical form of the species and the var. *comalensis.* The worker is somewhat smaller and often of a paler color, with the thoracic projections more feebly developed and more rounded and the vestiges of the epinotal spines even more insignificant. Both the petiole and postpetiole are considerably broader, each being fully twice as broad as long. According to Emery the male of *minutus* has the head rounded behind, but my specimens from the Bahamas and Porto Rico have the posterior border of the head straight and the posterior angles projecting as acute teeth. In the female the epinotum is very steep, with small, blunt spines. Forel seems never to have accepted this subspecies, and I am myself very doubtful whether it deserves to rank as such. It is certainly much less distinct and less easily recognizable than the following:

18. **Cyphomyrmex rimosus dentatus** *Forel.*

Cyphomyrmex rimosus race *dentatus* Forel, Ann. Soc. Ent. Belg., XLV, 1901, p. 124 ☿.
Cyphomyrmex rimosus subsp. *dentatus* Wheeler, Ann. Soc. Ent. Belg., XLV, 1901, p. 200.

Mexico: Cuernavaca (Wheeler).

The worker of this marked subspecies is described by Forel as follows: "Differs from the type in that the basal surface of the epinotum has two distinct teeth. The pronotal protuberances are stronger, more dentiform. The occipital ears are a little more pronounced than in the type of the species, and especially form a more complete and larger groove for the scape which surpasses them little if at all. Entirely pale ferruginous yellow, with the front and vertex indistinctly brown. The petiole is also broader. The postpetiole has a strong median notch at the middle of its posterior border and its sides are prolonged as dentiform cones which are curved backward. The sculpture is that of *rimosus,* but the gaster has a distinct but very fine system of minute, blunt tubercles. The pubescence is extremely short and very fine, not dilated nor brilliant, so that it is inconspicuous."

Two deälated females of *dentatus* in my collection measure 2.4 mm. in length, and have prominent but blunt and upturned prothoracic spines and strong laterally compressed epinotal teeth; the epinotal declivity is very concave, the posterolateral cones of the postpetiole are more prominent and the median dorsal region of the same segment is more concave than in the worker. The head and thorax are much rougher than in the females of the typical *rimosus* and the gaster is more strongly tubercular, with a short but deep median depression at the base of the first segment. The body is dark brown, the upper surface of the head and thorax blackish and covered with a bluish bloom.

19. **Cyphomyrmex rimosus transversus** *Emery.*

Cyphomyrmex rimosus subsp. *transversus* Emery, Bull. Soc. Ent. Ital., XXVI, 1894, p. 90, ☿ ♀ ♂.

Cyphomyrmex dentatus race *olindanus* Forel, Ann. Soc. Ent. Belg., XLV, 1901, p. 337, ☿.

Cyphomyrmex rimosus transversus Emery, Bull. Soc. Ent. Ital., XXXVIII, 1905, p. 161, ☿ ♀ ♂.

Brazil: Matto Grosso (Emery); Ceara and Olinda (P. J. Schmitt).

The worker of this subspecies resembles *dentatus* in sculpture and in the development of the thoracic projections, but the appressed hairs on the body are broader and more scale-like even than in the typical *rimosus,* the petiole and postpetiole broader, and the median dorsal impression on the latter and on the base of the first gastric segment deeper and longer. The epinotum has blunt but distinct teeth.

In the female the epinotal teeth are very large, compressed and obtuse, the pedicel even broader than in the worker.

The male has the posterior border of the head broadly excised and the posterior corners with acute, slightly recurved teeth. Except in pilosity *transversus* is closely related to *dentatus,* as Forel has observed.

20. **Cyphomyrmex rimosus salvini** *Forel.*

Cyphomyrmex rimosus race *salvini* Forel, Biol. Centr.-Am., Hymen., III, 1899–1900, p. 40, pl. iii, fig. 2. ♀.

Forel described only the female of this form from a specimen taken at Bugaba, Panama. The late Dr. F. C. Paulmier brought me from Port Limon, Costa Rica two males and several workers which seem to me to belong to this same form. The worker is larger than that of any of the other subspecies of *rimosus,* measuring nearly 2.5 mm. The frontal lobes are very large and concave, the ear-like corners of the head much prolonged and pointed. The thoracic projections, especially the anterior pronotal pair, are long and acute, the epinotal teeth very faintly indicated. The petiole is more than twice as broad as long, the postpetiole about 1½ times as broad as long, with excised posterior margin and a posteromedian impression. There is also a distinct median impression at the base of the gaster. The hairs are much flattened and scale-like, pearly white and abundant, appressed on the body, but reclinate or even suberect on the legs and scapes. The body is light chocolate brown, the legs and antennæ paler.

The female according to Forel's description, measures 3.7 mm. and is very similar to the worker in the shape of the head. The superior pronotal teeth are stout and triangular, the epinotal teeth much reduced. The postpetiole is proportionally broader than in the worker, the gaster very convex, feebly marginate on the sides and without any indications of depressions and elevations.

The male, too, is decidedly larger than the corresponding sex in other forms of *rimosus,* measuring nearly 3 mm. in length. The superior occipital teeth are short and acute, the superior pronotal pair blunt and rather slender. In the place of the spines, the epinotum has a pair of broad, laterally compressed projections, which are continued forward and backward on the base and declivity as prominent ridges. The hairs on the body and appendages are all appressed and not very abundant, not dilated on the legs and only slightly scale-like on the body. The latter is chocolate brown like that of the worker, with the first gastric segment blackish, the mandibles, clypeus, frontal lobes, antennæ, legs, terminal gastric segments and genitalia dull yellow. The wings are very dark brown or blackish.

21. **Cyphomyrmex wheeleri** *Forel.*

Forel, Bull. Soc. Ent. Suisse, X, 7, 1900, pp. 282–284, ☿ ♀.

Worker. (Pl. XLIX, Fig. 2.) Length: 2.–2.5 mm.

Head, without the mandibles, longer than broad, broader behind than in front, with obtusely excised posterior margin and rather sharp, ear-like posterior corners. Eyes moderately large, convex, at the middle of the head. Mandibles acute, with five sharp teeth. Clypeus with thin, entire anterior border. Frontal area triangular. Frontal carinæ with large, rounded anterior lobes, each with a circular impression, and continued back as a pair of strong, straight, diverging ridges to the posterior corners, where they loop around and become continuous with the postorbital carinæ, thus enclosing deep grooves for the antennal scapes. Each postorbital carina bears a prominent tooth just behind the eye. Vertex with a pair of short longitudinal ridges as far apart as each is from the posterior ridge of a frontal carina and continued laterally along the occipital border to the posterior corner. Here also the 'ears' are joined by a pair of prominent ridges from the posteroinferior surface of the head. Antennal scapes very slender at the base, enlarged towards the tips which reach the posterior corners of the head; joints 2–8 of the funiculus a little broader than long. Pronotum with a pair of acute inferior teeth and above with a larger pair of angular humeral projections and a median pair of smaller projections. Mesonotum elevated in the middle in the form of an elongate elliptical, slightly concave disc, truncated behind, with a faint transverse depression on its posterior portion and bordered with a prominent ridge which is interrupted in the middle in front. Mesoëpinotal constriction short and deep. Epinotum as high as the mesonotum, its base very convex and nearly as long as the concave declivity with which it forms an obtuse angle in profile. Spines laterally compressed, short and triangular, as broad at the base as long, directed backward and continued forward and backward as ridges on the base and declivity. There is also a pair of lateral ridges on the base. Petiole nearly twice as broad as long, as broad in front as behind, with rounded anterior angles; node short, compressed anteroposteriorly, with two spines, directed upward and backward. Postpetiole trapezoidal, 1½ times as broad as the petiole and less than twice as broad as long, with two blunt anterior, two larger and more rounded posterior protuberances and a broad, longitudinal depression in the middle; posterior border entire. Gaster suboblong, distinctly longer than broad, as broad in front as behind; first segment convex above, with distinct lateral ridges and a faint median depression at the base. Tibiæ somewhat compressed; hind femora curved, angularly dilated and compressed near the base on the flexor side.

Opaque throughout; mandibles very finely and indistinctly striated. Remainder of body very finely granular-punctate; antennal grooves and gaster densely and distinctly punctate.

Hairs short, glistening white, scale-like and appressed, uniformly distributed over the appendages and upper surface of the body. Pubescence very fine, whitish, confined to the antennal funiculi.

Yellowish ferruginous; mandibular teeth black.

Female. Length: 2.5–2.7 mm.

Very similar to the worker. Pronotum with prominent inferior and superior teeth, the former acute, the latter larger and blunt. Mesonotum prominent, flattened, with a faint median furrow anteriorly and a pair of broader Mayrian furrows. Scutellum with very broadly and faintly excised posterior border separating a pair of broad, acute teeth. Epinotum with the base convex and only about half as long as the abrupt concave declivity; spines similar to those of the worker but somewhat stouter.

Sculpture and pilosity as in the worker.

Color a little darker in old specimens. Wings opaque, infuscated; the membranes and veins in the anterobasal portion of both fore and hind wings fulvous.

Male. Length: 2.4–2.6 mm.

Head, without the mandibles and eyes, narrow, longer than broad, with straight posterior border. Mandibles like those of the worker but less distinctly denticulate. Frontal carinæ with large, reflected lobes and strong, diverging posterior ridges reaching to the posterior corners where each terminates in a compressed, projecting tooth. Postorbital carinæ absent. Antennæ slender, scapes enlarged towards their tips which surpass the posterior corners of the head by about ⅓ of their length. Pronotum with indistinct inferior, but prominent and acute superior teeth. Mesonotum with distinct Mayrian furrows. Scutellum like that of the female, but with more deeply excised posterior border. Petiole and postpetiole like those of the worker and female. Gaster elliptical, convex above. Legs long and slender. Hind femora not angularly dilated below.

Opaque; very finely and densely punctate; gaster faintly shining or glossy.

Pilosity very similar to that of the worker and female.

Ferruginous; upper surface of head and the thoracic depressions blackish; basal segment of gaster dark brown above. Mandibles, antennæ, legs and tip of gaster yellowish. Wings like those of the female.

Texas: Austin, Belton, Langtry, Fort Davis (Wheeler).

California: Three Rivers (Culbertson).

The types from which the worker and deälated female were carefully described by Forel, are from Austin. The species is allied to the South American *C. strigatus* Mayr and *C. auritus* Mayr but differs from both in having larger frontal lobes and in lacking prominent ridges on the middle of the first gastric segment. The ear-like posterior corners of the head are much shorter than in *auritus* and the scapes are shorter than in *strigatus*.

22. **Cyphomyrmex flavidus** *Pergande.*

Cyphomyrmex flavidus Pergande, Proc. Calif. Acad. Sci. (2), V, Dec. 1895, p. 895, ☿.
Cyphomyrmex flavidus Forel, Biol. Centr.-Am., Hymen., III, 1899–1900, p. 41.

Worker. Length: 2.2–2.8 mm.

Head, without the mandibles, longer than broad, broader behind than in front, with obtusely excised posterior border and prominent posterior corners. Eyes convex, at the middle of the head. Mandibles small and acute, with oblique, apparently 5-toothed blades. Clypeus long and rather flat, with a minute median excision in its thin anterior border. Frontal area triangular. Lobes of frontal carinæ very large, horizontal, half as long as the head and extending out laterally a little beyond the borders of the head. Posteriorly each of these lobes has a deep subtriangular depression in its surface. The ridges of the frontal carinæ diverge backward to the posterior corners where they pass over into the postorbital carinæ, not through a rounded arc but rectangularly, so that the termination of the antennal groove is broad and truncated. There is a ridge on each side of the inferior occipital portion of the head and a pair of projections on the vertex, which are continued laterally along the occipital border as a pair of blunt ridges to the posterior corners. Antennal scapes enlarged towards the tips, which extend a little beyond the posterior corners; joints 2–7 of the funiculus a little broader than long. Thorax robust; pronotum with a pair of acute inferior teeth, which are directed forward, and a blunt protuberance on each side above. Mesonotum in the form of an elevated, elliptical and slightly concave disc, bordered with a low ridge which is interrupted in the middle behind and in the middle on each side. This ridge bears a pair of rounded swellings just in front of its lateral interruptions. Mesoëpinotal constriction deep and narrow. Epinotum with a pair of swellings at its base; declivity sloping, longer than the base; spines reduced to a pair of laterally compressed and rather acute teeth which are as long as they are broad at the base. Petiole and postpetiole resembling each other in shape, the former twice as broad as long, broader behind where its sides are produced as a pair of blunt angles; it is flattened above, without spines or teeth and with a small semicircular impression in the middle of its posterior border. Postpetiole ⅓ broader than the petiole, more than twice as broad as long, rounded in front, with a median groove, broadening behind; posterior margin with three semicircular impressions of which the median is the largest. Gaster longer than broad, suboblong, with straight, feebly marginate sides, rounded anterior and posterior borders, and a short median groove at the base of the first segment. Hind femora curved, with an angular, compressed projection near the base on the flexor side.

Opaque throughout, very finely and densely punctate-granular.

Hairs minute, appressed, slightly dilated, glistening white, rather sparse and indistinct. Pubescence fine, whitish, confined to the antennal funiculi.

Ferruginous yellow; clypeus, frontal lobes, front and middle of vertex more or less brownish; mandibular teeth black.

Mexico: Santiago Ixtquintla, Tepic (Eisen and Vaslit).

This species, which I have redescribed from a type specimen kindly sent me by Mr. Pergande, at first sight closely resembles *C. wheeleri.* It may be distinguished, however, by the absence of teeth on the petiole, the much broader and more truncated ear-like corners of the head, longer antennal scapes and much blunter ridges and projections on the thorax. *C. flavidus* is thus intermediate in several respects between *wheeleri* and *rimosus,* but is undoubtedly a distinct species. Although at present known only from northern Mexico, it may be expected to occur as far north as the southern portions of Arizona and California.

23. **Myrmicocrypta brittoni** sp. nov.

Worker. (Pl. L, Figs. 18 and 19.) Length: 2.3–2.5 mm.

Head, without the mandibles, about as broad as long, slightly broader behind than in front, with obtusely excised posterior border, rather straight sides, rounded posterior corners and a narrow median longitudinal groove. Eyes distinctly in front of the middle, of moderate size and convexity. Mandibles large, convex, with straight outer and inner borders, the latter with about ten teeth which grow gradually smaller towards the base. Clypeus short, with entire, flattened and very broadly rounded anterior border. Frontal carinæ with flattened but slightly reflected lobes, which are much longer than broad, with roundly angular external edges reaching only half the distance between the median line and the external border of the head. Mesially these lobes are fused with the posterior portion of the clypeus and enclose the small, indistinct frontal area which is triangular and longer than broad. The lobes of the frontal carinæ are not continued behind in the form of diverging ridges as in other Attii. Lateral carinæ sharp and distinct, continued to the posterior orbits and bounding a broad, short and deep antennal groove. There are no postorbital carinæ. Antennæ rather slender; scapes slightly curved at the base and enlarged towards their tips, which slightly surpass the posterior corners of the head; funicular joints all considerably longer than broad, terminal joint nearly as long as the four preceding joints together. Thorax long and rather narrow, in front about $\frac{2}{3}$ as broad as the head. Pronotum with small, acute inferior angles. There is a pair of blunt epinotal teeth, but otherwise the thorax is smooth and without spines or projections. Mesoëpinotal constriction distinct, but long and rather shallow. Humeral angles rounded, mesonotum about as long as the pronotum, elongate elliptical, flattened, slightly higher than the epinotum. Epinotum with subequal base and declivity, the former straight and horizontal, the latter concave and sloping, without longitudinal ridges. Metasternum with a small rounded tubercle on each side. Petiole oblong, a little broader than long, with slightly rounded anterior and acute posterior corners; node evenly convex above, suddenly constricted anteriorly into a very short peduncle. Postpetiole nearly twice as broad as the petiole, somewhat broader than long, with straight posterior border, rounded anterior corners and straight, subparallel sides; convex and evenly rounded above without a posteromedian impression. Gaster smaller than the head, longer than broad, elliptical, with straight anterior border and convex upper surface, without lateral ridges or median impression on the first segment. Legs slender, hind femora straight and without an angular projection on the flexor side.

Opaque throughout; mandibles slightly glossy, very finely and densely striated; remainder of body very densely and uniformly punctate.

Hairs short, glistening white, dilated and scale-like, appressed, uniformly distributed over the body and appendages. Antennal funiculi and tarsi with delicate whitish pubescence.

Black; clypeus, antennal grooves, inferior corners of pronotum, antennal scapes, coxæ and legs, dark brown; mandibles, except the teeth, tips of scapes, funiculi, tarsi and articulations of legs light brown or yellowish.

Porto Rico: Santurce (Wheeler).

Though at once recognizable as an Attiine ant, this species is nevertheless so unlike any of the species of which I had seen specimens or descriptions that I at first decided to make it the type of a new genus or subgenus. Professor Forel, to whom I sent specimens, has kindly given me a worker of a species which he took some years ago in Colombia. This species, which he will describe as *M. emeryi*, is intermediate in certain characters, such as the structure of the frontal lobes, between the above described *brittoni* and *M. squamosa* F. Smith (= *uncinata* Mayr). *M. emeryi* differs from *brittoni* in having a much longer and more slender thorax, pedicel, legs and antennæ, in being of a lighter (brown) color and in having the appressed hairs on the body and legs, long and not scale-like. The clypeus, lower surfaces of the mandibles and the gula have conspicuously long and projecting hairs. The petiole is nearly twice as long as broad, the postpetiole slightly longer than broad and with a deep rounded excision in the middle of its posterior border. The mandibles are more slender, with more oblique blades and fewer teeth. The epinotal teeth are distinctly longer and directed upward. The frontal carinæ are smaller and the tips of the antennal scapes extend further beyond the posterior corners of the head. According to Mayr's description the thorax in the worker of *squamosa* is furnished with teeth and projections like the more typical Attii. The Porto Rican and Colombian forms therefore approach *Apterostigma* and *Sericomyrmex* much more closely than do the other known species of *Myrmicocrypta* and may be regarded as the simplest and most generalized members of the genus, if not of the whole Attiine tribe. I take great pleasure in dedicating the Porto Rican species to the distinguished botanist, Professor N. L. Britton, with whom I passed many delightful and profitable hours collecting plants and insects in Culebra and Porto Rico.

PART III. ETHOLOGICAL OBSERVATIONS.

1. **Atta texana** Buckley.

In the United States this large "cutting" or "parasol" ant (Fig. 7, and Pl. XLIX, Figs. 11–14), is the only species of the tribe Attii that forms sufficiently populous colonies to be of any economic importance, or, indeed, to be sufficiently common and conspicuous to attract the attention of any one but a myrmecologist. Although unable to determine its exact range, I have found no indications of its occurrence outside of a rather restricted area in Texas. This area appears to have its center at Austin and to comprise the territory for some hundreds of miles north and south in a narrow belt where there is a moderate annual rain-fall and where the forests are of a mesophytic character. I have never seen it in the dry western portions of the state nor have I heard of its occurrence in the more humid eastern counties, in Louisiana or the other Gulf States. It was seen as far south as Alice in Nueces County, and probably occurs as far north as Waco and Fort Worth. It certainly could not endure the winters of the "Panhandle" region nor even those of the extreme northeastern portion of Texas. Even in the vicinity of Austin large colonies of *Atta texana* are rather sporadic. It prefers the neighborhood of rivers and creeks and especially the rich soil of the pecan and the pure sand or somewhat clayey soil of the post-oak woods. In such spots one is always sure of finding it along the banks of the Colorado, Comal and Guadeloupe Rivers.

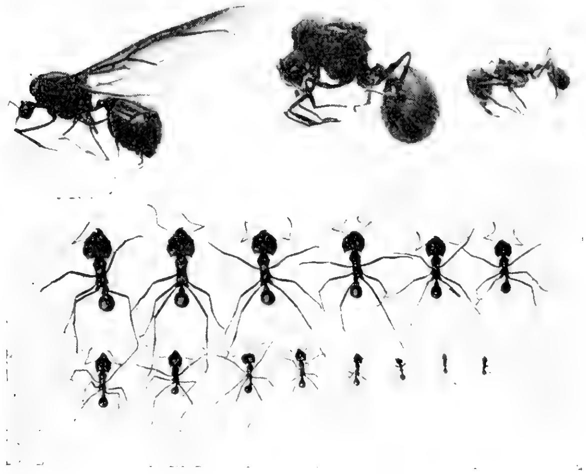

Fig. 7. *Atta texana* Buckley; male, deälated female, soldier and series of workers; natural size. (Photograph by Messrs. C. T. Brues and A. L. Melander.)

The nests are nearly always situated in places fully exposed to the sun, in clearings of the woods, in fields, along roads, etc. In some localities, as at Elgin, I have found them in the sand-ballast of the railway tracks. The nests can be recognized even at a distance as very flat mounds usually not more than one to two dcm. high, with very uneven surface and consisting of sand or soil of a lighter color than the surface of the surrounding country. Closer inspection shows that these mounds, which may cover an area of many square meters, have been derived from the walls of craters, washed down and fused with one another by the rains. Several perfect and recently constructed craters are commonly found on the top or about the edges of the mound, and in the case of large and active colonies these may be numerous, as in the nest shown in Fig. 8, which was situated on the left bank of the Colorado River between Austin and Montopolis. The craters in this instance covered an area of more than 100 sq. m. although the nest had not been in existence long enough to form a distinct mound. They varied from a dcm. to half a m. in diameter and from a few cm. to a dcm. high. Their typical form is shown in Fig. 9, which is taken from the nest represented in the preceding figure. The wall of the crater is often higher on one side than on the others, or it may be crescentic, that is, interrupted at one part of the circumference. The opening at the bottom varies from 3–6 cm. in diameter, is often very irregular in outline and leads vertically or somewhat obliquely downward into a gallery of the same diameter. The large size of the opening is evidently an adaptation for two very different purposes, first, for enabling the ants to carry in their pieces of leaves more

Fig. 8. Large *Atta texana* nest on the left bank of the Colorado River between Austin and Montopolis, Texas. (Photograph by Mr. C. G. Hartmann.)

easily, and second, for ventilating the subterranean portions of the nest. In the nests of *Atta texana* I have been unable to detect two kinds of craters, one used as entrances, the other for ejecting the exhausted portions of the fungus gardens, as Forel has observed in the Colombian *Atta cephalotes* and as I have observed at Cuernavaca, Mexico, in the nests of *A. mexicana*. All the craters when fresh, consist of large, uniform pellets of earth or sand, 3–5 mm. in diameter, which are carefully compacted and carried to the surface by the workers. The grains of sand or earth seem to be held together merely by the moisture that permeates the soil at the depth from which they are dug, rather than by any salivary secretion such as von Ihering supposes the Brazilian *A. sexdens* to employ for this purpose. The pellets disintegrate in the first rain, so that the walls of the craters become lower and more rounded and fuse with one another to form the low mound of older nests. The ants usually work at only a few of the craters at a time, and as only one or two of the openings are used when the ants are busily engaged carrying in leaves, it seems probable that the greater number of craters is constructed for the aëration of the nest and not for entrance or exit.

Fig. 9. One of the craters of the *Atta texana* nest represented in the preceding figure, about $\frac{1}{6}$ natural size. (Photograph by Mr. C. G. Hartmann.)

The depth and extent of the excavations vary, of course, with the size of the colony, its age, and the character of the soil. This is evident from the following notes on three nests examined at different seasons of the year.

April 10, 1900, Messrs. A. L. Melander and C. T. Brues assisted me in excavating a moderately large nest situated at the base of a juniper on the banks of Waller Creek, at Austin. There were at least twenty craters on the summit of the flat mound, which was about 5 m. across. These entrances measuring 2.5–4 cm. in diameter, were found to lead downward as tubular galleries converging towards and uniting with one another more and more, till a depth of about a meter was reached. Here each of the galleries, now greatly reduced in number, entered the top of a large chamber with vaulted roof and level floor. Some of these chambers were fully 30 cm. in diameter and 25 cm. high and as broad as long, others were much elongated. They were sometimes connected with one another by means of broad galleries, especially when lying at different levels. The rootlets of the juniper ran through some of the chambers or hung down freely into their cavities. Each chamber had a large placenta-like gray or white fungus garden covering the greater portion of its floor. Small gardens of a more nodular form also hung suspended, enveloping the juniper roots, which seemed to have been left untouched by the ants, during their excavations, for this very purpose. Each garden was a comb-like or sponge-like mass of triturated leaves and juniper berries, permeated and covered with a mould-like mycelium. This mass exhaled a rather pleasant odor not unlike that of stale honey, and crumbled so readily under the touch that it was impossible to remove it entire. It swarmed with workers, the soldiers being least, the mimims most numerous, whereas the mediæ were intermediate in numbers as well as in size. In one of the gardens we found the aged mother queen of the colony, three winged males, and a number of larvæ. Several of the disintegrated gardens together with many of the ants were carried to the laboratory and placed in large glass jars. By the following morning the insects had completely rebuilt their gardens. The coarser work of carrying and building up the particles of leaf-pulp fell to the lot of the mediæ, while the minims went about planting and pruning the tufts of fungus hyphæ. The huge soldiers merely stalked about on the surface of the gardens, often breaking down under their weight the walls of the delicate comb. The ants were confined in the jars for several days, and after the expiration of a week I made an observation that did not impress me as important at the time: the gardens, which were in a much less flourishing condition than when first installed in the jars, were seen to be covered with droplets of a brown liquid. As these droplets closely resembled those since described by J. Huber (*vide ante*, p. 698) as the excrement of the female *Atta sexdens*, it is probable that the soldiers and mediæ, unable to add fresh leaves to their rapidly deteriorating gardens, resorted to the very same method of manuring the mycelium as that employed by the queen *Atta* while she is founding her colony.

November 3, 1900, I excavated a large nest of *Atta texana* situated on the left bank of the Colorado River about a mile west of Austin. This nest was in pure sand at the edge of a sorghum field about 15 m. above the river bottom where it was overgrown with low willow, pecan and Texas persimmon trees. The ants were busy defoliating the willows and carrying their leafy burdens up the bank and into the nest along a path about 80 m. long. At intervals along this path piles of leaf-clippings, dropped by the ants, lay drying in the sun. The leaves were cut by the mediæ in the manner described by Mœller for the South American *Acromyrmex discigera*. The nest was in a promontory accessible from three sides, one of which formed the wall of a small ravine. The craters were very numerous and nearly all on the summit of the bank. The arrangement of the galleries and chambers was very similar to that described for the nest on Waller Creek, except that the chambers were at a lower level (1.5 to 2.3 m.) below the surface and much larger. One of them, of a crescentic form, measured nearly 1 m. in length and 30 cm. broad and high. All of the chambers, of which I examined fully a dozen, were situated in a damper layer of sand than

Fig. 10. Barton Springs, near Austin, Texas, the classic locality for the study of *Atta texana*. (Photograph by Messrs. Brues and Melander.)

that overlying them and contained huge fungus-gardens on their flattened floors. These gardens were 10–15 cm. high, of a yellowish color below and made up very largely of triturated sorghum leaves. Above they were bluish or greenish gray and this was the only portion that was permeated and covered with the living mycelium, the lower portions having lost their fungus-nourishing substances. The large amount of this exhausted leaf-pulp still retained in the chambers, showed that *Atta texana* must differ from some of the tropical species of this genus, which carry it to the surface and eject it from the craters. The Texan species simply keeps on building up its gardens till they reach a considerable thickness while the mycelium retreats to the more nutritive superficial layer. Many of the gardens in the nest under discussion contained worker larvæ and pupæ in abundance, but no sexual forms, either mature or immature. Both in this and in the previously described nest I found many specimens of a little myrmecophilous cockroach, of which I shall have more to say in the sequel. Although the

Fig. 11. Large *Atta texana* nest on the right bank of Barton Creek near Austin, Texas. (Photograph by Messrs. Brues and Melander.)

nest was easily excavated, owing to its location in an exposed bank of pure sand, nevertheless I was made very uncomfortable by the attacks of the soldiers, who actually drew blood with their sharp mandibles.

An interesting nest was excavated and measured by Messrs, Brues and Melander during the spring of 1903. This was situated on the right bank of Barton Creek (Fig. 10) near Austin, about 15 m. above the bed of the stream. In surface view (Fig. 11) it presented a low, irregular mound, consisting of fused or contiguous craters of pure sand resting on a layer of blue clay. As shown in the diagram, Fig. 12, galleries descended vertically from these craters through the blue clay layer, which was nearly 2 m. thick, and continued down through an equally thick layer of red clay, where they entered a layer of pure sand about a meter in thickness. At the top of this last layer they opened into a number of large chambers communicating with

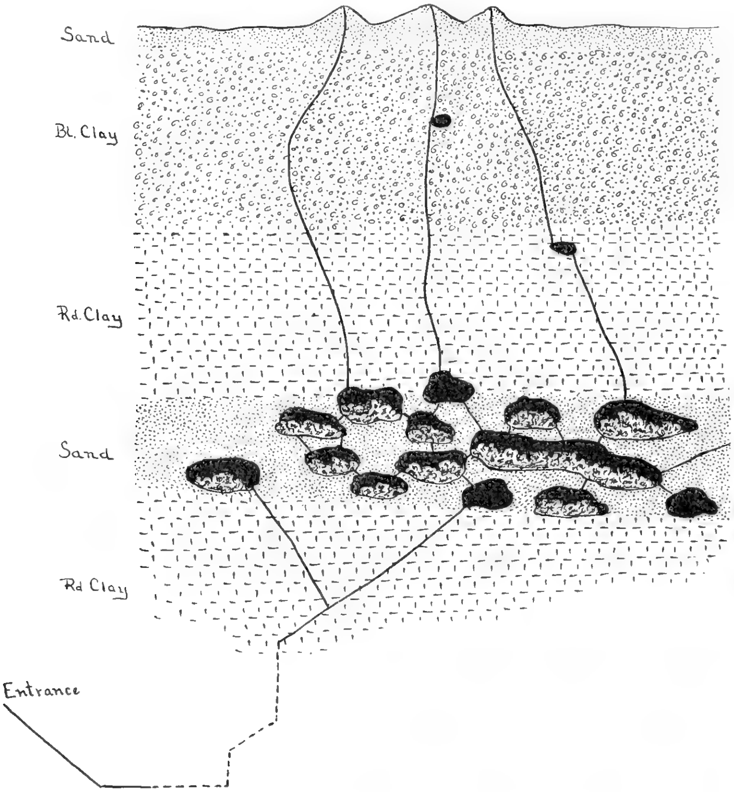

Fig. 12. Diagram of the *Atta texana* nest represented in the preceding figure. (From a sketch by Messrs. Brues and Melander.)

one another by means of short galleries. The chambers occupied the entire layer, so that the total depth of the nest was very nearly 5 m. Some of the chambers broken open by the pick, are represented in Fig. 13. In the lowermost of these one of the large fungus gardens is seen *in situ* resting on the floor. From the lower series of chambers a number of galleries continued down through another layer of clay, and finally united to form a single long gallery, which ran at first horizontally and parallel with the stream, but finally rose obliquely and opened on the surface of the bank a few meters above the water level and at a distance of fully 65 m. from the nest! This remarkable tunnel was the entrance through which the long file of workers brought the leaf-clippings to the chambers. The crater openings on the top of the bank seemed to be used only for excavating and ventilating purposes. That some of these, however, were the original entrances of the nest was proved by the presence of small dilatations or chambers only a few cm. in diameter in the course of the vertical galleries.

Fig. 13. Exposed chambers of nest represented in the two preceding figures A large fungus garden is shown *in situ* in the lowermost chamber. (Photograph by Messrs. Brues and Melander.)

These dilatations, two of which are indicated in the diagram, must have represented the chambers of the incipient nest and one of them was undoubtedly the original cell excavated by the mother queen of the colony.

In collecting the vegetable substances to serve as a substratum on which to grow their fungus, the workers of *Atta texana* seem to show no evidences of discrimination, further than that a colony usually concentrates its attention on one kind of material on each of its forays. I have seen workers of the same colony at different times cutting and carrying home the leaves of plants belonging to the most diverse natural orders. They seem indeed to prefer plants with small or rather narrow leaves, but the texture of the leaves is apparently a matter of little importance, for the ants may be seen defoliating soft herbs like the sheep sorrel (*Rumex acetosella*) or the clover, and anon attacking the tough leathery foliage of the live oak (*Quercus virginiana*). But even hard berries like those of the juniper are collected and embedded entire in the gardens. Once I saw a colony carrying away the cracked grains of maize from a hominy mill, and on another occasion the same colony was assiduously gathering large caterpillar droppings that had rained down from a plane tree near the nest. These ants occasionally enter gardens and defoliate rose-bushes or other ornamental shrubs or destroy tender vegetables, but their inability to concentrate their attacks for several consecutive days on particular species of plants, and the somewhat smaller size of their colonies than those of the tropical *Attæ*, make them much less dangerous economically than might be supposed.

Like many other Texan ants, *Atta texana* is more sensitive to the heat than to the sunlight. I infer this from the fact that during the winter and cool autumn and spring months it forages at all times of the day but during the hot summer months carries on its excavations and goes abroad only during the cool night hours. The sensitiveness of these ants to heat and to the humidity of the air is also shown by the fact that they carefully close their nest craters with earth, leaves, or sticks during hot, dry spells. This seems to be an adaptation for preventing the escape of the moisture from the nest through the large ventilating galleries and the consequent injury to the proliferating mycelia in the gardens. While opening the nest chambers of this and other species of Attii I have often seen the delicate fungi wither up within a few moments after exposure to the dry air.

I have not observed in *Atta texana* the method of comminuting the leaf-clippings but there can be little doubt that it is very much like that employed by *A. cephalotes* and *Acromyrmex discigera* as described by Tanner and Mœller. The macroscopic structure of the gardens (Figs. 14 and 15) has been correctly described by McCook (*ante*, p. 679). Their microscopic structure resembles very closely that of the *Acromyrmex* studied by Mœller.

There is the same beautiful, white mycelium with hyphæ .6–.8 μ in diameter everywhere threading and covering the comb-like leaf-pulp and densely dotted with clusters .2–.3 mm. in diameter of the small spherical or pear-shaped food-bodies (Kohlrabiköpfchen) 3–5.5 μ in diameter. As Mœller's terms for these structures are rather far-fetched, since to English-speaking peoples at least the kohlrabi is by no means a familiar vegetable, and as the structures really deserve somewhat more dignified or at any rate more technical appellations, I would suggest that the globular swellings of the hyphæ be called *gongylidia* and the grape-like clusters which they form, *bromatia*. The arrangement of the leaf-pulp at the surface of the gardens in the form of thin walls or plates greatly extends the exposed surface of the substratum, favors the growth of the plant, and thus increases the amount of it that can be raised in a circumscribed cavity. This arrangement also facilitates the control of the fungus and its cultivation and makes it more accessible as food.

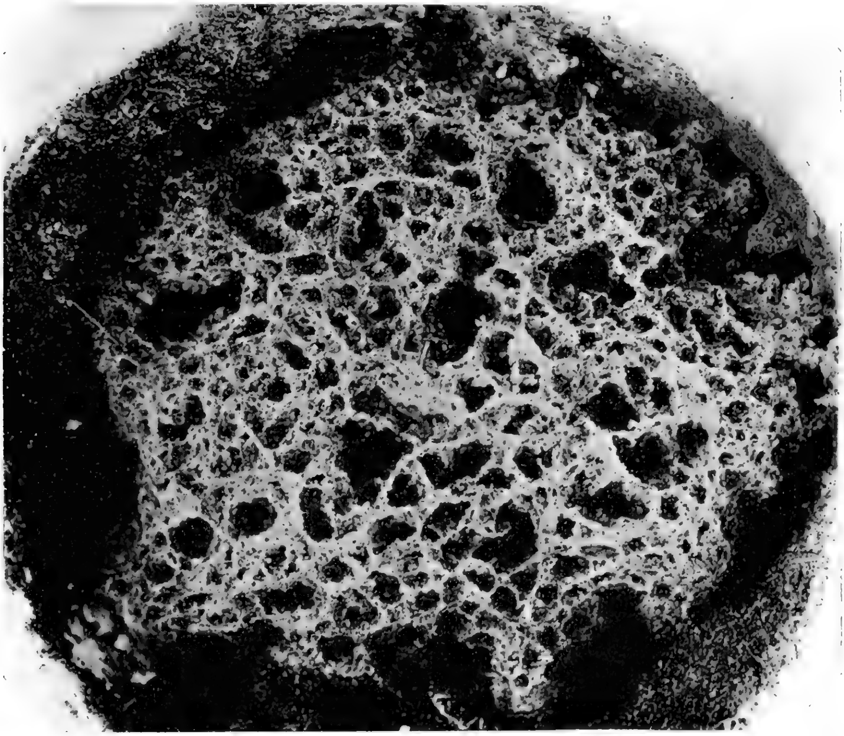

Fig. 14. Entire fungus garden of *Atta texana*, about ¼ natural size. (Photograph by Messrs. Brues and Melander.)

Some well-developed means of intercommunication would seem to be necessary for ants like *Atta texana* which live in great colonies and coöperate so intimately both on their foraging expeditions and in the cultivation of their delicate food plant. I am convinced that this means is supplied by the stridulatory organs which are highly developed in all the castes of the species. As I have shown in a former paper,[1] the stridulation of the huge females of *Atta texana* is audible when the insect is held a foot or more from the ear. The male and soldier to be audible must be held somewhat closer, the largest workers still closer, whereas the smaller workers and mimins, though stridulating, as may be seen by the rapid movements of the gaster on the postpetiole, are quite inaudible to the human ear. It is probable that all these differences in the rate of vibrations, or humanly speaking, of pitch, correlated as it is with a differentiation in the size and functions of the various castes, is a very important factor in the coöperation of these insects, especially in the often widely separated subterranean cavities in which they spend so much of their lives. Miss Fielde and Prof. Parker[2] have recently given good reasons for concluding that these vibrations are transmitted through the soil or other solids and not through the air, and that they are therefore perceived by the ants through their legs as tactile rather than as

Fig. 15. Portion of fungus garden of *Atta texana* built up by ants in confinement. (Photograph by Messrs. Brues and Melander.)

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[1] Ethological Observations on an American Ant (Leptothorax Emersoni Wheeler). Arch. f. Psychol. u. Neurol., II, 1903, p. 19, foot-note.

[2] The Reactions of Ants to Material Vibrations. Proc. Acad. Nat. Sci. Phila., Sept. 1904, pp. 642–650.

auditory sensations. This result agrees also with the accounts of others who have investigated the perception of vibrations in insects.

Of all ants the Attii would seem, at first thought, to offer in the great sponge-like masses of decomposing vegetable matter of their fungus gardens the most favorable of resorts for all kinds of myrmecophiles and synœketes. But the number of such animals hitherto observed in the nests of these ants is very small. This is probably due to the exquisite care and diligence with which the ants patrol and cultivate all parts of their gardens to prevent the growth of the aërial hyphæ, alien fungi and bacteria, for under such circumstances any intruder might be easily detected and ruthlessly destroyed. Nevertheless a few animals have managed to secure a foothold in the nests, but so far as known, only in those belonging to species of *Atta* s. str. and *Acromyrmex.* I have never seen any traces of myrmecophiles in the many nests of *Trachymyrmex*, *Mycetosorites* and *Cyphomyrmex* which I have examined. Bates (1892) and Brent (1886) state that certain Amphisbænian lizards manage to live in the *Atta* nests of Brazil and Trinidad. It is probable that these reptiles feed on the ants. Belt (1874) mentions a large *Staphylinid* beetle as occurring on the *Atta* nests of Nicaragua, and Wasmann (1900) concludes that this beetle, which he identifies as *Smilax pilosa* Fabr., is probably a true myrmecophile, because it so closely resembles the large *Atta* workers in its dark brown color and abundant pile. The same author (1894, 1895) mentions several Histerid beetles (*Philister rufulus* Lewis, *Hister* (?) *costatus* Mars, *Reninus salvini* Lewis and *Carcinops* (?) *multistriata* Lewis) as having been taken from the nests of *Atta mexicana,* and three Staphylinidæ belonging to the genera *Aleochara* and *Atheta* from the nests of *A. sexdens.* These are probably all not true guests but synœketes. To the same group belong also a number of specimens of the myriopod *Scutigera* which I found running about in the galleries of an *A. texana* nest.

The only myrmecophiles known to live in intimate relations with Attiine ants are the small and aberrant cockroaches of the genus *Attaphila* of which I described the first species (*A. fungicola*, Pl. LIII, Figs. 47–49) from Texas (1900). This insect, which is very common in the fungus gardens of *A. texana,* measures only 3–3.5 mm. in length. It is yellowish brown and has very small eyes, one-jointed cerci, and peculiar antennæ, consisting of a few cylindrical joints. The females are wingless, the males have vestigial tegmina and hind wings. The antennæ are always imperfect, their terminal joints having been bitten off, in all probability, while the ants are clipping the fungus mycelium. The structure of the remaining antennal joints is so unlike that of all other Blattidæ that *Attaphila* must be regarded as the type of a distinct subfamily, the Attaphilinæ. Since publishing my description of this singular insect, I have had an opportunity of observing it in artificial nests. It does not feed on the fungus hyphæ as I at first supposed, but mounts the backs of the large soldiers while they are stalking about the garden and licks their surfaces after the manner of some of the myrmecophiles of other ants, notably the little cricket *Myrmecophila nebrascensis,* the Staphylinid beetle *Oxysoma oberthueri,* and the guest ant *Leptothorax emersoni.*

In 1901 Bolivar described a second species of *Attaphila* (*A. bergi*), which was discovered many years ago by Berg in the nests of *Acromyrmex lundi* in Argentina and Uruguay. This species (Pl. LIII, Figs. 50–54) is very similar to the Texan form and it too, seems always to have multilated antennæ. According to Berg "it is found in the nest of the ants, sitting on the back, neck or even on the head of the sexual individuals (never on the neuters), and when these swarm forth during the spring or summer, it is also carried out of the nests, still attached to its host."

Fig. 16. Nest craters of *Atta* (*Mœllerius*) *versicolor* Pergande in a sandy "draw" at Yucca, Arizona. (Photograph by the author.)

2. **Atta (Mœllerius) versicolor** *Pergande.*

This ant is unquestionably a Mexican species which enters the United States only along its southwestern frontier where it inhabits the arroyo bottoms in the most arid regions. I have observed the typical form of the species only in two localities, at Tucson, Arizona, and at Yucca in the same state, a few miles east of the Californian boundary. At Tucson several colonies were found in an arroyo near the Carnegie Desert Botanical Laboratory where the soil was probably somewhat moist at a depth of several feet, but where the surface was very hard and dry and covered with typical desert plants such as the retama (*Parkinsonia*), the small acacia known as "cat-claw" or "uña de gato" (*Acacia greggi*), the Mexican grease-wood (*Covillœa tridentata*), the ocotillo (*Fouquiera splendens*) and several cacti (*Opuntia*). At Yucca the ants occur in similar arroyos bordered with the beautiful pod-willows (*Chilopsis saligna*) in the midst of a very hot, dry desert, studded

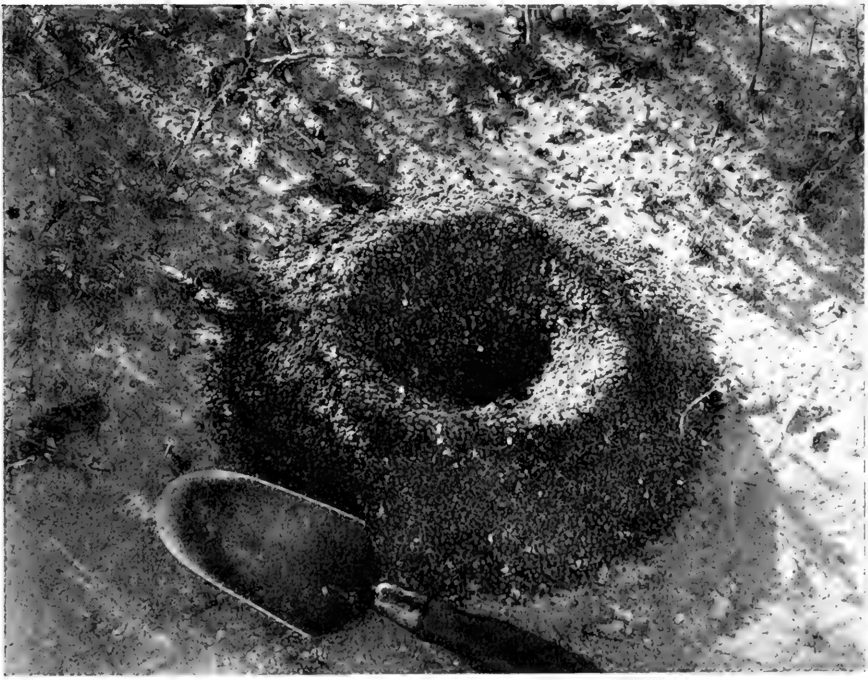

Fig. 17. One of the craters of the group represented in the preceding figure, about ¼ natural size, showing the difference between the pellets brought up by the ants and the surrounding soil. (Photograph by the author.)

with clumps of cañatilla (*Ephedra*), huge tree-like yuccas, and "allthorn" bushes (*Kœberlinia*). In both localities the nests were surmounted by from one to a dozen craters, varying from 10–30 cm. in diameter, and of very elegant and regular structure (Figs. 16 and 17). This was noticeably the case at Yucca, where the craters were built of the coarse, uniform sand of the arroyo bed. The earth or sand of the crater walls was often of a different color from the surrounding surface, showing that it had been brought up from a considerable depth. The opening at the bottom of the crater was 2–3 cm. in diameter and was often closed with earth. Even about the open craters no ants were to be seen during the intense heat of the day. Between four and five o'clock in the afternoon, however, they were seen leaving the nests in files, and slowly moving towards some desert shrub in the neighborhood for the purpose of cutting and carrying home its leaves. At Tucson some of the colonies were collecting the entire young and tender leaves of the

Fig. 18. Small crater of *Atta* (*Mœllerius*) *versicolor* covered with leaves of grease wood (*Covillæa*) collected by the ants at Tucson, Arizona. These leaves are also scattered along the path leading to the crater (upper right hand corner of figure). (Photograph by the author.)

"cat-claw," and had completely defoliated some of the bushes (Figs. 18 and 19). Other colonies were carrying in the small leathery leaves and yellow flowers of the grease-wood. Considerable quantities of these leaves had often been gathered and dropped along the path or on the craters, as shown in Fig. 18, and left to wither in the sun when the ants withdrew into their nests during the night or early morning hours.

The colonies were much smaller than those of *Atta texana*, although they comprised several hundred workers. These varied considerably in size, especially at Yucca. Dr. William Cannon, director of the Desert Laboratory, kindly assisted me in excavating one of the nests which had only a single crater. The entrance gallery, about 2 cm. in diameter broke up into a number of small anastomosing galleries just beneath the surface and these reunited to form a single gallery extending down into coarse, friable sand to a depth of about a meter and terminating in a single small chamber which contained a fungus garden about the size of a walnut. This garden was

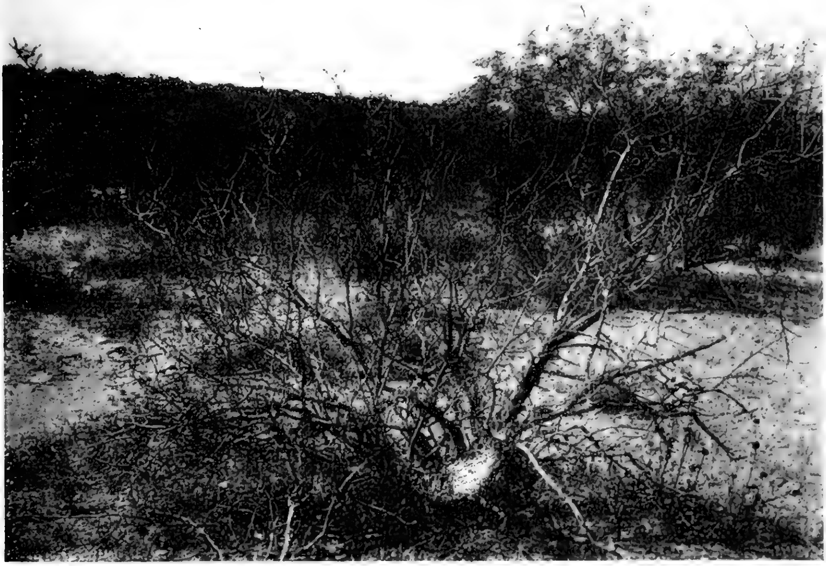

Fig. 19. Acacia bush defoliated by *Atta* (*Mœllerius*) *versicolor* at Tucson, Arizona. (Photograph by the author.)

lying on the floor of the chamber and consisted of fine leaf-pulp covered with a brilliant white mycelium dotted with bromatia. No other chambers or galleries could be found, and as the nest contained only about one hundred workers, the colony must have been incipient or enfeebled by age or adverse conditions. As we had spent a great deal of time excavating this nest, and as the heat was intense, so intense, in fact, that it caused the gutta-percha plate-holders of my photographing outfit to soften and crumple, we could not command sufficient energy to excavate a larger and more typical nest. Unfortunately my stay of only a few hours at Yucca did not suffice for the exploration of one of the much finer nests of that locality. Judging from the single nest examined at Tucson, *Mœllerius versicolor* resembles most of the species of *Acromyrmex* described by Mœller, Tanner, von Ihering and Forel in having only a single chamber and garden.

My notes on the subsp. *chisosensis* are even more fragmentary. At Terlingua, Texas, in the Great Bend of the Rio Grande, I found a few dead workers of this form in a spider's web under a stone, but was quite unable to locate the nest from which they came. Judge O. W. Williams, however, brought me a number of fresh specimens from a nest in a dry arroyo at the foot of the Chisos Mountains some miles southeast of Terlingua. Both localities are in very arid deserts, riven with cañons, though the vegetation is of a different type from that of southern Arizona. The red quicksilver-bearing soil supports a sparse growth of the sotol (*Dasylirion texanum*), desert spurges (*Euphorbia antisyphilitica* and *Iatropha spathulata*) and lechugilla (*Agave lechugilla*), and the steep cañon walls are spangled with star-like resurrection plants (*Selaginella lepidophylla*) and xerophytic ferns. Such a region, with an annual rainfall of barely 25 cm., is certainly a remarkable environment for an ant compelled to subsist on fungi that can grow only in a humid atmosphere, an ant, moreover, belonging to a group which was probably first developed in the rain-forests of the tropics.

3. **Atta (Trachymyrmex) septentrionalis** *McCook.*

The species of *Trachymyrmex* form small colonies of at most two or three hundred, and often of only a few dozen individuals, and are so timid and retiring in their habits that they are readily overlooked unless their nests happen to be numerous and close together. And even when numerous the nests are not often seen as their earth-works disintegrate and their entrances are kept closed during considerable periods of the year.

Our best known species, *T. septentrionalis*, is widely distributed over the Gulf and South Atlantic States, the var. *obscurior* ranging from central Texas to Florida and the typical form from Maryland to New Jersey. There are no observations to show that either of these forms extends equally far north in the Mississippi Valley. Mr. Wm. T. Davis has found the typical form as far north as the Raritan River in New Jersey and although he has hitherto failed to take it on Staten Island, it may yet be found in certain parts of Long Island. Both forms of the species have the same habits, although the southern variety often makes larger and more complicated nests and lives in larger colonies than the typical northern form, which is always more or less depauperate, like all ants at the limit of their geographical range. The following description, except in so far as it relates to the size and complexity of the nest, will apply to both forms of the species.

According to my observations, *T. septentrionalis*, even in widely separated localities, always occupies a very precise ethological station. I have never found it except in pure sand and in open woods. It is abundant in the post-oak woods of Texas, especially in the neighborhood of Milano and Montopolis, wherever the red clay is replaced by sand, in the hummocks of Florida (Miami, Jacksonville) and the pine barrens of New Jersey (Lakehurst, Toms River, etc.). The plant associations in all of these localities have a common *facies* in that they always comprise several species of oaks and many other plants and animals peculiar to the Louisianian portion of the Austroriparian subprovince.

Externally the nest of *T. septentrionalis* is very unlike that of any other North American ant known to me. It consists of a little mound of sand varying from 10 to 20 cm. in diameter, and a few cm. in height, of an elliptical, round, or crescentic form and placed at a distance of 5 to 10 cm. from the entrance. The latter is circular and varies from 4 mm. to 1 cm. in diameter, and the gallery into which it leads invariably slopes so as to form an angle with the surface. The sandpile lies in front of the entrance. The external appearance of one of these nests is shown in Fig. 20, from a photograph taken at Lakehurst, where the sand is often covered with the needles, twigs and cones of *Pinus rigida* and *inops.* The subterranean portion of the nest consists of from one to three series of straight galleries alternating with more or less spherical chambers, so that it is possible to distinguish a simple and a racemose type. To the former belong the young nests of the var. *obscurior* and all the nests of the typical *septentrionalis,* whereas the racemose type seems to occur only in old and flourishing colonies of the southern variety.

In the table on page 749 are given the dimensions in cm. of the galleries and chambers of ten nests of *T. septentrionalis* var. *obscurior* examined in three localities about Austin, Texas, nests A to F being of the simple, and G to J of the racemose type. Diagrammatic sections of nests C, D, F, and G–J, drawn to scale, are represented in Pls. LI to LIII, Figs. 37–42, 45. The entrance gallery is called gallery I, that between chambers I and II, gallery II and so on. Of the two measurements recorded for each chamber, the first is the depth or vertical, the second the breadth or transverse diameter. The chambers are either spherical, or if one diameter exceeds the other, it is most frequently the transverse, so that the chambers are often oblately spheroidal. As the galleries enter and leave the chambers at opposite points on their roofs and floors, the globular cavities have the appearance of being strung on the galleries like beads on a string. The most frequent nests are those of the form A–C, comprising only two galleries and two chambers, and these are the only ones described by previous observers (Morris, McCook, Swingle, Forel). The entrance gallery is commonly a few cm. in length and the first chamber is very small (2.8 × 3.2 cm. on an average). These represent the whole of the nest dug by the mother queen while establishing her colony, the other chambers and galleries being added subsequently by the workers. The table and the figures show very clearly that the length of Gal. II and the size of Ch. II, greatly exceed the queen's excavations and are in turn surpassed by subsequent excavations (Gals. III–IV and Chs. III–V). Nests with three, four and five chambers, like D, E, and F, are rarely encountered. Of the last I have seen only a single example and this was peculiar in having Chs. III and IV deeper than broad.

Fig. 20. Nest of *Atta* (*Trachymyrmex*) *septentrionalis* in pine barren near Lakehurst, New Jersey, about ⅓ natural size. The circular entrance is in the middle of the figure; the excavated sand is dumped out in a heap in front of it (below). (Photograph by the author.)

Atta (Trachymyrmex) septentrionalis McCook

Nest	Gal. I	Ch. I	Gal. II.	Ch. II.	Gal. III.	Ch. III.	Gal. IV.	Ch. IV.	Gal. V.	Ch. V.	Total Depth.
A	2.5	2.5×3.2	7.7	7.7× 7.7	—	—	—	—	—	—	20.4
B	3.8	3.8×4.5	7.7	6.4× 6.4	—	—	—	—	—	—	21.7
C	5.	4. ×4.	5.	6.5× 6.5	—	—	—	—	—	—	20.5
D	2.5	1.9×2.	5.	6.4× 6.5	0.	6.5×10.3	—	—	—	—	22.3
E	3.	3.5×4.	13.5	3.8× 5.	10.2	3.8× 5.	15.3	2.5× 3.8	—	—	55.6
F	1.3	1.3×1.3	1.8	2.5× 2.5	2.5	7.8× 3.8	12.7	12.8×12.	23.	6.4×7.8	72.1
G	2.5	3.8×5.	a. 11.4	a. 6.3× 8.	—	—	—	—	—	—	25.1
	—	—	b. 2.5	b. 6.3× 9.	5.	5. × 6.4	—	—	—	—	
H	2.5	3.8×5.	a. 7.8	a. 5. × 6.4	—	—	—	—	—	—	38.5
	—	—	b. 12.8	b. 7.8× 8.3	7.8	3.8× 3.8	—	—	—	—	
I	2.5	2.2×2.2	a. 12.8	a. 7.8× 7.8	a. 7.8	—	—	—	—	—	46.7
	—	—	b. 7.8	b. 2.5× 3.2	b. 6.4	b. 5. × 7.	12.6	7.7× 8.9	—	—	
J	1.3	1.3×1.3	a. 7.8	a. 6.4× 6.4	a. 5.1	a. 5. × 5.	—	—	—	—	33.1
	—	—	b. 7.1	b. 7. ×10.2	b. 2.5	b. 7.6× 7.6	—	—	—	—	
	—	—	c. 8.9	c. 7.6× 7.6	c. 7.6	c. 6.4× 7.6	—	—	—	—	
Ave.	2.7	2.8×3.2	7.9	6.0× 6.7	5.5	5.6× 6.3	13.5	7.6× 8.2	23.	6.4×7.8	35.6

Nest D was unique in having Chs. II and III opening directly into each other. Nests of the simpler racemose type, like G, are more frequent than simple nests with as many as four and five chambers, like D and E. In nests G–I the second gallery sent off a branch terminating in a chamber of its own (Ch. II*a*). The terminal chamber of nest H (Ch. III), like that of nest E (Ch. IV), was very small and obviously in process of being excavated by the ants. In nest I the insects had completed at least a portion of the gallery (Gal. III*a*) leading from Ch. II and the ants, had they been left undisturbed, would probably have widened its end into another chamber (Ch. III*a*). In nest J, the largest and most complicated of the series, not only did Gal. II form two branches, but one of these divided in turn, so that there were three galleries, each terminating in two chambers (Chs. II a, b, c, and Ch. III a, b, c) separated by a gallery (Gals. III a, b, c). Since in all of the nests the galleries formed an angle with the surface of the sand, their total depth, as given in the last column of the table, does not represent the vertical distance of the floor of the terminal chamber from the surface, but the oblique distance from the entrance. Both simple and racemose nests, moreover, though represented in the figures as lying in a single plane, are often bent, or, like nest I, of the latter type, radiate out from the entrance in three different intersecting planes.

When establishing their formicaries the ants select only those spots in the woods where the sand is permeated with fine rootlets. They are careful to leave these untouched, while hollowing out their chambers, as supports for their gardens, which in this, as in other species of *Trachymyrmex,* are always pendent and do not rest on the floor of the chamber like the gardens of *Atta* s. str., *Acromyrmex* and *Mœllerius.* The substratum on which the fungus is grown consists very largely of caterpillar excrement and withered oak-catkins, both picked up under the trees, but often small dead leaves or berries are used, and occasionally as Morris and McCook observed, flowers or green leaves are cut from the small herbaceous plants in the neighborhood. These substances are comminuted and placed on the pendent rootlets where they become knitted together by the rapidly proliferating fungus mycelium. The whole garden then hangs from the roof of the chamber as a cluster of nodular strands or plates separated from the walls and from one another by spaces sufficiently large to admit the ants to all parts of the structure. The first chamber, in which the original worker brood was reared by the queen, is often empty or has lying on its floor particles of exhausted vegetable substances ready to be carried out of the nest, or materials that have just been brought in. This chamber seems to be the work-shop in which the materials are prepared for insertion into the hanging gardens of the lower chambers. The appearance and arrangement of several of these gardens are shown in

Pls. LI–LIII, Figs. 30–46. The mycelium in flourishing colonies has a bluish tint, somewhat like that of *Penicillium glaucum*. The hyphæ measure .78 μ in diameter. The gongylidia are subspherical or pear-shaped, and average 4.5 μ in length and 3.6 μ in breadth, and are grouped in compact clusters or bromatia averaging .4–.5 mm. in diameter.

In Texas the most favorable time to study the nests of *T. obscurior* is during the month of April. Then the ants are actively enlarging and deepening their nests and bringing in supplies for their gardens. While excavating they advance in a small phalanx up the inclined entrance gallery, each laden with a cuboidal sand pellet about 2 mm. in diameter, walk slowly to the sand pile, deposit their burdens and then return for others. The deälated females, of which there may be as many as four or five in a nest, toil in the phalanx like the workers. At the slightest alarm the ants immediately retreat into the nest and usually a single worker takes up her position in the entrance and holding a sand-pellet in her jaws, waits patiently till all danger has passed, before venturing forth and leading the troop of her sand-laden sisters. When foraging the ants go out singly and in various directions, pick up what they can find and return with it to the nest, moving slowly and sedately over the sand. The deälated females may also be seen in the act of carrying caterpillar droppings and leaves to the nest. If rudely touched with the finger or a stick, the insect drops her burden, curls herself up, folds her legs and antennæ and "feigns death." At such times her rough yellowish brown body is almost indistinguishable from the sand on which she lies. When the nest is ruthlessly torn open, the ants, especially

Fig. 21. Brood of *Atta* (*Trachymyrmex*) *obscurior*. About twice natural size. Three packets of eggs are shown enveloped in fungus mycelium. (Photograph by Mr. A. Beutenmüller.)

if they are numerous and have a large brood, do not feign death but boldly assail the intruder with their mandibles.

The nests remain in fine condition throughout May and the early part of June, while the young are being reared. The eggs are broadly elliptical and embedded in masses in pure white hyphæ. (Fig. 21.) These delicate vegetable strands serve to keep the eggs together, thus enabling the ants to carry them about in packets, afford an admirable protection and, as soon as the larvæ hatch, represent a supply of very accessible food. The older larvæ and young pupæ, however, are always free from adhering hyphæ, so that their surfaces are smooth and glistening, till they develop the rough, tuberculate integument of the adult stage. The brood is undoubtedly moved from chamber to chamber to suit the varying conditions of heat and moisture. Throughout the warm days of May and June it is kept in the superficial apartments. On the morning of June 11, 1903, after an unusually cool night, I found the ants and entire brood of several nests huddled together in the lowermost chambers, but during the warm afternoon of the same day the young had been brought very near the surface. At Miami, Florida, the males and females were mature and ready for the nuptial flight as early as May 9; in Texas I have not seen them in this condition till the second week in June, and to judge from the date on the label of a winged female in my collection the sexual phases of the typical form do not mature in New Jersey till some time in August.

Fig. 22. Nest of *Atta* (*Trachymyrmex*) *septentrionalis* var. *obscurior* in sandy post-oak wood near Delvalle, Texas. About ¼ natural size. This represents the condition of the nest during the dry summer. A few sticks and dead leaves cover the entrance just below the middle of the figure. (Photograph by Mr. C. G. Hartmann.)

When its nest is disturbed, *T. septentrionalis,* like other Attii is very careful to rescue portions of its fungus gardens as well as its brood. A number of colonies, whose nests I had excavated in the post-oak woods at Montopolis, were found a few days later to have made new nests a few feet from the old sites and to have carried with them such fragments of their gardens as they could rescue. They had suspended these to the rootlets in one or two chambers which they had succeeded in excavating in the meantime, and were busy carrying in caterpillar excrement and withered oak catkins.

During the spring and autumn *T. septentrionalis* may be found abroad at all hours of the day, but with the growing heat of the summer it becomes increasingly crepuscular and nocturnal. And as soon as the dry weather sets in, it greatly contracts or completely closes with dead leaves and twigs the orifice of its nest to reduce or prevent the evaporation of the moisture from the chambers. The sandpile subsides under the influence of the elements till the nest becomes barely distinguishable from the surrounding leaf-strewn surface (Fig. 22). It is then almost impossible to find the nests even in localities where previous exploration has shown them to be very numerous. The ants no longer venture forth but spend all their time weeding and rearranging their gardens in the moist subterranean chambers. Immediately after the first warm rain, however, the nests are reopened, excavations and repairs to the chambers are renewed, the exhausted portions of the gardens are ejected and the ants sally forth in quest of fresh supplies.

4. **Atta (Trachymyrmex) turrifex** *Wheeler.*

As this species is even more timid and retiring than *T. septentrionalis,* it was some time before I learned to find its colonies and gained an acquaintance with its habits. Its geographical range covers the dry deserts of Trans Pecos Texas, and slightly overlaps the range of *septentrionalis* along the escarpment of the Edwards Plateau in the central portion of the state. That it is a more adaptable ant than its eastern and northern congener, is shown by its occurrence in the following diverse stations:

1. In the treeless deserts at Del Rio, Langtry, Marfa, Alpine and Ft. Stockton, in dry stony soil fully exposed to the glare of the sun. In these localities the colonies are widely scattered.
2. In the clayey soil of the post-oak woods and "cedar-brakes" (*Juniperus sabinoides*) near Austin (Fig. 23), along the Perdenales River, and at Marble Falls. Here the colonies are often numerous and close together.
3. In the pure sand of open fields at Montopolis on the Colorado River. In this locality the colonies are infrequent and mingled with those of *sep-*

Fig. 23. "Cedar Brake" (*Juniperus sabinoides*) near Austin, Texas. Home of *Atta* (*Trachymyrmex*) *turrifex*. (Photograph by Prof. W. L. Bray.)

tentrionalis, a condition which also obtains in sandy portions of the post-oak woods.

Though structurally closely resembling the eastern species, *T. turrifex* may be readily distinguished by a number of ethological characters. Its colonies are much smaller, often consisting of only two or three dozen individuals. Nevertheless a single nest may contain as many as four or five deälated females. The nesting habits are most conveniently studied in the post-oak woods, where the ants prefer to live in the shade of the trees. Here the red clay is overlaid with a stratum of less compact black soil two or three decimeters deep. The external structure of the nest is very different from that of *septentrionalis.* The orifice is only 3–4 mm. in diameter and in typical nests, does not open on the surface of the soil but at the top of a cylindrical turret or chimney about 10 mm. in diameter and from 10–40 mm. high. The walls of this turret, which are made of earth particles, small juniper twigs and other vegetable débris (Fig. 24) are sufficiently resistant to withstand heavy showers. As the nests are often located on sloping ground the turret would seem to be an ingenious adaptation for keeping the water from entering the subterranean galleries and chambers. Occa-

Fig. 24. Turret-shaped entrance to nest of *Atta* (*Trachymyrmex*) *turrifex* in a cedar brake near Austin, Texas. (Photograph by Mr. A. L. Melander.)

sionally I have found nests with abnormal turrets, like the one represented in Pl. L, Fig. 27, which has the summit enlarged and spreading and provided with three distinct orifices. The pellets of earth brought up by the ants are cuboidal or polyhedral, of uniform size and measure about 2 mm. in diameter. They are not cast to one side as in *septentrionalis* but in a closed circle at a distance of 8–12 cm. from the entrance. As this circle grows in height it forms a very shallow crater with the turret rising abruptly in its center. In the post-oak woods and cedar-brakes the castings are red or dull vermilion and contrast strongly with the black soil or dead leaves of the surface.

The galleries and chambers alternate with one another as in the simple type of *septentrionalis* nests, but the chambers are smaller and the galleries are much longer and usually descend vertically into the soil. These differences are distinctly shown in the figures (Pl. LI, Figs. 33–36) and in the measurements (in cm.) of the accompanying table.

Atta (*Trachymyrmex*) *turrifex* Wheeler.

Nest	Gal. I	Ch. I	Gal. II	Ch. II	Gal. III	Ch. III	Gal. IV	Ch. IV	Gal. V	Ch. V	Total Depth
K	3.7	1.8×1.8	4.2	1.8×2.5	5.	3.8×3.8	6.3	4. ×4.2	7.7	——	38.3
L	1.8	1.3×1.3	8.2	2.8×2.8	9.5	.4×6.5	13.4	3.2×6.5	17.4	4.5×3.8	66.1
M	2.5	.8×1.	11.5	3.2×3.2	14.6	4.2×6.4	15.3	5. ×5.	—	——	57.1
N	3.6	1.3×1.8	6.5	3.5×3.8	11.5	3.8×7.6	7.5	1.5×1.5	—	——	39.2
O	3.6	1.3×1.3	2.5	2.5×5.	12.8	5. ×6.4	7.5	5.2×7.5	—	——	40.4
P	3.8	2.5×2.5	1.5	2.5×3.8	6.3	4. ×5.2	9.	4. ×6.5	10.5	6.5×7.8	50.6
Q	3.5	2.5×2.5	5.	4. ×4.	18.	2. ×2.5	16.5	3.5×5.	15.	——	70.
R	10.2	2. ×2.	23.	5. ×6.4	19.	2.5×3.8	30.5	6.5×7.8	8.	3.8×3.8	110.5
Ave.	4.1	1.7×1.7	7.8	3.8×3.9	12.	3.6×5.2	13.2	4.1×5.5	11.7	4.9×5.1	59.0

All of these nests were located in the clayey soil of the post-oak woods except the last (R) which was in pure sand. Owing to the length of its galleries, this is exceptional in its total depth (110.5 cm.), and therefore abnormally increases the average length of the galleries I to V in the table. The average depth of nests K to Q is only 50.8 cm. which is less than half the depth of nest R. The nests usually comprise four chambers (Fig. 25), but five are often met with, and here, as in *septentrionalis,* the galleries and chambers have their dimensions suddenly increased, below the first chamber, which is the work of the mother queen. I have seen but one *turrifex* nest that resembled the racemose type of *septentrionalis* in having two branches to Gal. IV, each terminating in a chamber. Comparing the nests of the two species we see that both start with the simple, primitive type consisting of alternating galleries and chambers and that *turrifex* continues its excavations according to this pattern, whereas flourishing colonies of *septentrionalis* change to the racemose type which bears an unmistakable resemblance to the nests of *Atta* s. str.

The greater length of the *turrifex* galleries in pure sand is undoubtedly due to the need of reaching a stratum of greater dampness. In the dry Trans Pecos deserts the same tendency is observable. In that region I repeatedly endeavored to excavate nests, but was never able to reach the chambers on account of the extreme hardness of the stony soil. I am convinced, how-

Fig. 25. Section of nest of *Atta* (*Trachymyrmex*) *turrifex* showing four chambers exposed (at points of paper triangles numbered 1 to 4). About ½ natural size. (Photograph by Mr. C. G. Hartmann.)

ever, that these nests were more than a meter deep. That *T. turrifex* requires rather moist soil is also shown by a peculiarity of its nests in the post-oak regions. Here, as I have said, the subsoil is red clay overlaid with a dryer, and more porous black earth. The ants not only carry their excavations down into the subsoil but carefully line the galleries and chambers in the black soil, to the very orifice of the turret, with a thin layer of clay brought up from below. Thus the nest becomes a bottle with thin clay walls, alternately constricted into slender tubes (the galleries) and dilated into ampulliform enlargements (the chambers). This clay lining is probably a very efficient means of preventing both the escape of the moisture from the chambers during dry spells and the entrance during rainy weather of too much moisture from the soil. Unlike the nests of *septentrionalis*, those of *turrifex* are not closed during the dry season. Such closure is in fact unnecessary because the nests are considerably deeper, situated in soil which retains the moisture much longer, and have very small orifices.

The first chamber, like that of the *septentrionalis* nest, is used as a workshop and temporary repository for fresh and discarded vegetable substances. The rootlets of plants are also left dangling into the remaining chambers as a suspensorium for the fungus gardens. These resemble the gardens of *septentrionalis* but are smaller, whiter, and of a more delicate texture, as if the vegetable substratum on which they were grown had been more finely comminuted. In the confection of this substratum the same materials are used, viz., the withered catkins of oaks, the scales of buds, bits of dead leaves and the excrement of caterpillars. I have never seen these ants cutting or bringing in green leaves of any description. At Marfa and Ft. Stockton they were collecting the withered florets of a small yellow composite (*Pectis tenella*). The nest openings were often surrounded by a circlet of these florets, so that to one riding over the desert each nest seemed to be marked by a small handful of saffron. All of the vegetable substances are picked up by the ants from the ground and not collected directly from the plants, as *turrifex* is even less inclined than *septentrionalis* to climb about on the vegetation. The microscopic structure of the fungus gardens is very much like that of *septentrionalis.* The hyphæ measure .78 μ in diameter; the bromatia .3–.4 mm. and consist of beautifully developed gongylidia 3.5–4.7 μ in length and somewhat less in breadth.

The deälated females of *turrifex* take part in excavating and foraging, like the workers. On one occasion, early in the morning of June 14, in the midst of the desert at Marfa, I came upon a whole colony of this ant, comprising some thirty workers and five deälated females, in the act of digging a nest in the hard adobe soil. They had evidently been compelled to forsake their old nest during the night on account of the drought, which was almost unprecedented even in that region, as it had not rained for nine months. As I have also found many abandoned nests of this ant in the cedar brakes about Austin, I infer that it not infrequently migrates to more favorable spots. It would be interesting to know whether on such occasions the old queens carry over to the new quarters portions of the fungus gardens in their hypopharyngeal pocket, or whether the workers transfer the old gardens piece-meal during the cool night hours. The latter would seem to be the more probable procedure.

T. turrifex is, if anything, slower and more sedate in its movements than *septentrionalis.* It also "feigns death" more readily and never seems to resent the destruction of its nest. Only a few workers are seen at any one time outside the nest. The slightest disturbance causes these to withdraw into the turret, and one may sit motionless near the nest for many minutes before they muster sufficient courage to venture forth again. When several of these ants, together with pieces of their gardens, were placed in a dish with a number of *septentrionalis* workers, a conflict ensued, in which the latter were the aggressors and came off victorious. They carried the *turrifex* garden piece by piece into a wide chamber they had excavated in some sand at the bottom of the dish, but by the following morning they had thrown it all out again and, although they had been without food for several days, they would have nothing to do with it.

The breeding season of *turrifex* must come later in the summer than that of *septentrionalis.* During early June I found a few young larvæ in the nests of the former species, but the only winged female I have seen was captured in flight by Mr. W. H. Long on September 27. I have never been able to obtain a male of this species.

5. **Atta (Trachymyrmex) jamaicensis** *Ern. André.*

Like the preceding two species of *Trachymyrmex, T. jamaicensis,* though confined to the West Indies, occurs only in association with a xerophytic flora. It is a larger, much darker ant, with unusually long legs and antennæ. I found it first in the Bahamas, on both Andros and New Providence Islands. On the former it was seen wherever I landed and searched for it—at Big Wood Key, Mangrove Key, on several of the uncharted keys along the course of the Southern Bight and about Crawl Creek. On New Providence it was found in the neighborhood of Fort Charlotte. It prefers to nest in the pure white foraminiferous sand of the sea-beach, at or just above high water mark, along the edges of the 'coppets' which consist very largely of coarse grasses, sea-grape, cocoa-plum, wild sapodilla, sea-lavender and palmettos. Its nest, which is most readily found by tracking foraging workers, is surmounted by a very flat and obscure crater about 30 cm. in diameter with an oblique and somewhat eccentric orifice 5–10 mm. in diameter. The ants collect buds, small flowers, bits of dead and living leaves and caterpillar excrement as a substratum for their fungus gardens. When rudely touched the workers fall over and "feign death." At first I was inclined to believe that this species is restricted to the sandy seabeaches, but on walking inland about two miles from All Saint's Rectory at Mangrove Key, I found it nesting also in clearings among the 'coppets' wherever a small amount of rich black soil in the cavities of the rough Æolian limestone had induced the negroes to plant maize and other vegetables. Here the ants were busily engaged in cutting and carrying into their nests bits of the green maize leaves after the manner of the species of *Atta* s. str. In other places, like Fort Charlotte, on New Providence Island, the ants were nesting in the dry shady 'coppets.' In all of these localities the nests extended down through holes or crevices in the limestone, so that I was unable to obtain a satisfactory conception of their structure.

On a recent trip to the Island of Culebra, a few miles east of Porto Rico, I again encountered this ant but under conditions more favorable for study. The vegetation on Culebra, which is too low to intercept the rain-laden trade winds from the Atlantic, is decidedly xerophytic. There is no standing water on the island and the short arroyos dry up very soon after a shower. A number of colonies of *T. jamaicensis* were found in the shade of the trees on the banks of these arroyos. The colonies, at the time of my visit (March 2–9), were in an opulent condition and each comprised numerous larvæ, pupæ and winged males and females in addition to about a hundred workers. Externally the nests, though in black friable soil, were like those on the sandy beaches of the Bahamas. Their subterranean structure closely resembled that of the simplest, two-chambered nests of *septentrionalis.* The entrance descended into the soil obliquely and at a distance of 2–3 cm. below the surface, widened into a small spherical chamber 2.5 cm. in diameter. This chamber contained no fungus garden but only a few workers apparently engaged in comminuting leaf clippings and caterpillar excrement. A second gallery 5–10 cm. in length led off obliquely from the bottom of this chamber and terminated in a larger spheroidal cavity 6.5–9 cm. in diameter, filled with a flourishing fungus garden of coarse and nodular structure and suspended from rootlets. The brood, callow and recently matured sexual forms were ensconced among the pendent folds and strands. The mycelium was of a bluish color, like that of *septentrionalis,* with hyphæ .58 μ in diameter. The bromatia measured .36 mm. and consisted of well-developed pyriform gongylidia 4–4.6 μ long and 1.5–3 μ broad.

6. **Atta (Mycetosoritis) hartmanni** sp. nov.

This interesting little ant was discovered May 9, 1903, in the sandy country on the left bank of the Colorado River at Montopolis and Delvalle, near Austin, Texas, while, with the assistance of Mr. C. G. Hartmann, I was examining and photographing the nests of *Trachymyrmex turrifex* and *septentrionalis*. At first I was inclined to regard the diminutive workers as merely belonging to incipient *Trachymyrmex* colonies, but closer study soon showed that these little ants were not only specifically distinct but also represented a new and interesting subgenus, in certain respects intermediate between *Trachymyrmex* and *Cyphomyrmex*. There were hundreds of their nests, often within a few decimeters of one another, in the fields or in clearings among the oaks and wherever the sand was fully exposed to the sun. These regions were also inhabited by several species of solitary wasps (*Microbembex* and *Pompilus*) and numerous colonies of ants (*Trachymyrmex turrifex* and *septentrionalis*, *Aphænogaster treatæ*, *Pheidole splendidula* and *morrisi*, *Solenopsis geminata*, *Pogonomyrmex comanche*, *Prenolepis arenivaga*, etc.). The herbaceous flora of the region consisted of a sparse growth of bull-nettles (*Iatropha stimulosa*), showy gaillardia (*Gaillardia pulchella*), butterfly weed (*Asclepias tuberosa*), white prickly poppy (*Argemone alba*), stone crop (*Sedum*) and cactus (*Opuntia engelmanni*), all in full bloom.

Fig. 26. Crater of *Atta* (*Mycetosoritis*) *hartmanni* from sandy post-oak woods at Montopolis, Texas. Natural size. (Photograph by Mr. C. G. Hartmann.)

The nests of the *Mycetosoritis* are small turriform craters of pure sand 5–8 cm. in diameter at the base and tapering rapidly to the summit, which is 2.5–4 cm. high and perforated with a circular orifice barely 2 mm. in diameter (Fig. 26). Occasionally the summit is double (Pl. L, Fig. 28) and furnished with two entrances, which, however, soon unite to form a single gallery. The internal structure of the nest resembles on a small scale that of *Trachymyrmex turrifex.* It consists of from two to four alternating vertical galleries and spheroidal chambers. As the former are very tenuous and run through pure sand, the excavation of the nests is rather difficult. The measurements of six of these nests (S to X) are given in the accompanying table, diagrams of three of them are represented in Figs. 30–32, Pl. LI, and photographs of portions of one of them in Figs. 27 and 28.

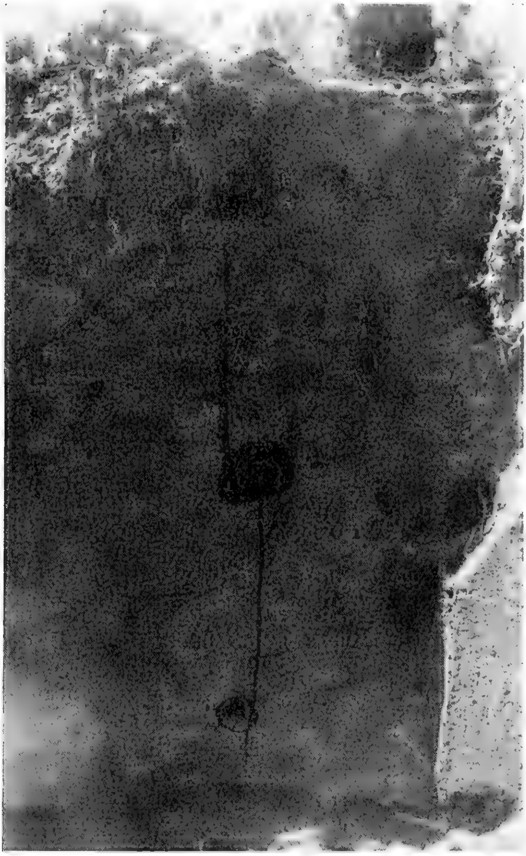

Fig. 27. Section of nest of *Atta* (*Mycetosoritis*) *hartmanni* in pure sand at Delvalle, Texas. About ⅙ natural size. (Photograph by Mr. C. G. Hartmann.)

Atta (Myceetosorites) hartmanni sp. nov.

Nest	Gal. I	Ch. I	Gal. II	Ch. II	Gal. III	Ch. III	Gal. IV	Ch. IV	Total Depth
S.	5.	2. ×2.5	15.	2.6×4.	—	——	—	——	24.6
T.	6.3	1.3×2.	20.5	2.5×4.	18.5	2.5×3.4	—	——	51.6
U.	5.	1.4×1.4	13.	2.5×4.	29.4	2.5×4.5	—	——	53.4
V.	7.6	1.3×1.3	13.3	3.3×3.8	7.	4. ×4.	—	——	36.5
W.	6.	1.2×1.3	18.7	2.3×3.7	20.	2.9×4.1	14	2.×3.4	67.1
X.	5.2	.8×1.5	28.	1. ×3.2	25.3	2.5×4.5	14	2.×3.4	78.8
Ave.	6.5	1.3×1.6	18.1	2.3×3.8	19.8	2.8×4.1	14	2.×3.4	52.1

The galleries are proportionally longer than those of *turrifex* nests in clay or black soil, and the chambers are absolutely smaller and more oblately spheroidal. On an average, however, the *Mycetosoritis* nests are quite as deep (55.1 cm). Their resemblance to *turrifex* nests in pure sand, like nest

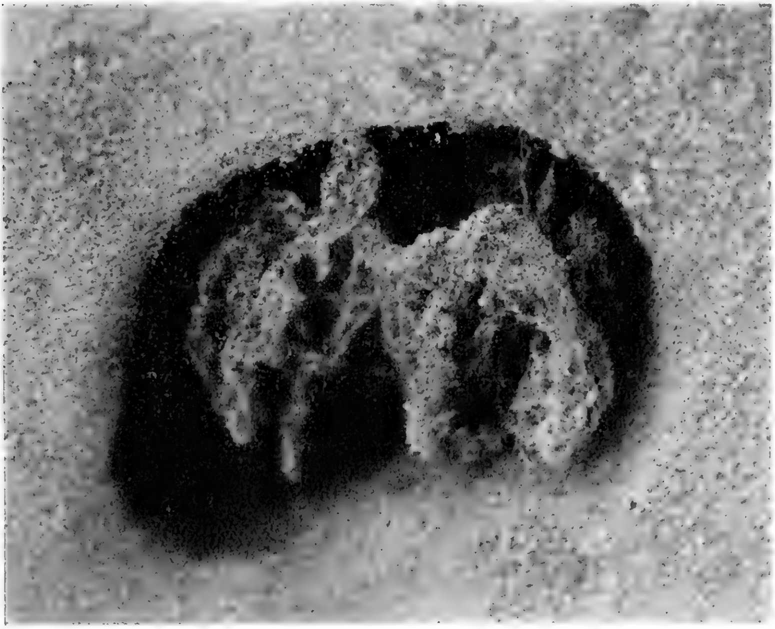

Fig. 28. One of the pendent fungus gardens of the nest shown in the preceding figure, slightly enlarged. (Photograph by Mr. C. G. Hartmann.)

R of the table on p. 756, is greater owing to the elongation of the galleries of the latter species.

Like the species of *Trachymyrmex, M. hartmanni* leaves the rootlets dangling into the chambers as suspensoria for its fungus-gardens (Fig. 28). These gardens, however, have a much more delicate and flocculent texture and are made up almost exclusively of the anthers of plants, knit together by a snow-white mycelium consisting of slender hyphæ .58 μ in diameter. The bromatia, which measure .3–.4 mm. consist of typical pyriform gongylidia 1.5–4.3 μ in length and 1.3–4 μ in breadth.

The colonies are small, not exceeding 60 to 70 workers. Only a single deälated female was found in each of the nests. I was unable to find any larvæ or pupæ. Mr. A. M. Ferguson, who helped me excavate a number of the nests on one occasion, and kept the ants with some of their gardens in an artificial nest, succeeded later in the summer in rearing the males and winged females described on pp. 715–716. The workers are extremely timid and "feign death" with the utmost readiness. Their small rough bodies are then quite indistinguishable from the sand grains among which they lie. Only a few workers forage or excavate at a time. They seek the withered anthers where they have fallen or have been drifted by the wind on the surface of the sand and slowly and laboriously transport them to their nests. These anthers, many of which still contain pollen grains, are inserted entire in the gardens and are evidently responsible for the light and flocculent

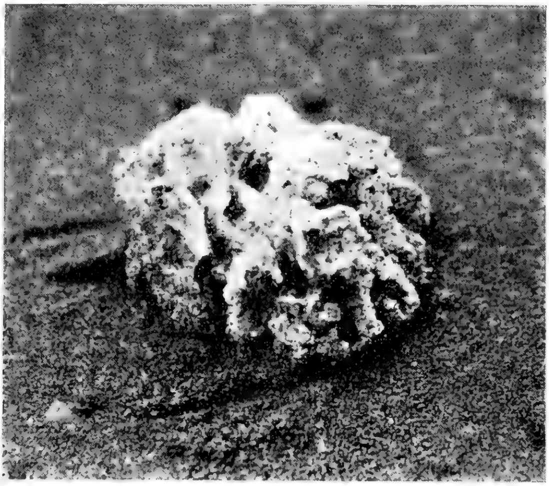

Fig. 29. Fungus garden of *Atta* (*Mycetosoritis*) *hartmanni*, removed from the nest intact and placed on the ground. (Photograph by Mr. C. G. Hartmann.)

texture. Exposure of only a few moments to the air causes the delicate mycelium to wither and contract. The garden of the chamber represented in Fig. 28 was thus dried, but the one in Fig. 29 was photographed immediately after its removal from the nest. The ants appear to be crepuscular or nocturnal. I have not seen them at work after ten o'clock in the morning except on very cloudy days.

On June 5, when I paid a second visit to the sandy country at Montopolis and Delvalle, all the nests were closed and the craters revealed no signs of recent excavation. They had merely crumbled, marking the sites of the nests as obscure little piles of sand. I opened several of the nests and found the workers moving diligently about in their gardens, which were in fine condition. On June 26, when, just before leaving Texas, I paid a final visit to the dry post-oak woods, not a trace of the nests could be found. The wind and rain had completely obliterated the fragile turrets and fused their sandgrains with the surrounding surface, so that even the closest observer would never have suspected the existence of innumerable colonies of little ants diligently cultivating their hanging gardens in the dark bosom of the yellow sands.

The foregoing description of the nests of *Mycetosoritis* shows that this ant is closely related to *Trachymyrmex*. The members of the genus *Cyphomyrmex*, as will be seen from the following accounts of two species have very different habits.

7. **Cyphomyrmex wheeleri** *Forel.*

This species appears to be more widely distributed than most of the preceding, since it ranges from Central Texas to California and probably also over a large portion of northern Mexico. In Texas it is rather rare and, according to my observations, occurs only in arid regions, especially on the Edwards Plateau and Grand Prairie and in the stony deserts of the Trans Pecos country about Langtry and Fort Davis. Although several of the preceding Attii prefer to live in dry localities among plant associations of a more or less xerophytic habitus, the abode of *C. wheeleri* is characterized by even greater aridity. Most of my observations on the habits of this ant were made among the lime-stone hills of the plateau escarpment just west of Austin. Some of these hills, which are often beautifully stratified and terraced and belong to lower cretaceous formations, are shown in Fig. 30, from a photograph taken in the early morning when the long shadows accentuate their peculiar structure. The terraced slopes are strewn with blocks of limestone of different sizes. Among these hills, from early spring to late autumn, the heat and the glare of the sun reflected from the white

Fig. 30. Limestone hills of the Edwards Plateau, near Austin, Texas. Home of *Cyphomyrmex wheeleri.* (Photograph by Prof. W. L. Bray.)

rock are exceedingly oppressive. Water is very scarce and the vegetation is so sparse and stunted or of such a xerophytic character as to yield little shade except in the deeper cañons. The trees and shrubs comprise such species as the mountain cedar (*Juniperus sabinoides*), several hackberries (*Celtis helleri, reticulata* and *pallida,*) oaks (*Quercus fusiformis breviloba* and *schneckii*), buckeyes (*Ungnadia speciosa* and *Æsculus octandra*), dwarf mulberry (*Morus celtidifolia*), dwarf walnut (*Juglans rupestris*), frijolillo, or coral bean (*Sophora secundiflora*), Texas persimmon (*Brayodendron texanum*), madroña (*Arbutus xalapensis* var. *texana*), algerita (*Berberis trifoliata*), *Eysenhardtia amorphoides, Leucophyllum texanum, Rhus microphylla* and *virens*, and *Ephedra antisyphilitica.* During the spring the bare rocks are beautiful with a profusion of smaller plants (*Gilia rigidula, Castilleia, Salvia texana, Stillingia angustifolia, Palafoxia texana, Androstephium violaceum, Camassia fraseri, Yucca rupicola* and *Nolina*)

It is only on the higher and more arid terraces that *C. wheeleri* manages to live and cultivate its fungus gardens, where long after other plants have bloomed and deep into the winter the golden heads of *Actinella scaposa* nod on their long stems. The nests are always under large stones covering a little lingering moisture in the hard soil, which consists very largely of disintegrated limestone. Each colony comprises only a few dozen workers and a single deälated female except during the spring and early summer, when one finds also several callow workers, males and females and a variable number of eggs, larvæ and pupæ. The workers are nocturnal, at least during the warm seasons of the year, a peculiarity which is indicated by their yellow color. They are very slow in their movements and readily "feign death."

The excavations though extensive for such small ants, are unlike those of *Atta, Trachymyrmex* and *Mycetosoritis.* A few rough and occasionally branching galleries about 1–2 cm. in diameter run along the surface covered by the stone, and descend vertically into the ground to a depth of 10–15 cm. One of the surface galleries terminates in a small entrance at the edge of the stone where its opening may be marked by a small crater. Irregular and indistinct dilatations in the galleries represent the chambers of other Attii, and in one of these dilatations, which is often fully exposed when the stone is removed, or may be readily uncovered at a depth of a few cm., the single fungus garden is found. This rests directly on the ground and is spheroidal or ovate, usually about the size of a filbert or pecan nut, more rarely half as large as a hen's egg. It consists of a delicate flocculent substratum made of small vegetable slivers covered with a dense snow white mycelium. The slivers average from 1–3 mm. in length and appear to have been torn from the stems of herbaceous plants. They undergo no trituration or comminution before they are inserted in the garden. The mycelium which binds these slivers together bears distinct bromatia .6–.7 mm. in diameter and consisting of pear-shaped gongylidia 1.5–3.5 μ in length and .78–1.56 μ broad. They are less globose than the gongylidia of *Atta* and *Trachymyrmex* and less club-shaped than those of the South American species of *Cyphomyrmex* represented in Mœller's figures. Sometimes as in these species, however, they are not terminal but appear as mere swellings in the course of the hyphæ. The brood is embedded in the fungus gardens and the eggs and young larvæ and often also the older larvæ and pupæ are covered with a delicate film of mycelium.

The ants carry all the exhausted particles of the substratum out of the galleries and build them into a flat mass which adheres to the lower surface of the stone. More rarely this refuse is dumped outside the entrance of the nest at the edge of the stone. As the mass of slivers is sometimes nearly as large as a man's hand and therefore greatly exceeds the size of the flourishing gardens, one is compelled to conclude that the vegetable particles contain but little available nutriment for the fungus and have to be continually renewed by the workers. Moreover, as these masses of exhausted substratum are often found under stones covering completely deserted galleries, it is probable that the ants keep moving to new nesting sites. This moving must be necessitated by the small amount of moisture in the soil and the rapidity with which it evaporates even from under large stones.

In the vicinity of Austin, *C. wheeleri* is not confined to the limestone hills of the Edwards Plateau. On three occasions I found small isolated crater nests of this species in the hard pebbly soil of the open woods at a lower altitude in the outskirts of the town. The exhausted substratum was dumped to one side of the small circular entrance which descended vertically into the soil. These nests must have been much deeper than the ones above described as I never succeeded in excavating them completely or in finding the fungus garden.

The males and winged females were found in the nests on the Edwards Plateau June 26th, and as early as June 8th in the somewhat warmer country about Fort Davis. In the latter locality I noticed among the vegetable slivers of the exhausted substratum a number of elytra, thoraces, etc., of small beetles, but whether these insects had been collected for food or merely formed a part of the substratum, I am unable to say.

8. **Cyphomyrmex rimosus** *Spinola.*

The stations inhabited by the various subspecies and varieties of this widely distributed ant afford a striking contrast with the arid environment of *C. wheeleri* and entail a corresponding contrast in habits. All the forms of *rimosus* that have come under my observation live in the shade of trees and bushes in rather moist, black soil. These ants are, in fact, restricted to such localities on account of the material they require for constructing their gardens and the peculiarities of the fungus which they cultivate. The habits of the subspecies *minutus* which I have had abundant opportunities of observing in the Florida Keys, Bahamas, Culebra and Porto Rico, and those of the subspecies *dentatus* which I first found in the lovely barrancas about Cuernavaca, Mexico, resemble so closely the habits of the var. *comalensis* at New Braunfels, Texas, that I may confine my remarks very largely to this form.

At New Braunfels a number of beautiful springs, the sources of the Comal River, gush forth from the foot of Mission Mountain, one of the limestone hills that constitute the Grand Prairie escarpment (Fig. 31). The volume and temperature of these springs is practically constant during the entire year. They nourish an exuberant vegetation consisting of ash-trees, live-oaks and shittim wood (*Bumelia lycioides*) and a dense undergrowth of subtropical shrubs and herbaceous plants too numerous to mention. The entomologist who enters this undergrowth must be prepared to endure the fiery torments of the "red-bugs" or "coloradillos" ("*Leptus*" *irritans*) and exercise some care lest he tread on a water moccasin. But, if he be in search of ants he will be rewarded by finding a number of interesting subtropical species, among others three species of *Pseudomyrma* (*pallida, brunnea* and *flavida*), a singular little *Strumigenys* (*S. margaritæ* Forel) hitherto known only from the island of St. Vincent, besides the fungus-growing ant with which we are here concerned.

This ant, owing to the close agreement between its color and the black soil over which it moves, is more difficult to detect than any of the other small Attii described in the preceding pages. Single workers wander about slowly in the damp shade of the plants in search of the caterpillar excrement with which they construct their gardens. As soon as one of the short, cylindrical, ribbed pellets is found, the ant seizes it in her jaws, raises it above her head like a man shouldering a cask and returns home with accelerated pace. The slightest touch causes the ant to drop her load, draw up her legs and antennæ and "feign death." And he must have exceptionally good eye-sight who can distinguish her rough, opaque and inert body from the particles of earth among which it falls.

The colonies of *C. comalensis* are larger than those of *C. wheeleri*, sometimes comprising a hundred or more workers and from one to three deälated queens. The nests are under rather small flat stones or pieces of wood, with the entrance sometimes nearly a cm. in diameter, at the periphery. On

Fig. 31. One of the sources of the Comal River at New Braunfels, Texas. Home of *Cyphomyrmex rimosus* var. *comalensis*. (Photograph by Prof. W. L. Bray.)

removing the stone or piece of wood the galleries are seen to be very irregular, running along the surface as in the nests of *C. wheeleri* and extending down into the soil to a depth of 20 to 35 cm. They adapt their course to the many small fragments of limestone on or below the surface. The single fungus garden, of irregularly flattened or sometimes of elongate and straggling form lies in dilated portions of the gallery, usually completely exposed by the removal of the stone. In many nests the garden rests on a small stone, piece of bark or dead leaf from which the earth has been carefully removed by the ants. So different is this garden from that of the other Attii heretofore described that it has been completely overlooked by all previous observers. The substratum consists of a mass of caterpillar droppings a few cm. in diameter, which have undergone so little manipulation by the ants that the individual pellets may be distinctly recognized even to the peculiar ridges produced by the rectal folds of the caterpillars.

The fungus grown on this substratum is not a mycelium as in all the species above described, but is in the form of a number of isolated whitish or yellowish bodies .25–.55 mm. in diameter, of the appearance and consistency of cheese crumbs and of an irregularly polygonal or pyriform shape (Pl. L, Fig. 29). Each of these bodies may be said to correspond to a cluster of gongylidia and may therefore be called a bromatium. It rests with one of its angles or surfaces on the caterpillar excrement, but no rhizoids or mycelial threads can be seen at this point entering and ramifying in the substratum. The whole garden is kept so moist that when first exposed to the air the surface glistens with a film of greenish liquid. As the bromatia rest on this liquid, which evidently represents a thick solution of fecal and vegetable substances, they are in a position to absorb nutriment directly. It is probable that the habit of placing the excrement on the surface of a small stone, bit of wood or dead leaf which happens to be found in the gallery of the nest, is for the purpose of retaining this nutrient moisture and preventing its absorption by the soil. All of these conditions are such as to restrict *C. comalensis* and the other forms of *rimosus* to moist, shady localities. Such situations are of course, also the only ones in which tropical and subtropical plants are sufficiently abundant to furnish an unfailing supply of caterpillar droppings.

When the bromatia are crushed and examined in water under a high power of the microscope, they are seen to consist of a dense mass of elliptical or subspherical cells measuring .78–2 μ in length and .78–1 μ in breadth. Among these there are also cells of other shapes and even smaller sizes as shown in Pl. LII, Fig. 43. The cytoplasm of all of these cells is colorless and finely granular and contains one or more clear vacuoles and a few small refractive corpuscles. A nucleus is probably present, but I have been unable to find it in my preparations. The cell wall is always very thin and transparent. These cells closely resemble those of the common yeast (*Saccharomyces*) except that they are considerably larger. Like the yeast cells they may often be found in the act of budding or dividing. In this manner probably arise the minute cells scattered about among those of much larger dimensions. All the cells are held together in the bromatial mass merely by cohesion of their surfaces without assuming polyhedral shapes from mutual pressure, and there is no perceptible intercellular substance nor any trace of an envelope enclosing the mass as a whole.

Neither the mycologists with whom I am acquainted nor the botanical works to which I have access, have given me any satisfactory information concerning the natural affinities of this singular fungus. That it must be in a purely vegetative stage of growth will probably be admitted, since there is nothing to suggest sporulation in the structure of the bromatia or the cells of which they consist. It is also evident that this plant must represent an entirely different fungus from any of those described by Mœller. Its cultivation on some artificial medium, such as agar mixed with sterilized extract of caterpillar excrement, may be expected to throw light on its affinities and to show that it belongs to some well known genus or species, but this can be undertaken only by a trained mycologist. It will be a long time, however, before we are in possession of any information in regard to these matters, if botanists continue to manifest as little interest in the fungi cultivated by ants as has been the case during the past fifteen years. In the meantime the singular fungus cultivated by *C. comalensis* and the other forms of *rimosus* over such an extensive area of the American tropics certainly deserves a name, and even at the risk of creating a synonym, I propose to call it *Tyridiomyces formicarum* gen. et sp. nov. and to assign it provisionally to the order Exoaceæ, a group which also includes the well-known yeast fungi.

I have proved that the ants eat the *Tyridiomyces*, by observing their behavior in artificial nests. On several occasions colonies were brought from New Braunfels to Austin, where they were kept in Petri dishes for periods of from one to four weeks and provided with the excrement of caterpillars (*Hyperchiria io*) which feed on the leaves of the southern hackberry (*Celtis mississippiensis*). The captive ants were as careful of the bromatia as of their brood. When the garden was disturbed they rearranged the pellets of excrement and deftly replaced the scattered and detached fungus bodies. Workers, females and males were frequently seen holding these bodies between their forelegs and eagerly rasping off portions of them with their tongues. Sometimes an ant would consume a whole bromatium, but more frequently only a portion was eaten. The irregular polygonal shape of the bodies is undoubtedly due to this method of feeding. It is equally certain that these bodies keep growing in size and regenerating the consumed portions by a rapid proliferation of their component cells. Caterpillar excrement freshly introduced into the nest was "seeded" by the workers either with entire bromatia brought from older portions of the garden or with small pieces bitten off from the bromatia and sprinkled over the new substratum. In the artificial nests the ants were unable to raise sufficient fungi for their consumption, so that in the course of a few weeks they devoured all of the bromatia and eventually died of starvation. As a rule the substratum employed by *C. comalensis* and the other forms of *rimosus,* that have come under my observation, consists exclusively of caterpillar droppings, but in several of the nests of the subspecies *minutus* in the island of Culebra, I also found small pieces of plant substances which I was unable to identify and a few small decomposing insect larvæ. These were mingled with the caterpillar excrement and also dotted with flourishing bromatia.

On one of my artificial nests of *comalensis* I made an observation which proves that this ant can also eat animal food. Several of the larvæ and pupæ that had been injured while the colony was being captured were eaten with avidity not only by the workers but also by the males and winged females. They did not, however, eat other insects, such as flies and small beetles, which I placed in their nest. The remains of the larvæ and pupæ were eventually inserted among the caterpillar excrement and carefully seeded with pieces of bromatia. This would seem to indicate that the beetle fragments seen in the nests of *C. wheeleri* at Fort Davis may have been similarly employed as a portion of the substratum.

Both in the natural and artificial nests of *C. comalensis* and *minutus* the brood was carefully kept to one side of the damp fungus garden, which would certainly be a very unwholesome and inappropriate nursery compared with the flocculent gardens of other Attii. The larvæ of *comalensis* were fed by the workers with small pieces of the bromatia. I have seen a few virgin females in the nests of this variety as early as May 10, but these and the males were not found in numbers till June 10 to 21. In the more southern countries, such as Culebra and Porto Rico, the winged phases appear as early as March and April. They "feign death" like the workers, but the males less readily than the females.

9. **Atta (Mycocepurus) smithi** *Forel.*

This species, originally described from the island of St. Vincent, seems to be widely distributed through the West Indies and Mexico, but I have seen it only in Porto Rico, where it is represented by the variety *borinquenen-*

sis. Owing to its retiring habits and small size, it is very easily overlooked. A few isolated nests were found in the open fields and among the cafetals and platanals along the turnpike which winds through the picturesque mountains between Arecibo and Ponce. These nests and one found in the curiously eroded country about Vega Baja between San Juan and Arecibo, were small, obscure craters less than 8 cm. in diameter, made of earth of a different color from that of the surrounding surface and therefore brought up from some little depth. I made several attempts at excavation but was never able to find the fungus gardens. Finally I discovered a nest in moist red clay under a stone on the shady slope of Mount Morales near Utuado at an altitude of about 400 m. The ants, about 30 in number, had constructed a small tubular entrance at the edge of the stone and had excavated a tenuous gallery about 5 mm. in diameter for a distance of several cm. along the surface covered by the stone to a small irregular chamber. In this I found the fungus garden which consisted of a mass, hardly more than 2 c. cm. in volume, of caterpillar droppings, studded with bromatia which differed from those of *Cyphomyrmex rimosus* only in the somewhat greater volume of their component cells (Pl. LIII, Fig. 44). This difference is, however, probably of little importance, as the material from which the figure was drawn was more recently preserved than that represented in Pl. LIII, Fig. 43. As *C. minutus* and *Mycocepurus borinquenensis* occur in the same localities it is quite possible that both ants may cultivate the same species of fungus.

These observations though very meagre, are nevertheless sufficient to prove that in its habits *Mycocepurus* is much more closely related to *Cyphomyrmex* than to any of the subgenera of *Atta*. It would be permissible therefore to regard *Mycocepurus* as an independent genus.

10. **Myrmicocrypta brittoni** sp. nov.

My brief glimpse of the habits of this Porto Rican ant would be hardly worth recording, were it not that no observations have been published on the habits of the remarkable genus *Myrmicocrypta*. *M. brittoni* was seen only at Santurce, a suburb of San Juan, while I was accompanying Professor N. L. Britton on a botanical excursion. The ants were nesting in the sea-beach just above high-water mark and over a narrow strip of the adjacent shore in a large grove of cocoanut palms. The black workers stood out in strong contrast with the white sand over which they were moving in the bright sunlight. The nests, which were very numerous and often only a few meters apart, resembled those of *Trachymyrmex turrifex* as they were in the form of flat, circular craters, 8–10 cm. in diameter, very shallow in the middle and with the vertical entrance gallery terminating on a small turret about a centimeter high. Under the palms the sand of the craters was often of a deep red color, unlike that of the surrounding surface, so that the galleries must have been rather deep. Unfortunately my stay in this locality was so brief that I could not examine the nests at my leisure. Although I subsequently collected in many localities on the island, I never again encountered *M. brittoni.* Santurce is, however, easily accessible from San Juan, and the future observer will have no difficulty in finding the nests and of learning much more concerning the habits of this interesting ant.

Part IV. The Attii and the Other Fungus-growing Insects.

Many insects, especially of the orders Coleoptera and Diptera, either in the larval or imaginal stages, are known to feed on fungi, but the ability to cultivate or to control the growth of these food plants is, so far as known, restricted to certain termites, Scolytid beetles and ants. The taxonomic relationships of these three groups to one another are so remote that we are compelled to regard this control as the result of convergent development. In other words, the fungus-growing habit must have arisen independently on three separate occasions in the phyletic history of the Insecta. In order to secure a broader comparative basis for a discussion of the fungus-growing habits of the Attii it will be necessary to summarize our knowledge of the similar habits in the termites and ambrosia beetles.

1. *The Fungus-growing Termites.*

Several observers have undoubtedly seen and described the fungus gardens of termites without being aware of the full significance of their observations. As these gardens are perforated sponge-like masses filled with the insects and their brood and lying on the floors of subterranean chambers, they have often been regarded as the true nests of the termites. The earliest author to call attention to these structures seems to have been König (1779). After describing the vaulted, smooth-walled earthen chambers of *Termes fatalis* at Tanjore, he mentions the gardens full of holes and lying on the floors as being "covered with little knots on their outer and inner surfaces, like chagrin skin. This texture is most clearly seen at their margins near the openings and entrances. Under a magnifying glass they appear fibrous or woolly." In the light of our present knowledge it is evident that this fibrous or woolly appearance was caused by the fungus mycelium.

Smeathman (1781) was the first to recognize the growth covering the garden as being that of a fungus, although he was not aware that it bore any important relation to the insects. In his interesting account of the African *Termes bellicosus* he refers to the gardens as "nurseries." "There is one remarkable circumstance attending the nurseries. They are always slightly overgrown with mould, and plentifully sprinkled with small white globules about the size of a small pin's head. These, at first, Mr. S. took to be the eggs; but on bringing them to the microscope, they evidently appeared to be a species of mushroom, in shape like our eatable mushroom in the young state in which it is pickled. They appear, when whole, white like snow a little thawed and then frozen again, and when bruised seem composed of an infinite number of pellucid particles, approaching to oval forms and difficult to separate; the mouldiness seems likewise to be the same kind of substance. The nurseries are inclosed in chambers of clay, like those which contain the provisions, but much larger. In the early state of the nest they are not larger than a hazel-nut, but in great hills are often as large as a child's head of a year old." I reproduce in Plate LIII, Figs. 55 and 56, Smeathman's figures of a "nursery," and of three of the "mushrooms" enlarged, as these are the earliest known illustrations of the fungus garden of any insect.

Hagen (1860), in his well-known monograph of the Termitidæ, quotes a communication which he received from Nietner of Ceylon on a species referred to *Termes fatalis.* This observer describes the vaulted earthen chambers of the nest and the fungus gardens which they contained. The latter "are hemispherical or broadly conical, flat or concave at the base. They are nowhere attached, but stand out freely in the chambers, from which they may be removed without injury. They consist of a soft bread-like mass of gnawed wood; are brown in color and when broken open golden gray. These nests are always found to be full of minute microscopic fungi, the finest and most beautiful imaginable. The corpuscles, as large as a fine pin's head and composed of small beads, grow in clusters on a net-work of roots and young brood; all resembling crystals of ice or silver." Nietner "does not believe that this fungus bears any other relation to the termites than that the substance of the nest conduces to its growth. The bread-like nests, threaded with fungi, consist of small galleries and cells which often contain so many eggs and young that the whole appears to form one living mass."

Although, as shown by these citations, the termite gardens were known long before those of the ants, their true significance was not understood till after the publication of Mœller's work (1893) on the South American Attii. Holtermann in 1899 made the first careful study of the gardens of *Termes* *taprobanes* and *fatalis* in India and the Malay Archipelago (Singapore, Java and Borneo.) He says: "These animals build their nests in the ground; once only did I find them nesting in a log. Notwithstanding their clandestine mode of life, I have been able to investigate hundreds and hundreds of their singular habitations, for I was able to find them easily by means of a species of *Agaricus* which was always rooted in a termite nest. It was only necessary to follow the stem of the pileus into the earth, although in some cases I had to dig to a depth of a meter." Like Nietner, Holtermann refers to the fungus gardens as "nests." These varied from the size of a walnut to that of a man's head and were of a sponge-like structure, full of holes and galleries containing termite eggs, larvæ and nymphs. The gardens were found resting on the floor of the earthen chambers and were separated from the walls by a space as broad as one's finger. They consisted of finely comminuted vegetable substances (portions of dead leaves and stems) that had passed through the bodies of the termites. Under the microscope "the surfaces of the galleries were seen to be covered with a white felt-work of mycelium. Usually the hyphæ were loosely united but sometimes they were combined in strands. The individual hyphæ were richly septate but showed no 'Schnallenbildung' at the septa." Even with the unaided eye Holtermann could detect aërial hyphæ projecting from the general felt-work of the mycelium. "The terminal and often the penultimate cells of these hyphæ were filled with strongly refractive, hyaline protoplasm, whereas the remaining cells contained remarkably little plasma. The terminal cells were often swollen and club-shaped. Sometimes the tip even became spherical but only in its upper portion. In exceptional cases the hyphæ anastomosed, most frequently through confluence of the terminal cells." This mycelium ramified through the whole substratum which it perhaps served to bind together. The swollen tips of the hyphæ were often aggregated to form bromatia like those of *Atta*, but Holtermann failed to find them in all termite colonies, and believes that they may occur only in the gardens of certain species. In addition to these structures he describes others of a more interesting character, namely, small spherical bodies distributed everywhere on the mycelial net-work. They were white, varied from .25–2 mm. in diameter and were usually attached by a peduncle .5–1 mm. in length. The minute structure of these spherules which were not abundant in the interior of the garden, is described as follows: "The peduncle consisting of nearly parallel hyphæ becomes wider below and loses itself in the substratum; otherwise it is of uniform thickness and the head is sharply marked off from its end. The rudiment of the head appears as a distinct thickening at the tip of the stem and as soon as the head is established the stem ceases to grow. In every chamber are found all the transitions from completed heads to their earliest development in the form of a rich branching at the tip of the bundle of hyphæ forming the stem. The otherwise parallel filaments ramify more and more, till the head is formed. It should be noted that the ends of the filaments do not become thinner while branching but always retain the thickness of the general mycelium. The outer cells grow less rapidly than the others and after a time become passive, thus forming an envelope which later appears as a kind of peridium. The limits of the envelope subsequently become more distinct through the gradual drying up of the outer cells. The inner cells, on the contrary, actively proliferate. The head continues to enlarge owing to the numerous ramifications of the hyphæ, till it has become a sac-like apical thickening. With this increase in size its spherical form changes to an oval. Some time before it attains its complete development, a rapid formation of oïdia takes place in its interior, as the hyphæ break up into very short oval cells. Only here and there a few of the main filaments remain intact, but the lateral branches and greater portion of the hyphæ everywhere break up into short rows of oïdia." These oïdia are 8–25 μ long and 6–10 μ broad and have one or two vacuoles in their protoplasm. So complete is this resolution of the hyphæ of the head into oïdia that a slight pressure on the cover glass causes the dry peridium to burst and thousands of oïdia to escape. Holtermann found that the oïdia are eaten by the termites, but he expressly states that these insects also feed on dead leaves, stems, etc. When the insects are removed from the garden, the cavities of the latter become stuffed with masses of aërial hyphæ, the ripe oïdial heads wither up and alien fungi may make their appearance. Holtermann does not believe that the termites are instrumental in preventing these changes under normal conditions since they occur even when termites are present, if the garden is exposed to the light. The normal condition of the gardens may be due to their confinement in dark subterranean chambers, where the spores of alien fungi are unable to germinate. Holtermann is also of the opinion that the above described fungus represents a form of the mushroom which he found growing out of the nests and calls *Agaricus rajap.* This mushroom has an umber-brown pileus and long gray stem. Its spores are rose-red. He succeeded in growing these spores in a culture liquid, but no oïdial heads were produced although the hyphæ sometimes bore club-shaped swellings. Oïdia from the termite gardens were also sown and slowly produced hyphæ with swollen ends and indistinguishable from those grown from the *Agaricus* spores. This is not, however, conclusive proof of the identity of the two fungi, although it seems to be regarded as such by Holtermann.

Karawaiew (1901) has published in Russian an account of this same fungus which he observed at Buitenzorg, Java. His article is accompanied by some excellent photogravures of the fungus gardens. In Plate LIII, Fig. 57, I have reproduced a portion of one of his figures showing the small oïdial heads apparently of the natural size.

Knuth (1899) observed the fungus gardens of a couple of unidentified species of *Termes* at Buitenzorg, but his description is very meager.

Mme. Errington de la Croix (1900) has published some notes on the Malaccan *Termes carbonarius* which show that the nests of this species contain fungus gardens, although they were not recognized as such. She merely states that they were "formed (perhaps?) by agglomerated eggs in a nutritive substance."

Haviland (1902) figures the nest and gardens of *Termes malayanus* and mentions a number of species of this genus from Africa and southern Asia as fungus growers. These comprise the species of the *bellicosus* group (*T. bellicosus, dives, fatalis, gilvus, azarelli, carbonarius, malaccensis, malayanus, natalensis*), of the *vulgaris* group (*T. vulgaris, angustatus, capensis, taprobanes, badius, latericius*), and of the *incertus* group (*T. incertus* and *pallidus*). Among these are the largest forms of the genus. He states that neoteinic forms, that is, fertile males and females which never develop wings, are not known to occur among fungus-growing termites. The soldiers of some of the species are aggressive and able to make sounds, thus recalling the behavior of the *Atta* soldiers. He says "In the section of the fungus-growers to which *T. bellicosus* belongs the workers run away to their subterranean passages when the nest is being opened, whilst the soldiers stay to defend the nest; generally the smaller soldiers are more active than the larger, for they run about whilst the larger occupy the crevices of the nest and the cavities of the fungus beds, where they wait and bite at anything which comes within reach. The soldiers of this group can generally produce the rattling sound. In this accomplishment, *T. carbonarius* has reached the highest stage of development for the soldiers can hammer in rhythmic unison. At first a few begin irregularly, then they get into time, and the others take it up. Every soldier in the exposed portion of the nest stands up and hammers with its head; the blow is given thrice in very quick succession, and then there is an interval of two seconds. The noise they produce reminded me of wavelets lapping on a shore. This trick of hammering is seen in only a few species; it is clearly a modification of the shaking movements so often seen in workers."

Sjöstedt (1896, 1900, 1903, 1904) has added a number of species to the list of fungus-growing termites from Africa. Such are, for example, *Termes lilljeborgi* and the allied *goliath, gabonensis, nobilis, amplus, gratus* and *vitrialatus.* According to his latest paper (1904) *T. transvaalensis* is also to be included in this series of forms. In his monograph on the African termites (1900) he figures the gardens of *Eutermes heterodon* and describes them as follows: "May 30, 1891, while digging in a hill-slope near the factory N'dian just beside the water fall of the N'dian River a considerable number of the fungus gardens of this species were unearthed. They were as large as walnuts or somewhat smaller and of a light brownish yellow color. They were scattered about in the earth, some a few inches below the surface, others somewhat deeper. The earth between them was perforated with a net-work of galleries, which connected the different beds with one another. Each of the latter was lying free in a cavity so that the termites could move about over it without obstruction. Only here and there were they attached to the adjacent earthen wall. The nest or fungus garden itself is rather fragile and made up of morel-like, folded, and rounded disks separated by a labyrinth of long ventricose or more rarely rounded cavities. The surface is lumpy and shows that the whole consists of spherical particles. The cavities are filled with milkwhite larvæ, workers, and soldiers, the two latter with yellowish brown heads." Sjöstedt's figures of the gardens of *E. heterodon* are reproduced in Plate LIII, Fgs. 60 and 61.

In 1904 Trägårdh published an interesting account of three fungus-growing termites from the Sudan (*T. natalensis*, *vulgaris* and *trægardhi*). The first builds large conical earthen mounds .8–2.1 m. in height and 1.4–5.5 m. in diameter at the base. There are no openings on the surface of these mounds, but within they have a number of large chambers, of which only the peripheral ones contain fungus gardens. These are like sponges and conform in shape to the earthen cavities on the floors of which they lie. They are perforated with galleries and consist exclusively of finely comminuted vegetable substances that have been voided and welded together by the insects, for under the microscope they are seen to be made up of pellets that have been flattened into lenticular forms. The fungus growth is described as follows: "Under the microscope the surface of the substratum is seen to be covered with a white felt-work of mycelium and under still higher magnification small hyphæ may be detected. These are aggregated here and there to form small round plates as much as 1 mm. in diameter and consisting of dense branched hyphæ. These apparently correspond to the structures mentioned and described by Holtermann, but differ from these, so far as I have been able to observe, in not having the tips of the hyphæ swollen. Here and there on the inner walls, usually not in any great abundance, but more sporadic, at least in the gardens I have examined, there are small round bodies, which may be as much as 2.5 mm. in diameter. They are of a brilliant white color and are unlike those mentioned by Holtermann in always lacking a peduncle. These spherules are of rather solid consistency and have an external tougher envelope, the whole forming a compact mass of very much branched and contorted hyphæ. The formation of the oïdia, or process whereby, according to Holtermann, the hyphæ in the interior of the spherules breaks up almost completely into very short oval cells, is by no means so complete in our species. To be sure, the hyphæ are constricted in the interior so that they appear as rows of short oval cells, completely filled with protoplasm, but these cells even in the largest spherules, which have reached their full development, remain attached to one another so that when a thin section is pressed under the cover glass, only a few of the cells escape. In the spherules described by Holtermann, on the contrary, slight pressure on the cover-glass sets free thousands of oïdia."

The mounds of *T. vulgaris* (= *affinis* Trägårdh) are as large as those of *natalensis* (1.4 m. high and 5.5 m. in diameter at the base), but the structure and arrangement of the chambers is very different. They are separated by thick walls and communicate with one another by very tenuous galleries. Each chamber has a flat floor with a peripheral groove and an arched roof. The gardens, which are shaped like inverted dishes and are not confined to the smaller peripheral chambers, are often concave beneath, with a ridge around their border fitting into the circular groove in the floor of the chamber. The substratum consists of the same materials as in *natalensis* and is perforated with numerous transverse galleries. Concerning the fungus Trägårdh says: "The spherules are much smaller than in *natalensis*, are like these nonpedunculate, and occur in great numbers on the walls and especially on the roofs of the cavities and galleries in the peripheral portions of the gardens. These portions are also stuffed with larvæ and nymphs. The spherules are unlike those of *T. natalensis* in structure, since as shown in Figs. 2 & 3 Pl. III [reproduced in the present paper as Figs. 58 & 59, Pl. LIII], the cells in the outer layer of the spherules are larger than those in the interior. Both the inner rows of cells, which ramify dichotomously, and the outer ones, are in part empty, in part filled with finely granular protoplasm." Although Trägårdh found fungus-gardens in the nests of *T. trægardhi* (= *incertus* Trägh.) which seems to live as an inquiline in the nests of *T. bellicosus, natalensis* and *vulgaris*, he believes that these had been stolen from the host termites and that *trægardhi* does not itself grow fungi.

Doflein (1905, 1906) has contributed more recent observations on the gardens of termites. He studied colonies of *T. obscuriceps* in Ceylon. The mounds of this species are about 2 m. high and terminate above in one or more huge tubular, chimney-like orifices which open into the galleries and chambers in the interior of the nest. The chambers are about as large as a cocoa-nut or smaller, with smooth walls and excavated to a depth of 1½ m. below the surface. The gardens, which consist of comminuted wood that has passed through the bodies of the insects, are dish-shaped, and there may be several piled one on top of the other in a single chamber. They are perforated with galleries filled with the termites and their larvæ. "On taking one of these brown cakes in the hand, one can see with the unaided eyes that its whole surface is covered with a fine bloom of fungus mycelium. When broken open the interior of the galleries is found to be covered with peculiar white spherules about as large as a pin-head (1–2 mm. in diam.)." Doflein's description of the minute structure of these spherules is less explicit than that of Holtermann and Trägårdh, but he actually saw the termites swallow these bodies when they were presented on the point of a sterilized needle. They were eaten by the larval workers and soldiers and by the adult kings and queens, but the adult workers and soldiers would not take them. The intestines of the latter contained only comminuted wood in which no fungus elements could be found. Doflein, is, therefore, of the opinion "that in this species the larvæ are fed with a concentrated and easily assimilated food in the form of mycelial spherules, and that these constitute the permanent food of the sexual forms, whereas the larvæ of the workers and soldiers are not fed with these after reaching a certain age but with other substances [dead wood] instead. This suggests the further inference that this food may play an important role in the differentiation of the castes of *Termes obscuriceps* Wasmann."

Doflein found that when the fungus garden of this insect is placed in the light under a bell-jar to protect it from evaporation "the termite fungus can easily be induced to fructify, a peculiarity in which it differs from the fungus cultivated by the South American leaf-cutting ants. In the course of a few days numerous long, club-shaped fruiting organs grow up out of the dense mass of hyphæ, which has developed in the meantime. As time goes on these club-shaped bodies develop pilei, which, as Mr. Green of Peradenyia informs me, are now known to be those of an *Agaricus,* a fact which is also indicated by my own observations. While the fungus is growing up freely in this manner, one is surprised to find alien fungi gradually making their appearance in the garden, and other objects in the neighborhood taking on the usual mouldiness. The tendency of the termite fungus to grow as a pure culture must therefore be very great. This is the case even when very few termites are present. Hence the purity of the culture cannot be ascribed to a ceaseless weeding process carried on by the termite workers, like that assumed by Mœller in the case of the South American *Attæ.*"

When the garden is left under the bell-jar the under surface of the latter soon becomes wet, showing that the fungus gives off a great deal of water. In a day or two the termites become suffocated, although masses of these insects hermetically sealed between pairs of watch glasses manage to live in perfect condition. On raising the bell-jar a peculiar odor is noticeable, which Doflein believes to be a gas fatal to the insects. In the wild nests this gas must be carried off by the chimneys which thus act as ventilating shafts.

All of the foregoing observations relate to Old World Termites. One is naturally led to inquire whether any of the American species raise mushrooms. Haviland was of the opinion that certain of the South American forms such as *T. dirus* are "almost certainly fungus growers." The only observations I have found on the habits of this species are contained in Silvestri's work (1903). He says: "I have seen in the galleries (Fig. 298) pieces of grass 10 mm. long, of leaves 6–10 mm. long and twigs 30 mm. long and 2 mm. in diameter. I have found such materials accumulated in small quantities at various points in the galleries, but I believe that they are not utilized in this form but are brought together in some more subterranean portion of the nest for the development of a fungus on the mycelium of which the termites feed." He found similar vegetable fragments in the nests of *T. grandis* and *molestus*. Of the latter species he says: "I was unable to reach the center of the nest, but I succeeded in finding small masses of grass with the mycelium already developed." From these, which he figures, he concludes that the species grows fungi. But these observations are by no means conclusive as is evident from a comparison with the above cited observations on the Old World species. These do not raise fungi on pieces of dead leaves, twigs, etc., but on finely comminuted particles voided from the alimentary canal and built up in the form of a sponge. Moreover the temporary stores of leaves, etc. which are brought into the nests as food may easily mould when left in the moist galleries. We may conclude therefore that there is really nothing in Silvestri's observations to prove that any of the South American termites eat and grow fungi.

The most important study of the fungus-growing termites has been recently contributed by Petch (1906). Unfortunately I could not consult this work till after the present article had gone to press, so that I am unable to review it at length. Petch carefully investigated the habits and fungus gardens of the Ceylonese *Termes obscuriceps* Wasm. and *T. redemanni* Wasm. In several particulars his account differs from those of Holtermann and Doflein. I quote from the summary of his beautifully illustrated paper the passages relating to the fungi for the purpose of showing how complex and difficult are the problems with which the mycologist is confronted in any critical study of the fungus-growing insects. After describing the sponge-like combs in the chambers of the nest, he says:[1]

"The mycelium on the comb bears small white, stalked or almost sessile

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[1] In the quotation I have omitted the numerals belonging to the paragraphs and have run the latter together.

'spheres.' These consist of branching hyphæ bearing either spherical or oval cells. The spherical cells do not germinate. The oval cells germinate readily, but it has not been possible to reproduce the 'spheres' from them. When the comb is old an agaric grows from it. This agaric appears in two forms, one of which has been assigned by various mycologists to *Lentinus, Collybia, Pluteus, Pholiota* and *Flammula,* and the other to *Armillaria.* It develops in a cartilaginous, almost gelatinous, universal veil and is a modified *Volvaria.* Sclerenchymatous cells occur at the base of the agaric stalk and in aborted agarics. It has not been possible to germinate the spores of the agaric or to grow the sphere-producing mycelium from its tissues. When the comb is enclosed in a bell jar, *Xylaria* stromata are produced. Sclerotia may also be formed: the same stromata grow from these. This *Xylaria* is probably *X. nigripes.* The shape of the stroma and conidiophore depend on the age of, and amount of moisture in, the comb. When sown on agar the spores of these reproduce the *Xylaria* stromata. These stromata occur most abundantly in combs which have produced an agaric. After continued rain *Xylaria nigripes* grows from deserted termite nests. Other fungi which grow on combs removed from the nest include *Mucor, Thamnidium, Cephalosporium, Peziza.* As these are not found in the nest though some of them are capable of development under ground, it is probable that the termites 'weed out' foreign fungi from the cultivation of the comb. The comb material is probably sterilized by its passage through the alimentary canal. That the 'spheres' form the food of the termites is probable, as in the case of the leaf-cutting ants: neither case can be considered definitely proved. *Termes redemanni* and *T. obscuriceps* undoubtedly prefer fungi, or wood which has been attacked by fungi. Whether a difference in food causes the differentiation of termites into workers, soldiers, and sexed insects, is not decided. A Ceylon agaric, *Entoloma microcarpum,* possesses a mycelium composed of spheres of swollen cells: the details of these spheres resemble the parts of the termite spheres, but are not so highly developed. It is most probable that the 'spheres' in the termite comb and the 'Kohlrabihäufchen' of the leaf-cutting ants investigated by Mœller are parts of a normal mycelium, and that their shape is modified by the insects only in a very slight degree, if at all. The available evidence appears to show that the 'spheres' are part of the mycelium of the *Volvaria,* but it has not been possible to connect these forms experimentally." A review covering some other features of Petch's work has just been published by Harris in the American Naturalist (1907).

The foregoing accounts from several observers show that the fungus-growing termites differ from the Attiine ants in several important particulars. In the first place the termites use their own excrement as a substratum, moulding it into the form of a sponge containing numerous habitable chambers and galleries. This substance is, of course, much harder and more compact than the comminuted leaves, etc., employed by the Attii. Second, the fungus grown on this substratum forms bromatia (the spherules or oïdial heads) of a very different type from those found in the gardens of the Attii. And third, the termites that are in the habit of growing fungi are not exclusively mycetophagous like the Attii, but subsist also and probably very largely on dead wood, twigs and leaves. If it be true as Holtermann and Doflein believe, that the termites are not instrumental in maintaining the purity of the fungus culture, we should have another striking difference, but it is quite conceivable that both in the termites and the ants some effluviæ emanating from the myriads of insect bodies may be responsible not only for the suppression of alien fungi but also for the aberrant growth of the food-plant.

I have already called attention to the fact that Holtermann cannot be said to have demonstrated that the *Agaricus rajap* is the fruiting form of the fungus which grows in the gardens as a mycelium with oïdial spherules. And Doflein's and Petch's observations are open to similar doubts. Not only is there no satisfactory proof that the termite fungus is a basidiomycete, but the same is true also of Mœller's statement that the South American *Attæ* cultivate the mycelium of a fungus (*Rozites gongylophora*) belonging to the same group. A careful perusal of Mœller's observations shows an important lacuna at this point. That his *Attæ* ate portions of the pileus and stem of the *Rozites* does not prove that it is the fruiting form belonging to the fungus they habitually cultivate and eat. Nor is Mœller on much surer ground when he assumes that the mycelia cultivated by different genera of Attii belong to different species of fungi, for it is very probable that the ants of one species would avoid fungus taken from the nest of another on account of the alien nest-aura. Certainly, to the human olfactories the fungus gardens of *Atta texana* have a very striking odor which is altogether lacking in the gardens of *Trachymyrmex*, and it would be strange if these differences did not affect the appetites of such sensitive insects as the ants. In my opinion, it is not improbable that the fungi cultivated both by the termites and ants may be more closely related to the moulds (Ascomycetes) than to the mushrooms (Basidiomycetes). Mœller does in fact, call attention to certain ascomycete peculiarities in the mycelium cultivated by *Acromyrmex disciyera*. This is a matter, however, to be settled by the mycologist, and I merely call attention to it in this connection, because Mœller's somewhat guarded statements have assumed an unduly positive form in the writings of subsequent reviewers of his work.

2. *The Ambrosia Beetles.*

The beetles of the family Scolytidæ may be divided into two groups exhibiting very different ethological peculiarities: the bark-borers, which excavate and inhabit tubular galleries between the bark and the splint and eat the substance of the tree, and the wood-borers, or ambrosia beetles, which extend their galleries into the wood and subsist on delicate fungi growing on their walls. All Scolytidæ are of small size and dark color, with cylindrical bodies and short legs adapted to the shape and size of their galleries (Pl. LII, Figs. 62 and 63), but the mouth-parts differ in the two groups; the bark-beetles having strong maxillæ armed with 12–20 spine-like teeth in adaptation to their hard food, whereas the fungus-eating wood-borers have weak maxillæ with 30–40 flexuous bristles. Unlike the Attii and fungus-growing termites, the wood-borers are not confined to the tropics or to a single hemisphere, but are cosmopolitan in their distribution and well represented even in the north temperate zone. The species have been assigned to a number of genera (*Platypus, Gnathotrichus, Trypodendron, Xyleborus, Xyloterus, Corthylus* and *Pterocyclon* [*Monarthrum*]). As these insects are very destructive to wood, they are well known to economic entomologists, who have described their habits in journals or text-books devoted to forestry. The remarkable habits have therefore been little noticed by entomologists interested in general biological questions.

There has been considerable difference of opinion in regard to the feeding habits of the ambrosia beetles since the time of Schmidberger (1836) who believed that *Xyleborus dispar* Fabr. fed on the sap exuding into its burrows from the surrounding wood. The mother beetle was supposed to mould this sap into a coagulated, albuminoid mass and to feed it to her young. This substance Schmidberger called "ambrosia." Various conjectures concerning its nature were expressed by Ratzeburg (1839–1844), Altum (1872–1875), and Eichhoff (1881). In 1844 Hartig discovered a fungus in the galleries of *Xyleborus dispar* and described it as *Monilia candida.* Several years later (1872*a*, 1872*b*) he described similar conditions in *Xyloterus lineatus* Oliv., which lives only in conifers, and *X. domesticus* L., which is confined to deciduous trees. In 1895 Goethe published a good description and figure of the fungus of *X. dispar.* At about this time Hubbard took up the study of the North American ambrosia beetles and published most interesting accounts of their habits (1897*a*, 1897*b*). Hopkins, too, who has given special attention to our Scolytidæ, has published a number of valuable observations (1898–1904*b*), and Hedgcock (1906) has made some important observations on the fungi. In the following paragraphs I shall confine myself to an account of the investigations of these three authors.

The ambrosia beetles resemble the ants and termites and differ from other Coleoptera in living in societies and in caring for and feeding their larvæ. The arrangement of the galleries, which have walls stained dark by the fungus, differs in different species. Those of *Xyleborus celsus* Eichh., living in the hickory, are shown in Pl. LII, Fig. 64, taken from Hopkins (1904). The galleries ramify into the sapwood from a single entrance gallery that opens on the bark. These perforations do not necessarily kill the tree, but they spoil the wood for many commercial purposes. When made in young growing trees they may be overgrown by succeeding layers of wood. Hopkins (1903) has given an interesting account of this condition in trees infested with the Columbian timber-beetle (*Corthylus columbianus* Hopkins). This beetle which is responsible for losses to the lumber interests of North America "amounting to millions of dollars, attacks the sap-wood of the young, living, healthy tree, in which the adults excavate their brood galleries and deposit their eggs. These hatch and develop into beetles and emerge within one year. The next year the operation is repeated in another place in the same tree, and so on for hundreds of years, or as long as the tree lives, so that the galleries excavated in different years and periods occupy their respective positions in the heartwood and sapwood of the full-grown and old tree. Nearly all the damage by this insect, as affecting the best part of the trees, was done 50, 100, 200 or in some cases, as noted in an old tulip tree, over 400 years ago. The age of each gallery observed in the end of the log is easily determined by counting the number of annual layers of wood between the old healed-over entrance to the galleries and the bark. Within recent years, examples of the species which do this work have been exceedingly scarce; consequently but little evidence of its work can now be found in the sapwood and outer heartwood of living trees. Therefore there is no remedy for the old work and probably no need of trying to combat an insect which is apparently becoming extinct."

Hubbard's general account (1897*a*) of the fungus growing habits of the ambrosia beetles is worth quoting *in extenso*, as it is one of the most important of recent contributions to the study of insect ethology: "A small fragment of ambrosia taken from the gallery of any species of these timber beetles, if placed on a glass slide, with a drop of water or glycerine and examined with an objective of moderate power, is plainly seen to be a fungus. It will be found, however, that the different kinds of ambrosia fungi are connected with certain species of the beetles irrespective of the sort of timber in which the galleries are constructed. So far as we yet know the food of each species of ambrosia beetles is limited to a certain kind of ambrosia, and only the most closely related species have the same food fungus.

"Two principal types exist among the varied forms of these minute fungi: (1) Those with erect stems, having at the termination of the stems, or their branches swollen cells (conidia) [Pl. LII, Fig. 65]. (2) Those which form tangled chains of cells resembling the piled-up beads of a broken necklace. The erect or stylate forms are found among those species of the beetles whose larvæ live free in the galleries (*Platypus* and *Xyleborus*). The bead-like or moniliform kinds appear to be peculiar to the species whose larvæ are reared in separate cells or cradles (*Corthylus, Monarthrum,* etc.).

"All the growing parts of the fungus are extremely succulent and tender. The conidia especially are always pellucid, and glisten like drops of dew. When the plant is in active growth, conidia are produced in the greatest abundance, growing sometimes singly, at the end of short straight stems, sometimes in grape-like clusters among interlacing branches. At such periods the fungus appears upon the walls of the galleries like a coating of hoarfrost. The young larvæ nip off these tender tips as calves crop the heads of clover, but the older larvæ and the adult beetles eat the whole structure down to the base, from which it soon springs up afresh, appearing in little white tesselations upon the walls.

"The growth of ambrosia may in fact be compared to asparagus, which remains succulent and edible only when continually cropped, but if allowed to go to seed is no longer useful as food. In like manner the ambrosia fungus must be constantly kept in fresh growth, otherwise it ripens; its cells burst and discharge the protoplasmic granules which they contain in myriads, and the entire plant disappears as if overwhelmed by a ferment.

"Various disturbances of the conditions necessary to its growth are apt to promote the ripening of the fungus, and this is a danger to which every colony of ambrosia beetles is exposed. If through any casualty the natural increase of a populous colony is checked, there results at once an overproduction of the ambrosia. It accumulates, ripens, and discharges its spores, choking the galleries and often suffocating the remaining inhabitants in their own food material. The same results may sometimes be brought about by closing the outlets of the galleries through the bark, or by spraying into them kerosene or some other noxious liquid. The inmates of the colony are thereby thrown into a panic, the beetles rush hither and thither through the galleries, trampling upon and crushing young larvæ and eggs, breaking down the delicate lining of ambrosia on the walls of the brood chambers and puddling it into a kind of a slush, which is pushed along and accumulated in the passage ways, completely stopping them in places. The breaking down of the food fungus follows and in a few days the galleries are filled with a paste-like mass of granules or spores, or with threads of mycelium, in which the living insects are suffocated and destroyed.

"The ambrosia does not make its appearance by accident or at random in the galleries of the beetles. Its origin is entirely under the control of the insect. It is started by the mother beetle upon a carefully packed bed or layer of chips, sometimes near the entrance, in the bark, but generally at the end of a branch gallery in the wood. In some species the ambrosia is grown only in certain brood chambers of peculiar construction. In others it is propagated in beds, near the cradles of the larvæ. The excrement of the larvæ is used in some and probably in all species to form new beds or layers for the propagation of the fungus.

"It is not alone, however, the excreta of the living beetles or their young that is required for the development of ambrosia; there must be present a certain amount of moisture or sap, and the sap in most species must be in a condition of fermentation. Certain ambrosia beetles, as for example the species of *Corthylus,* seem not to need fermentation in the propagation of their fungus; their galleries are constructed in the sap-wood of vigorous plants. The great majority of the species, however, attack the wood of such trees only as are moribund; in which the natural circulation of the sap has ceased, and fermentation has begun. Some of the number are also able to produce their food fungus in wood which is saturated with a vinous or alcoholic ferment, and they attack wine and ale casks, perforating the staves with their galleries and causing serious loss by leakage.

"The precarious conditions under which their food is produced limit the life of a colony of ambrosia eaters in most cases to a single generation.

"Under favorable conditions, and in large tree trunks, colonies may continue their excavations during two or three generations before the failure of the sap or change in its condition puts an end to their existence and forces the adult beetles to seek new quarters.

"When their galleries are disturbed and opened to daylight, the adult beetles generally fall to eating their ambrosia as rapidly as possible. Like other social insects they show their concern at the threatened loss of their most precious possession and try to save it, just as bees, when alarmed, fill themselves with honey.

"As its honey is to the bee, so to the ambrosia-feeding beetle its food fungus is the material the propagation and preservation of which is the chief concern of its life. Its solicitude concerning it is not surprising when one considers the herculean labors which it undergoes in the effort to produce it, the frequent failures, and the difficulties and uncertainties that at all times attend its preservation in the vegetative form, in which alone it can serve the insect as food."

The life-histories of the ambrosia beetles described and copiously illustrated by Hubbard suggest a wide range of habits within the group. The genus *Platypus*, though best represented in the tropics, contains several of the largest and most destructive species in the United States. "They are powerful excavators, generally selecting the trunks of large trees and driving their galleries deep into the heart-wood. They do not attack healthy trees but are attracted only by the fermenting of the sap of dying or very badly injured trees. The death rattle is not more ominous of dissolution in animals than the presence of these beetles in standing timber. . . . The female is frequently accompanied by several males and as they are savage fighters, fierce sexual contests take place, as a result of which the galleries are often strewn with the fragments of the vanquished. The projecting spines at the end of the wing-cases are very effective weapons in these fights. With their aid a beetle attacked in the rear can make a good defense and frequently by a lucky stroke is able to dislocate the outstretched neck of his enemy. The females produce from 100 to 200 elongate-oval pearl-white eggs, which they deposit, in clusters of 10 or 12, loosely in the galleries. The young require five or six weeks for their development. They wander about in the passages and feed in company upon the ambrosia which grows here and there upon the walls. . . . The older larvæ assist in excavating the galleries, but they do not eat or swallow the wood. The larvæ of all ages are surprisingly alert, active and intelligent. They exhibit curiosity equally with the adults, or show evident regard for the eggs and very tender young, which are scattered at random about the passages, and might easily be destroyed by them in their movements. If thrown into a panic the young larvæ scurry away with an undulatory movement of their bodies, but the older larvæ will frequently stop at the nearest intersecting passage and show fight to cover their retreat." The ambrosia of *P. compositus* Say consists of hemispherical conidia growing in clusters on branching stems. The long continued growth of this fungus blackens the walls of the older galleries.

Xyleborus saxeseni Ratzb., instead of producing ramifying galleries, excavates in hardwood trees (oak, hickory, beech, maple) a flat, leaf-shaped brood chamber connected with the surface of the bark by one or a few tubular galleries. The chamber "stands vertically on edge, parallel with the grain of the wood. The space between the walls is not much greater than the thickness of the bodies of the adult beetles. The larvæ of all ages are able to cling to the vertical walls, and to progress over them by an adaptation of the end of the body which aids them in progression. The entire surfaces of the walls in the brood chamber are plastered over with ambrosia fungus. It consists of short erect stems, terminating in spherical conidia. The freshly grown fungus is as colorless as crystal, but it is usually more or less stained with greenish yellow, and sometimes resembles a coating of sublimed sulphur. The brood chamber is packed at times with eggs, larvæ, pupæ and adults in all stages of maturity. The larvæ aid in extending the brood chamber. They swallow the wood which they remove with their jaws, and in passing through their bodies it becomes stained a mustard-yellow color. Great quantities of this excrement are ejected from the openings of the colony, but a portion is retained and plastered upon the walls, where it serves as a bed upon which there springs up a new crop of the food fungus. In populous colonies it is not unusual to find the remains of individuals which have died packed away in a deep recess of the brood chamber and carefully inclosed with a wall of chips." Hubbard found one of these catacombs containing "the multilated bodies of a dozen or more larvæ and immature imagoes, together with the fragments of a predatory beetle, *Colydium lineola* Say." In a short branch gallery of the same chamber he also found the lifeless body of the mother of the colony carefully sealed up by the surviving insects.

In the species of *Pterocyclon, Xyloberus* and *Gnathotrichus* the young are reared in cradles, or short diverticula of the main galleries, and fed by the mother beetles. In species of *Ptercyclon* (*mali* Fitch and *fasciatum* Say) "the sexes are alike, and the males assist the females in forming new colonies. The young are raised in separate pits or cradles which they never leave until they reach the adult stage. The galleries, constructed by the mature female beetles, extend rather deeply into the wood, with their branches mostly in a horizontal plane. The mother beetle deposits her eggs singly in circular pits which she excavates in the gallery in two opposite series, parallel with the grain of the wood. The eggs are loosely packed in the pits with chips and material taken from the fungus bed which she has previously prepared in the vicinity and upon which the ambrosia has begun to grow. The young larvæ, as soon as they hatch out, eat the fungus from these chips and eject the refuse from their cradles. At first they lie curled up in the pit made by the mother, but as they grow larger, with their own jaws they deepen their cradles, until, at full growth, they slightly exceed the length of the larvæ when fully extended. The larvæ swallow the wood which they excavate, but do not digest it. It passes through the intestines unchanged in cellular texture, but cemented by the excrement into pellets and stained a yellowish color. The pellets of excrement are not allowed by the larvæ to accumulate in their cradles, but are frequently ejected by them and are removed and cast out of the mouth of the borings by the mother beetle. A portion of the excrement is evidently utilized to form the fungus bed. The mother beetle is constantly in attendance upon her young during the period of their development, and guards them with jealous care. The mouth of each cradle is closed with a plug of the food fungus, and as fast as this is consumed it is renewed with fresh material. The larvæ from time to time perforate this plug and clean out their cells, pushing out the pellets of excrement through the opening. This débris is promptly removed by the mother and the opening again sealed with ambrosia. The young transform to perfect beetles before leaving their cradles and emerging into the galleries." The ambrosia of *Pterocyclon* "is moniliform and resembles a mass of pearly beads. In its incipient stages a formative stem is seen, which has short joints that become globular conidia and break apart. Short chains of cells, sometimes showing branches, may often be separated from the mass. The base of the fungus mass is stained with a tinge of green, but the stain on the wood is almost black."

In *Xyloterus retusus* Lec., which lives in the broad-toothed aspen (*Populus grandidentata*) of the northern States, and is the largest of our ambrosia beetles, still other peculiarities are observable. "Several pairs of the beetle unite in colonies having a single entrance, but each family occupies its own quarters, consisting of one or two branch galleries. The galleries do not penetrate deeply into the heart-wood. Each female attends her own brood, which are raised in cradles extending upward and downward at right angles to the main passage-way. She feeds the young with a yellowish ambrosia grown in beds in the neighborhood of the cradles. The mouth of each cradle is constantly kept filled with a plug of the food fungus. The ambrosia consists of oval cells which form upright sticks resembling some forms of styliform ambrosia, but they do not branch and are capable of being broken up into beadlike masses without losing their vegetative powers. Although the color of the fungus is yellowish, the galleries are stained intensely black."

The foregoing account of the ambrosia beetles suggests a number of intricate and important problems for future investigation. That these insects have developed unusually advanced social habits for Coleoptera is certain. It is also evident that the fungi which they cultivate are not basidiomycetes but chromatogenic or wood-staining ascomycetes. Hedgcock (1906) who has recently studied these fungi, describes a number of species referable to the genera *Ceratostomella* (wood-bluing), *Graphium, Hormodendron, Hormiscium* (wood blackening and wood-browning), *Penicillium* and *Fusarium* (wood-reddening). Cultures of one of the species (*Graphium ambrosiigerum* Hedgc.) were made from material taken from the burrows of ambrosia beetles in the wood of *Pinus arizonica* Eng. The mycelium was seen to develop stromata with heads, and both primary and secondary conidia, but the author records no observations on the relations of the beetle to the fungus or the modifications produced in the food plant when in the presence of the insect. From some investigations now in progress at the Royal School of Forestry at Tharandt, Saxony, and communicated to me by Professors K. Escherich and F. W. Neger it would seem that in the case of the ambrosia beetle *Trypodendron lineatus* the fungus is found only in the mycelial and conidial stages when the insects are present, but that when these have been removed stromata with globular or flattened heads, similar to those figured by Hedgcock for *Graphium atrovirens* and *ambrosiigerum*, are produced on the walls of the galleries.

The constant association of certain species of ambrosia beetles with certain species of fungi, irrespective of the kind of wood on which they grow, indicates that the mother beetles must be instrumental in transferring the plant from colony to colony and from tree to tree in some manner analogous to the fungus transfer of the *Atta* queen when establishing her formicary. Hedgcock seems to have found evidence of some such transference of *Ceratostomella* conidia. He says: "These are readily disseminated by the wind and are probably carried by insects which penetrate the wood and bark of trees, like most of the ambrosia and bark beetles. At the stage in which the conidia form a mucilaginous mass, they adhere readily to any insect that may pass over them. In the laboratory a number of species of mites which feed on fungi carried spores on their bodies from colony to colony in an agar plate to a sterile portion of the surface of the medium and started new colonies of the fungus. Bark beetles were placed in a dish with the conidial stage of *Ceratostomella* and after allowing them to remain a short time were transferred to sterile agar plates which were inoculated with spores from the insects. It is probable that some species of insects feed on the conidial stage of *Ceratostomella,* especially one or more species of ambrosia beetles and a number of mites infesting their channels in the wood; but proof is yet lacking on this point. The constant occurrence of this fungus in the channels of a number of wood boring beetles indicates that the conidia or the ascospores must be carried in some manner by these insects."

Interesting as are the observations on the fungicolous ants, termites and beetles collated in the preceding pages, we must admit that they are still fragmentary and leave many fundamental questions unanswered. It will be seen that our knowledge of the fungi cultivated by all three of these insect groups is very unsatisfactory and that many more investigations must be undertaken before we shall be able to determine the precise taxonomic affinities of the plants and to estimate the extent of the modifications induced in their growth by the symbiotic insects. Equally fragmentary is our knowledge of the phylogenetic origin and development of the fungus-growing habit. Indeed, this problem in the termites and ambrosia beetles has scarcely been recognized a yet. The views that have been entertained in regard to the phylogeny of the Attii and their habits are perhaps, of sufficient interest to command attention till further observations are forthcoming.

3. *The Phylogeny of the Attii and of the Fungus-growing Habit.*

The Attii belong to a complex of Myrmicine genera once grouped together as Cryptocerides on account of their superficial resemblance to the ants of the genus *Cryptocerus.* Forel in 1892 was the first to split up this artificial group. He divided the genera into four tribes, the first including the Attini, the second the Dacetonini, again divisible into three subgroups: *a, Strumigenys, Orectognathus, Epitritus* and possibly *Hypopomyrmex*; *b, Daceton* and *Acanthognathus,* and *c, Rhopalothrix, Ceratobasis* and *Cataulacus.* To a third tribe he assigned *Meranoplus* and *Calyptomyrmex,* which were recognized as having affinities with the Tetramorii, and to a fourth tribe he assigned *Cryptocerus* and *Procryptocerus.* In 1893 he said: "Taxonomy has proved to me that the Attini are intimately related to the Dacetonini (*Strumigenys,* etc.) and has led me to suppose that the Attini are of secondary derivation. This is all the more probable, because they are confined to the American continent, whereas the Dacetonini are distributed over the whole world, even to New Zealand."

Emery, writing in the same year (1893), expresses himself somewhat more explicitly. "If we separate from the *ensemble* of the ancient Cryptocerides, on the one hand *Cryptocerus* and *Procryptocerus* (group Cryptocerini), on the other hand *Cataulacus* (forming by itself a distinct group), and if furthermore, *Meranoplus* and *Calyptomyrmex* be attached to *Tetramorium* and its allies, all that remains of M. Forel's Attini may be divided into two groups according to the venation of the wings. In the genera *Atta, Sericomyrmex, Cyphomyrmex, Glyptomyrmex* [*Myrmicocrypta*], *Apterostigma,* the radial cell is closed and there is no trace of a discal cell nor of a recurrent nervure, the trunk of the cubital nervure being straight or feebly sinuous. In the genera *Rhopalothrix, Strumigenys* and *Epitritus* the radial cell is open; in the female *Rhopalothrix petiolata* Mayr I find a vestige of a recurrent nervure, and in the male *Strumigenys imitator* Mayr the trunk of the cubital vein is strongly arcuate behind at the base, indicating the point of insertion of a recurrent nervure that has disappeared. According to Smith's figures, *Daceton,* which has a discal cell, belongs to this latter group; probably the same is true of *Acanthognathus, Ceratobasis* and *Orectognathus,* whose wings are still unknown. The former of these two groups, which we may call the *Attini genuini* is exclusively American, whereas the latter, which may bear the name Dacetini, is represented in all the zoological regions except the Ethiopian. These two groups are, however, very closely allied, and the fossil genus *Hypopomyrmex,* which undoubtedly approaches the ancestors of *Strumigenys* very closely, has a discal and a closed radial cell. The closed radial cell is an archaic character and is found only in a few Myrmicine genera, such as *Cryptocerus, Atopomyrmex, Myrmecina, Pheidologeton, Aëromyrma, Carebara, Lophomyrmex* and certain species of *Tetramorium.* In my opinion no great taxonomic importance is to be attached to this character; nevertheless its constant occurrence in the true Attini must be taken into consideration."

In a later paper (1895) Emery groups the genera above mentioned as follows:

Tribe Dacetii: *Daceton, Acanthognathus, Orectognathus, Strumigenys, Epitritus, Rhopalothrix, Ceratobasis.*

Tribe Attii: embracing besides the genera and subgenera enumerated in the introduction to this paper, *Wasmannia* and possibly also *Ochetomyrmex.*

Tribe Cryptocerii: *Procryptocerus* and *Cryptocerus.*

Tribe. Cataulacii: *Cataulacus.*

Emery is apparently of the opinion that the Attii are related to the Tetramorii through such intermediate genera as *Wasmannia* and *Ochetomyrmex,* whereas Forel is inclined to seek their origin among the Dacetonii through such a series of genera as *Cyphomyrmex, Rhopalothrix* and *Strumigenys.* Morphological considerations may be adduced in support of either of these contentions. The question then naturally arises as to whether there are in the Dacetonii or Tetramorii any ethological peculiarities which by further development could lead to the highly specialized fungus-growing habits of the Attii.

Forel (1902) regards *Cyphomyrmex* as the most primitive genus of Attii and believes that some of the species do not raise fungi, whereas the others make very imperfect gardens on insect excrement. These ants would thus be transitional in their habits to the Dacetonii, many of which also live in damp places in rotten wood, where fungi grow in abundance and where there is plenty of insect excrement that might gradually come to be employed as a substratum. In an earlier paper (1893) Forel quotes in support of his view an observation of H. Smith on the West Indian *Strumigenys smithi* Forel, a species which nests in rotten wood. Smith says that "the cavities in which these ants are found are *always* black inside, as if with some fungoid growth." Forel infers from this that some species of *Strumigenys* cultivate fungi. It seems to me, however, that his view evaporates into a mere hypothesis when the facts are more closely scrutinized. In the first place, there is no known species of *Cyphomyrmex,* nor in fact any Attiine ant, which does not cultivate fungi. I have shown in the third part of the present paper that statements to the contrary in regard to *C. rimosus* are false and due to superficial observations. In the second place, there is not a particle of evidence to prove that the Dacetonii cultivate fungi. The species discovered by Smith may have been nesting in the abandoned fungus-stained galleries of ambrosia beetles, or the dark color of the walls may have been due to other causes. I may say also that in no colonies of the various species of *Strumigenys* which I have found in the United States and West Indies were there any traces of fungi. These ants live in rather small communities under stones or in rotten wood and feed on insects. Many of our species live as thief ants, after the manner of *Solenopsis molesta* Say, in the nests of larger ants. *Rhopalothrix* seems to have similar habits, to judge from some field notes accompanying a colony of an undescribed species taken, with all its larvæ and pupæ, under a stone in Jamaica.

Forel's view, however, contains an interesting suggestion, for the nature of the substratum on which the fungi are grown may be supposed to throw some light on the origin of the habit under discussion. In all the fungicolous insects there is an unmistakable tendency to employ vegetable substances that have passed through the alimentary tract of insects. This is the case in all fungus-growing termites, and in the ambrosia beetles. Among the Attii, as I have shown, this tendency is apparent in nearly all the species that have been closely observed. Though most pronounced in the lower genera and subgenera (*Cyphomyrmex, Apterostigma, Mycocepurus, Trachymyrmex*), it is not wholly lost even in the leaf-cutting *Attæ*, and the method employed by the *Atta* queens in manuring their incipient fungus-gardens suggests that the food plant may have been originally grown on fecal substances. It is quite possible, however, that in the Attii this habit is secondary and that it was preceded phylogenetically by culture on some other substance since generally abandoned as less suited to the purpose. This leads us to a consideration of another view on the origin of the fungus-growing habit.

Von Ihering (1894) advances the following opinion: "We know quite a number of ants, like the species of *Pheidole, Pogonomyrmex* and furthermore species of *Aphænogaster* and even of *Lasius,* which carry in grain and seeds to be stored as food. Such grain carried in while still unripe, would necessarily mould and the ants feeding upon it would eat portions of the fungus. In doing this they might easily come to prefer the fungi to the seeds. If *Atta lundi* still garners grass seeds and in even greater than the natural proportion to the grass blades, this can only be regarded as a custom which has survived from a previous cultural stage." Thus von Ihering would explain the origin of fungus cultivation and the supervention of the leaf-cutting habit.

This view, like Forel's, is, of course, purely hypothetical. There are, however, a few facts which indicate that the Attii may have developed from grain-storing species allied to the Tetramorii (*Meranoplus* and *Tetramorium*) as Emery has suggested. That certain harvesting species form nests and have many peculiarities of behavior similar to those of the smaller Attii is shown by Santschi's observations on *Oxyopomyrmex santschii* Forel of the Tunisian deserts. In a letter to Forel, Santschi states that the nests of this ant are "so characteristic that when one has once seen one of them, nothing is easier than to find others. I am surprised to find that they have not attracted the attention of other observers. Especially remarkable is the tiny crater, which has the form of a cone, hardly more than 4–5 cm. in diameter and 2.5–3 cm. high. The circumference of its funnel-shaped top is 3–4 cm. across and its margin is always perfectly circular and entire, except in nests in process of construction, where it is at first semilunar like the very small nests of *Messor arenarius*. At the bottom of the funnel the small entrance is found, 1–2 mm. in diameter, just large enough to permit one of the workers to pass. A single nest has rarely two entrances and two cones. A single perpendicular gallery descends below the surface. A first chamber is found at a depth of 2–3 cm. It is horizontal, attaining a length of 5 cm., a breadth of 1 cm. and a height of 5 cm. In this first chamber the pupæ are kept for the purpose of enjoying the warmth and here I have found a number of workers and winged females. Thence the gallery continues to descend to a depth of 15–20 cm. and finally opens into two or three chambers of the same dimensions as the first. These contain pupæ and an ample provision of very small seeds. This ant is therefore granivorous. I surprised a few of the workers entering the nest with seeds in their mandibles. They go out foraging singly and not in files like *Messor* and other genera. They are very slow in their movements and are very apt to stop motionless at the least alarm. Day or night one or two of the workers may be seen on the outer surface of the crater scarcely moving unless molested, but when disturbed they hurriedly retreat into the nest to spread the alarm. Their habits are rather nocturnal. If a light is brought near the nest when a worker is on the point of leaving it with a grain of sand she hurriedly backs into the entrance and there stops, closing it perfectly with her burden. If the observer remains very quiet, she eventually comes forth and deposits her load on the slope of the crater. There are scarcely more than thirty individuals in a nest."

Although *Oxyopomyrmex* has no close taxonomic relations with the Attii or Tetramorii, but rather with members of the complex genus *Stenamma*, it closely resembles *Trachymyrmex turrifex* and *Mycetosoritis hartmanni* in the small size of its colonies, the slowness of its movements and the structure of its nests. These resemblances are in all probability, due to convergent development. Nevertheless, species with habits like *Oxyopomyrmex* might conceivably become fungicolous by some such substitution of instincts as that suggested by von Ihering. So many assumptions, however, would have to be made in order to account for the delicate and intricate adaptations shown by existing Attii in the cultivation of their fungi, that further speculation seems idle till we are in possession of a greater body of careful observavations.

Less hypothetical and worthier of confidence are the views of Forel and von Ihering concerning phylogenetic development within the narrow confines of the Attiine tribe itself. But here, too, we must proceed with caution. The ants of the genera and subgenera *Cyphomyrmex, Myrmicocrypta, Sericomyrmex, Apterostigma, Mycocepurus* and *Mycetosoritis* on the one hand, are obviously primitive, for they form small colonies and have monomorphic workers and proportionally small males and females. On the other hand, *Atta* s. str. would seem to be the most recent and highly specialized genus of the tribe, because the colonies are very populous, the workers are polymorphic with marked division of labor, and the males and females are very large. Between these two groups, *Trachymyrmex, Acromyrmex* and *Mœllerius* occupy an intermediate position. Mœller and subsequent writers have been inclined to find a parallel development in the instincts, but this is not so clear as the morphological sequence and relations of the various genera and subgenera, for we find *Atta* s. str. and *Acromyrmex* building gardens on the floors of their chambers like *Cyphomyrmex,* whereas *Apterostigma* has highly specialized gardens, suspended and enveloped in a mycelial web not known to occur in any other Attii. Moreover, at least one species of *Cyphomyrmex* (*rimosus*) and a species of *Atta* s. lat. (*Mycocepurus smithi*) cultivate a very different fungus from that known to occur in the nests of any other species; *C. wheeleri* does not, at least as a rule, use caterpillar excrement as a substratum but only small plant slivers; *Mycetosoritis* specializes to the extent of using only the anthers of flowers, and *Sericomyrmex opacus* has a predilection for fruit pulp. All of these species are therefore aberrant in their habits, though belonging to primitive genera. Mœller has certainly overestimated the primitive nature of the treatment bestowed on the fungi in the nests of *Cyphomyrmex* as a group, and although the bromatia of the *Apterostigma* gardens may be of a generalized type, this genus is in many other respects more highly specialized than *Atta* s. str.

Granting the cogency of these considerations, it still remains true that the Attii in general present a series of increasingly specialized forms as we pass from the species of *Cyphomyrmex* through the subgenera *Mycetosoritis, Trachymyrmex, Acromyrmex* and *Mœllerius* to *Atta* s. str. in which we see the culmination of a wonderful progress in adaptation. These insects in the fierce struggle for existence, everywhere apparent in the tropics, have developed a complex of instinctive activities which enables them to draw upon an ever-present, inexhaustible food-supply through utilizing the foliage of plants as a substratum for the cultivation of edible fungi. No wonder therefore, that, having emancipated themselves from the precarious diet of other ants, which subsist on insects, the sweet exudations of plants and the excrement of phytophthorous Rhynchota, the Attii have become the dominant invertebrates of tropical America!

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EXPLANATION OF THE PLATES.

PLATE XLIX.

Fig. 1.— *Cyphomyrmex rimosus* Spinola var. *comalensis* var. nov. Worker.
Fig. 2.— *Cyphomyrmex wheeleri* Forel. Worker.
Fig. 3.— *Atta* (*Trachymyrmex*) *turrifex* Wheeler. Worker.
Fig. 4.— *Atta* (*Trachymyrmex*) *septentrionalis* McCook. Worker.
Fig. 5.— *Atta* (*Mœllerius*) *versicolor* Pergande. Worker.
Fig. 6.— *Atta* (*Mycetosoritis*) *hartmanni* sp. nov. Worker.
Fig. 7.— The same in profile.
Fig. 8.— *A.* (*M.*) *hartmanni* sp. nov. Male.
Fig. 9.— *Atta* (*Trachymyrmex*) *arizonensis* sp. nov. Deälated female in profile.
Fig. 10.— Head of same from above.
Fig. 11.— *Atta texana* Buckley. Soldier.
Fig. 12.— Thorax of same in profile.
Fig. 13.— *Atta texana.* Media.
Fig. 14.— *Atta texana.* Minima.

PLATE L.

Fig. 15.— *Atta* (*Mycocepurus*) *smithi* Forel. Worker.
Fig. 16.— Same in profile.
Fig. 17.— *Sericomyrmex opacus* Mayr. Worker.
Fig. 18.— *Myrmicocrypta brittoni* sp. nov. Worker.
Fig. 19.— Same in profile.
Fig. 20.— *Apterostigma pilosum* Mayr. Worker.
Fig. 21. *Atta sexdens* L. Brazil. Hypopygium of male.
Fig. 22.— *Atta cephalotes* L. Panama. Hypopygium of male.
Fig. 23.— *Atta insularis* Guérin. Cuba. Hypopygium of male.
Fig. 24.— *Atta texana* Buckley. Texas. Hypopygium of male.
Fig. 25.— *Atta mexicana* F. Smith. Mexico. Hypopygium of male.
Fig. 26.— *Atta* (*Mœllerius*) *versicolor* Pergande. Male. Genitalia from above.
Fig. 27.— Unusual triple nest-entrance of *Trachymyrmex turrifex.*
Fig. 28.— Unusual double nest-entrance of *Mycetosoritis hartmanni.*

Fig. 29.— Bromatia of fungus (*Tyridiomyces formicarum* gen. et sp. nov.), cultivated and eaten by *Cyphomyrmex rimosus* and its various subspecies and varieties.

PLATE LI.

Fig. 30.— Nest diagram of *Mycetosoritis hartmanni* (Nest X of the table on p. 763), showing four chambers, the connecting galleries, and the pendent fungus gardens.

Fig. 31.— Nest diagram of *M. hartmanni* (Nest T of the table on p. 763), with three chambers all containing fungus gardens.

Fig. 32.— Nest diagram of *M. hartmanni* (Nest U of the table on p. 763), with three chambers.

Fig. 33.— Nest diagram of *Trachymyrmex turrifex* (Nest L of the diagram on p. 756), with five well-developed chambers and pendent fungus gardens in all but the first.

Fig. 34.— Nest diagram of *T. turrifex* (Nest N of the table on p. 756), with four chambers, the lowermost small, recently excavated, and with an incipient garden suspended from rootlets.

Fig. 35.— Nest diagram of *T. turrifex* (Nest O of the table on p. 756), with four well-developed chambers and flourishing gardens in three of them.

Fig. 36.— Nest diagram of *T. turrifex* (Nest P of the table on p. 756), with five chambers and poorly developed fungus gardens in three of them. This nest shows very clearly the suspension of the substratum from the rootlets hanging into or traversing the chambers.

Fig. 37.— Nest diagram of *Trachymyrmex septentrionalis* var. *obscurior* (Nest C of the table on p. 749), consisting of only two chambers, both containing pendent fungus gardens.

Fig. 38.— Nest diagram of *T. obscurior* (Nest D of the table on p. 749), consisting of three chambers two of which open directly into each other. The mound of sand is shown in the typical position in front of the oblique entrance gallery. The first chamber contains exhausted substratum ready to be carried out of the nest.

Plate LII.

Fig. 39.— Nest diagram of *Trachymyrmex obscurior* (Nest I of the table on p. 749), of the racemose type, with five chambers. Extending from the single chamber on the right is an unfinished gallery. All the chambers contain well-developed pendent gardens except the first, which is partially filled with exhausted substratum.

Fig. 40.— Nest diagram of *T. obscurior* (Nest J of the table on p. 749) of the racemose type, with seven chambers, six of which are of large size. Of the latter, five contain flourishing gardens but one (to the extreme right) seems to have been only recently excavated by the ants. The crater of this nest was best developed behind the entrance.

Fig. 41.— Nest diagram of *T. obscurior* (Nest G of the table on p. 749) of the racemose and horizontally spreading type, with four chambers. The first chamber, in which the mother queen established her colony, had been subsequently enlarged by the workers.

Fig. 42.— Nest diagram of *T. obscurior* (Nest H of the table on p. 749) of the racemose type, with four chambers. As in the preceding, the first chamber had been enlarged by the workers, the lowermost was apparently in process of excavation.

Fig. 43.— Cells composing the bromatia of *Tyridiomyces formicarum,* the peculiar fungus grown by *Cyphomyrmex rimosus.*

Fig. 44.— Cells composing the bromatia of the same or an allied species of *Tyridiomyces* grown by *Mycocepurus smithi* var. *borinquenensis.*

Plate LIII.

Fig. 45.— Nest diagram of *Trachymyrmex obscurior* (Nest F of the table on p. 749), resembling the nests of *T. turrifex,* with five chambers.

Fig. 46.— Nest diagram of *Trachymyrmex turrifex* (Nest R of the table on p. 756) in pure sand, showing the elongation of the galleries.

Fig. 46a.— Deeper portion of the same nest with incipient gardens on the rootlets traversing the two lower chambers.

Fig. 47.— *Attaphila fungicola* Wheeler. Male. From nest of *Atta texana.*

Fig. 48.— *A. fungicola.* Female; dorsal view.

Fig. 49.— Same, ventral view.

Fig. 50.— *Attaphila bergi* Bolivar. Male, from nest of *Acromyrmyx lundi.* (After Bolivar.)

Fig. 51.— *A. bergi,* Female. (After Bolivar.)

Fig. 52.— Head of same. (After Bolivar.)

Fig. 53.— Hypopygium of same. (After Bolivar.)

Fig. 54.— *A. bergi.*— Hypopygium of male. (After Bolivar.)

Fig. 55.— Fungus garden of *Termes bellicosus* Smeathm. (After Smeathman.)

Fig. 56.— Bromatia of same more highly magnified. (After Smeathman.)

Fig. 57.— Portion of the fungus garden of a Malayan *Termes,* showing spherical bromatia of *Agaricus rajap* Holtermann. (After Karawaiew.) Natural size.

Fig. 58.— Bromatium from the fungus garden of an African Termite, *Termes vulgaris* Havil. (After Trägårdh.)

Fig. 59.— Portion of same crushed under a cover-glass and more highly magnified, to show the component cells. (After Trägårdh.)

Fig. 60.— A fungus garden of the African *Eutermes heterodon* Sjöst. $\frac{2}{5}$ natural size. (After Sjöstedt.)

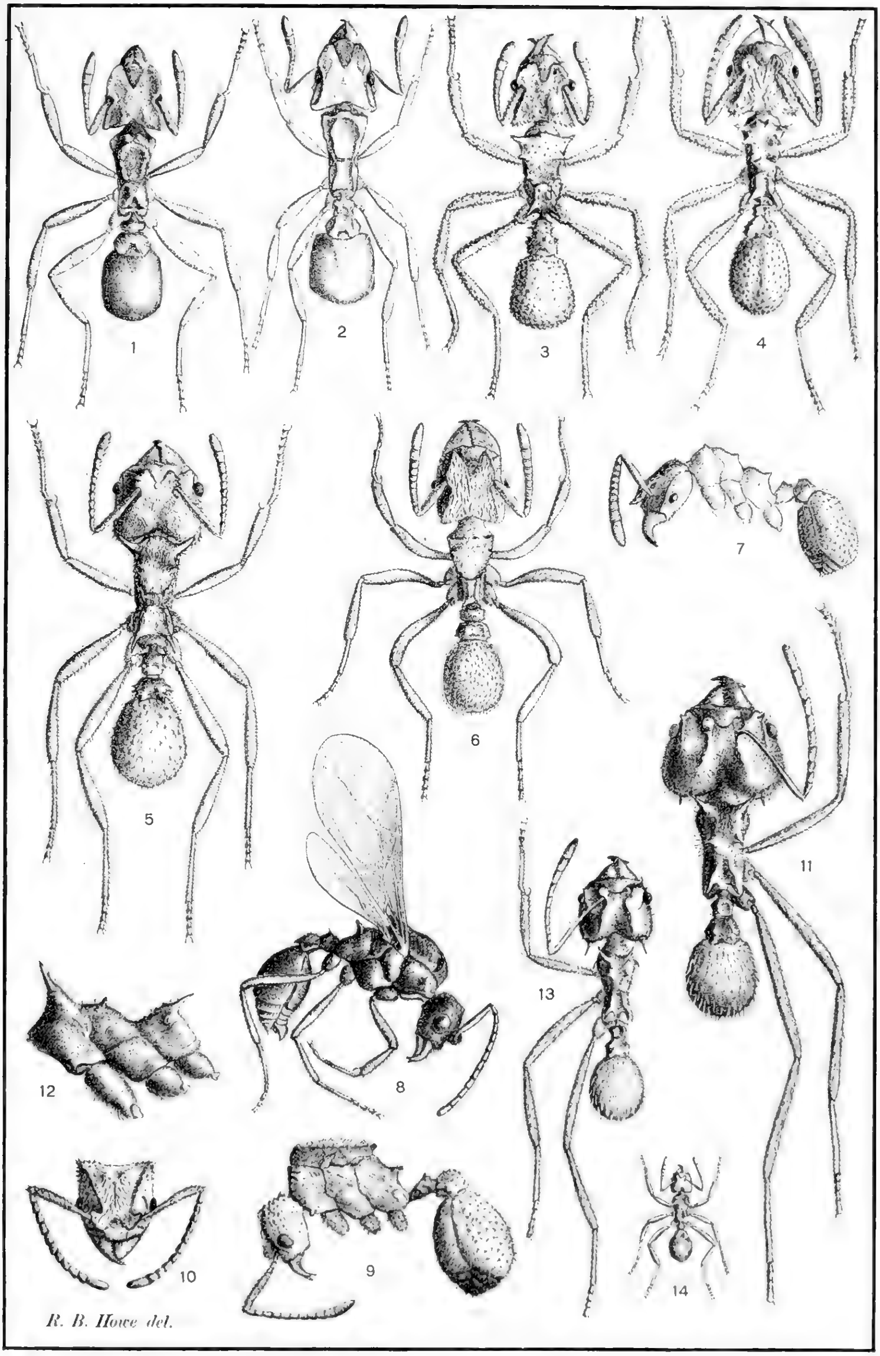
Fig. 61.— Section of same. (After Sjöstedt.)

Fig. 62.— Ambrosia beetle (*Xyleborus celsus* Eichh.) of the hickory. Female, enlarged. (After Hubbard.)

Fig. 63.— *X. celsus,* Male. (After Hubbard.)

Fig. 64.— Piece of hickory showing burrows of *X. celsus* in the sapwood. (After Hopkins.)

Fig. 65.— "Ambrosia" or fungus grown by *X. celsus* enlarged. On the right a few of the filaments more highly magnified.



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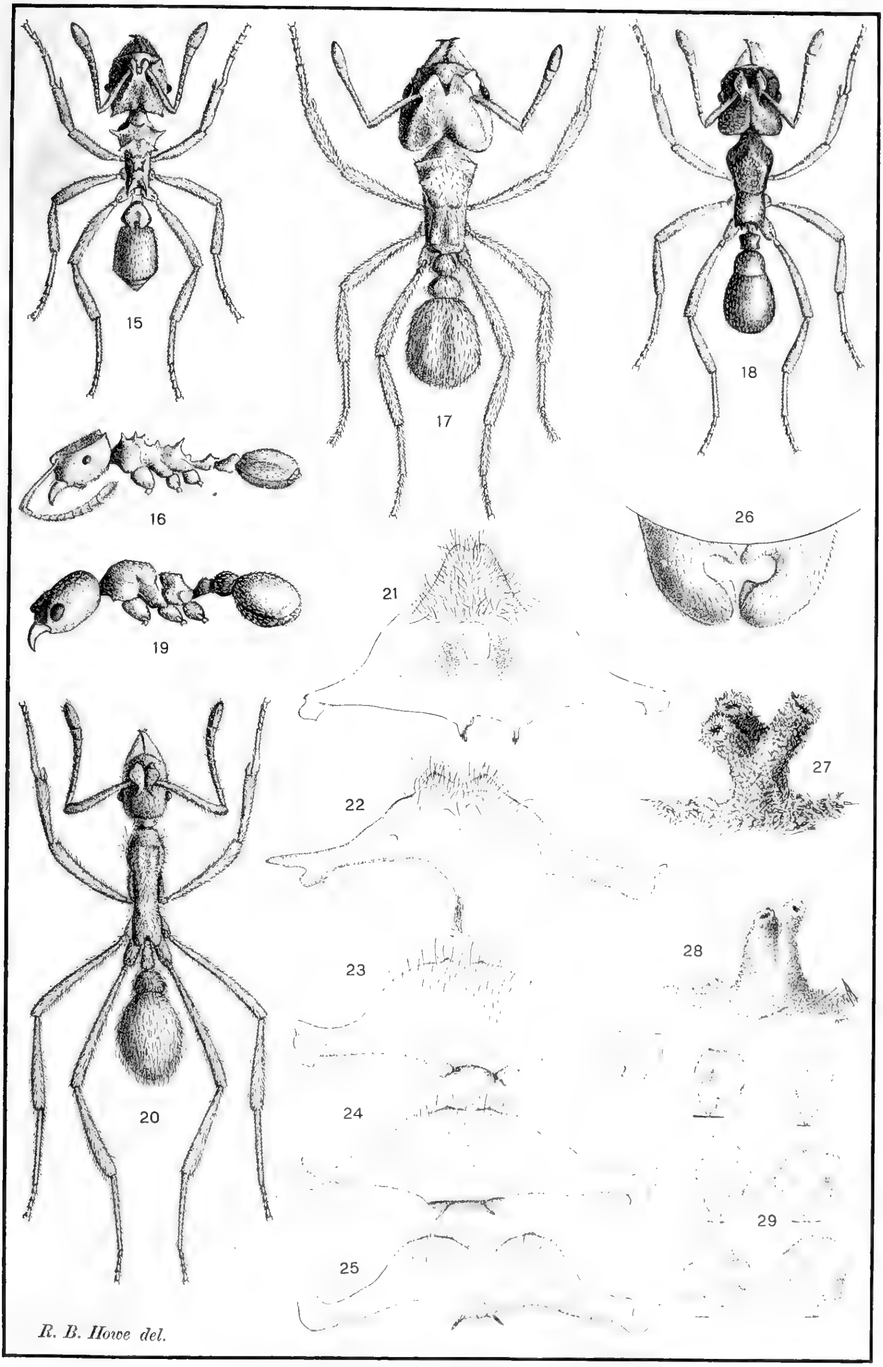
FUNGUS-GROWING ANTS OF NORTH AMERICA.



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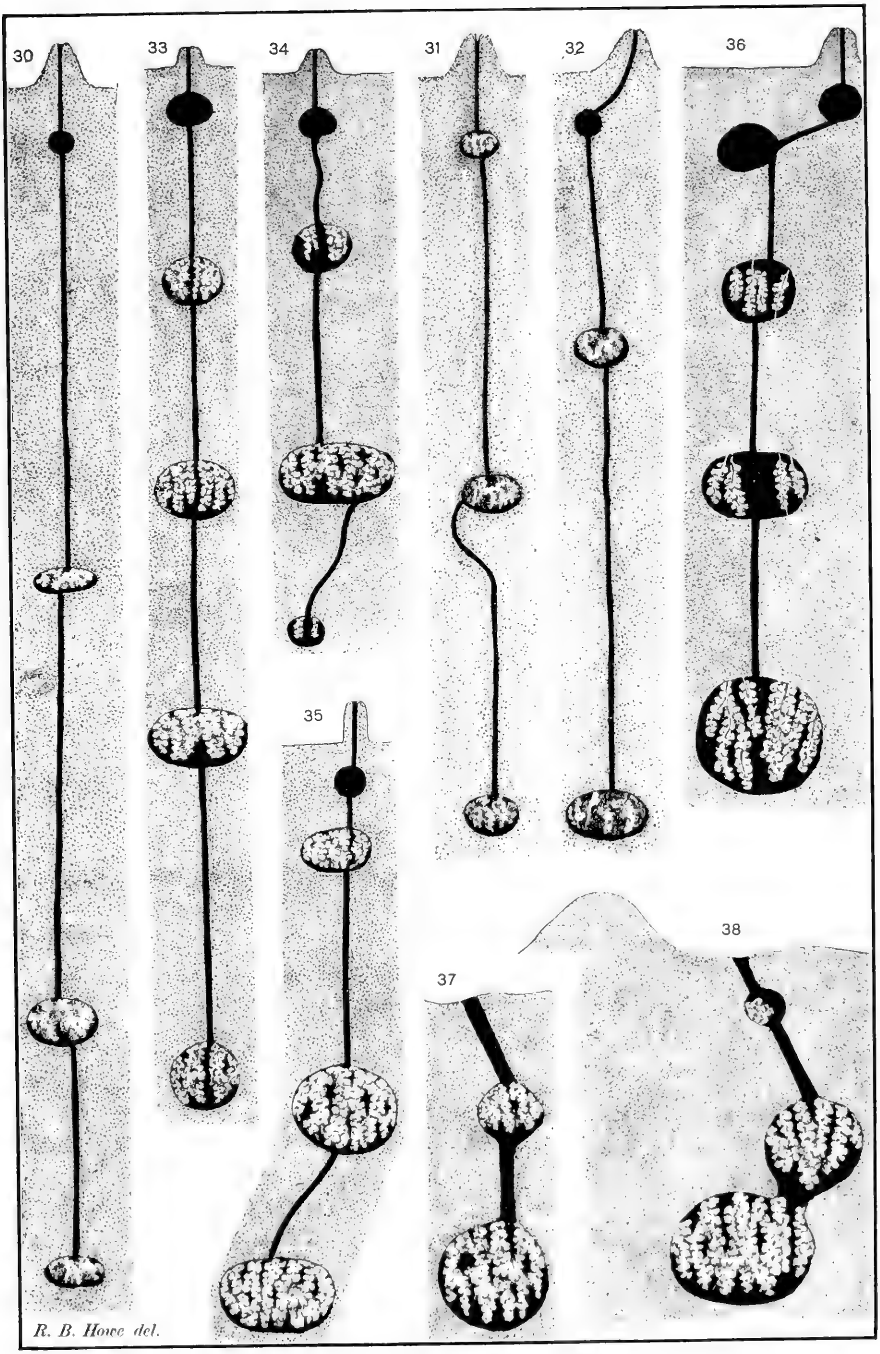

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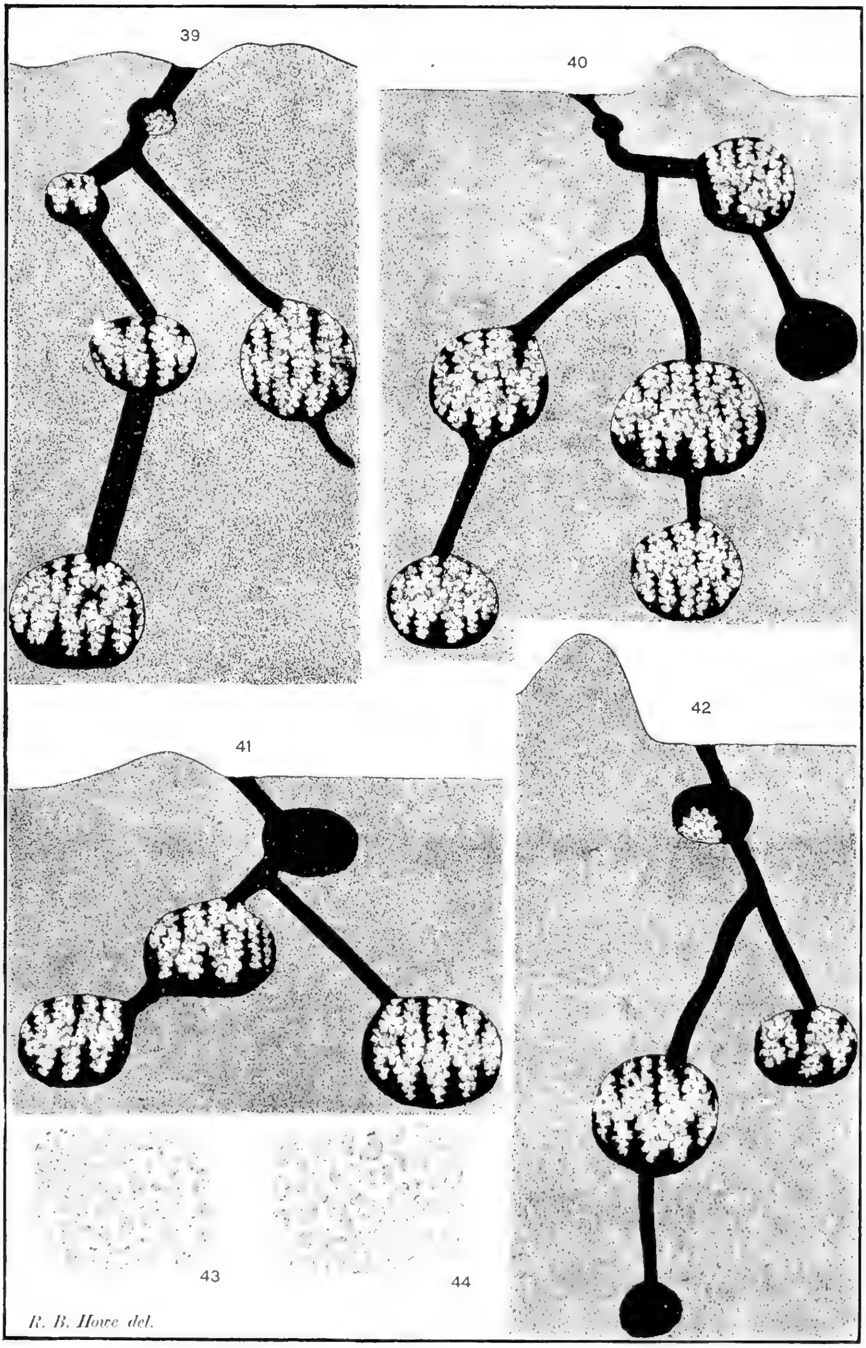

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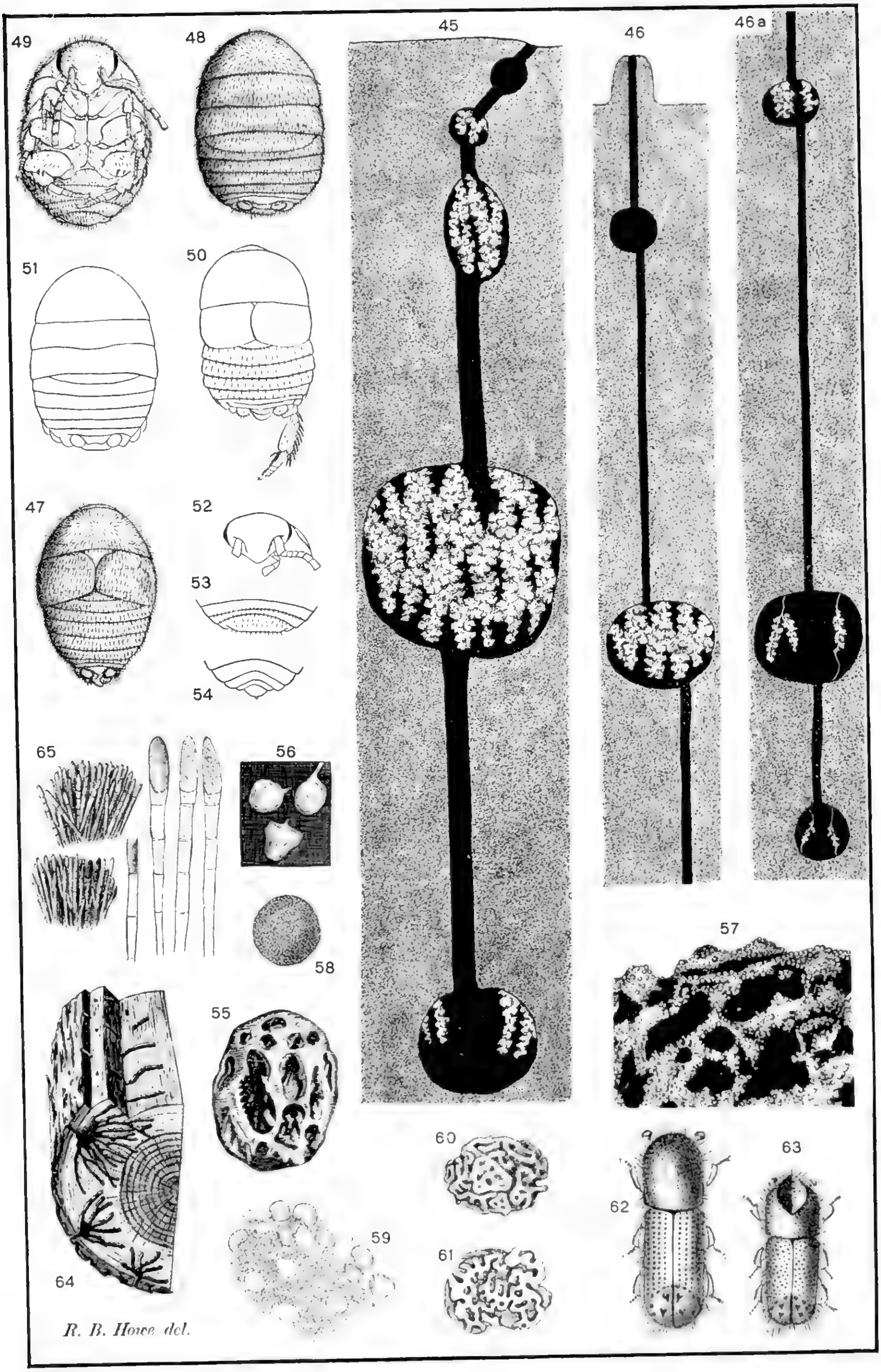

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