59.57, 96 : 15.5

# 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.

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."

[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

[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

[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

[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

[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 'Içа' 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: *subænescens* 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.

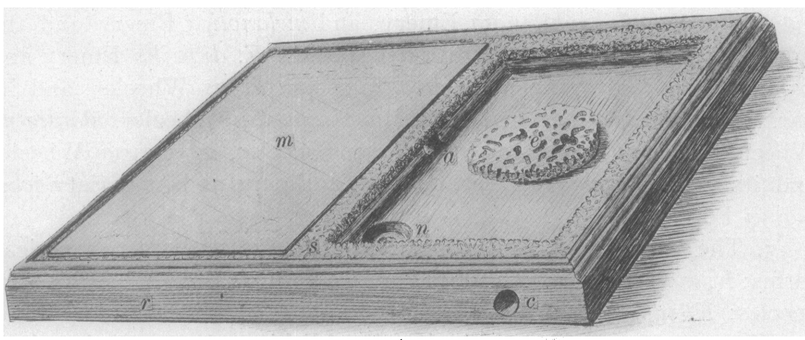



Fig. 1. Artificial ant nest, constructed on the combined principles of the Fielde and Janet nests; with one of the roof-panes removed. *r*, plaster of Paris base, cast in a single piece; *c*, entrance to be plugged with cotton after the admission of the ants from the Forel arena; *m*, glass roof-pane, 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

[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. The 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 *incertv* 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.

[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

[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:

[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

[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

[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 *subs sericea* 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 con ave 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 $2\frac{2}{3}$ 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 ho d. 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)

[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

[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

[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

[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.

[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

[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]

[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

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

[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

[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 $\frac{1}{8}$ 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. $\frac{3}{8}$ 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. $\frac{1}{2}$ 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 $\frac{1}{8}$ 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 $\frac{1}{6}$ 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.

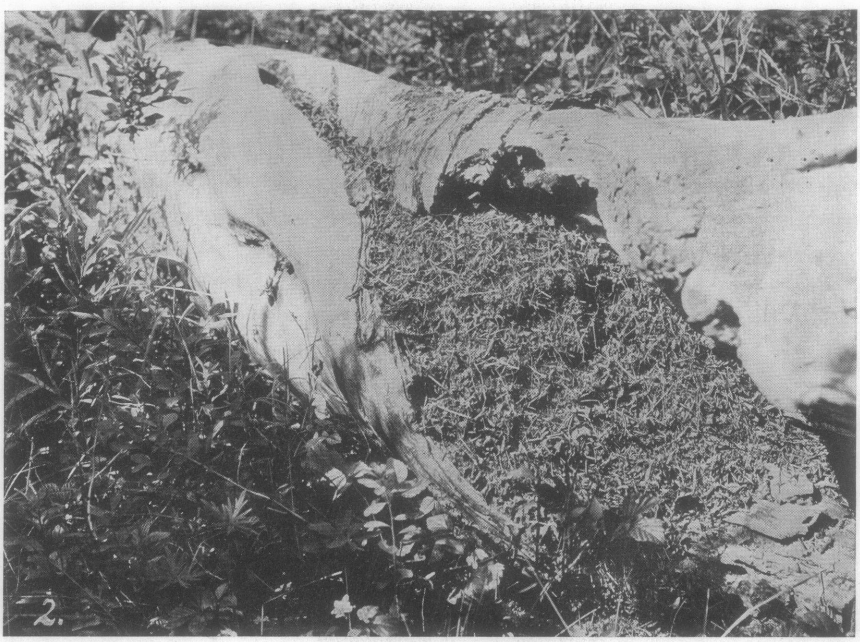
FIG. 2.—Nest of same species from the same locality, showing zone of green grass around the base and covering the entrance

PLATE XIV.

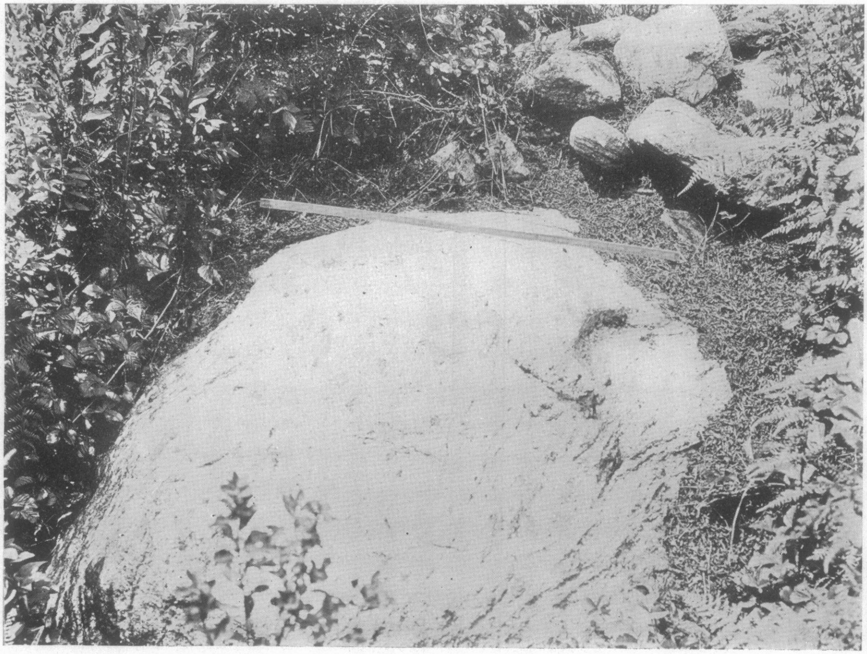
FIG. 1.—*Formica exsectoides* mound shot through with the stems of plants that have been killed by the ants. Staten Island.

FIG. 2.—Large mound nest of *Formica exsectoides*, showing the numerous entrances around the base, Colebrook, Conn.


INCIPIENT ANT NESTS.

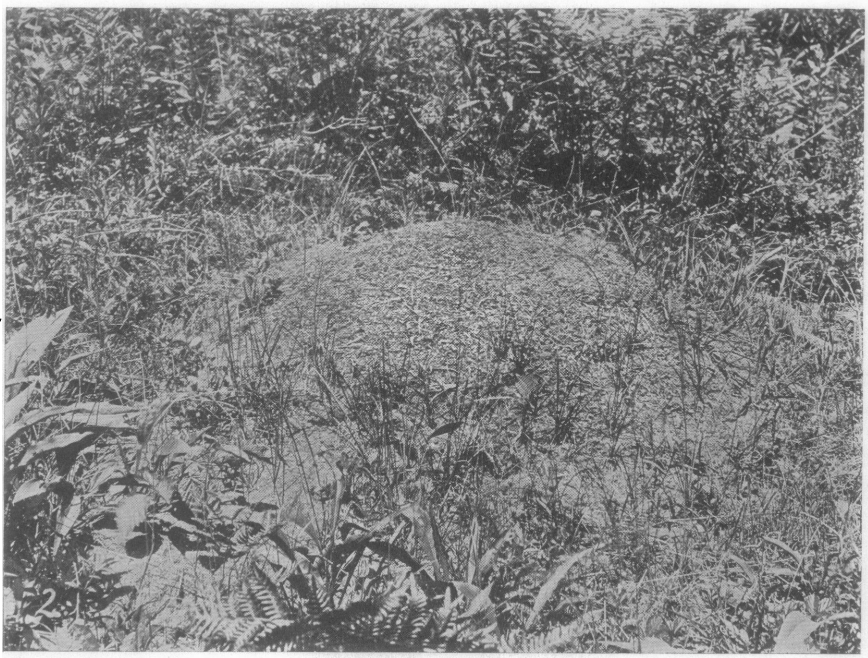



NESTS OF FORMICA INTEGRA.



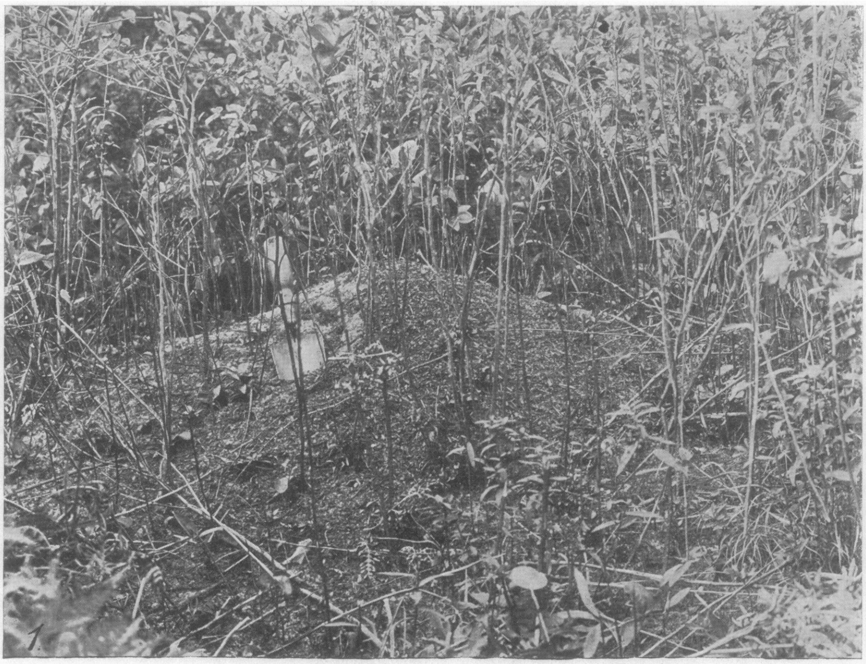

NESTS OF FORMICA INTEGRA AND F. CONSOCIANS.


NESTS OF FORMICA INCERTA.



SMALL NESTS OF FORMICA EXSECTOIDES.

LARGE NESTS OF FORMICA EXSECTOIDES.





LARGE NESTS OF FORMICA EXSECTOIDES.