

**Article XXXIII.—THE ANTS OF CASCO BAY, MAINE, WITH
OBSERVATIONS ON TWO RACES OF FORMICA SAN-
GUINEA LATREILLE.**

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The following study of the ants of Casco Bay was made during July of the current year while I was spending my vacation at the Tuft's College Marine Laboratory at South Harpswell. In making this study I am greatly indebted to the director of the laboratory, Professor H. V. Neal of Knox College, who not only interested himself greatly in the work but put himself to considerable inconvenience to take me in the laboratory launch to several points in the bay.

As yet no systematic study of the ants of Maine has been undertaken. In my list of the Formicidæ of New England ¹ I recorded 14 forms from the State. Those since collected in the Casco Bay region comprise twice that number. It is certain that these represent only a portion of the fauna, but I believe that there can be hardly more than 35 or 40 species, subspecies and varieties in the whole State. On this supposition, Maine, though four times as large as New Jersey, would have less than half as large a formicifauna. The boreal character of this fauna is very pronounced, especially in the Casco Bay Region. Indeed, the rocky, heavily glaciated southernmost islands and the tips of the slender peninsulas, which are bathed by the icy Arctic Current and in winter swept by bleak winds from the ocean, have an ant-fauna essentially like that of the White Mountains and Nova Scotia. Unquestionably this is true also of the remaining islands and peninsulas of the Maine coast northeast of Portland. The bases of the peninsulas, the adjacent continental shores, and the more sheltered islands in their immediate neighborhood, however, are considerably warmer and are therefore inhabited by many forms common to Massachusetts, Connecticut, New York and other more southern localities. This striking contrast between the regions exposed to the cold currents of air and water and the inland regions is beautifully apparent in the flora, and can be readily followed during a journey of less than 20 miles from the tip of Harpswell Neck to its junction with the mainland. At the tip and on the adjacent islands the forests are almost pure formations of black spruce (*Picea nigra*), but pines and deciduous trees increase in number to the northward and the

¹ Fauna of New England, 7. Occas. Papers Boston Soc. Nat. Hist., VII, 1906, pp. 1-24.

latter predominate near the Gurnet. The conditions are therefore comparable to a descent from the cold bogs and spruce woods of the White Mountains at an altitude of 1500 to 2000 feet to the deciduous forests of much lower elevations. Sensitive insects like the ants, would, of course, be expected to vary adaptively in different portions of such a region, and we find, therefore, at the southern extremity of Harpswell Neck, on Haskell Island and Ragged Island, only a few decidedly boreal species, whereas nearly the entire series of the subjoined list occurs in such sheltered spots as Prince's Point near the Gurnet and at the north end of Sebascodegan Island. One species, *Formica fusca*, exhibits a very interesting geographical variation. Out in the cold current among the spruce trees, and even on bleak and treeless islands, almost the only ant is a boreal variety, *glacialis*, closely resembling the typical *fusca* of the Alps and northern Europe, but further inland, among the deciduous forests, it is replaced by the larger and more silvery pubescent variety *subsericea*, which is the common form throughout the Northeastern States and Canada. There occurs also in the Casco Bay region, but very sparingly, a third variety, *argentata*, with very silvery body and reddish legs. This is also a boreal form, with its true center of distribution in the mountains of British Columbia and Colorado. Although the title of this paper may seem to be somewhat presumptuous, since I have explored only a small portion of Casco Bay, I nevertheless believe that further researches will add few species to my list or materially modify the general remarks which I have deemed it safe to make.

I expected to find at South Harpswell an excellent field for continuing my studies on *Formica sanguinea*, an ant by no means abundant in the neighborhood of New York. I was not disappointed. Colonies of two of our American subspecies, *subintegra* and *aserva*, are extremely common in several places on Harpswell Neck, within easy walking distance from the laboratory, so that I was able to add materially to my former account of these slave-makers.¹ I could have wished to devote the entire summer to my observations and experiments on these insects, but my vacation came to an end and I was obliged to return to New York the first of August.

¹ On the Founding of Colonies by Queen Ants, with Special Reference to the Parasitic and Slave-making Species. Bull. Am. Mus. Nat. Hist., XXII, 1906, pp. 33-105, pls. viii-xiv.

I. LIST OF SPECIES, SUBSPECIES AND VARIETIES.

Ponerinæ.

1. ***Ponera coarctata pennsylvanica* Buckley.**—A single worker taken in a spruce clearing under a bit of wood near a nest of *Formica aserva*.

Myrmicinæ.

2. ***Cremastogaster lineolata* Say.**—A few colonies of a small dark form of this species, nesting under the bark of spruce stumps near the Austin cottage, South Harpswell and on Ragged Island.

3. ***Stenamma (Aphænogaster) fulvum* Roger** var. ***piceum* Emery.**—Only two colonies seen, both nesting under stones, one at South Harpswell, the other on Sebascodegan Island.

4. ***Myrmica rubra brevinodis* Emery** var. ***canadensis* Wheeler.**—Very common in the bogs, nesting in hummocks of moss (*Polytrichum commune*), or under stones and bits of wood.

5. ***Myrmica rubra scabrinodis* Nylander,** var.—The workers of this form are large and reddish and resemble those of the var. *sabuleti* but the lobe at the base of the antennal scape is much larger and more cup-shaped. A few colonies were found among the grass and lichens on the dry heaths near South Harpswell.

6. ***Myrmica rubra scabrinodis* var. *fracticornis* Emery.**—This form occurs in dry bogs and shady spruce clearings. Several fine colonies were found on Lower Goose Island and Sebascodegan Island.

7. ***Leptothorax acervorum canadensis* Provancher.**—Isolated workers taken on the bark of spruce logs and stumps at Stover's Point, near South Harpswell, and on Ragged Island.

8. ***Leptothorax emersoni* Wheeler.**—This interesting little ant, which always lives in symbiosis with *Myrmica canadensis*, was found in several localities near South Harpswell. It is particularly abundant in a bog near the spring at Stover's Point.

9. ***Leptothorax curvispinosus* Mayr.**—A fine colony of a small, pale variety of this species was found living in a curled dead leaf at the roots of a huckleberry bush in a dry bog near the Austin cottage at South Harpswell.

Dolichoderinæ.

10. ***Dolichoderus pustulatus* Mayr.**—The typical, coarsely sculptured form of this species, with large yellow spots on the gaster, is common in the

bogs near the Austin cottage and on Sebascodegan Island. Its colonies are small and live under the dead leaves about the roots of shrubs. The workers wander about singly and attend aphids. July 24 a fine dealated female was found running over the ground.

11. *Dolichoderus taschenbergi* Mayr var. *gagates* Wheeler.—Several files of foraging workers of this form were seen in the same locality as the preceding, but I was unable to locate any of the nests. The colonies were smaller and more depauperate than those which I have observed at Lakehurst, N. J. July 24 several dealated females, evidently just alighted from their nuptial flight, were found running over the ground.

12. *Tapinoma sessile* Say.—This ant seems not to occur at the lower end of Harpswell Neck or on the outlying islands, but is common in dry, sunny places at Prince's Point and on Lower Goose Island. The workers are smaller and more silvery than the typical *sessile* and have yellow knees and tarsi. This same form is common in the mountains of New Jersey and New York.

Camponotinae.

13. *Brachymyrmex heeri depilis* Emery.—A few colonies of this minute ant were found under lichens and stones at South Harpswell, Lower Goose Island and Prince's Point.

14. *Lasius niger* L. var. *neoniger* Emery.—The worker of the typical form of this variety has the large stature and pilosity of the typical palearctic *niger*, but it is of a pale yellowish or brownish color and has very distinct ocelli. Smaller, darker forms, with less pubescence and forming transitions to some of the subvarieties of var. *americanus* Emery and the European *alienus* Först. occur in many localities throughout the Northern States. *L. neoniger* is also closely related to the var. *sitkaënsis* of Alaska but, according to Pergande's description, must be somewhat smaller and more pilose. The female of *neoniger* is much larger (9–10 mm.) than that of *americanus*, and has the coloring and pilosity of the worker. The wings are long (9–9.5 mm.) and tinged with yellowish.

I have found this variety only in moist localities, especially in sunny, subalpine meadows and, in the Casco Bay region, in bogs near the seashore. It is very common at South Harpswell and on Ram, Haskell, Ragged, Lower Goose and Sebascodegan Islands. The specimens from these localities are exactly like a long series in my collection taken at Digby, Nova Scotia (J. Russell), Montreal, Canada (Miss A. Rucker), Selkirk Mts., British Columbia (J. C. Bradley), Fabyan, N. H.; Litchfield Hills, Conn.

(W. M. Wheeler), Black Mts., N. C. (W. Beutenmüller), Giant Forest, Cala. (J. C. Bradley), King's River Cañon, Cala. (H. Heath), Moscow, Idaho (J. M. Aldrich), Corvallis, Oregon; Olympia, Washington (T. Kincaid), and Beulah, New Mexico (T. D. A. Cockerell).

15. ***Lasius niger* L. var. *americanus* Emery.**—Common on dry, sunny heaths where it builds small crater nests or lives under stones, boards, etc. Like the European *alienus*, this is a hairless or nearly hairless xerothermic variety of *niger*. When nesting in shady woods or damp spots it usually has a darker color and may develop a few erect hairs on the scapes and legs, thus approaching the smaller and darker forms of *neoniger*.

16. ***Lasius brevicornis* Emery.**—Common under stones and in dry bogs in the northern portions of Casco Bay. One colony was found on Haskell Island.

17. ***Lasius* (*Acanthomyops*) *claviger subglaber* Emery.**—Several large colonies of this beautiful ant, containing mature winged females, were observed on Sebascodegan Island, July 23. In the evening while returning from this locality to South Harpswell in the launch, I saw thousands of these females on the surface of Harpswell Sound where they had fallen from their nuptial flight during the afternoon. They were, of course, unable to rise in the air and were eagerly devoured by the fishes.

18. ***Formica exsectoides* Forel.**—Only three colonies of this ant, and these all of small size, were seen; one in a dry bog at South Harpswell and two in an open, sunny pasture at Prince's Point. None of the nests measured more than two feet in diameter. The depauperate condition of these colonies indicated that Casco Bay must be near the northernmost limit of the range of this "mound-building ant of the Alleghanies."

19. ***Formica rufa obscuriventris* Mayr.**—A fine colony of this form, which I had redescribed as *F. dryas* before seeing Mayr's types in Professor Forel's collection, was found nesting under a pile of stones at Doughty's Point on Sebascodegan Island. There were many winged males but no females in the nest.

20. ***Formica rufa integra* Nylander.**—A few fine colonies of this subspecies were seen on Lower Goose Island and at Prince's Point. One of these colonies contained many males and a few winged females (July 24). It is a significant fact that both *F. integra* and *F. exsectoides* were found only in localities where *F. subsericea*, their temporary host, abounds, and not in colder regions where *glacialis* is the prevailing or only form of *fusca*.

21. ***Formica sanguinea aserva* Forel.**—Very common on Harpswell Neck, at Ash Point, and Prince's Point, on Lower Goose and Sebascodegan Islands, but no trace of it could be found on Haskell or Ragged Islands. A fuller account of this and the following subspecies is given below.

22. **Formica sanguinea subintegra** Emery.—Emery regarded this as a variety of the subspecies *rubicunda*, but after examining a long series of specimens from many localities in the Northern States, I deem it preferable to regard it as an independent subspecies. It is common in the same localities as the preceding form and is also absent on Haskell and Ragged Island, though its slave, *F. glacialis*, is extremely common in both of these places.

23. **Formica fusca** L. var. **glacialis** var. nov.

The worker of this form averages smaller than those of vars. *subsericea* and *argentata* (5–6 mm.) and is deep black, with only the mandibles, scapes, base of funiculus, knees, trochanters and tarsi reddish. The pubescence on the body is decidedly shorter and more dilute, so that the surface appears smoother and more shining, but less so than in the var. *subaenescens* Emery.

The female, too, is smaller than in the varieties *subsericea*, *subaenescens* and *argentata* (7–8 mm.), and the gaster is decidedly shining. Color and pubescence as in the worker. Wings tinged with greyish as is *subsericea* and *subaenescens*, not colorless as in *argentata*.

The male, measuring 9–10 mm. is slender, with black antennæ and yellow legs; coxæ, trochanters, and bases of femora black or infuscated. Wings as in the female. External genitalia infuscated; pubescence of gaster longer than in *subaenescens* but shorter than in *subsericea*.

The type locality is South Harpswell. It is common also in most of the above mentioned localities in Casco Bay but is replaced by the var. *subsericea* in warmer and more sheltered spots. There are series of the var. *glacialis* in my collection from the following localities: Digby, Nova Scotia (John Russell), Cod Roy, Newfoundland (L. Gratacap), Bedford, N. Y. (Wheeler), Franconia, N. H. (Mrs. A. T. Slosson), Fabyan, N. H. (Wheeler).

F. glacialis is the most abundant and conspicuous ant of the Casco Bay region, as it constructs large masonry dome nests from one to four feet in diameter at the base and four to ten inches high, often covered with grass or *Polytrichum commune*. They appear as hummocks both in clearings in the spruce woods and in the open fields. Less frequently this ant is found nesting in old stumps or under stones. It is certainly very closely related to *subaenescens* and to the typical European *fusca*, but differs from the former in the smaller size and greater number of its workers. Moreover, I have never found *subaenescens* living in masonry dome nests but only under bark or stones in woods, nor are the domes of the European *fusca* as large or conspicuous as those built by the new variety. The males and winged females appear during the latter half of July. The workers are the normal slaves of *F. subintegra* and *aserva* in the Casco Bay region and, of course,

the only slaves in the cold localities where *F. subsericea* is lacking. On the golden rod plants near the laboratory at S. Harpswell I found the workers of *glacialis* assiduously attending small Membracids (*Publilia concava* Say), which were all stationed singly on the leaf petioles a short distance from the points where they had oviposited.

24. ***Formica fusca* L. var. *subsericea* Say.**—Rare and sporadic near South Harpswell and apparently lacking on the outlying islands (Haskell, Ragged, Ram and Orr's), this form is more abundant at the northern end of Sebascodegan and Lower Goose Islands and on Prince's Point. The colonies are smaller and more concealed and the workers are conspicuously larger than those of *F. glacialis*.

25. ***Formica fusca* L. var. *argentata* Wheeler.**—A few colonies of this form were taken from small concealed nests under stones at South Harpswell, on Sebascodegan and Lower Goose Islands.

26. ***Formica subpolita* Mayr var. *neogagates* Emery.**—Common on the dry heaths near the Austin cottage at South Harpswell and on Prince's Point, Lower Goose and Sebascodegan Islands.

27. ***Camponotus herculeanus* L.**—Not uncommon in the decaying logs and stumps in the spruce clearings. I have taken it on Harpswell Neck, Lower Goose Island, Prince's Point and Sebascodegan Island. On Ram Island I took a single winged female which must have flown from the adjacent islands or mainland, as there is no timber on this island.

28. ***Camponotus herculeanus ligniperdus* Latr. var. *novæboracensis* Fitch.**—This is the more common form of the species in all the localities mentioned and also on Ragged and Haskell Islands. Like the European *ligniperdus* it often nests under stones. I could find no traces of the entirely black subspecies *pennsylvanicus* De Geer or its variety *ferrugineus* Fab., both of which are the most common forms further south and west.

II. MYRMECOPHILES.

The only myrmecophiles encountered in ant-nests in the vicinity of S. Harpswell were the following:

1. ***Microdon tristis* Loew.**—July 11 a single young larva of this Syrphid was found in Basin Cove on Harpswell Neck in the gallery of a *Formica aserva* colony that was nesting in a rotten stump. In the same locality and in another nest of the same ant a number of old and empty puparia were seen.

2. ***Cremastochilus castaneæ* Knoch.**—July 18 I found in a nest of *F. glacialis* at Stover's Point 11 larvæ of this beetle. The nest was a typical

masonry dome with some vegetable detritus collected on its summit. The larvæ, mostly full grown, were scattered through the earth at a depth of between three and six inches below the surface. As soon as they were exposed by the trowel the ants attacked them furiously. A twelfth larva was found enclosed in a broadly elliptical earthen cocoon, and preparing to pupate after the manner of other Cetoniids. The larvæ and incipient pupa were carefully imbedded in earth in a glass jar and by August 3 had nearly all pupated. The adult beetles hatched August 14-22. As the larva and pupa of this singular myrmecophilous beetle have not been noticed heretofore, I subjoin a description:¹

Larva.—Length 12-14 mm. Of the usual clavate, scarabæidoid shape and pale drab color, with the abdomen in the region of the ninth and tenth segments darker, owing to the black contents of the intestine. Head moderately convex, but little narrower than the prothoracic segment, nearly twice as broad as long, broadest at its anterior border which is straight; surface obscurely reticulate, rather shining; front with a rather faint Y-shaped sulcus. Ocelli absent. Clypeus regularly transversely rectangular, somewhat more than three times as broad as long, its anterior and posterior angles rather sharp, its disc crossed by an impressed transverse line parallel with the posterior and anterior borders; its surface obscurely rugulose. Labrum longer but somewhat narrower than the clypeus, with rounder anterior corners and faintly trilobed anterior border; surface reticulate, shining, with two obscure longitudinal impressions converging in front. Antennæ turned forward, rather stout, 4-jointed, inserted on conical eminences which simulate basal joints; first joint slightly obconical, three times as long as broad; second joint shorter but of the same form; third but little shorter than the second, produced at the tip on the ventral side into a blunt tooth; fourth as long as the first joint, slightly fusiform, with blunt tip and slightly constricted and attenuate base. Mandibles somewhat shorter than the head, distinctly ridged above, opaque and depressed at the tips, smoother and more convex at the base; right mandible obscurely tridentate, with sharp, blade-like masticatory border, left quadridentate. Legs raptorial, with rather dense, coarse hairs; length slightly increasing from the first to the third pairs; coxæ subequal, subcylindrical, flattened externally, much longer than broad; trochanters obconical, third pair somewhat longer than the others, as is also the case with the femora, tibiæ and ungulæ; femora and tibiæ slightly clavate; ungulæ narrow, subulate, nearly straight, much shorter than the tibiæ. Prothorax duplicate above, meso- and metathorax and first eight abdominal segments triplicate, gradually enlarging posteriorly; ninth and tenth abdominal segments still larger and smooth. Pleuræ triangular, plicate. Spiracles broadly elliptical, with subcentral bulla and minutely cribrate respiratory area. Body covered with sparse, coarse, rather straight, fulvous hairs.

Pupa.—Length 9 mm. Enclosed in an elliptical earthen cocoon 11-12 mm. long, 8-9 mm. in diameter and about .5 mm. thick. The larval exuviae are crowded to the anal pole and the free pupa has the form of the adult beetle except for the undeveloped condition of the wings and elytra. The scutellum is longer than broad and has a pointed tip.

¹ I have recently brought together what is known of the habits of *Cremastochilus* in an article entitled: Studies on Myrmecophiles. I *Cremastochilus*. Journ. New York Entom. Soc., Vol. XVI, June 1908, pp. 68-79, 3 figg.

The larva of *Cremastochilus castaneæ* resembles that of *Osmoderma*, so carefully figured and described by Schiødte,¹ but the body is shorter and more robust, with a proportionally larger head and stouter legs; the head is shorter, the anterior corners of the clypeus are less acute and its sides are more parallel; the tibiæ are not ovate and the ungulæ are not conical. In the structure of the head and legs (except the ungulæ), the larval *Cremastochilus* is more like the larval *Cetonia*, figured by Schiødte.

III. FORMICA SANGUINEA SUBINTEGRA EMERY.

The great abundance of fine colonies of this slave-making ant in the neighborhood of South Harpswell enabled me to gain a much more satisfactory acquaintance with its habits than has been possible heretofore. Though not uncommon in many localities in the Northeastern States, one rarely happens on localities where its nests can be readily found and inspected, since its usual host, or slave in these regions is *F. subsericea*, an ant which resembles the European *fusca* in concealing its nests. Moreover, the few experiments which I had made at Colebrook, Conn., on its methods of colony formation gave indecisive or negative results so that I desired to reinvestigate the subject.

In the Casco Bay region *subintegra* nests almost exclusively in the typical masonry domes of *F. glacialis*. Nests containing the *subintegra* are usually at once recognized by their very large size (3 and 4 feet in diameter! and this is due to the very pronounced slave-making habits of this race of *sanguinea*. It is never found in unmixed colonies, and not only are its own workers very numerous but they are associated with three to five times as many workers of *glacialis*, so that a single mixed colony often comprises thousands of individuals. The nests are always of the pure *glacialis* type, and if the *subintegra* assists in their construction, as is very probable, it must adhere rigidly to the plan adopted by its slaves. The intense dulotic instincts of *subintegra* are also shown by the magnificence and frequency of its forays. These, as in other races of *sanguinea*, do not begin till the latter part of July, after both the colonies of this species and of the *glacialis*, which it plunders, have given off their yearly brood of males and winged females. Both species are colonially proterandric, that is, the males hatch from the cocoons and mature before the females. The earliest date on which I found mature male *subintegra* was July 10. On the following days callow females made their appearance and both sexes had left their parental col-

¹ De Metamorphosi Eleutheratorum Observationes. 2 vols. Thiete, Copenhagen, 1861-1883.

onies by July 24. The first slave-making foray was witnessed on Sebascodogan Island July 23. It is probable that both the maturing of the sexual phases and the occurrence of the forays were much advanced during the past summer, owing to the unprecedented heat and drought during June and July. In normal seasons these occurrences are probably delayed in boreal regions like Casco Bay till the first week in August.

On the afternoon of July 26 I witnessed at Prince's Point two forays of *subintegra* which for magnitude and interest surpassed any that I had previously seen. Both colonies inhabited large mound nests and behaved in precisely the same manner. The army from one was plundering, about 85 feet from the home nest, a concealed colony of *F. subsericea* in an open field, the other was similarly engaged on a large mound nest of *glacialis* about 60 feet away, and reached by a tortuous path through a dense cluster of spruces. In neither case did the workers of the nest attacked offer any resistance, nor did the *subintegra* exhibit any marked hostility, but hastily carried away the larvæ and pupæ. Strange to relate, however, the marauders did not confine themselves to this booty but carried home also the callow and mature *subsericea* and *glacialis* workers. The latter were seized by the mandibles, curled themselves up in a quiescent attitude and permitted themselves to be borne without remonstrance to the nests of the slave-makers. On stationing myself at these nests I repeatedly saw a few of these deported individuals escaping and making for home. Often they had secured a larva or pupa in the galleries of the *subintegra* nest, where they had been released, and attempted to carry it home. It was surprising to see them timidly avoiding the great army of returning slave-makers by mounting the grass blades and nervously moving back over the heads of their foes. They were often detected, however, and compelled to drop their burdens, or were driven off into the grass where they wandered about disconsolately and as if they had completely lost their bearings. It would be of interest to know whether any of the deported workers remain in the *subintegra* nest and become a part of the mixed colony or are merely carried home in obedience to an impulse which prevents the slave-makers from returning empty-handed, or, more accurately speaking, with empty jaws.

The large number of *subintegra* forays which I witnessed before leaving South Harpswell convinced me that this ant, in the proper season or whenever the weather is propitious, must be almost constantly employed in plundering the nests of *glacialis* and *subsericea*. Hence there is nothing surprising about the size of its colonies and the number of its slaves.

In the light of these observations my former failure to find similar dulotic instincts in the young *subintegra* females while engaged in founding their colonies, called for further investigation. I therefore captured a

number of females and performed two different sets of experiments, one similar to those described in my former paper and consisting in placing a female in a nest with a number of *glacialis* workers and their larvæ and pupæ, and another in which the female was confined with a diminute colony comprising the mother queen as well as the workers and brood of the slave species. The results of a considerable number of these experiments were fairly uniform and in all cases the behavior of the *subintegra* queen, to my surprise, was essentially like that of the *rubicunda* queens, which gave the first clue to the method employed by the slave-makers in establishing their fornicaries. I subjoin a condensed statement of the results in both sets of experiments:

1. When the female *subintegra* was introduced into a nest with a small number of *glacialis* workers (3-12) and their brood, she was at once seized in the usual manner by her antennæ and legs. She always succeeded in freeing herself and soon became aggressive but at first merely seized the attacking workers in turn by their legs and antennæ as if to dissuade them from further hostilities. If they became more persistent her excitement increased and she no longer hesitated to kill them by piercing their heads, thoraces or abdomens with her mandibles. Sometimes her mere presence frightened the workers so that they scurried about the nest like so many sheep. Without waiting to dispose of all her persecutors, she began to collect the larvæ and pupæ and tuck them away in some corner or under a lump of earth. This she did with great precision and perseverance, interrupting her task only to punish or kill some bold worker that came up to snatch one of its own cocoons. By the following day she had killed all the *glacialis* workers, had brought all the brood together and was resting on it with open mandibles, alert and ready to pounce on any intruder. From time to time she left the cocoons and carefully explored the chamber in which she was confined as if to satisfy herself that there were no foes lurking in the background. The regularity of these exploring movements was similar to that described by Huber for the queens of the Brazilian *Atta*, while establishing their colonies and fungus gardens in their small earthen chambers. After the lapse of several days the *subintegra* queen could be surprised in the act of opening the cocoons and assisting the callow *glacialis* workers to hatch. And gradually the number of these increased till she was surrounded by a loyal colony of jet-black attendants, who now completed the work of divesting the remaining workers of their swaddling clothes, while the queen, like the old mother queens of adult colonies, became more timid and negatively heliotropic and sought refuge in corners whenever the nest was uncovered.

This was the course of events in several cases, but often the queen suc-

cumbed to the attacks of the workers within a few hours or days. Yet even in these cases she exhibited the same aggressive behavior and interest in the brood till she was overcome by her assailants. For some of the experiments the queens were artificially deälated, but even when introduced in the winged condition, they were soon deälated by the workers. In three of the experiments I used fecundated and deälated females found running on the ground, but their behavior and that of the *glacialis*, among whom they were placed, was essentially the same as when virgins were employed. In no case was a queen adopted by adult workers. These never showed any inclination to tolerate her, and if she survived their attacks she never permitted any of them to remain alive in the nest.

2. The second series of experiments was undertaken with a view to determining the behavior of the *subintegra* queen on entering a small *glacialis* colony possessing its own queen. One of several possible fates could be supposed to await this unfortunate insect: she might be driven away or killed by the *subintegra* queen; she might be tolerated and permitted to survive till the workers hatched from their cocoons and be destroyed by these members of her own species. The results obtained in six experiments were quite uniform and indicated that the *glacialis* queen shares the fate of her own workers. When the *subintegra* was attacked by the latter, on being placed in their midst, the *glacialis* queen showed no interest in the struggle, but on encountering the intruder fled in dismay to a corner of the nest, and the *subintegra* queen was so busy defending herself from the hostile workers that she ignored the frightened mother. After the workers had been dispatched, however, and the brood appropriated, the *glacialis* queen was often seen to approach the pile of larvæ and pupæ as if drawn to them by an irresistible longing, but she was again and again driven away by the *subintegra*. The latter made quick dashes at the black queen but did not grapple with her. But as in every experiment the *glacialis* was found dead on the day following the usurpation of the brood by the *subintegra*, I have no doubt that she shared the fate of her worker daughters.

I next attempted to secure the representation of *subintegra* queens in *glacialis* colonies by introducing queen cocoons of the former species, but these were always rejected or the pupæ were prematurely taken out of their cocoons and thrown on the refuse heap. Introducing cocoons of *glacialis* queens among the worker cocoons appropriated by the *subintegra* queen also led to no result as the insect simply threw them out and permitted them to die in a remote corner of the nest. It is therefore impossible to say how the host queen would be eventually suppressed if a *subintegra* queen happened to gain adoption in her colony. Among my published experiments on *rubicunda* (*loc. cit.*, p. 78) was one (No. 35) in which a female *subsericea*

was reared and lived in a nest with a *rubicunda* queen and 175 *subsericea* workers. Both of the females lived peacefully side by side for two weeks, when the nest was abandoned, but I failed to record that during the last days of this period the host queen was repeatedly attacked and pulled about by her own workers. I remember wondering at this strange performance. Now that Santschi has shown that in nests of the North African *Monomorium salomonis* that are invaded by a queen of the parasitic *Wheeleriella santschii*,¹ the host queen is actually massacred by her own workers, my observation acquires significance and I am inclined to believe that it illustrates the method of eliminating the host queen not only in the rare cases in which *sanguinea* queens may be adopted in colonies of adult *fusca* workers and queen, but also when such colonies are invaded by temporary social parasites (*F. consocians*, *rufa*, *integra*, *truncicola*, *exsecta*, etc.).

IV. FORMICA SANGUINEA ASERVA FOREL.

My previous acquaintance with this boreal subspecies, of which a single slaveless colony was first found by Forel at Toronto, Canada, was confined to four colonies at Colebrook, Connecticut, and a few incomplete and unsatisfactory experiments with artificially deälated queens. In the vicinity of South Harpswell this form is as common as *subintegra* but prefers to nest in and under old spruce stumps and logs, and is much less frequently found in the open fields. Its colonies are often very large, a single one sometimes occupying every stump in a clearing and spreading over twenty or thirty nests. I have been able to study colonies of all sizes. These may be arranged in three groups representing as many stages of ontogenetic development.

1. July 7 I found at Ash Point a very small colony containing a deälated queen and a single callow worker of *aserva*, about 70 *glacialis* workers and about 200 larvæ and small cocoons. Nearly the entire colony was captured and placed in an artificial nest; only a few of the *glacialis* workers managed to escape into the grass. During the remainder of the month the cocoons hatched and all yielded small *aserva* workers. This colony was therefore in its second year, having been founded during the summer of 1907, and this must have been accomplished either by a number of adult *glacialis* adopting the *aserva* queen or by this queen appropriating *glacialis* pupæ. That the latter alternative is to be accepted will be shown presently.

2. Medium sized colonies presumably in their third and fourth years

¹ See Forel: Moeurs des fourmis parasites des genres *Wheeleria* et *Bothriomyrmex*. Rev. Suisse Zool., XIV, fasc. 1., 1906, pp. 51-69, and Santschi: Moeurs parasitiques temporaires des fourmis du genre *Bothriomyrmex*. Ann. Soc. Entom. France, LXXV, 1906, pp. 363-392.

were occasionally found. In these the *aserva* workers were large and very pugnacious and at least two to three times as numerous as the *glacialis* workers. Males and winged females were often present in these colonies during July.

3. Many much larger colonies were found in different localities, occupying several nests and comprising thousands of belligerent workers. Among these it was often impossible to find more than a few dozen *glacialis* workers and in some cases none was to be observed. Males and winged females were sometimes present, the former appearing first as in the *subintegra* colonies.

On clear, sunny days during the latter part of July I devoted much time to watching the *aserva* colonies but in no instance were any of the ants seen to make a foray. The nests, moreover, were often situated in the immediate vicinity of flourishing *glacialis* colonies which showed none of the signs, so often visible in colonies of this same ant when nesting near *subintegra* nests, of being harassed or of losing their brood.

A series of experiments performed with both artificially deälated and winged virgins, and with fecundated queens of *aserva*, introduced into nests containing several *glacialis* workers and their broods, gave essentially the same results as described for *F. rubicunda* and *subintegra*. The *aserva* queens were, however, fiercer than those of *subintegra* and did not stop to tweak the legs and antennæ of their assailants but killed them outright and appropriated the brood. The secreting and guarding of the brood and the assistance given to the hatching callows exhibited the same picture as in the other subspecies, and when the *aserva* queens were placed in small colonies containing a mother *glacialis*, the latter was also eventually killed or injured.

From these observations and experiments we are justified in concluding that, though the *aserva* queen founds her colony in the same manner as the queens of *rubicunda* and *subintegra*, the workers do not make forays. The small number of *glacialis* seen in old colonies are, therefore, the last survivors of the brood which was hatched under the guardianship of the young *aserva* queen when the colony was being founded. This is not surprising, for it is known that the workers of *fusca* may live several years and the largest *aserva* colonies are probably in many cases not more than five or six years old.

I am able to account for the discrepancy between my experiments on the founding of colonies by the *subintegra* and *aserva* queens at South Harpswell and those which I performed at Colebrook, Conn., only on the supposition that the queens in the latter locality were immature or weak. It is indeed probable that there is in the life of the *sanguinea* queen a 'psycho-

logical moment' which is necessary to the release of the catenary reflexes of colony formation, and that the individuals on which I experimented during the summer of 1905 either had not attained or had already passed this critical point in the maturation of their instincts.

V. REMARKS ON THE ONTOGENETIC AND PHYLOGENETIC DEVELOPMENT OF SLAVERY AND TEMPORARY SOCIAL PARASITISM.

Since my account of the American *F. rubicunda* was published, my method of experimentation has been applied to the typical European *sanguinea*. Wasmann¹ at once sought to discredit my work on the ground that I had employed only virgin queens, and that his own experiments with fecundated individuals indicated that the *sanguinea* colony is formed by adoption. Viehmeyer² repeated my experiments with the European *sanguinea* and obtained precisely the same results as I had described for *rubicunda*. Now Wasmann returns to the subject in a rather voluminous paper,³ and relates a number of observations and experiments which have induced him to agree with Viehmeyer and myself.

It is naturally a source of no little gratification to me to find that at last the eminent Jesuit has not only confirmed my predictions of 1904,⁴ by showing that the European *F. rufa*, *pratensis*, *truncicola* and *exsecta* are temporary parasites like the allied American forms, but has also accepted my views on the formation of colonies by the sanguinary ants so fully that there remains between us no dissension in regard to the facts. There is, indeed, an outstanding difference in interpretation, but this relates almost exclusively to a purely speculative matter, the phylogenetic origin and development of slavery. As the observations on *F. subintegra* and *aserva* above recorded have a bearing on this interpretation I may be pardoned for again returning to the discussion.

Wasmann is still desirous of deriving the dulotic from the adoptive method of colony formation as is shown by a tendency in many parts of his work to obliterate the boundaries between these two methods. It may be granted that such a procedure is more consonant with the fluently variable character of living phenomena, and also that the term adoption has been used rather loosely both by Wasmann and myself, but I nevertheless believe

¹ Die moderne Biologie und die Entwicklungstheorie. 3d edit. Freiburg i. Br., 1906, p. 402, Anm. 2.

² Zur Koloniegründung der parasitischen Ameisen. Biol. Centralbl. XXVIII, No. 1, Jan. 1, 1908, pp. 18-32.

³ Weitere Beiträge zum sozialen Parasitismus und der Sklaverei bei den Ameisen. Biol. Centralbl., XXVIII, Nos. 8-13, 1908, pp. 257-271, 290-306, 321-333, 353-382, 417-441; 3 figg.

⁴ A New Type of Social Parasitism among Ants. Bull. Amer. Mus. Nat. Hist., XX, Oct. 11, 1904, pp. 347-375.

that the two processes are quite distinct genetically and that it is expedient and desirable to distinguish them carefully in all future investigations on the founding of colonies by queen ants. We have been using 'adoption' first, in a general sense, to designate the founding of colonies by queens of one species with the aid of workers of the same or an allied species. In this sense the term is equivalent to 'consociation' or 'affiliation' and is, of course, merely a brief description of the fact that mixed colonies of the same or of two or more species are formed. Second, the term 'adoption' is used in a special sense to designate the amicable reception and retention of a strange queen in the colony of an allied species (social parasitism, temporary and permanent). And third, the term is used in another special sense to designate the direption and appropriation of the brood of one species by an alien queen who is accepted and retained by the hatching workers (dulotic parasitism). Here it is obviously only a matter of words whether we say that the queen adopts a strange colony in a juvenile condition or is adopted by that colony when it has matured, since the pragmatic result is the same in both cases. In the general sense, above referred to, the term 'adoption' is merely a description of a condition which is the very basis of colonial organization in the social Hymenoptera; in each of the special senses, however, it designates a particular method of bringing about this condition when the ants concerned belong to different species.

Now the discrepancy between Wasmann's position and that of Viehmeyer and myself is this: Wasmann contends that phylogenetically dulotic arises out of temporary social parasitism and tends to return to social parasitism of the permanent type. Viehmeyer and I are perfectly willing to grant the degeneration of dulotic into permanent parasitism in cases like *Polyergus*, *Harpegoxenus* (*Tomognathus*) and *Strongylognathus*, but we are not convinced of its origin from temporary parasitism.

In order to understand Wasmann's position it will be necessary to review his facts. He has found that the workers of adult *F. truncicola* colonies, which are temporary parasites in their juvenile stage, will appropriate worker *fusca* pupæ placed in or near their nest and permit the hatching ants to survive as auxiliaries. He gave a *truncicola* colony a large number of pupæ belonging to the following species: 660 *F. fusca*, 100 *rufibarbis*, 100 *rufa*, 300 *pratensis*, 50 *exsecta*, 50 *sanguinea*, 50 *Camponotus ligniperdus* and 100 *Lasius niger*. The *Camponotus* and *Lasius* pupæ were at once rejected, the pupæ of *F. rufibarbis*, *sanguinea* and *exsecta* were retained, but not reared. The following were hatched and adopted: *F. fusca* (about $\frac{1}{3}$ of the total number), *pratensis* (about $\frac{2}{3}$), *rufa* (about $\frac{1}{2}$). He concludes from this and similar experiments performed with wild colonies that "*F. truncicola* even in its old and independent colonies preserves a pronounced

penchant for rearing the pupæ of the very species of *Formica*, with whose aid its colonies are established." He reached the same conclusion as the result of experiments with *F. exsecta*, which he now finds, as I predicted, to be a temporary social parasite like *truncicola* and the long series of allied North American and European species of the *rufa* and *microgyna* groups. He failed, however, to find any such tendency in the typical *rufa* and *pratensis*, which are, nevertheless, temporary parasites of much the same character. The following quotation seems to contain the gist of Wasmann's present views on the relations of social parasitism to slavery: "We are unable to draw a hard and fast line between the founding of colonies by robbing the pupæ (pupillary parasitism of Santschi and Wheeler) and by adoption (tutelary parasitism of Santschi and Wheeler). Both types seem to occur and sometimes pass over into each other. In nature the union of these types may occur when the old *fusca*, that have fled with their brood on the invasion of a *sanguinea* queen, gradually return and associate themselves with the young workers that have hatched in the meantime from the captured pupæ. In this manner we can perhaps explain more satisfactorily the large number of auxiliaries in young *fusca* colonies than by the robbing of pupæ alone.

"My experiments also show several striking transitions between the colony founding of *rufa* and *sanguinea*. The *rufa* queen often defends herself violently from the assaults of the *fusca* and kills a number of her assailants. On the other hand she sometimes appears much interested in the worker cocoons of the *fusca*, collects and defends them and even prefers to remain with them rather than be adopted by the old workers. Nevertheless *F. rufa*, in a state of nature, is not a slave-holding ant, and when she employs alien auxiliaries in founding her colonies, this is usually accomplished by adoption and not by robbing the pupæ.

"Indeed, the analogies between the colony founding of *rufa* and *sanguinea* deserve careful consideration in connection with the question under discussion. In both species colonies are frequently formed by detachment ('Zweigkolonienbildung') and just as the queen of the former species is readily accepted by workers of her own species, and with them establishes a new colony, so also in the case of *sanguinea*. Just as the former, if she is unable to find workers of her own species with which to found a colony, turns to alien auxiliaries (social parasitism), so also the latter. As in the former so also in the latter two forms of parasitic colony-founding occur: by adoption on the part of adult *fusca* and by appropriation of the brood. In *rufa*, however, the parasitic method is still facultative, in *sanguinea* it is more obligatory. We see, moreover, that of the two tendencies which diverge from the facultative parasitic founding of colonies, one, leading to

the adoption colonies, has become obligatory in *truncicola*, while the other, leading to the predatory colonies, is more or less obligatory in its development. There exist, therefore, manifold transitions between the facultative and obligatory types of parasitic colony formation on the one hand, and between the two types of parasitic colony formation (by adoption and the robbing of pupæ) on the other. At any rate, if we are to form a conception of the phylogenetic origin of the regular types of adoption colonies on the one hand and of predatory colonies on the other, we must start with a species of *Formica* in which the parasitic method was facultative, one in which there already existed the possibility of developing both forms of parasitic colony formation.

"Accordingly, we may say that the origin of slavery in *F. sanguinea* is not to be sought in a 'truncicola-like form,' but rather in a 'rufa-like form'; for in *truncicola* the parasitic founding of colonies by adoption has already become obligatory. On the other hand the inclination of *F. truncicola* to select for rearing, among different pupæ, the very ones (*fusca*) belonging to its former auxiliary species, makes it possible to understand why the slave-makers (like *sanguinea*) also continue to rear the pupæ of the original auxiliaries with which their colony was founded, and do not at once devour them as they do with the pupæ of strange species. Hence the results derived from a study of *truncicola* retain their decisive importance in any hypothetical explanation of the origin of slavery. One may also designate the *truncicola*-stage as a preliminary to the *sanguinea* stage to the extent that the former species produces only temporary mixed colonies of three years duration, while the latter, on the contrary (at least in the case of the typical European *sanguinea*), produces permanently mixed colonies; for there can be no doubt that the permanent are to be derived from the temporary mixed colonies. But this derivation must proceed from temporary mixed colonies in which adoption has not yet become so obligatory as it is in *truncicola*, but in which the possibility of founding colonies with robbed pupæ is still open (as in *rufa*) and capable of a gradual development."

With most of this passage I agree, but there are in its last paragraphs certain statements to which exception may be taken. I am unable to find in any of the facts hitherto published by Wasmann on *truncicola*, a sufficient basis for conclusions concerning the phylogenetic origin and development of slavery. *F. truncicola*, according to his account, behaves like any other temporary parasite, except that its pure adult colonies will rear the pupæ of *fusca*. It is not a little strange that *F. consocians*, which on account of its much smaller queens, may be supposed to be in an even more advanced stage of temporary parasitism, will not, as I have shown (The Founding of Colonies, etc., *loc. cit.*, p. 61) rear the auxiliary *incerta* in adult colonies.

In the case of *truncicola* and *exsecta* Wasmann claims that the rearing of auxiliaries is due to a harking back, so to speak, to the mixed juvenile stage of the formicary. But why do not *consocians* and *rufa* behave in a similar manner? In the above described experiment, in which he gave the *truncicola* colony the cocoons of a variety of *Formicæ* and other ants, it is seen that the number of *fusca* (660) is greater than the sum total of all the others (600). Is it not possible that these proportions were such as to develop a tendency or habit to prefer the *fusca*, quite irrespective of any inherited reminiscence? And is it not probable that the greater survival of *fusca* in an alien living environment may be due to the greater vigor of its brood? That *fusca* is a very hardy species in all its ontogenetic stages is shown by the great abundance of its colonies, notwithstanding their exploitation by a whole series of parasitic *Formicæ* and *Polyergi*, its wide distribution and its occurrence in the most diverse conditions of soil, moisture, temperature and altitude. At any rate, the experiment to be conclusive, should have been made with equal numbers of pupæ of the various species of *Formica*, *Lasius*, and *Camponotus*. But even granting Wasmann's interpretation of *truncicola's* motives for rearing *fusca*, what bearing does this have on the slave-making colonies more than is already indicated in the founding and development of these colonies themselves? That the workers of *sanguinea*, *rubicunda* and *subintegra* continue the tactics of their young queens and rob the *fusca* pupæ, has its *raison d'être* in the behavior of the queens and does not need to be explained by reference to *truncicola* or any other temporary parasites. What requires explanation, however, is the fact that the *aserva* workers, if my observations are correct, do not make slaves, although their queens behave like the queens of *subintegra*, *rubicunda* and the typical *sanguinea*. It may be true, as Wasmann maintains, that *sanguinea* queens are sometimes adopted by adult alien *fusca* workers, but I have never seen anything to suggest this in my numerous experiments on the three American sub-species. If it occurs in a state of nature it must be very exceptional. But even if its frequent occurrence be granted, it does not throw any light on the origin of dulosis. This still remains a distinct phenomenon which may have been grafted on to an incipient form of temporary social parasitism, or develop within its sphere but is not, properly speaking, a stage in its development.

Wasmann's observations on *rufa* are of unusual interest because they seem to indicate that we have in this species two tendencies, coëxisting Janus-faced, so to speak, in the directions of temporary social and dulotic parasitism. In this species both tendencies are probably useful, according to the benign or belligerent attitude assumed by the workers of her own or the alien species among which the queen is endeavoring to establish herself.

F. aserva perhaps represents the next stage in the phylogenetic development of dulosis, one in which the dulotic tendency has supplanted that of adoption, but without being transmissible by the queen to her worker offspring. The European *sanguinea* and the American *rubicunda* would represent a somewhat more advanced stage, with the workers becoming dulotic, but without a very strong tendency to make forays; and lastly the subspecies *subintegra*, with its very numerous slaves and frequent forays, would represent the culmination of dulosis in the sanguinary series. That phyletic development has followed some such course is suggested by the small stature of all three phases in *subintegra*, which in this respect is further removed from *rufa* than any of the other forms of *sanguinea*, including the type.

There are, however, other conditions which lead me to believe that the phylogenetic origin of slavery may not be so clear as I have just indicated:

1. It is not improbable that the young queens of many ants that are in no sense temporary social parasites, will nevertheless usurp and guard the brood of other species with which they may come in conflict. In other words, the tendencies of the *sanguinea* queen may be very general among the *Formicidæ* although this has not been established by experiment. I had hoped to investigate this matter during the past summer, but the work on *subintegra* and *aserva*, together with a faunistic study of the Casco Bay ants, consumed all my time. Experiments must be performed, however, before it can be positively stated that the dulotic instincts are necessarily associated with those of adoption, as they seem to be in *F. rufa*.

2. The behavior of the young *sanguinea* queen is evidently a mixture of predatory and philoprogenitive reactions. Is it not possible that the former, which are the more characteristic, have their phyletic roots in the ancient predatory habits of the solitary wasp-like or mutillid-like ancestors from which, by common consent, the *Formicidæ* have been descended? These ancestors, like the existing solitary wasps, probably provisioned their nests with insect prey. Certainly the behavior of the young *sanguinea* queen while collecting and defending the brood which she has captured, is very suggestive. If she deposited her eggs immediately after capturing the brood and her larvæ fed directly on this brood after the manner of Ponerine larvæ, we should have a condition like that seen in existing solitary wasps, excepting that these do not feed on the larvæ of allied wasps, but on caterpillars, spiders, crickets, flies, aphids, etc. The *sanguinea* larvæ do not feed on the *fusca* brood directly, but both they and the queen are fed by the adult workers, so that in this case we have an example of the transition from predatism to parasitism.

3. This transition is very instructive because zoologists have long been of the opinion that parasitism usually arises from predatism, that it is, in

fact, merely a refined (in the sense of the German "raffinirt") method of predatism. In the animal kingdom, at least, there are many cases which point to this as the regular phyletic sequence, but it would be difficult to cite a case in which parasitism has given rise to predatism, and this is, if I am not mistaken, the sequence postulated by Wasmann in his interpretation of dulosis.¹

In my opinion we may seek the origin of dulosis, even of the *sanguinea* and *Polyergus* types, in such predatory habits as are still exhibited, albeit in a degenerate and specialized form, among the thief ants (*Solenopsis fugax*, *molesta*, etc.), which live in the gallery walls of the nests of many different *Formica* and prey on their larvæ and pupæ. Viehmeyer has, in fact, given good reasons for supposing that the dulotic habits of *Harpegoxenus* (*Tomognathus*) have had such an origin, and the same is probably true of *Strongylognathus*, in which we also have the mature females of parasite and host coexisting in the same formicary. In both of these genera, however, the dulotic instincts have degenerated secondarily. Dulosis, on this supposition, would be either the continuation or revival of an ancient predatory habit, merging into and modified by the general adoptive instincts. This interpretation would also account for the predatory habits of the worker *sanguinea*, which have been emphasized by Forel, Darwin and myself, and finally also by Wasmann, in a passage in which he admits that the inclination of the workers to rob pupæ has its foundation largely in the "karnivore Ernährungsweise" of *sanguinea*. In this connection it is interesting to note that the annual dulotic forays of *sanguinea* do not begin till immediately after the marriage flight of the males and females and hence at the very time when the latter are founding their colonies by an activity essentially like that of the workers. This simultaneity of impulse in the workers and young queens, like the migratory instincts of many animals and the marriage flights of the ants themselves, probably depends on meteorological conditions.

Polyergus presents an interesting problem for future investigation, as Emery has shown in a recent paper.² Forel, Wasmann and Viehmeyer concluded from their experiments that young queens of *P. rufescens* are adopted rather readily by strange *fusca* and *rufibarbis* workers. I found that the young queen of our American *P. lucidus* is not readily adopted but received with marked hostility and usually killed by strange workers of the slave species, *F. incerta*, and that she shows no interest in the brood. Emery

¹ In the plant kingdom parasitism seems to proceed from saprophytism and there are probably among animals (e. g., among myrmecophiles) several cases in which scavengers have developed into parasites.

² Osservazioni ed Esperimenti sulla Formica Amazzone. Rendic. Accad. Sci. Ist. Bologna, Sess. Feb. 1908, pp. 49-62.

has performed similar experiments with *rufescens* with precisely the same results. Concerning the probable method employed by this ant in establishing its formicaries, he says:

"Huber found that the workers of *Polyergus* do not begin their forays till after *F. fusca* and *rufibarbis* have completed the education of their young males and females. This observation is accurate only in part, as Forel has observed. The fact is that *F. fusca* and its subspecies are more precocious than *Polyergus* by about a month.

"The female *F. fusca* is therefore capable of founding a nest before the *Polyergus* can emigrate from their natal formicary. A female *F. fusca* which Wasmann captured in April, 1886, had already produced worker pupæ by the middle of June. In September, 1894, Wasmann found a nascent formicary of *rufibarbis*, containing in addition to the queen, three callow workers.

"Might not a female *Polyergus* occupy one of these nascent nests containing only the female of the host species and her still immature offspring?

"Another hypothesis seems to me more probable, namely, that the *Polyergus* female selects a colony in its second year, containing a *fusca* female surrounded by workers, still few in number, with abundant eggs, larvæ and pupæ, assassinates the mother and usurps her position."

From the fact that in artificial nests the female *Polyergus* remains indifferent to the brood, Emery concludes that she "seeks only adoption and something mysterious besides (ancora qualcosa di misterioso)." This mysterious something, he believes, may be the eggs of its host, and he cites in support of this suggestion some unpublished observations of Santschi, who found that the queen of the temporary parasite *Bothriomyrmex medianalis*, after killing the queen of her host (*Tapinoma erraticum*), remained several months without laying, and that it was only after she had been fed with the eggs from another *Tapinoma* nest that she began to lay. In this connection Emery cites an observation of Wasmann, who found *Polyergus* workers licking up the juices of larvæ and eggs which they had perforated with their sickle-shaped mandibles. I may add that I have made similar observations on *P. lucidus* workers in artificial nests. There is no doubt that the workers occasionally eat the eggs and it is quite probable that Emery, with his usual perspicacity, has suggested an interesting matter for future experimentation. His supposition, if it proves to be correct, would support my views on the predatory significance and origin of dulosis.¹

¹ Emery confirms Forel's account of the participation of the young dealated females of *P. rufescens* in the forays of the workers. He believes that these females mate with the males in the parental nest and that the same is true of the peculiar ergatoid females which occur rather frequently in colonies of the European amazon. He even doubts whether copulation takes place in the air as in other species, although both Huber and Forel have witnessed marriage flights of *Polyergus*. Burrill (A Slave-making Foray of the Shining Amazon. Journ. New York

In conclusion I append the following notes on some imperfectly known species which are, in all probability, temporary social parasites:

1. *Lasius fuliginosus* Latr.—De Lannoy¹ has recently found a mixed colony of *L. mixtus* and *fuliginosus*, which Emery² is probably right in regarding as indicating that *L. fuliginosus* founds its colonies by temporary parasitism on *L. mixtus*. He calls attention to the fact that "*L. fuliginosus* differs from most of its congeners in having females that are only a little larger than its workers. *L. carnolicus* and, to some extent, also *L. bicornis* are in the same condition. The great majority of species of the genus *Lasius*, on the contrary, have females that are much larger than the workers; they have large rotund gasters, full of stored fat, capable of nourishing the mother during her long fast and while engaged in establishing a family and compelled to subsist exclusively on the resources of her own body." We are justified in inferring that the microgynous and macrogynous species of *Lasius* bear the same relation to each other as is borne by the microgynous and mesogynous species of *Formica* to the various macrogynous varieties and subspecies of *F. fusca* and *pallidefulva*.

2. *Formica exsecta suecica* Adlerz.—Wasmann, in his latest paper, calls attention to the small size of the queens of *F. exsecta* and its subspecies *pressilabris*, a fact which impressed me while I was studying these ants in Switzerland and Germany during the summer of 1907. In his 'Fourmis de la Suisse' Forel long ago mentioned several small mixed colonies of *exsecta-fusca* and *exsecta-pressilabris-fusca*, which I pointed to as evidence of temporary social parasitism. Early in July, 1907, I found a small col-

Entom. Soc., XVI, Sept. 1908) has recently described a feeble marriage flight of our American *lucidus*, and August 20, 1903, I saw a large and very typical flight of this ant near Colorado Springs. Burrill saw a male attempting to mate with a female, and I am unable to believe that copulation does not occur during flights like the one I witnessed. It is true, nevertheless, that the mature males and females linger long in the parental formicaries. I have noticed this in a beautiful *lucidus* colony which I have had under observation for the past five years near Bronxville, N. Y. During four years this colony produced numbers of males and females, both winged and ergatoid, and the winged females lingered for weeks in the nest without déallation. The first week of the past April I found the whole community with its larvæ and mother queen enjoying the spring warmth in the superficial galleries just under the large flat stone with which I had covered the nest in September, 1903. I captured the queen and part of the colony and transferred them to an artificial nest. August 9 I again visited the nest, and to my surprise, found it teeming with several hundred mature males clinging to the lower surface of the stone, but with no winged or déallated females. Besides the males I found only a single large ergatoid female, several dozen workers and slaves and half a dozen cocoons enclosing nearly mature male pupæ. Without doubt, the ergatoid had usurped the rôle of the mother queen and, being unfertilized, had produced only male offspring. The comparatively small number of slaves had been able to rear an enormous number of these little creatures although the absence of *incerta* pupæ in the nest indicated that the *Polyergus* workers had made no forays during the past summer.

I find in one of my note-books an observation which is very significant in connection with the foregoing quotation from Emery. August 12, 1903, I discovered under a small stone near Colorado Springs, Colorado, an incipient mixed colony of *P. breviceps* and *F. fusca* var. *argentina*. It consisted of a fine déallated queen and 7 or 8 diminutive workers (micrergates) of the former species, a few small cocoons, apparently also belonging to the *Polyergus*, and about a dozen small *argentina* workers. This was doubtless a colony in its second year, strictly comparable to second year colonies of *sanguinea* and the temporary social parasites.

¹ Notes sur le *Lasius niger* et le *Lasius fuliginosus*. Ann. Soc. Ent. Belg., LII, 1908, p. 47-53.

² Remarques sur les Observations de M. de Lannoy touchant l'existence de *Lasius mixtus* dans les fourmilières de *Lasius fuliginosus*. Ann. Soc. Ent. Belg., LII, 1908, pp. 182-183.

ony of *exsecta*-*pressilabris*-*fusca* on the slopes of Monte Generoso in Canton Ticino, and Wasmann has just described a small *exsecta*-*fusca* colony which he discovered in Luxemburg during October, 1906. Adlerz has described as *suecica* a Swedish subspecies of *exsecta*. A type female of this form received from Professor Forel proves to be even smaller than that of *exsecta*. The latter measures 6.5-7 mm., whereas the former is no larger than the largest workers and measures only 5 mm. *F. suecica* is therefore the most microgynous of all the European *Formicæ*. Its queen is, in fact, as diminutive as those of the North American *microgyna*, *impexa*, *nepticula* and *nevadensis*, and must have very pronounced parasitic habits. As the only American species of the *exsecta* group, *exsectoides* and *ulkei*, have queens as large as those of *F. rufa* and *truncicola*, we have in the *exsecta* group a series of micro-, meso- and macrogynous females strictly comparable to the series which I have established for the *rufa* group. It is interesting to note that on both continents the microgynous species and subspecies are decidedly boreal or monticolous, whereas the meso- and macrogynous forms often extend down into the lowlands and have a more southerly distribution.

3. *Formica dakotensis* Emery.—The taxonomy of this species needs some rectification. Emery first described the workers of the typical form from Hill City, South Dakota.¹ In the same paper (p. 663) he described a small female ant from Wisconsin as var.? *specularis*, denoting by the query that the insect might prove to be either a variety of *F. fusca subpolita* Mayr or an independent subspecies of *fusca*. Wasmann afterwards sent females, males and workers of this same *specularis*, collected by Muckermann at Prairie du Chien, Wis., to Forel, who recognized them as a form of *dakotensis* but described them as a new variety under the name of *wasmanni*.² Emery wrote me some time ago that he had compared some of the females with his type of *specularis* and found them to be identical. *F. wasmanni* is therefore merely a synonym. Like Forel I have been guilty of making a synonym in redescribing specimens of the typical *dakotensis* from Colorado, as *F. montigena*.³ Examination of one of Emery's types in Forel's collection convinced me of this error.

At Prairie du Chien Muckermann found several mixed colonies of *F. dakotensis* var. *specularis* and *F. subsericea* and other larger colonies containing *specularis* only. Wasmann, although he had never seen this variety in the field but knew its habits only from Muckermann's notes, jumped to the conclusion that it is probably incipiently dulotic or, at any rate, represents a stage midway between *truncicola* and *sanguinea*.⁴ And, notwithstanding

¹ Beiträge zur Kenntniss der nordamerikanischen Ameisenfauna. Zool. Jahrb., Abth. f. Syst., VII, 1893, p. 652.

² Fourmis de British Columbia. Ann. Soc. Ent. Belg., XLVIII, 1904, p. 153, nota.

³ A New Type of Social Parasitism, etc., loc. cit., pp. 374, 375.

⁴ Ursprung und Entwicklung der Sklaverei bei den Ameisen. Biol. Centralbl., 1905, p. 277 et seq.

my comments on this prognostication, he seems still to adhere to it in a table published in his latest paper.¹ Now, although, like Wasmann, I have never studied the var. *specularis* in the living condition, I have nevertheless become well acquainted with the typical *dakotensis*. This ant is not uncommon in certain localities in Colorado at altitudes above 6000 ft. (Pike's Peak, Ute Pass, Florissant and Buena Vista). Its adult colonies are very much like those of *truncicola* and *consocians* but more populous. They sometimes occupy several nests near one another, under stones, about the roots of bushes and in old stumps. During the summer of 1903 I found two juvenile mixed colonies of this ant with *F. incerta*, and this discovery, combined with the fact that the females are very small, shows that the species must be a temporary social parasite. As the adult colonies often occur in the very midst of *incerta* and *fusca* (var. *argentata*) colonies, without exhibiting any tendency to mix with them, I fail to perceive the slightest suggestion of dulosis. The presumption is therefore very strong in favor of the same condition obtaining in the var. *specularis*. At any rate we should drop all further allusions to incipient dulosis in this ant till it has been studied by some one thoroughly familiar with the subject under discussion.

4. *Stenamma (Aphænogaster) mariæ* Forel.—In his original description of the worker of this species, Forel² called attention to its close resemblance to the worker of *S. (A.) tennesseense* Mayr, an ant which I have given good reasons for regarding as a temporary social parasite on *S. (A.) fulvum*. According to my experience, *S. mariæ* is a rare species confined to the Atlantic States. It has been taken in Connecticut, New Jersey, North Carolina and Florida. Sept. 8, 1901, I captured a winged female running in the grass of a door-yard at Colebrook, Connecticut, and I have since received a dealated specimen taken by Mr. Wm. Beutenmüller in the Black Mts. of North Carolina. Both of these females are remarkable on account of their small stature (4.5 mm.) which does not exceed that of the worker. In this respect it closely resembles the female of *tennesseense* and contrasts with the large females of all our other North American species of *Aphænogaster*. But although the epinotal spines are large and robust, they are not so enormously developed and flattened as is *tennesseense*, and the head, thorax and pedicel are rugose and much less shining. The body and appendages are reddish brown, with more yellowish coxæ and tarsi; the wings are slightly infuscated, with pale veins and brown stigma. I believe there can be little doubt that this species is, like *tennesseense*, a temporary parasite on one or more of our numerous varieties of *S. fulvum*. Owing to the

¹ Weitere Beiträge, etc., *loc. cit.*, p. 430.

² Espèces Nouvelles de Fourmis Américaines. Compt. R. Soc. Entom. Belg., Séance^e du 6. Fév. 1886, p. 4.

close agreement in size, color and form between these two species, however, it will require extremely close observation to detect a mixture of their colonies in the field.

5. *Oxygyne*.—Forel has assigned to a special subgenus, *Oxygyne*, an interesting series of *Cremastogaster* species (*emmae*, *ebenina*, *soror*, *travancorensis*, *dalyi*, *aberrans*, *ranavalonæ*, *paulinæ*, *agnetis*, *daisyi*, *marthæ* and *depressa*) from Madagascar, India and the Malayan region, because they have unusually small, glabrous females, with falcate, pointed or very oblique mandibles, abbreviated frontal carinæ and sometimes very strong epinotal spines and a robust abdominal pedicel.¹ The workers of these forms are, however, essentially like those of the ordinary macrogynous species of *Cremastogaster*. In one species of *Oxygyne* (*ranavalonæ*), according to Emery,² the mother queen has the gaster enormously enlarged and subspherical as in the old mother queens of the permanently parasitic *Anergates atratulus* of Europe. Forel suggests that the structural peculiarities of the *Oxygyne* females may be correlated with peculiarities of habit. Comparison of a series of these insects, kindly presented to me by the eminent myrmecologist, with the microgynes of *Formica*, and especially with those of *Aphaenogaster tennesseensis* and *mariaæ* leaves no doubt in my mind that they are temporary parasites on other species of *Cremastogaster*. Their sickle-shaped mandibles, so much like those of *Polyergus* and *Strongylognathus*, point to a method of assassinating the host queen similar to that employed by *Bothriomyrmex*. At any rate, such a supposition would constitute a good working hypothesis in carrying on further researches on the species of *Oxygyne*. In this case, also, extremely close observation in the field will be required to detect the existence of mixed colonies.

The foregoing notes suggest that the results hitherto obtained in the study of dulosis and temporary social parasitism are only a beginning in a subject of extraordinary interest. Although at present this interest is mainly theoretical, it is not improbable that the results already obtained may be capable of some practical application as soon as we have acquired a more accurate knowledge of the economic status, especially in forestry, of some of our more abundant ants, such as *F. rufa* of Europe and *exsectoides*, *integra* and their allies in the United States. If these insects are really as useful in destroying forest pests as some authors have maintained, their colonies may, perhaps, be greatly increased by an adroit introduction

¹ These species are described in the following papers: Les Formicides in Grandidier's *Histoire Physique, Naturelle et Politique de Madagascar*, 28 fasc. 1891, 280 pp.; 7 pl.; *Nouvelles Espèces des Formicides de Madagascar* (Recoltées par M. Sikora), *Ann. Soc. Entom. Belg.*, XXXVI, 1892, pp. 516-536; Les Formicides de l'Empire des Indes et de Ceylan. *Journ. Bombay Nat. Hist. Soc.*, VII, VIII, IX, XIII, XIV, 1892-1902; Myrmicinae Nouveaux de l'Inde et de Ceylan. *Rev. Suisse Zool.*, X, 1902, pp. 165-249.

² Descriptions de deux Fourmis. *Bull. Soc. Entom. France*, 1897, pp. 12-14, 2 figg.

of their temporary hosts (*F. fusca* and *subsericea*) in certain regions. It is probable, however, that taking advantage of the tendency of most of these ants to form colonies by detachment or budding may lead to the same results. Field study of the Formicidæ is certainly becoming much more interesting and precise through our increasing knowledge of dulosis and temporary social parasitism, since every ant colony examined no longer represents to the observer merely a meaningless aggregate of individuals, but a definite stage in the life-cycle of a colonial organism. Thus the myrmecologist is prompted to attack a host of fascinating problems suggested by the origin, development and decline, both onto- and phylogenetic, of a living community and the instinctive processes involved in the numerical regulation of its polymorphic components.

