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THE COMPOUND AND MIXED NESTS OF AMERICAN ANTS.

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PART II (*continued*).

V. DULOSIS.

UNDER this heading we may include all those remarkable mixed nests which owe their origin to the enslavement of one species of ant by another. This condition is characterized by Wasmann ('**91**, p. 43) as follows: "Here ants of different species dwell together, not only on the same spot, but coalesce to form one colony, a single social whole. In such communities the unity of the colony is of paramount importance, and the specific differences between the various components of the colony lapse so far into abeyance that they appear to be non-existent; the consociating ants, belonging originally to different nests, behave towards each other as if they were kith and kin, and carry on in common the construction of the nest, the acquisition of food, the education of the offspring, the defense of the nest, etc., so far as this is permitted by their physical and psychical endowments and the law of the physiological division

of labor. Hence the term 'slaves' is much less appropriate than the term 'helpmates' (auxiliaries)."

While the various forms of social symbiosis hitherto considered may exist between ants belonging to very different taxonomic subfamilies, dulosis is known to occur only between species of the same subfamily. This rule is based on but few cases, for only four genera, two belonging to the Camponotinæ and two to the Myrmicinæ, *viz.*, Formica, Polyergus, Strongylognathus, and Tomognathus, are known to contain dulotic species. Still it seems obvious that such close symbiotic relationships as those under consideration could be entered into only by species of very similar habits and phylogenetic derivation.

With the exception of Strongylognathus, the above-mentioned genera are all known to occur on our continent, the dulotic species of Formica (*F. sanguinea* Latr.) and Polyergus (*P. rufescens* Latr.) being represented by distinct races, or subspecies, the genus Tomognathus by a distinct species (*T. americanus* Emery). So little attention, however, has been devoted to our ants, that we may yet look forward to the discovery of an American Strongylognathus, for there are in America several species of the genus Tetramorium (including the subgenus Xiphomyrmex) which are allied to the *Tetramorium cæspitum* auxiliary of the European Strongylognathus.

The meagre work which has been done on our American dulotic ants is barely sufficient to show that their behavior is essentially like that of their European allies. Since these ants in America select their auxiliaries, or slaves, from a slightly different though allied ant fauna, we may yet expect to find some interesting differences in the details of habit and behavior.

Before enumerating the American species, together with their auxiliaries, it will be convenient to present a much condensed résumé of the splendid accounts of the European observers, Forel, Wasmann, and Adlerz.

Formica sanguinea Latr. — This species is a true Formica, which is sometimes found living without auxiliaries. It has broad, toothed mandibles, of the type characteristic of its

genus, and is naturally carnivorous, though it has been observed to attend aphides for the purpose of collecting their sugary excrement. Although this ant is, therefore, quite able to exist alone, it nevertheless has a very pronounced *penchant* for robbing the larvæ and cocoons of other species of Formica, eating great numbers of them but allowing others to develop and to function as its slaves, or auxiliaries. The latter feel themselves to be members of the colony in which they emerge from their cocoons, and direct all their activities to maintaining and defending their foster nest and its occupants. In Europe, as a general rule, the normal slaves of *F. sanguinea* are the workers of *F. fusca*, less frequently the workers of *F. rufibarbis*. Sometimes both species of auxiliaries may be found in the same mixed nest. In extremely rare instances the workers of *F. rufa* and *F. pratensis* may serve as slaves. The expeditions for robbing cocoons are usually carried out during July and August, but they seem to be rather infrequent or irregular and are not often observed. The tactics of *F. sanguinea*, like those of other dulotic ants, consist in surprising the colony they wish to rob and in carrying away the pupæ as rapidly as possible without engaging in unnecessary slaughter. Only the ants that offer active resistance are dispatched.

F. fusca is most frequently enslaved because it is a weaker and more tractable species and forms smaller colonies than *F. rufibarbis*. The rare occurrence of *F. rufa* and *pratensis* in *sanguinea* nests is due to the more savage nature of these species, which are enslaved only when they belong to small colonies or when they are of small size individually.

The number of auxiliaries in nests of *sanguinea* varies greatly. In Holland, in more than 100 nests, Wasmann ('91) found the ratio of *sanguinea* to slaves varying between 1 : 0 and 1 : 3. Most frequently the *sanguinea* are from 2 to 5 times as numerous as their slaves. The number of the latter depends on various circumstances, such as the abundance or scarcity of nests of the auxiliary species in the vicinity. It is a singular fact that the weakest colonies of *sanguinea* contain the greatest number of slaves, so that it would seem as if the dominant species tried to make good the deficiency in the

number of its workers by importing and employing foreign labor. This may result naturally from the fact that in weak colonies on an average a larger percentage of the stolen pupæ are permitted to develop into slaves. In populous *sanguinea* colonies, on the other hand, a considerable portion of the prey is devoured even when there is plenty of other insect food within reach.

The relations implied by the terms "slave" and "master" do not adequately express the conditions existing in these mixed nests, since *sanguinea* works side by side with its auxiliaries, which are neither a mere luxury nor an absolute necessity. Still, although *sanguinea* is capable of excavating and maintaining its own nest, the auxiliaries appear to be more enthusiastic and skillful workers in the earth. And although *sanguinea* looks after its own brood and the hatching of the cocoons of the auxiliary species, it must, nevertheless, derive some advantage from the assistance of its slaves. The latter, moreover, bring into the nest a good deal of food from the aphides, which they assiduously attend.

F. sanguinea, on moving to a new nest, usually carries its slaves, and is rarely carried by them. This is probably due to the fact that the *sanguinea* are of a more excitable temperament and therefore have a greater tendency to take the initiative in a change of dwelling than their more stolid auxiliaries.

Continental authorities uniformly maintain that the *sanguinea-fusca* nests contain only workers of the auxiliary species. In England, however, Rev. T. D. Morice ('00, p. 98) recently found a nest which contained also *fusca* males and queens in addition to the workers of this species. This very exceptional condition would seem to have arisen either from the failure of the *sanguinea* to consume all the pupæ of the fertile sexes of *fusca*, or less probably from the formation of an alliance colony between fertile queens of *sanguinea* and *fusca*.

Polyergus rufescens Latr. — The "amazon," as the paragon of dulotic ants, has been observed with great care by a number of investigators, among whom Pierre Huber ('10) and Forel ('74) hold the first place. It is a rather large, brown-red ant, allied to Formica, but characterized by the possession of slender,

sickle-shaped mandibles, the cutting edges of which are furnished with minute serrate teeth. Such mandibles are beautifully adapted to fighting, but scarcely fitted for the many other uses to which these organs are put by most ants. Polyergus is therefore a warrior, and on this account its life presents two very different phases, one replete with the brilliant tactics whereby it gains possession of the larvæ and cocoons of its

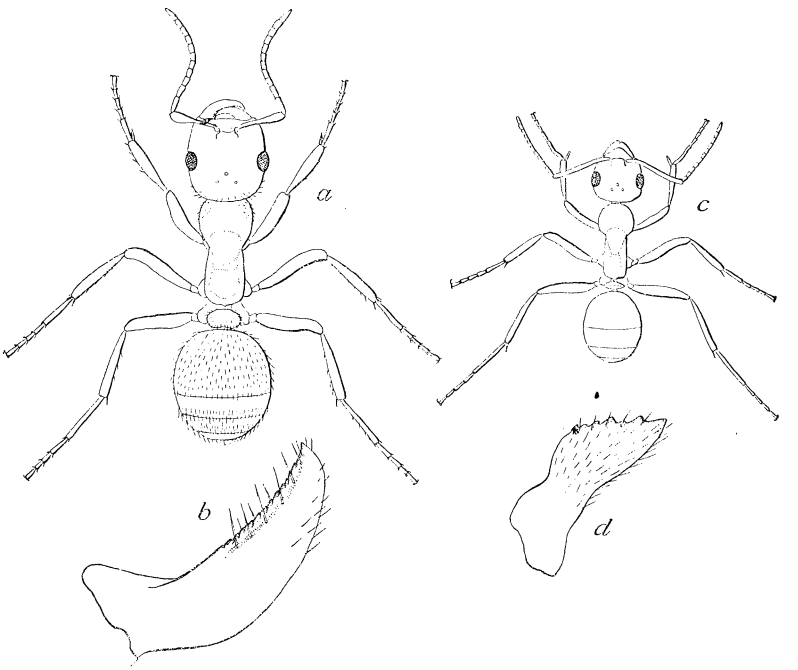

FIG. 15.—*a*., *Polyergus rufescens* Latr., subsp. *breviceps* Emery, worker; *b*., mandible of same; *c*., *Formica fusca* L., var. *subsericea* Say, subvar.; *d*., mandible of same.

slaves, the other characterized by abject helplessness and complete dependence on these same auxiliaries.

The auxiliaries of Polyergus are furnished by the very same species as in the case of *F. sanguinea*. In this case, also, *F. fusca* is most often victimized, *rufibarbis* less frequently. Occasionally, too, both species are found in the same nest. The number of slaves, however, is much greater than in *sanguinea* nests, being about seven-eighths of the entire colony. The dulotic expeditions of Polyergus have been often observed

since the days of Pierre Huber ('10, p. 210 *et seq.*). They have been admirably described by Forel ('74), who has also estimated (pp. 320, 321) the number of expeditions undertaken by a single powerful colony of these ants during a single summer. In thirty days (from June 29 to August 18, 1873) he witnessed forty-four expeditions of the amazons. These usually occurred between 2 and 5 o'clock P.M., the time limits being from 1.30 to 6 P.M. Among the forty-four expeditions there were forty-one attacks, nineteen on *fusca* and nineteen on *rufibarbis*, and three of which only the return was observed. The total number of cocoons robbed was estimated at 29,300 (14,000 *fusca*, 13,000 *rufibarbis*, and 2300 of unknown origin but probably *fusca*). Counting in the expeditions after August 18, which he was unable to witness, Forel concludes that not far from 40,000 larvæ and pupæ of the auxiliary species were appropriated during the summer of 1873 by a single Polyergus colony! Most of the pupæ were consumed, so that few of them ever hatched and became auxiliaries. And although two species were pillaged the colony later became almost entirely *F. fusca*.

Wasmann ('91, pp. 61, 62) has observed that the *fusca* auxiliaries are noticeably fiercer and more courageous than when nesting alone. The same is true of *fusca* in *sanguinea* nests. This is explained by Wasmann as merely a special case of the general rule that all ants are more courageous when they feel themselves backed by numbers.

The shadow side of the life of Polyergus is seen within its nest, where it is abjectly dependent on its slaves. Here it spends most of its time preening its legs and antennæ, as it is quite unable to excavate. On this account the character of the nest architecture is entirely determined by the auxiliary species. Moreover, the conformation of its mandibles is such that Polyergus cannot care for its own young or the pupæ of its slaves, though it sometimes licks the newborn callows. After a minute investigation of the question as to whether Polyergus is able to feed itself, Wasmann concludes that it can lap up liquids but is usually fed by the slaves. This mode of obtaining its food is, in fact, so essential, that it dies of starvation when deprived of its helpmates.

Polyergus goes on its cocoon-robbing expeditions unattended by its auxiliaries. When the colony moves to a new nest the Polyergus are nearly always carried by their slaves (*cf. F. sanguinea!*). In this case the slaves commonly initiate the change of dwelling. At home the Polyergus appear to be under the guardianship of their slaves and to be treated like helpless dependents. They are sometimes even held back from their sorties by the auxiliaries.

The way in which the fertilized Polyergus queen starts her colony has not been observed. Forel and Wasmann have demonstrated that a friendly alliance may be easily effected in artificial nests between Polyergus queens and strange workers of *F. fusca*, and Wasmann concludes from this fact that new mixed colonies may be started by such consociations under natural conditions. But it does not appear to be necessary to accept this inference. The fertilized Polyergus queen may be quite as well able as other queen ants to raise unaided an incipient colony of small workers which could then pillage adjacent nests of *fusca* and provide themselves with the necessary auxiliaries. It has, moreover, been observed that Polyergus queens occasionally accompany the workers on their raids, and this habit may be still more pronounced in the queens of incipient colonies. I deem this probable because the young queens of other species very generally perform nearly all the functions which are later delegated more or less completely to the workers alone.

Tomognathus sublævis Mayr (Fig. 16). — This is a small, rather hairy ant, with broad and edentulous mandibles. It occurs only in northern Europe (Finland, Sweden, and Denmark). Two very careful studies of its habits have been published by Adlerz ('86 and '96). The auxiliaries are furnished by *Leptothorax acervorum* or *L. muscorum*, more rarely by *L. tuberum*. Adlerz's observations show that the Tomognathus secure these auxiliaries by attacking a Leptothorax colony, driving away the ants, and taking possession of the nest, together with the larvæ. The latter are then reared as helpmates. It is probable, however, that the Tomognathus may occasionally recruit the number of their slaves by making

sorties like Polyergus, for Adlerz succeeded in finding a nest of Tomognathus with two species of auxiliaries (*L. acervorum* and *muscorum*).

The mixed nests of Tomognathus-Leptothorax may contain males, queens, and workers of both the dominant and victimized species, a condition not known to occur in the case of other dulotic nests. The males of Tomognathus (Fig. 16, *a*) resemble the males of Leptothorax so closely that Adlerz failed

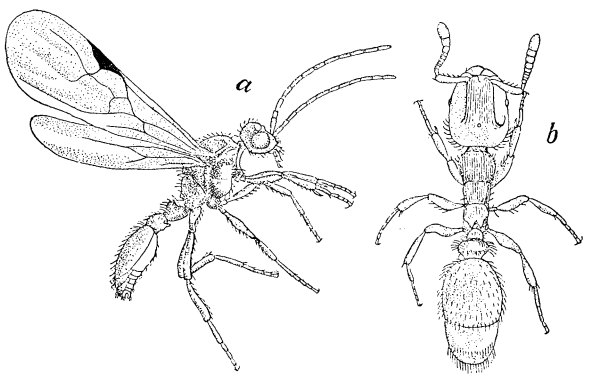

FIG. 16. — *Tomognathus sublævis* Mayr (after Adlerz); *a.*, male; *b.*, female (ergatoid).

to distinguish them till he published his second study ('96). The female is also of such a remarkable character that it, too, was originally overlooked. This sex is apterous (Fig. 16, *b*) and resembles the worker except in possessing ocelli and a receptaculum seminis.

The industrial instincts of Tomognathus are very rudimentary. It rarely or never excavates. It is able to feed itself if food is within reach, but it does not go in quest of provisions. This it leaves to the Leptothorax auxiliaries, by whom it is usually fed. Occasionally it may be seen caring for the larvæ. A number of Tomognathus which were isolated with larvæ and some food managed to live for 135 days, but the larvæ died or shriveled up. It seems probable, therefore, that Tomognathus depends on its slaves to a certain extent even for the care of its larvæ. When the colony is compelled to move to a new nest, the Tomognathus are usually deported by the Leptothorax; only rarely are the rôles reversed.

Sometimes when they desire to leave the nest, the Tomognathus are detained by the auxiliaries in much the same manner as Polyergus.

The males of Tomognathus do not mate with the females of the same nest, but do so readily with the virgin queens of other nests. The larvæ are so similar to those of the Leptothorax that Adlerz was unable to distinguish them. They are nourished with both liquid and solid food. Adlerz's description of the manner in which the larvæ are fed with pieces of flies tallies exactly with my observations on the primitive method of feeding adopted by the Ponerinæ and the Myrmicinæ of the genera Stenamma (Aphænogaster) and Pheidole ('00[a] and '00[b]).

Strongylognathus. — The species of Strongylognathus have perfectly edentulous, falcate mandibles, and more or less projecting postero-lateral corners to the head. Four species of the genus are known to occur in Europe: *S. huberi* Forel, *S. testaceus* Schenk, *S. christophi* Emery, and *S. cæciliæ* Forel. The habits only of the first two have been observed (Forel, '74 and '00[a]; Wasmann, '91), and these present interesting differences. Both species form mixed nests with *Tetramorium cæspitum*: *S. huberi* in southern Europe and northern Africa, and *S. testaceus* in southern and central Europe.

S. huberi seems like a diminutive and feeble caricature of Polyergus. Forel ('74) found by experiment that it would rob the larvæ and pupæ of Tetramorium and fight with the rightful owners after the manner of Polyergus. But it is not known whether *S. huberi* under natural conditions really provides its nests with auxiliaries by carrying on regular marauding expeditions. Forel, in a more recent paper on this species ('00[a], p. 275), expresses the opinion that it may not make sorties but keep up the mixed colony by alliance with the Tetramoriums instead. The workers of Strongylognathus are able to excavate, but they are fed by the Tetramorium workers. The latter are present in considerable numbers in the mixed nests, but up to the present time fertile queens of Tetramorium have not been found with them, though from what is known of *S. testaceus* one or more of these queens may perhaps be present in some cases.

S. testaceus is a commoner and better known form than *S. huberi*, and is supposed to represent a further advance towards a condition of social parasitism. The number of workers of *S. testaceus* is decidedly smaller in proportion to the number of Tetramoriums. On this account Forel maintains that the worker cast of *S. testaceus* is on the road to disappearing (*cf.* Anergates !). As fighters these workers, though provided with sabre-like mandibles, are indeed but sorry caricatures of Polyergus and decidedly less valiant than the workers of *S. huberi*. They do not kill the Tetramoriums, but seem to frighten them into deserting their larvæ and pupæ. Their weakness is further shown by the fact that they do not undertake their pillaging expeditions alone, but accompanied by their Tetramorium auxiliaries, and it is these latter that determine the success of the enterprise undertaken for the sake of robbing their own species. The workers of *S. testaceus* are even awkward in their attempts to carry away the conquered larvæ and pupæ. Although the Tetramorium auxiliaries commonly do all the work within the nest, such as excavating the galleries, caring for the larvæ and pupæ, and feeding the Strongylognathus, the latter are, nevertheless, able to feed themselves and to dig the nest, but they are apparently unable to care for the young.

Forel and Wasmann have succeeded in throwing considerable light on the obscure problem of the origin of the *S. testaceus*-Tetramorium colonies. The former found a single fertile queen of the Strongylognathus living amicably in the midst of a colony of *Leptothorax acervorum;* and Wasmann made the significant discovery of a fertile queen of the Strongylognathus and a fertile queen of Tetramorium living side by side in the same nest. This nest contained workers of both species (15,000–20,000 Tetramoriums and some thousands of Strongylognathus), and pupæ, about 70% of which were males and females of Strongylognathus. The remainder included two large male pupæ of Tetramorium. From this discovery Wasmann infers that the mixed nests of *S. testaceus*-Tetramorium are alliance colonies brought about by the adoption of fertilized queens of Strongylognathus by Tetramorium colonies.

The fact that these mixed nests rarely contain male Tetramoriums and never, so far as known, queen pupæ of this species, is explained by Forel ('00[a], p. 273) as the result of a general regulative instinct: "The females and males of Strongylognathus are smaller and less troublesome to nourish. This is obviously sufficient to induce the Tetramorium workers to rear them in the place of their own enormous queens and males, the larvæ of which they therefore undoubtedly devour or neglect, as they do in the case of all that seems to be superfluous."

After this brief review of the European species we may turn to our American dulotic ants.

16. **Formica sanguinea** Latr., subsp. **rubicunda** Emery.

Although the typical *F. sanguinea* is not known to occur in America, the species is, as Emery has shown ('93[a], p. 647), far more variable on this continent than it is in Europe. We should therefore be prepared to find a corresponding variability in its instincts, though this may not be commensurate with its taxonomic variation.

F. sanguinea is also occasionally found without slaves in America, but far more frequently it is attended by ants belonging to the great group of forms which centers about *F. fusca*. The best known subspecies of *F. sanguinea* in the Northern and Atlantic States is undoubtedly *rubicunda*. This is usually found with slaves belonging to *F. fusca*, var. *subsericea* Say, but one colony which I observed near Rockford, Ill., Sept. 16, 1900, contained about equal numbers of auxiliaries belonging to two species, *viz.*, *F. pallide-fulva* Latr., subsp. *nitidiventris* Emery, and *F. fusca*, var. *subænescens* Emery.

The above assumption that the habits of *F. sanguinea* in America may differ to some extent from those of the European form seems to be borne out by some recent observations of Forel ('00[c], pp. 11–12). Owing to Forel's long and very intimate acquaintance with the European *sanguinea*, these observations on our American form are of great value. He had occasion at Cromwell, Conn., to witness the attack of a very

small troop of *F. sanguinea* (probably *rubicunda*) on a large formicary of *F. subsericea*. "There were scarcely thirty *F. sanguinea*, and a third of these were recently hatched workers, still immature. The troop was evidently from an incipient colony. The *subsericea* had their nest about the roots of a great mullein (Verbascum). Their numbers were at least ten times as great as that of their assailants, and it may be admitted that each of them was fully as well armed and on the average larger and more robust than the *sanguinea*. Well, the mere arrival of the little troop of *sanguinea* sufficed to spread consternation through the nest of the *subsericea*, which betook themselves to flight with their larvæ and pupæ, but permitted the *sanguinea* to snatch these away and to conquer their nest without even making a serious show of defending themselves. Not more than one or two small *sanguinea* were killed in the fray. This fact is of importance, for in this instance we cannot allege the redoubtable weapons, hard integument, or even the impetuosity of the analogous attacks of the little troops of *Polyergus rufescens* which I have described in my 'Fourmis de la Suisse.' The bold and courageous tactics of the *sanguinea* were even less noticeable than in the European form of this species, which wages war on smaller and more feeble species than itself. I have never yet seen such complete and absurd cowardice as that of the American *subsericea*, a cowardice which brings clearly into prominence the instinctive adaptation to attack on the part of the enslaving, and to flight on the part of the enslaved species."

At Colebrook, Conn., during August, 1900, I had an opportunity to see a colony of *rubicunda* moving to a new nest. Each of the ants was carrying a motionless, curled-up *F. subsericea* in its jaws. The rather open phalanx of ants presented a very striking appearance as it moved from a shady hedge where the old nest was located, across a dusty road and disappeared in the undergrowth of a wood on the opposite side.

17. **Formica sanguinea** Latr., subsp. **rubicunda** Emery, var. **subintegra** Emery.

This variety, originally found by Mr. Pergande in the District of Columbia, has the same slave as the preceding, *viz.*, *F. subsericea*. During July, 1900, I found a very large nest of this variety on Naushon Island, Mass. It contained the usual auxiliaries and was compounded with a large nest of *Solenopsis molesta*.

18. **Formica sanguinea** Latr., subsp. **rubicunda** Emery, var. **subnuda** Emery.

This form was discovered by Mr. Dieck near Yale, D. C. Its auxiliaries are also furnished by *F. subsericea*.

19. **Formica sanguinea** Latr., subsp. **puberula** Emery.

This small form, which occurs in Colorado, is probably the one observed by McCook ('**82**, pp. 152–153). Its auxiliaries, according to this observer, belong to *F. schaufussi* and to a small black species (probably one of the western varieties of *F. fusca*).

20. **Formica sanguinea** Latr., subsp. **obtusopilosa** Emery.

Emery described this subspecies from New Mexico. Its auxiliary is not recorded, but is probably furnished by some variety of *F. fusca*, like *neorufibarbis* Emery or *neoclara* Emery.

21. **Polyergus rufescens** Latr., subsp. **lucidus** Mayr.

P. lucidus, the "shining slave-maker" of McCook, is the best known of the three American subspecies. It has been taken in several of the Atlantic States from Cape Cod to North Carolina and westward into Pennsylvania, but its exact geographical distribution has not yet been determined. Rev. P. J. Schmitt has sent me specimens from New Jersey, Maryland, and North Carolina. The specimens from the last-mentioned locality are decidedly opaque, thus resembling the European

form much more closely than do the typical specimens from other localities.

The habits of *P. lucidus* were first observed by McCook fully twenty years ago ('80). His account is fragmentary and barely sufficient to show that the habits are essentially like those of the European form. In the nest which he observed the slaves belonged to *F. pallide-fulva*, subsp. *schaufussi*. The same slaves were observed in a mixed nest taken on Cape Cod by Mrs. Mary Treat (Mayr, '86, p. 424). According to Pergande's observations cited by Wasmann ('94, p. 164), *F. pallide-fulva*, subsp. *nitidiventris*, is the auxiliary species in the District of Columbia. In the case observed by McCook it was, of course, the *F. schaufussi* which determined the character of the nest, since Polyergus does not excavate. Hence the title of McCook's paper is misleading. His observations on the feeding habits of *P. lucidus* are, as he remarks, "chiefly confirmatory of those recorded by Huber, Forel, and others in the European Polyergus." These, and a few additional notes on the belligerent disposition of this ant, are not, however, sufficient to leave no doubts in our minds that "our American species has precisely the same habit" of carrying on its dulotic expeditions, which he did not observe. Its slaves are certainly somewhat different in this country, and it is therefore to be presumed that the military tactics of the dulotic species may also be different.[1]

To McCook's inapposite criticism of Darwin's views concerning the phylogenetic origin of dulosis, I shall have occasion to return in the sequel.

22. **Polyergus rufescens** Latr., subsp. **breviceps** Emery.

This subspecies (Fig. 15, *a*, *b*), founded on specimens from South Dakota and Colorado, resembles the European *rufescens* still more closely than does *lucidus*, since it has the same sculpturing, opacity, and pilosity. It is, however, somewhat smaller, with a relatively shorter head, and its antennal scape is distinctly enlarged towards their tip. *P. breviceps* is evidently the form observed by McCook ('82, p. 384) in the

[1] *Cf.* the above-quoted observations of Forel on the American *F. sanguinea*.

Garden of the Gods. The slaves, according to McCook, belonged to *F. schaufussi*. Recently Rev. P. J. Schmitt has sent me specimens of *P. breviceps* from Breckenridge, Col. In this case the slaves accompanying the specimens belong to a rather small, monticolous subvariety of *F. subsericea* (Fig. 15, *c*, *a*).[1]

23. **Polyergus rufescens** Latr., subsp. **mexicanus** Forel.

This Mexican subspecies (Forel, '**99**, p. 129) is related to *breviceps*, but is larger, and without pubescence on the upper surface of the body. The exact locality of Forel's specimens is not given. It is safe to say that they must have been taken somewhere on the high plateau of central or northern Mexico. The auxiliary species is not recorded, but it is probable that the varieties of *F. fusca* (*F. subsericea* and *F. neorufibarbis*) recorded from the Mexican plateau (Forel, '**99**, p. 128) furnish the requisite slaves.[2]

24. **Tomognathus americanus** Emery.

This species (Fig. 17), which is both smaller and in other respects quite distinct from the European *sublævis*, appears to be very rare. The type specimens were taken by Mr. Pergande at Washington, D.C., in a nest of *Leptothorax curvispinosus* Mayr (Fig. 18), but no observations on the mutual relations of the two species were recorded. Rev. P. J. Schmitt of Beatty, Pa., writes me: "I have taken this species on but one occasion, — when I carried home a bushel of sifted vegetable matter from the woods. On examining this carefully

[1] While this article was going to press I discovered a fine large colony of *P. breviceps* in some woods near Rockford, Ill. The ants with their slaves — in this instance *Formica fusca* L., var. *subænescens* Emery — were living in a rotten stump in cavities excavated and long since abandoned by *Camponotus pennsylvanicus*. The Polyergus workers, like the Colorado specimens, are of small size with distinctly club-shaped antennal scapes. The head and thorax are opaque and the hairs on the abdomen are long and projecting. The abdomen is shining and nearly black in color.

[2] Buckley ('**66**, p. 170) describes a black female ant from Texas as *Polyergus texana*, but no one has since succeeded in recognizing this species. It is probably not a Polyergus at all.

I found about a dozen of the ants, which were readily recognized as Tomognathus. There may have been a few Leptothorax in the material,—certainly very few, if any,—but when

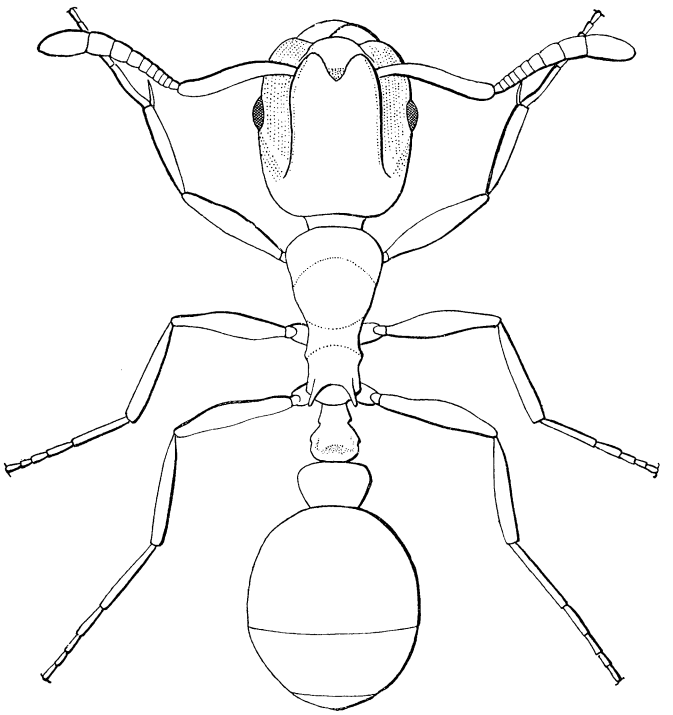

FIG. 17.—*Tomognathus americanus* Emery. Worker.

collecting with the sieve it is hazardous to affirm that any ants that are found belong to mixed or to independent colonies."

VI. COLACOBIOSIS.

It is very difficult to establish a clear distinction between the ants of this and the preceding category, since Strongylognathus is obviously transitional. Forel even includes this genus among the social parasites, while Wasmann includes the whole of Forel's category among the forms which I have designated as dulotic. I believe, however, that I am justified in erecting a special category for Anergates, which is the only well-known

social parasite, and for the American *Epœcus pergandei*, since these forms have become so extremely dependent on ants of other species that they have even lost the worker caste, thus leaving the species to be represented only by the fertile sexes like the vast majority of living organisms. The following condensed account of the work of European observers on *Anergates atratulus* is translated from Janet ('**97**, p. 58 *et seq.*), who incidentally adds to it some valuable observations of his own:

Anergates atratulus is a very bizarre ant, which inhabits central and northern Europe. It has been studied by Schenck ('**52**),

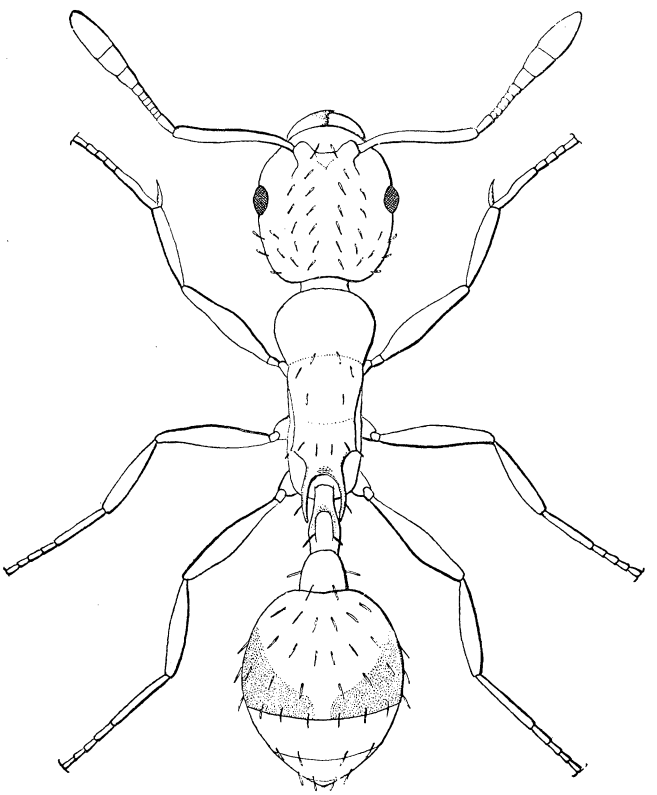

FIG. 18.—*Leptothorax curvispinosus* Mayr. Worker.

von Hagens ('**67**), Forel ('**74**), Adlerz ('**86**), and Wasmann ('**91**). As indicated by its name, it is a species which possesses no worker form. At the time of hatching from the pupa the

female presents very nearly the normal shape of queen ants and possesses wings. After fecundation, however, owing to an extraordinary development of the ovaries, her abdomen takes on the appearance of a sphere 4 mm. in diameter (Fig. 19, *b*), on which are seen in the form of little plates, isolated by the distention of the articular membranes, the strongly chitinized rings which constitute the whole external surface of the abdomen in the young individual (Fig. 19, *c*). The male (Fig. 19, *a*) is apterous, and its abdomen is strongly curved downwards. He has a dawdling gait. The strigil is well developed in the

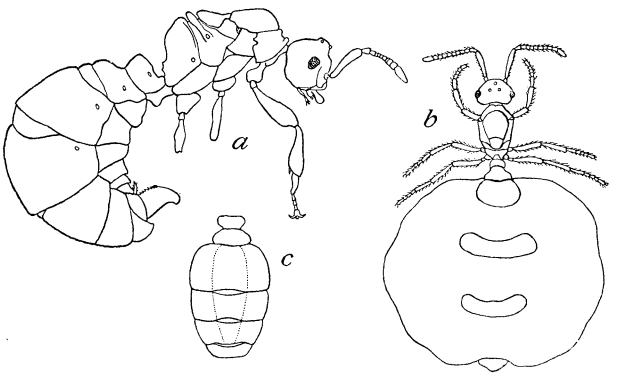

FIG. 19.—*Anergates atratulus* Schenck. *a.*, male (after Adlerz); *b.*, fertile female (after Forel); *c.*, abdomen of virgin female (after Adlerz).

female, while in the male it is very small, but nevertheless pectiniform in certain specimens (Switzerland, Forel), although in others it lacks the teeth and is quite rudimental or even almost obsolete (Sweden, Adlerz; Holland, Wasmann; Beauvais, Janet).

In some young male specimens collected at Beauvais and preserved in alcohol, I observed by transmitted light, in the head, near the eyes, and of about the same size as these, the two mandibular glands and their excretory ducts opening at the base of the mandibles. These glands are therefore well developed, notwithstanding the fact that the mandibles, which are rounded at their tips, are much reduced. The male and female are both provided with well-developed ocelli. The antennæ are 11-jointed in both sexes.

Owing to the absence of wings in the males, mating takes place within the nests. This can be easily observed both in the natural and in the artificial nests. The couples may be killed without separating, by immersion in warm alcohol.

The nuptial flight of the females was observed by von Hagens ('**67**) on the 12th of August in the Rhine province. Some of the queens may perhaps fly to other nests and there be fertilized, and although there is usually only one fertile queen to a colony, it is possible that there may occasionally be several originating from different nests. If this were not the case we should have the condition to which Forel has called attention ('**74**, p. 343), *viz.*, that all mating must necessarily take place between brothers and sisters of the same colony.

The missing workers of *Anergates atratulus* are replaced in the mixed colonies by the workers of *Tetramorium cæspitum*. Whatever progeny is found in these colonies belongs exclusively to the Anergates. The Anergates of both sexes are nourished with food regurgitated from the mouths of their Tetramorium auxiliaries. They appear to be incapable of obtaining their food in any other manner.

Adlerz ('**86**, p. 231) and Wasmann ('**91**, p. 136) have ascertained that the Tetramorium auxiliaries of the Anergates pay relatively little attention to the young queens, while, on the other hand, they very frequently carry the males about and lick them long and assiduously. During this operation the males assume a characteristic motionless attitude. The two authors compare the attention thus bestowed on the male Anergates by the Tetramorium auxiliaries to that bestowed on myrmecophilous beetles that secrete certain substances of which the ants appear to be fond; *e.g.*, the attention bestowed on *Claviger testaceus* by *Lasius flavus*.

Adlerz and Wasmann have made experiments with a view to determining the method whereby a new mixed colony is formed, *i.e.*, by the association of the female Anergates with the Tetramorium workers. Adlerz ('**86**) in Sweden placed several unfertilized Anergates queens in a strange nest of Tetramorium. They moved about among the Tetramorium as if unperceived. He obtained nearly the same results on placing unfertilized

queens of Anergates in a normal colony of Tetramorium comprising a queen and her progeny. He also placed a considerable number of the larvæ, pupæ, and male and female imagines of Anergates in a normal colony of Tetramorium which were living in an artificial nest. In all cases the strangers were almost at once amicably received. Wasmann ('**91**, p. 142) obtained similar results in Holland. He observed that strange Tetramoriums did not in the least injure the male or female Anergates which he gave them, whereas they killed without mercy the *Strongylognathus testaceus* males or females that were placed in their nest. I have reported an experiment made on the same subject ('**96**, p. 27). I have also performed the following experiment: A normal colony of *Tetramorium cæspitum* provided with a deälated queen, and a normal colony of Anergates comprising an obese queen, some slender young queens, some males and some Tetramorium workers — both colonies comprising about the same number of individuals — were put together in an artificial nest. There ensued some struggles of relatively little importance, but some days later the obese queen was found lying dead in the midst of a cluster of Tetramoriums which seemed to be caring for her assiduously. Some weeks later all the Anergates males and females had disappeared, so that the colony again became a normal colony of Tetramorium. Von Hagens ('**67**) kept a single formicary of Anergates under observation during several consecutive years in the same place. It is difficult to assume that the number of Tetramoriums may be maintained in an Anergates colony by the introduction in one way or another of newcomers, so that I am inclined to believe with Wasmann ('**91**, p. 143) that the duration of such a colony is limited to the duration of the life of the Tetramoriums.

25. **Epœcus pergandei** Emery.

Emery ('**94**, p. 274) believes that this species, like Anergates, has no worker forms. Up to the present time it has been taken only once, when Mr. Pergande found it in a nest of *Monomorium minutum* Mayr, var. *minimum* Buckley, near Washington, D. C. This nest contained not only the winged

males and females of the parasitic species, but was also provided with the winged sexes of the Monomorium. When both species were put together in the same vial the Epœcus queens attacked and killed some of the males of Monomorium. These meagre data constitute all the forthcoming evidence for supposing that the habits of Epœcus are analogous to those of

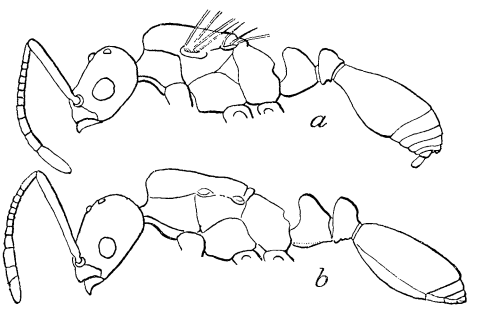

FIG. 20. — *Epœcus pergandei* Emery (after Emery). *a*., male; *b*., female.

the European Anergates. I may add that I have examined many dozens of *Monomorium minimum* nests in Texas in the hope of finding their rare parasite, but up to the present time my search has been in vain.

VII. SYNCLEROBIOSIS.

The mixed nests of uncertain origin and significance are of considerable interest, but unfortunately they are very rare, and as their origin has never been observed in any single instance either in Europe or America, it is possible to do little more in the present state of our knowledge than to catalogue the different cases. Mixed nests of this character are formed by the union of dominant species with unusual auxiliaries or *vice versa*, or by the close consociation of species which normally inhabit independent colonies. It is generally agreed that such nests must be either predatory unions, established after the manner of dulotic species by robbing the larvæ and pupæ of species which never function as normal auxiliaries, or by alliances between queens of different species before or soon after starting their colonies. Experiment may be expected to throw

considerable light on the extent to which such unions are possible. Forel ('74) and Wasmann ('91) have recorded a number of interesting observations, some of which are very similar to the following cases observed in America.

26. **Formica pergandei** Emery and **F. pallide-fulva** Latr.

Mr. Pergande (Emery, '93[a], p. 646) found near Washington, D. C., a mixed colony of *Formica pergandei* and the typical *F. pallide-fulva*, but the nature of the consociation was not determined. Emery suggests that the former species may be a true dulotic ant and *F. pallide-fulva* its auxiliary species. Mr. Pergande informed him that he had known of the existence of this colony for several years, but had seen only *pallide-fulva* in the nest till the summer of 1892, when the *F. pergandei* made their appearance in the colony. This observation would seem to favor an explanation by alliance rather than dulosis, or, at any rate, on the suppositon of dulosis the rôles of the two species would seem to be the reverse of that suggested by Emery, *pallide-fulva* being the dominant and *pergandei* the auxiliary species.

27. **Formica exsectoides** Forel and **F. subsericea** Say.

Forel ('00[c], p. 12) found a small mixed formicary of these species at Hartford, Conn. "There could be no doubt concerning the intimate life in common of the two species in the same nest. They entered and went out through the same doors, etc." Rev. P. J. Schmitt writes me that he has found at different times five different nests of *F. exsectoides-subsericea*. These invariably contained females of the *exsectoides* only. All these colonies were, moreover, obviously incipient, as shown by the fact that they contained scarcely more than fifty ants, including both species. These six cases observed by Forel and Schmitt are probably of the same nature as the very similar cases of *F. exsecta-fusca*, *F. truncicola-fusca*, *F. exsecta-pressilabris-fusca*, *F. pratensis-fusca*, and *F. sanguinea-rufa-fusca* described by Forel ('74) and Wasmann ('91). It is probable that the American *exsectoides*, like the European

exsecta, has dulotic proclivities which are shown only while the colony is young. In this connection the above-recorded fact, that weak colonies of *F. sanguinea* are found to have the most slaves, is perhaps significant.

28. **Dorymyrmex pyramicus** Roger, vars. **niger** Forel and **flavus** McCook.

A peculiar mixed colony containing both the common varieties of *Dorymyrmex pyramicus* was found by Forel at Faisons N. C. ('00c, p. 5). "There were two or three nests situated several meters apart. The yellow workers and the black workers entered and went out peaceably side by side, worked together and treated one another with every show of friendship. The two forms were, nevertheless, perfectly distinct, without presenting any transitional varieties. I completely demolished one of the nests and had the good fortune to find the females and males of *niger* and the male of *flavus*, the latter being larger and paler." Forel believes that this nest arose "without doubt by the fortuitous association of two fertile females, one of each variety." He therefore regards it as of the same nature as the peculiar mixed nest of *Tapinoma-Bothriomyrmex* which he described in the "Fourmis de la Suisse" ('74, p. 372).

29. **Pogonomyrmex barbatus** Smith and its var. **molifaciens** Buckley.

At Aguas Calientes, Mexico, Dec. 31, 1900, I happened on a huge gravel cone nest of the agricultural ant (*Pogonomyrmex barbatus*), containing about equal numbers of the typical species (with black head and thorax) and the entirely red var. *molifaciens*. There were no transitional varieties. Both forms were living together on the most amicable terms. As I entertained little hope of finding the queens, since this would, in all probability, have required a very careful excavation of the soil to a depth of from five to eight feet, I had to rest satisfied with digging into the nest a short distance and examining the hosts of belligerent workers that swarmed forth. As this was obviously an old and very flourishing colony, there can be little

doubt that it must have been formed by alliance between two or more queens representing the two distinct color varieties. The whole country about Aguas Calientes is covered with the most flourishing nests of these two forms, often very close to each other, so that it is not at all improbable that an occasional mixed nest should arise in this manner.

30. **Stenamma tennesseense** Mayr and **S. fulvum** Roger, subsp. **aquia** Buckley, var. **piceum** Emery.

Rev. P. J. Schmitt found this singular mixed nest near Beatty, Pa. The queen of the colony belonged to *S. tennesseense*. Rev. Mr. Schmitt was impressed by the fact that the nest was under a stone, whereas *tennesseense* normally occurs only in dead wood at Beatty. This seems to be generally true of the species. In Illinois and Wisconsin I have never taken it except in the old logs in the rather open forests.[1] It is a singular fact that in this and in nearly all the other cases of synclerobiosis the two consociating species or varieties represent a light and a dark colored form. This can scarcely be a mere coincidence, but I am unable to suggest any explanation of this peculiar phenomenon.

I cannot conclude this portion of my paper without expressing my indebtedness to Rev. P. J. Schmitt and to Professor Auguste Forel. These gentlemen have most generously sent me specimens of several of the rare and peculiar Formicidæ which I have figured.

(*To be continued.*)

[1] A somewhat similar mixed nest appears to have been found by Moggridge ('**73**, p. 37, footnote) at Mentone. This colony consisted of nearly equal parts of *Stenamma* [s. gen. *Messor*] *structor*, *barbara*, and the red-headed variety of *barbara*.