REPRINT

FROM

BIOLOGICAL BULLETIN

VOL. II. NO. 11

BOSTON, U.S.A.
GINN & COMPANY, PUBLISHERS
The Athenæum Press
1900

Volume II.] *November, 1900.* [*No. 2.*

BIOLOGICAL BULLETIN.

THE HABITS OF PONERA AND STIGMATOMMA.[1]

WILLIAM MORTON WHEELER.

IN a recent number of the *Biological Bulletin*[2] I described the habits of three Texan ants belonging to the subfamily Ponerinae. During the past summer an excellent opportunity presented itself to extend these observations to two other forms widely distributed in the Eastern and Northern States, *viz.*, *Ponera coarctata* Latr. and *Stigmatomma pallipes* Hald. These are of no little interest to the student of ant life, the former as a member of the typical genus, the latter as the only known North American representative of the most primitive tribe (Amblyoponii) of the subfamily. European myrmecologists have long wished to gain some knowledge of the habits of *P. coarctata*, but its rare and local occurrence on their continent has rendered this impossible up to the present time. The European type of the genus *Stigmatomma*, *S. denticulatum* Roger, is also rarely seen, and for the same reason its habits are all but unknown.

As both the ants to be considered in this paper are subterranean and very timid, it is impossible to learn much about them in their natural environment. It is therefore necessary to keep them in artificial nests. This is, fortunately, an easy matter, since the ants are very hardy. As the colonies are small, it suffices to use for this purpose the Petri dishes employed by

[1] *Contributions from the Zoölogical Laboratory of the University of Texas*, No. 10.

[2] "A Study of some Texan Ponerinae," *Biol. Bull.* Vol. ii, No. 1, pp. 1–31. October, 1900.

bacteriologists for growing cultures of micro-organisms. The ants are hastily scooped up, together with their larvae, pupae, and much of the earth in which they have excavated their nest, and the whole is transferred to a Petri dish. One or two glass slides are then placed on the earth, which is spread out till it forms a layer not more than about 5 mm. in thickness. The Petri dish is kept covered to retain the moisture in the soil. In the course of a day or two the ants excavate rough-walled chambers under the slide and galleries in the adjacent soil, of the same size and shape as those which they are in the habit of forming in their natural nests. They also gather their eggs, larvae, and pupae into these chambers, where they may be easily seen. When the slides become smeared or covered with earth they can at any time be hastily replaced by clean ones without greatly disturbing the ants.

The Ponerinae may appear to lead very monotonous lives to any one who has kept under observation the different species of *Myrmica*, *Pogonomyrmex*, *Lasius*, *Camponotus*, and *Formica*. But this very monotony is full of interest to the observer who sees in the rudimental activities of these ants a certain picture, however imperfect, of the simple stages through which the higher ants have passed in attaining to their present remarkably differentiated social organizations. It can hardly be doubted that there is a phylogeny of instincts, as there is a phylogeny of structures, and there is certainly no single animal group which more clearly illustrates the truth of this statement than the Formicidae.

PONERA COARCTATA LATREILLE.

Our American *P. coarctata* is considered by Emery[1] to differ sufficiently from the European form to be ranked as a subspecies, which he calls *pennsylvanica* Buckley. In the worker the single node forming the pedicel of the abdomen is somewhat thicker and much broader behind and less narrowed anteriorly than in the European forms. The punctation of

[1] "Beiträge zur Kenntniss der nordamerikanischen Ameisenfauna" (Schluss), *Zool. Jahrb.* Abth. f. System. Bd. viii, pp. 257–360, Taf. VIII. 1894.

the head is finer, that of the thorax and node much denser and more distinct. Emery also mentions some differences in the neuration of the wings of the male: "in den Flügeln verbindet sich aber die *Costa recurrens* etwas weiter von der Gabelung mit dem hintern Ast der *Costa cubitalis*, ungefähr wie bei der europäischen *P. punctatissima*."

Figs. 1, 2, and 3, from camera drawings, represent the outlines of the male, female, and worker of the American *coarctata*. The eyes of the worker are minute and vestigial, those of the female considerably and those of the male very much larger. The worker has no ocelli; those of the female are small, while in the male they are very prominent. The node in the male and female is more slender than that of the worker, and of a somewhat different shape. The antennae of the male are of nearly uniform thickness throughout and 13-jointed, whereas the geniculate antennae of the female and worker are 12-jointed, with a long basal joint, or scape, and a club-shaped funicular portion, with much shortened middle joints. The worker and female are provided with a long sting; while the pygidium of the male ends in an acute point.

The coloration of the female and worker is highly variable. Typical specimens have the head, thorax, node, and base of the abdomen black, the mandibles, clypeus, frontal carinae, antennae, legs, posterior third of the first abdominal segment, and the tip of the abdomen from the base of the fourth segment, red or yellow. Very often the ventral portions of the trunk are more or less suffused with red or yellow, especially when the specimens are immersed in alcohol. Some specimens, probably more or less immature, are red or yellow throughout. The body is covered in all cases with short pale pubescence, which on the head forms two lines, one on either side running parallel with the straight lateral edges. These lines are apparent only in dry specimens seen in a certain light. The male is black, with the palpi, trochanters, knees, tips of tibiae, and the tarsi light yellow. The genitalia and the incisures of the segments of the slender abdomen are also more or less yellow or piceous, as are also the stigma and veins of the colorless wings, both in this sex and in the female.

P. coarctata is a small ant, the male and female measuring scarcely more than 4 mm. in length, while the workers vary from 3 to 3.75 mm.

According to Emery this ant occasionally presents ergatoid females. He mentions[1] two of these wingless individuals from Sicily, with eyes somewhat larger than those of the worker, with ocelli and with the node somewhat higher and more slender above. I have been unable to find any such specimens among my American material, although I carefully scrutinized no less than two hundred wingless individuals from widely separated localities and from at least twenty different nests.

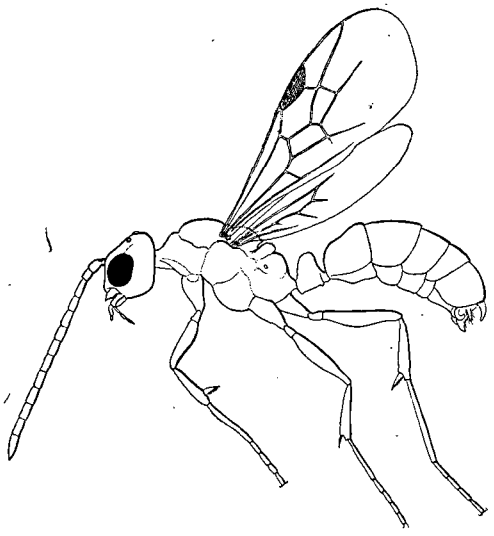

FIG. 1.—*Ponera coarctata* Latr., subsp. *pennsylvanica* Buckl. Male.

P. coarctata is the most widely distributed of the European Ponerinae and occurs even in northern Africa (Algiers), according to Emery.[2] In this country, too, its subspecies, *pennsylvanica*, is one of the most widely distributed forms in the subfamily. Emery[3] has examined specimens from Pennsylvania, New Jersey, Virginia, Maryland, Mississippi, Florida, and Ohio. Forel has observed it in North Carolina,[4] and I can add to this list four other states, *viz.*, Wisconsin, Illinois, Massachusetts, and Connecticut. It may, I think, be safely said to inhabit all the states east of the Mississippi, as well as Canada.

[1] "Sopra Alcune Formiche della Fauna Mediterranea," *Mem. letta alla R. Accad. delle Scienze dell' Istituto di Bologna.* Pp. 1–19, Tav. I. 21 Aprile, 1895.

[2] *loc. cit.*, p. 6.

[3] "Beiträge zur Kenntniss," etc., *loc. cit.*, p. 268.

[4] *Annales de la Soc. Entomol. de Belgique.* Tome xliii, pp. 438–447. 1899.

It is undoubtedly far more common in this country than in Europe. In July I found numerous nests at Rockford, Ill., both under the bark of old logs and under stones along the streets of the town. It is not uncommon in similar locations at Woods Holl, Mass., and very abundant under stones on the slopes of Mt. Pisgeh (altitude 1450 feet), at Colebrook, Litchfield County, Connecticut.[1]

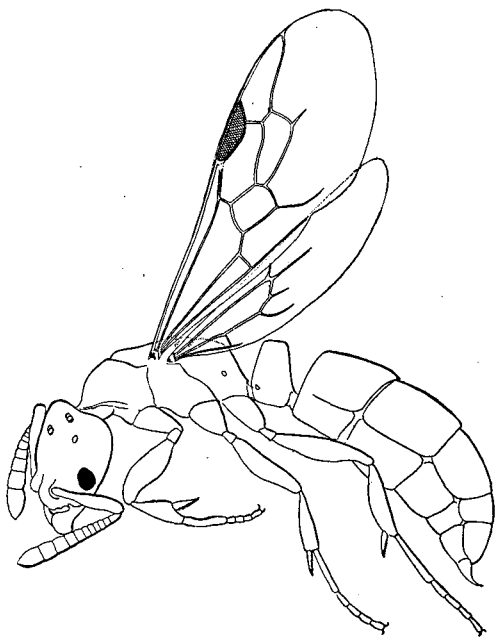

FIG. 2. — *Ponera coarctata* Latr., subsp. *pennsylvanica* Buckl. Virgin female.

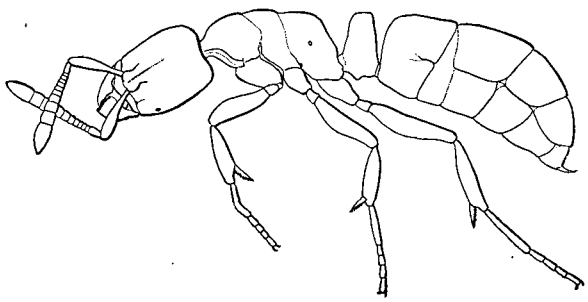

FIG. 3. — *Ponera coarctata* Buckl., subsp. *pennsylvanica* Buckl. Worker.

[1] This last locality, together with the slope of a small neighboring hill, is a rich collecting ground for ants. I give here the complete list of the forms taken there during August, as it probably embraces nearly all the species of Formicidae that occur in New England: *Brachymyrmex Heeri* Forel, subsp. *depilis* Emery; *Lasius niger* L.; *L. flavus* L.; *L. umbratus* Nyl., subsp. *mixtus*, var. *aphidicola* Walsh; *L. latipes* Walsh; *Formica sanguinea* Latr., subsp. *rubicunda* Em.; *F. exsectoides* Forel, var. *opaciventris* Em.; *F. pallide-fulva* Latr., subsp. *Schaufussi* Mayr; *F. pallide-fulva*, subsp. *nitidiventris* Em.; *F. fusca* L., var. *subsericea* Say; *F. fusca*, var. *subaenescens* Em.; *F. fusca*, subsp. *subpolita* Mayr, var. *neogagates* Em.; *Camponotus herculeanus*, subsp. *ligniperdus* Latr., var. *novaeboracensis* Fitch (= *pictus* Forel); *C. herculeanus*, subsp. *pennsylvanicus* de Geer; *Stigmatomma pallipes* Hald.; *Ponera coarctata* Latr.,

P. coarctata is not found in deep woods or in damp places, but prefers rather dry localities more or less open to the sunlight. The margins of woods and along stone walls are favorite haunts, under stones rather deeply imbedded in a rich soil, especially leaf mold. Here it excavates a small, irregular chamber, from which a few straggling burrows run off into the neighboring soil. In some cases the chamber and burrows are found under the lower surface of the stone, but I have gained the impression, from the examination of many nests, that the ants often prefer the vegetable mold nearer the surface, where it overlaps the sides of the stones. Chambers and galleries of the same irregular pattern are excavated in the rotten wood when the ants nest under the bark of old logs. The larvae and pupae are reared in the chambers. In late June and early July the nests contain eggs and larvae but no pupae; during the latter half of July and the month of August only cocoons are found, usually crowding the chamber so that the ants have little space in which to move over and among them. The imagines begin to hatch during the last two weeks of August and the first week of September. Even by the latter date I have seen no eggs nor larvae to represent a second brood.

The number of individuals composing a colony varies in different nests and with the advance of the summer. As the ants are very timid and at once seek refuge in their galleries as soon as the stone that covers the nest is moved, it is not easy to determine their precise numbers. None of the nests opened at Rockford, Ill., July 1, contained more than eight or ten ants, including a single female. As soon as the cocoons begin to hatch, the colony increases rapidly. One rather typical nest, opened at Colebrook, Conn., August 24, contained six males, one female (with wing stumps and evidently the mother of the colony), one callow virgin female, twelve

subsp. *pennsylvanica* Buckl.; *Myrmicina Latreillei* Curt., subsp. *americana* Em.; *Formicoxenus nitidulus* Nyl.; *Solenopsis molesta* Say; *Crematogaster lineolata* Say, var.; *Stenamma* (*Aphaenogaster*) *fulvum* Rog., subsp. *aquia* Buckl., var. *piceum* Em.; *Myrmica rubra* L., subsp. *scabrinodis* Nyl., var. *Schencki* Em.; *Tapinoma sessile* Say.

workers, and forty-four cocoons. A few nests examined somewhat later in the month contained a greater number of individuals, so that fifty to sixty is perhaps not too great an estimate for a large colony by the first week in September.

The winged males undoubtedly leave the nests like the males of other ants, as I have taken them in the sweep-net in the grass while collecting small Diptera. I have also seen the males copulating with the newly hatched females in the same nest. The small size of the nests in the early summer would seem to indicate that the large number of workers in the late summer and early autumn must split up into several detachments, each with a young queen, and migrate to different localities. My reasons for making this statement, apart from the above-mentioned mating of the young queens within the parental nest, are largely of a negative character, but they may be given for what they are worth. First, I have observed no tendency in the young queens, while they possess wings, to leave the nests like the males; second, the wings are often lost very soon after hatching, sometimes before the queen has acquired her deep adult coloration; and, third, I have never found a solitary queen in the act of founding a nest, either of this or of any other of the five species of Ponerinae I have studied, although I have frequently seen the young fertilized queens of *Camponotus*, *Formica*, *Lasius*, *Tapinoma*, *Crematogaster*, *Stenamma*, *Myrmica*, and *Pogonomyrmex* starting their colonies. The fact that the colonies seem to be annual instead of perennial growths, as among other ants like those above mentioned, is of considerable interest. It points to very primitive conditions in the Ponerinae, especially as the same is also true of tropical forms like *Pachycondyla* and *Leptogenys*, which can hardly be destroyed by severe winters. Thus what was at one time erroneously supposed to be true of the more specialized ants, *viz.*, the founding of a colony by a young female leaving the parental nest like the young queen of the hive bee, accompanied by a number of workers, may prove to be the normal method of nest formation with the Ponerinae. If this supposition is correct, there must be considerable inbreeding in the colonies of these ants, as the females would be regularly

fertilized by males from the same nest. There may be some connection between this condition and the limited productivity of these ants, and the strong tendency to parthenogenesis seen in some of the species (*e.g.*, in the ergatoid females of *Pachycondyla harpax*).

The behavior of *P. coarctata* towards individuals of the same species from different nests is very similar to that observed in *Pachycondyla*. If two nests be thrown together into the same dish, there may be no immediate signs of hostility; but after a few hours have elapsed, the ants are found struggling together in pairs. They interlock mandibles or tug at each other's legs and antennae, or even wrestle fiercely, intertwining their long bodies and trying to use their slender stings. These contests may be renewed from time to time for many days, whenever two individuals from different nests happen to meet, but deaths are rare, and ultimately the colonies fraternize completely. Long before the ants have settled their various difficulties, however, the cocoons and larvae of both nests are brought together as common property. A dozen different nests can be compounded quite as easily as two, and a few ants from one nest can be induced to adopt a large number of cocoons and larvae taken from half a dozen different nests.

The eyes of the workers of *P. coarctata* are so very small that they can hardly be of much service as visual organs. The actions of the ants indicate that they are guided very largely by their extremely sensitive antennae. They are, undoubtedly, able to detect the difference between light and darkness, but the fact that they do not seem to mind exposure to the light, provided they are covered with a glass plate, leads me to infer that they are rather positively stereotropic than negatively heliotropic. Of course their preference for an atmosphere charged with a certain amount of moisture — their positive hygrotropism — leads them to seek refuge in dark places, under stones or the bark of old logs.

I have not been able to ascertain the food of these ants in a state of nature. They probably kill and imbibe the juices of very small subterranean insects. In captivity they are omnivorous, feeding readily on raw or boiled meat, yolk of eggs,

corn bread, or even on "Boston brown bread." They do not appear to share the fondness of ants in general for sugar dissolved in water. When kept for a time without food they eat their dead companions or their own eggs, larvae, and pupae.

The workers of *Ponera* are never seen feeding one another with regurgitated food, like the different species of *Formica*, *Lasius*, and *Myrmica*. Even the queen is obliged to feed herself. The workers bestow on her no special attentions, nor does she enjoy any of the privileges of the queens of the above-mentioned specialized genera, after they have once established their colonies. Like any one of the workers, she takes part in digging the galleries, wanders out in search of food, assists in transporting and cleansing the eggs, larvae, and cocoons, and in feeding the larvae. Although not expressly stated in my former paper, this is also true of the ergatoid females of *Leptogenys* and *Pachycondyla*. This would seem to indicate a decidedly primitive condition, since the activities of the females of the Ponerinae never pass beyond the stage exhibited by the females of the more specialized ants only while they are raising their first batch of workers.[1]

In the scrupulous care of their nests, colonies of *P. coarctata* closely resemble the more specialized ants. They bury their food or any liquid or strong-smelling substance in their environment, and all refuse — dead ants, dead pupae, empty cocoons, etc. — is deposited in one corner of the nest.

The eggs of *P. coarctata* are oblong, like those of the other Ponerinae I have described (*Pachycondyla*, *Leptogenys*), and of very large size — fully .6 mm. long, or nearly as large as the thorax of the insect that lays them. The number produced at one time is, however, relatively small. Only three were deposited by one female in my nests July 20. As the larvae found in nests in early July are of very different sizes, we must assume that the queen lays a few eggs at a time,

[1] In this connection it is interesting to note that, as Janet has shown ("Nids artificiels en plâtre. Fondation d'une colonie par une femelle isolée," *Bull. Soc. Zoöl.*, tome xviii, p. 168, France, 1893), the female of the more specialized ants, when separated from all her workers, may return to and repeat all the activities which she displayed while founding her first colony.

probably at intervals of a few days or a week. It is quite possible that some of the workers, acting as ergatoid females, may contribute unfertilized eggs which give rise to the males that are found in nearly every colony late in August.

The larva (Fig. 4, *a*) is clearly of the Ponerine type, though differing in a few important particulars from any of the larvae of the five genera (*Leptogenys*, *Pachycondyla*, *Ponera*, *Odontomachus*, and *Diacamma*) described by Emery[1] and myself.[2] It is rather robust, with a large head succeeded by five distinct segments. The remaining segments, forming the swollen abdomen, are not distinctly marked off from one another. The body is furnished with outgrowths of three different types. The first of these is represented by a number of pointed bristles confined to the ventral surface of each segment. The second type is represented by several longitudinal rows of pointed tubercles, each of which, under a high magnification (Fig. 4, *b*) is seen to consist of a short distal spine and a long, tapering proximal base, directly continuous with the integument of the larva, and covered with transverse rows of serrated points. The distal spine is movably articulated with the proximal portion, and is so easily detached that it may be

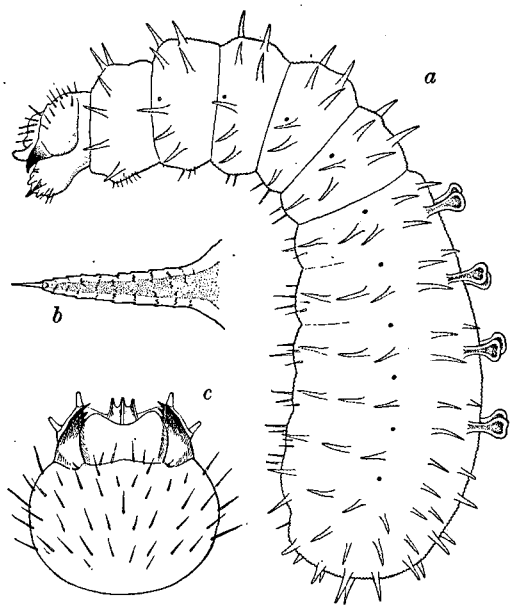

FIG. 4.—*a*, larva of *Ponera coarctata* Latr., subsp. *pennsylvanica* Buckl. Nearly ready to pupate. *b*, bristle-capped tubercle of same; *c*, head of same (dorsal aspect).

[1] "Intorno alle Larve di Alcune Formiche," *Mem. letta alla R. Accad. delle Scienze dell' Istituto di Bologna*. Pp. 1–10, 2 Tav. 7 Maggio, 1899.

[2] *Loc. cit.*, pp. 15–22.

overlooked. The third type of projection is found only on the dorsal surface of the third to sixth abdominal segment as four pairs of club-shaped structures which are glutinous to the touch. That these are peculiar modifications of the tapering tubercles seems to be indicated by the fact that they replace on either side in each of the four above-mentioned segments the more posterior of the two pointed projections seen in the thoracic, first and second, and seventh and eighth abdominal segments. The larva is usually kept on its back, so that the four pairs of glutinous tubercles act as suckers and fix it to the sides of the earthen chamber or to the glass of the artificial nest. The ants have to exert a slight effort in pulling the larva away from its attachment. The head of the larva in dorsal view is shown in Fig. 4, *c*. It is broad, evenly rounded behind, and beset with short stiff bristles. The labrum is bilobed and does not extend beyond the tips of the powerful tridentate mandibles. The fleshy maxillae and labrum project somewhat beyond the mandibles, the former being provided with robust tactile cones, the latter with a prominent median tubercle on which opens the duct of the spinning gland. Comparison of the figures in this and my previous paper shows that the larva of *P. coarctata* is peculiar in lacking the circlets of bristles on the pointed projections and in possessing clavate adhesive tubercles on the dorsal surface of the abdomen.

The larvae are fed in the very same manner as the larvae of the large Texan Ponerinae, *i.e.*, with pieces of food and not with liquid regurgitated by the ants. In confinement I did not succeed in inducing the ants to feed their larvae with fragments of insects, but they carried crumbs of moistened corn bread to them, and the larvae could be seen lying on their backs, attached by their glutinous dorsal tubercles, slowly consuming the morsels which had been placed on their flattened ventral surfaces. The fixation of the larva to the walls of the nest seems to be an adaptation for giving freer play to the head and slender neck during feeding.

The oblong elliptical cocoons of *coarctata* are of a light buff or cream color, and vary from 2 to 3.5 mm. in length. They closely resemble the worker cocoons of *Lasius umbratus mixtus*

Nyl., var. *aphidicola*, an ant which in Massachusetts and Connecticut is often found under the same stones with the Ponera. The larger cocoons belong to the males and females, the smaller ones to the workers.

The eggs and larvae are looked after with great care by the ants, as Forel has observed.[1] On a former occasion, however, I expressed doubt concerning the validity of Forel's further statement: "Lorsqu'on découvre un nid de *Ponera* dans un tronc pourri, on voit leur cocons jaunes assemblés dans un coin, mais absolument abandonnés des ♀ qui n'essaient pas de les sauver, ni de les recueiller." I have since had frequent opportunity to observe these ants, and I am convinced that the master myrmecologist is in error. It is true that the slightest disturbance of the nest causes the ants to retreat into their galleries and to forsake their cocoons, but when one stops to watch the nest a few moments, one is sure to see the ants returning one by one and stealthily removing their charges. This they do rather awkwardly, walking backwards and dragging the cocoons away without lifting them from the ground, in marked contrast with *Leptogenys elongata*, which straddles the cocoon with its long legs and carries it away with surprising dexterity. Simple experiment with the artificial nests shows that the cocoons of *Ponera*, when removed to a distance of three or four inches from the chamber in which the ants have stored them, are taken back in the space of ten to thirty minutes. Nevertheless, Forel certainly deserves credit for directing attention to this matter of the care of the cocoons, for if one has observed the way in which a large and highly specialized ant, like our northern *Formica pallidefulva Schaufussi*, *e.g.*, when its nest is uncovered, rushes out in the very face of danger to rescue its cocoons, the slow and awkward methods of *P. coarctata* certainly indicate a more primitive or possibly degenerate condition quite in harmony with the other habits of this feeble little ant. Further evidence that these ants care for their cocoons is seen in their habit of continually creeping in and out among them, and in the time which they devote to licking and cleansing them when there are no longer any larvae to require these attentions.

[1] *Loc. cit.*, p. 443.

Forel goes on to say of *P. coarctata*[1]: "Je soupçonne que chez ces fourmis, moins sociales que les autres, les nymphes sortent seules de leurs cocons, sans avoir besoin de l'aide des ☿." For the purpose of testing this supposition, I tried to surprise the ants in the act of leaving their cocoons, but I was not successful, notwithstanding numerous workers, males and females, were hatching in my artificial nests. A large number of cocoons from several different nests, and apparently in a healthy condition, were isolated in small dishes, but they failed to hatch. On the other hand, the workers opened many cocoons, extracted the dead or moldy pupae, cut them up into pieces, ate portions of them, and deposited the remainder on the refuse heap. I shall show when I come to consider *Stigmatomma pallipes* that these acts, which resemble what I formerly described for *Leptogenys* and regarded as indirect proof that the living callows are assisted in their escape from the cocoons, are of no value as evidence in this matter.

On hatching, the workers of *Ponera* are light dirty yellow, and very gradually, in the course of several days, acquire their dark color. The abdomen remains pale longer than the head and thorax. The females are more mature on hatching, having the head and thorax brown. The males are quite black and fully mature soon after leaving the cocoon.

In concluding this account of *P. coarctata* a few myrmecophiles that dwell with this ant may be mentioned. In two nests, one from Rockford, Ill., the other from Colebrook, Conn., I found a small brown Pselaphid beetle. In a single nest in the latter locality a minute Staphylinid was taken. In this locality also were found some peculiar mites, often attached in pairs on either side of the node and the first abdominal segment. Their symmetrical position resembles that of the mites *Antennophorus* and *Discopoma* infesting the *Lasius umbratus mixtus* Nyl. of Europe.[2] Wasmann[3] enumerates as

[1] *Loc. cit.*, p. 443.

[2] See Janet. Études sur les fourmis, les guêpes, et les abeilles. Note 13. Sur le Lasius mixtus l'Antennophorus Uhlmanni, etc. Pp. 1–62, 16 figs. Limoges, 1897.

[3] Kritisches Verzeichnis der myrmekophilen und termitophilen Arthropoden. Berlin, 1894.

myrmecophiles of *P. coarctata* in North America the Staphylinid beetle *Apocellus* (?) *sphaericollis* Say, and in Europe the two Pselaphid beetles: *Trichonyx sulcicollis* Rchbch and *Amauronyx Märkeli* Aubé.

STIGMATOMMA (AMBLYOPONE) PALLIPES HALDEMANN.

Although two species of *Stigmatomma* are known from southern Europe (*S. denticulatum* Roger and *S. impressifrons* Emery), both are of rare and local occurrence. On the former species Emery[1] has published the following note: "Dr. Alessandro Fosi had the good fortune to observe the nest of *S. denticulatum* while excavating antiquities at Verucchio near Rimini. These nests were found on several occasions in the Umbrian cinerary urns, and always at the surface of the layer of ashes with bone fragments found beneath the earth which had percolated in between the lid and the original contents of the urn. It was, however, impossible to obtain the winged individuals, nor could anything further be ascertained concerning the habits of these singular subterranean ants. The population of a nest which I had occasion to examine comprised about forty individuals, three of which were females."

Our American species, too, is considered to be an uncommon insect, although it is widely distributed through eastern North America, from Canada to North Carolina.[2] I have found it both on the Island of Naushon, near Woods Holl, Mass., and at Colebrook, Conn. In the former locality it was very common in some rather open oak woods at the north end of the island, under large stones, imbedded in rich vegetable mold. Here, on August 6, I uncovered some thirty nests in the course of three hours. At Colebrook, after the most careful search, I succeeded in finding only three nests (August 16 to 31), and these were in widely separated localities. All the nests on Naushon Island contained great numbers of cocoons, but in only three were there eggs or larvae. One of these contained a few mature larvae ready to

[1] "Sopra Alcune Formiche," etc., *loc cit.*, p. 3.

[2] Emery, "Beiträge," etc., *loc. cit.*; Forel, *loc. cit.*

pupate; the two others contained several packets of eggs and many young and half-grown larvae. One of the nests found in Colebrook, August 29, contained numerous callows and a few young larvae. These observations, together with the fact that the cocoons collected on Naushon Island nearly all hatched before August 20, show that *Stigmatomma* normally produces two broods during the summer. In this respect it may differ from *P. coarctata*; for, as I have said, no eggs or larvae of this species were found in several nests examined the last of August and the beginning of September.

S. pallipes seems to be so completely subterranean in its habits that it does not come to the surface even at night. Its nests are like those of *P. coarctata*, and it also often digs its galleries in the vegetable mold overlapping the edges instead of beneath the center of a stone. It is a much larger ant than *P. coarctata*, measuring 5.5 to 7.5 mm. One of the colonies taken on Naushon Island consisted throughout of very small individuals (5.5 to 6 mm.). The Colebrook individuals were all of smaller size than the majority of those from Massachusetts.

The females (Fig. 5), of which each colony contains from one to four before the hatching of the cocoons, are of the same size or slightly larger than the workers. They differ from the workers (Fig. 7) in having much larger lateral eyes, in having ocelli and wings, and in the structure of the thorax. Both females and workers are of a rich reddish-brown color; in older specimens the head, thorax, and node are almost or quite black, while the abdomen and legs are much paler. The male (Fig. 6) is black, with the two basal joints of the antennae, the trochanters, tibiae, and tarsi yellow; the remainder of the antennae reddish. The head, thorax, and anterior portion of the node are opaque and coarsely punctate or wrinkled, whereas the pleurae, scutellum, posterior edge of the node, and the abdomen are glabrous. The black stigma of the colorless wings in both sexes is large and conspicuous. Interesting morphological characters, such as the structure of the antennae in the two sexes, the remarkable dentate mandibles and clypeus in the female and worker, the venation, etc., are represented in

the figures and need no further description. There were no ergatoid females among the many specimens collected and reared, but it is quite possible that some of the workers may lay eggs, and, though lacking ocelli, such individuals could be called ergatoid females in

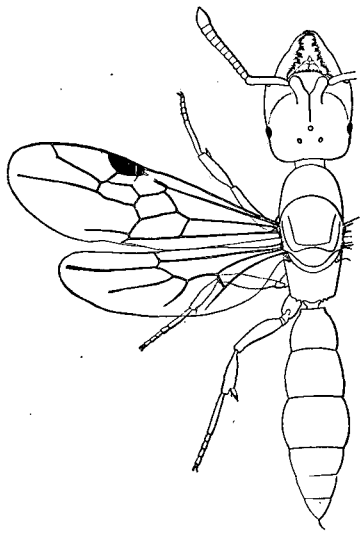

FIG. 5.

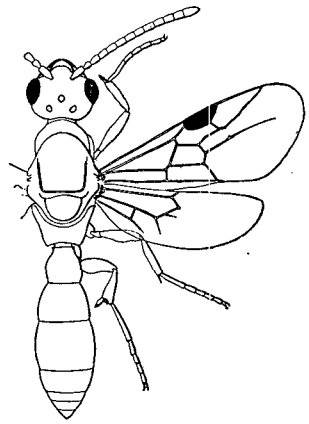

FIG. 6.

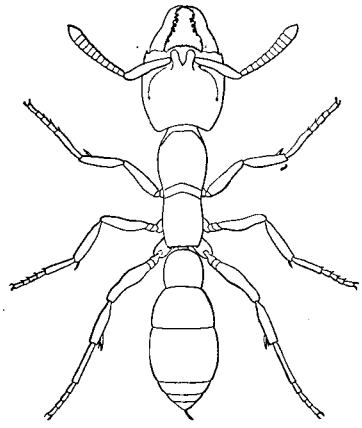

FIG. 7.

Stigmatomma pallipes Haldem. Fig. 5, Virgin female; Fig. 6, male; Fig. 7, worker.

the sense in which I have used that term (perhaps somewhat inaccurately) in my description of *Pachycondyla harpax*.[1]

[1] *Loc. cit.*, p. 5.

Much of what I have said concerning the size and growth of the colonies of *Ponera* may be repeated for *Stigmatomma*. One colony taken at Colebrook contained only two workers, and another seven workers and a female; but nearly all that were collected on Naushon Island were larger, varying from ten to twenty individuals. As some of these colonies had from four to six times as many cocoons as ants, the colonies in the artificial nests by the end of August contained from forty to sixty individuals, including in some instances ten or a dozen females and as many males.

Different nests of *S. pallipes* fraternize after a struggle in much the same manner as other species of Ponerinae. When my supply of vials gave out, while collecting the numerous nests of this species on Naushon Island, I was obliged to put some fifteen nests into a single glass jar. There was considerable struggling among the ants of the different nests for a few days, but eventually they settled down peacefully and attended to their cocoons in common. Very few of the ants were killed in the struggle, and these were usually small individuals. A portion of this compounded colony was taken in a small dish on a day's railway journey, August 9. On arriving at my destination I found most of the ants killed, and a few that were still fighting died a few days later. The unusual severity of the struggle in this case was probably due to the close confinement of the ants in a small receptacle and the jarring to which they had been subjected for several hours. Four ants and a number of larvae taken at Colebrook, Conn., August 28, were placed in a Naushon nest which had just hatched its last cocoons. The larvae were at once appropriated by the Massachusetts ants, and later in the evening a sharp struggle ensued between the members of the two colonies. On the following morning one Connecticut ant was found dead, the three others had gone over to the enemy, and the whole colony was busy cleansing the larvae.

The eyes of the workers of *Stigmatomma* are even more rudimental than those of *Ponera*. The reactions to light and darkness, to contact and to moisture, closely resemble those of the above-described species. The females, notwithstanding

their much larger eyes and their ocelli, have the same timid, groping habits as the workers. When fully mature the males, like the males of *Ponera*, are positively heliotropic and negatively stereotropic.

Stigmatomma appears to be very sensitive to low temperatures. It passes the cold nights and mornings even during August and September curled up, with its broad head covering the tip of its abdomen. When dug out of the soil some moments elapse before it straightens and begins to run about. It probably passes the winter in the convoluted conditions.

For fully four weeks after my colonies were placed in artificial nests the ants refused to eat, although I tried a great variety of foods. When small living insects were placed in the nest they were cautiously attacked, the ant advancing, snapping at them with its long mandibles, and then retreating. This whole action was a very feeble imitation of the snapping I have described for *Odontomachus*.[1] The insects thus killed were not eaten, but covered with particles of earth. Finally the ants consented to eat some of the larvae and pupae of *Formica pallide-fulva*, and a little later they became very fond of raw meat. While feeding, the huge mandibles are kept closed with overlapping tips. The insects are obliged to slide them over the food in order to reach it with the tongue and maxillae. Like other ants, they are unable to swallow solid food, but after rasping off a small mass with the tongue, they press it in the subpharyngeal pocket, thereby extracting its juices, and then spit out the small oblong ball of residue. The whole process of forming and disposing of these "boulettes de nettoyage" is exactly like that described by Janet for *Formica rufa*, *Lasius mixtus*, and *Vespa crabro*.[2] The workers of *Stigmatomma* were never seen feeding one another or their queens;

[1] *Loc. cit.*, pp. 12–14.

[2] "Sur l'organe de nettoyage tibio-tarsien de Myrmica rubra L.," *Ann. Soc. Ent. de France*, tome lxiii, p. 697, 1895; "Sur Vespa crabro, histoire d'un nid depuis son origine," *Mém. Soc. Zool. de France*, tome viii, p. 76, 1895; Sur le Lasius mixtus l'Antennophorus Uhlmanni, etc., pp. 16, 17. Limoges, 1897.—The agricultural ant, *Pogonomyrmex barbatus* Sm., when fed on starchy substances, like rolled oats, literally sprinkles the floor and walls of its nest with snow-white "boulettes."

nor can this be readily done by ants with such huge, horizontally projecting mandibles.

Stigmatomma has a singular habit of vigorously shaking its body from time to time, as if suffering with the ague. The motion is not unlike that of the Termites when they are supposed to be stridulating. It is possible that the action of the Ponerine may produce a sound through the rubbing of the various segments and joints on one another, but, though perfectly familiar with the sounds produced by the large Myrmicines *Pogonomyrmex* and *Atta*, I have not been able to detect them in *Stigmatomma*.

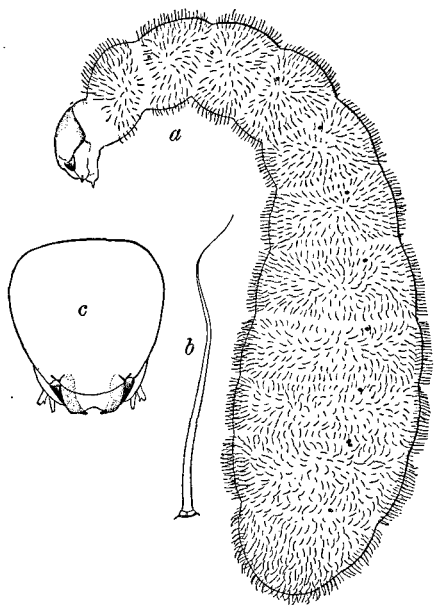

FIG. 8. —*a*, mature larva of *Stigmatomma pallipes* Haldem; *b*, bristle of same; *c*, head of same (dorsal aspect).

What I have said concerning the habits of cleanliness in *P. coarctata* applies also to the species under consideration.

The eggs of *Stigmatomma*, though deposited by a larger insect, are smaller than those of *P. coarctata*, being only .5 mm. long. They are, however, more numerous. A packet deposited by a female in one of my artificial nests contained thirteen eggs. In shape they are oblong elliptical, like the eggs of other Ponerinae. They are not arranged with their long axes parallel with one another, as in *Pachycondyla* and *Leptogenys*, but in an irregular mass, like the eggs of all the other subfamilies of ants, including the Dorylinae (*Eciton*).

The larva has the appearance of Fig. 8, *a*. The body is rather slender in alcoholic specimens, and the segments are all quite distinct and clothed rather uniformly and densely with yellowish hairs, which under a high power (Fig. 8, *b*) are

seen to taper into very slender flexuous points. The head is somewhat longer than broad and without hairs on its dorsal surface, the labrum is bilobed, the maxillae provided with the usual tactile cones. The outer one of these on either side appears to be bifurcate. The young differs from the mature larva only in having a relatively larger head and a sparser covering of bristles. Comparison of the larva of *Stigmatomma* with that of *Ponera*, *Pachycondyla*, *Leptogenys*, and *Odontomachus* shows that it does not conform to the Ponerine type but closely resembles, instead, the larvae of certain Myrmicinae, which are also covered with hairs instead of bristly tubercles.[1]

The cocoons of *Stigmatomma* are of a slightly darker, more brownish color, and somewhat more oval than the cocoons of *Ponera*. They measure from 4.5 to 6 mm. in length.

What I have said of the care of the eggs, larvae, and pupae of *P. coarctata* is equally true of *Stigmatomma*.

The larvae are fed in the very same manner as other Ponerine larvae. In one of the nests on Naushon Island a large larva was seen with its head and neck inserted in the two last segments of a beetle larva (*Tenebrionid*), which must have been captured and disarticulated by the ants. In my artificial nests the ants carried the larvae of *Formica pallide-fulva* to their own young. The latter could be distinctly seen sucking the juices of the *Formica* larvae till they were reduced to shriveled skins. These were then carried away and placed on the refuse heap.

I have succeeded in surprising the callows in the act of escaping from their cocoons. This they do, as Forel believed to be the case with *P. coarctata*, without any assistance from the workers. Several cocoons were isolated in a watch-glass, and I had an opportunity of seeing a female, two males, and several workers emerge entirely by their own efforts. The ant gnaws through the wall of the cocoon at a spot a short distance behind the anterior pole. The shape of the incision at once indicates whether a male or a female (or worker) is

[1] Compare, *e.g.*, my figures of the larvae of *Pogonomyrmex barbatus*, *loc. cit.*, p. 20, Fig. 9.

about to emerge. In the latter case the opening, which is produced by the huge mandibles, has the form of a transverse slit, extending halfway round the cocoon. The small, sharp mandibles of the male, however, gnaw a hole with irregular edges and of much smaller size. The insect, after periods of struggling, alternating with periods of rest, succeeds in getting first one antenna, then the other, and then the fore legs through the orifice, and finally, with considerable effort, creeps out. After making this observation on isolated cocoons I had an opportunity of making it in the artificial nests. In these the hatching cocoons were often carried about and placed on or under the stack of other cocoons, while the callows, struggling to emerge, seemed to hold out their antennae and fore legs in a supplicating attitude to the completely indifferent workers. In a few instances the callows died while halfway out of the cocoons and were carried to the refuse heap in this condition. Occasionally, when the young callows had emerged with their hind legs still enswathed and encumbered by the white pupal skin, the workers would pull this away. They also occasionally licked and fondled the newcomers, as if their bodies were covered with some pleasant secretion, but beyond these acts their helpfulness did not extend. These same workers, however, frequently opened cocoons and extracted dead immature pupae, cut them up, and then placed them on the refuse heap. This act shows that the statements concerning *Leptogenys* in my former paper[1] may require emendation.

The newly hatched *Stigmatomma*, as we should naturally expect from the above observations, is not as feeble as the callows of the more specialized ants. The males and females issue with their wings fully expanded; the former have their bodies completely pigmented and are able to run about briskly; the latter, as well as the worker callows, although of a rich yellowish-red, a color which they retain for several days, are nevertheless soon able to run about and to join in the labors of the colony. The queens show no tendency to leave the nest and usually lose their wings (after copulation?) while still in the red callow condition.

[1] *Loc. cit.*, pp. 29, 30.

Careful search in and about the natural nests of *Stigmatomma* failed to reveal the presence of any myrmecophiles. Wasmann, however, mentions[1] a Pselaphid beetle, *Araniops amblyoponica* Brend., as occurring with these ants in Pennsylvania and North Carolina.

GENERAL CONSIDERATIONS.

The foregoing observations on *Ponera* and *Stigmatomma*, together with those contained in my former paper, suggest some considerations of a more general nature.

First, the appearance of the larva of *Stigmatomma*, differing so widely from the known larvae of other Ponerinae, is calculated to raise some doubts on the subject of taxonomy. Forel[2] has been of the opinion that the group of genera including and allied to *Amblyopone*, viz., *Stigmatomma*, *Mystrium*, *Prionopelta*, and *Myopopone*, should be separated from the Ponerinae as an independent subfamily, the Amblyoponinae. The main characters used as an argument for this change are the presence of two spurs on the hind tibia of these ants, and the very broad and peculiar articulation of the node with the succeeding abdominal segment. Emery, on the other hand,[3] has protested against raising this group to the rank of a subfamily and its separation from the Ponerinae.[4] He argues that double spurs occur also on the hind tibiae of nearly all Ponerinae and of several Myrmicinae as well, that the articulation of the node is highly variable among the Ponerinae, and that the Cerapachyi (which Emery insists on placing with the Dorylinae) present the same conditions of the node as in *Amblyopone*. He also calls attention[5] to the important fact that the

[1] *Loc. cit.*, p. 94.

[2] "Sur la classification de la famille des Formicides," *Annales de la. Soc. Entomol. de Belgique.* Tome xxxvii, pp. 161–165. 1893.

[3] "Die Gattung Dorylus Fab. und die systematische Eintheilung der Formiciden," *Zool. Jahrb.* Abth. f. System. Bd. viii, pp. 685–778, Taf. XIV–XVII, 41 text-figs. 1895.

[4] "Die Abtheilung der Amblyoponinae darf nach meiner Ansicht nur als Tribus in der Subfamilie der Ponerinen beibehalten werden."

[5] *Loc. cit.*, p. 694, footnote.

male genitalia of *Stigmatomma serratum* Hald. are constructed "soweit es ohne Zergliederung zu sehen ist, ganz nach dem gewöhnlichen Ponerinentypus."

It would seem, therefore, that there are no very cogent reasons for adopting the subfamily Amblyoponinae, so far as characters drawn from the adult structure are concerned. The habits of *Stigmatomma*, as I have shown, are essentially the same as those of the Ponerinae, so that there exist no ecological grounds for accepting Forel's suggestion. The larva, however, seems to me to show very clearly that there is a greater gap between the Amblyoponii as a tribe of Ponerinae, and the tribes Ponerii and Odontomachii, than between the two last-mentioned groups. It must be remembered, however, that the larvae of two tribes of Ponerinae, the Australian Myrmecii and the cosmopolitan Ectatommii, have not been described, and that when these are known the striking differences between the Amblyoponii and the Ponerii may be reconciled. If, as Emery suggests,[1] the Myrmicinae are descended from the Ponerinae, it is obvious from a study of the larvae that the former subfamily must have come from forms with larvae like the Amblyoponii, a group which in other respects also is generally regarded as very primitive.[2] For the present I can see no reasons for altering the excellent classification outlined by Emery in his *Dorylus* paper.

There still exists an ecological (or biological, in the German sense) connection between the Ponerinae and the Myrmicinae, as I have lately ascertained. Since describing the peculiar method employed by the Texan Ponerinae in feeding their larvae, I have found that one of our New England Myrmicine ants, *Stenamma* (*Aphaenogaster*) *fulvum* Rog., subsp. *aquia* Buckl., var. *piceum* Emery — an ant very common under stones and in rotten logs along the edges of woods — has essentially the same method of feeding its young! My attention was first

[1] *Loc. cit.*, p. 773. "Dagegen liefern die Ponerinen offenbar die Wurzel, aus welcher die übrigen Unterfamilien der Ameisen (*i.e.*, after excluding the very primitive Dorylinae!) d. h. die Myrmecinen, Dolichoderinen und Camponotinen entsprossen sind."

[2] Emery, *loc. cit.*, p. 774, suggests that the Myrmicinae may be related to the Ectatommii, while the Dolichoderinae are more closely allied to the Ponerii.

called to this fact in an artificial nest belonging to Miss Adele M. Fielde, at Woods Holl, Mass. One afternoon Miss Fielde left a lot of queen pupae and larvae of *Crematogaster lineolata* within reach of the *Stenamma* colony. By the following morning the Stenammas had carried these into their nest, cut off their heads and abdomens, and had distributed the pieces freely among the larvae, which could be seen singly and in groups of from two to five eagerly feeding on the juices in the same manner as Ponerine larvae. Thinking that this might be a very exceptional action, due to the confinement of the colony, I opened numerous nests in the woods during the month of August, while the ants were rearing their second brood. In nearly every one of these nests I found one or more larvae feeding on substances left among them by the workers. In one nest three larvae were feeding on a small Geometrid caterpillar; in another several had their heads and necks inserted into the thoraces of some small Carabid beetles that had been decapitated by the ants; in still another nest several larvae were devouring the pulp of a blackberry, etc.[1]

Since making the above observation I find that Janet has recorded some very similar facts.[2] He saw several large larvae of *Lasius mixtus* and *L. flavus* sucking the juices from the cadavers of small larvae of their own species. Another more detailed observation I quote *in extenso*: "C'est dans un nid artificiel de *Tetramorium caespitum* que j'ai pu faire, à ce sujet, l'observation la plus précise. Au moment où les Fourmis récoltées venaient de terminer leur emménagement, j'ai vu, de la façon la plus nette, une larve d'ouvrière sucer une petite larve jaune de Coléoptère. La larve de *Tetramorium* n'était pas très éloignée d'avoir atteint sa taille définitive. Elle était suspendue par ses poils d'accrochage contre la paroi du nid, immédiatement sous le plafond en verre. Elle était placée horizontalement, le dos en haut, mais un peu de côté.

[1] *Stenamma fulvum* also brings into its chambers numerous seeds and the corollas of small white flowers. I mention this fact because it shows that this ant, which is normally carnivorous, nevertheless has proclivities that ally it by instinct as well as by structure to the harvesting ants of the subgenus *Messor*.

[2] Le *Lasius mixtus*, etc., *loc. cit.*, pp. 10–12.

Au-dessous d'elle, placée tête-bêche, parallèlement à son corps et soutenue en partie par les poils d'accrochage de l'abdomen du *Tetramorium*, se trouvait la petite larve jaune vermiforme, ayant ½ millimètre de diamètre et 2 millimètres ½ de longeur. Cette larve jaune avait certainement été placée là par une ouvrière, car pendant l'emménagement, j'en avais vu une qui introduisait une larve semblable dans le nid. La larve de *Tetramorium* avait sa tête infléchie et appliquée contre la larve jaune. Elle laissait voir, très nettement, sa bouche et ses pièces buccales. Grâces à ces circonstances exceptionnellement favorables j'ai pu examiner, avec une forte loupe, ce qui s'est passé, et cela pendant plus d'un quart d'heure. J'ai d'abord constaté le mouvement incessant de la bouche et vu nettement l'absorption du liquide transparent qui sortait de la plaie. Libre dans sa partie moyenne, la petite larve jaune était soutenue dans sa région céphalique par les poils d'accrochage de l'abdomen du *Tetramorium*. Ce dernier maintenait, au moyen de ses mandibules crochues, l'extrémité anale de sa proie, et cette extrémité était animée d'un mouvement rhythmé de balancement résultant des mouvements de succion. Pendant ce repas, et sans que la larve du *Tetramorium* parut en être dérangée, une ouvrière est venue la lécher. Cette ouvrière est allée, ensuite, dégorger de la nourriture contre la bouche d'une larve voisine. Au bout d'un quart d'heure j'ai du interrompre l'observation parce qu'une ouvrière est venue, malencontreusement, intercaler une nymphe entre la larve et le verre. J'ai alors pris la larve avec un pinceau et une petite cuiller et j'ai constaté qu'elle avait ramené sa bouche contre son corps, et que le repas était interrompu. Quant à la petite larve jaune dont j'avais vu le corps bien gonflé au commencement de l'observation, elle était, maintenant, surtout dans la région sucée, flasque et en partie vidée." Janet concludes his observations on this subject with the words: "Cette observation, venant confirmer celles, un peu moins précises, que j'ai faites chez d'autres espèces, ne me laisse plus aucun doute sur la faculté que les larves de Fourmis possèdent de sucer directement les liquides contenus dans le corps de larves, probablement blessées au préalable, qui les ouvrières deposent auprès

d'elles. Toutefois, cette manière de prendre la nourriture doit être considerée comme tout à fait exceptionelle."

The fact that this peculiar method of feeding the larvae is the only method adopted by the Ponerinae, and, I believe, also by the Myrmicine *Stenamma fulvum*, and that it occurs as an exception in such highly specialized ants as *Lasius* and *Tetramorium*, is of considerable interest from the standpoint of the phylogeny of instincts. It not only spans a gap between the generalized Ponerinae and the more specialized Formicinae, but it would seem to indicate that the method of feeding the larvae by regurgitation was grafted on to this original method in the more recent ants, possibly in connection with their habit of feeding one another by regurgitation in their adult conditions.[1]

In conclusion, the various peculiarities which indicate that the Ponerinae are a very primitive and generalized subfamily of ants may be enumerated[2]:

1. The colonies of the Ponerinae consist of a comparatively small number of ants, like the incipient colonies of the Myrmicinae, Dolichoderinae, and Formicinae.

2. These small colonies appear to be annual growths, formed by swarming, as in the bees, and not by single fertilized female ants unaccompanied by workers, as in the above-mentioned subfamilies.

3. Two or more colonies of Ponerinae of the same species can be fused to form a larger colony without much difficulty. This is not so easily accomplished with many species of the more specialized ants.

[1] Since completing my manuscript I find that one of our Texan Myrmicine ants (*Pheidole* sp. near *P. fabricator* Smith) resembles *Stenamma fulvum* in its manner of feeding the larvae. September 27 I opened a small nest of the *Pheidole* near Austin and found dozens of larvae feeding on fragments of different insects collected and comminuted by the workers. This is of interest because the *Pheidole*, like its congeners, is a harvesting ant, storing the large flat chambers of its nest with many seeds.

[2] While I have assumed in this and in my former paper that the Ponerinae may be regarded as the group from which the Myrmicinae, Dolichoderinae, and Formicinae (Camponotinae) have developed, I am quite of Emery's opinion that the existing Ponerinae are not ancestral forms. Emery calls attention to the fact that the palpi are aborted in all the tribes of Ponerinae except the Myrmecii, whereas many of the genera of higher ants have retained the undiminished number of joints in these organs.

4. The architecture of the Ponerinae is of a primitive character, consisting of a few irregular and unfinished galleries and chambers. The latter are not even formed by all the species.

5. The queen and worker differ but little in size and structure.

6. Ergatoid females, or forms intermediate between the queens and workers, are of normal and comparatively frequent occurrence in some species.

7. The habits of the queen and worker are very similar. The female is not an individual on whom special attention is bestowed by the workers.

8. The workers show no tendency to differentiate into major and minor castes.

9. The Ponerinae are carnivorous and live by hunting (in contrast with the various harvesting, fungus-growing, honey-collecting, and aphidicolous members of the more specialized subfamilies).

10. They do not feed one another by regurgitation.

11. The larvae are not fed by regurgitation, but are given pieces of insects from which they suck the juices.

12. The cocoon is retained as a pupal envelope throughout the group. (The Ecitonii among the Dorylinae have lost this envelope, although the Dorylii still retain it; it is lost in the Myrmicinae, and is apparently in the process of disappearing among the Formicinae.)

13. In at least one genus (*Stigmatomma*) the callows are able to escape from their cocoons without the assistance of the workers.

14. The callows of the Ponerinae are more mature on leaving the cocoon than the newly hatched Formicinae.

COLEBROOK, CONN., Sept. 5, 1900.