# XVI.—MERMIS PARASITIC ON ANTS OF THE GENUS LASIUS.

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Twelve Text-Figures.

## I. Account of the Occurrence of the Worm and its Effect on its Hosts.—W. C. Crawley.

It was hoped to give in this paper a complete account of the life-history of the parasite, but the evidence obtained after nearly a year's continuous observation suggests that it may possibly be longer than was anticipated, and we have therefore thought it better to give the results already obtained, with the hope of adding to them later on.

There is a fair amount of literature dealing with the infestation of ants by nematode worms. W. Gould, whose little book, "An Account of English Ants," published in 1747, contains many shrewd observations on the habits of these insects, says, "Amongst other incidents that tend to lessen and destroy Ant-Flies" (by this he means the males and winged females) "it is observable that abundance of them are demolished by a white and long kind of worm, which is often met with in their bodies. You may frequently take three from the insides of the large, but seldom more than one from a small Ant-Fly. These worms lie in a spiral form, and some of them may be extended half an inch." As will be seen below, Gould's account, as far as it goes, is remarkably accurate. By the "small ant-flies" he presumably means the males, as he is speaking of the common yellow ant, *Lasius flavus*, but it is possible he may be mistaken here, as no *Mermis* has since been found to be parasitic on the male ant of this species. Gould's worm was subsequently named *Gordius formicarum* by Diesing, but no description of it appears to exist. Forel (1874) mentions having found nematodes in the abdomen of *L. flavus*, and refers to Gould's account. A small worm was found in the labial glands of *Formica fusca* by Janet (1893, 1894, 1897), and in the pharyngeal glands of *F. rufa* and *L. flavus* by the same author, and this latter form was described by de Lacaze-Duthiers under the name of *Pelodera janeti*, and later referred to *Rhabditis*.

W. M. Wheeler (1901, 1907) found in the gaster of the Texan ant *Pheidole commutata* a worm which he considered to belong to the genus *Mermis*, with which we are here concerned. He concluded that the worm lay in the crop of the worker ant, whose fat body and reproductive organs seemed to have disappeared entirely. The worms were 50 mm. in length, ten times that of the host, and one host contained two worms. He says ("Ants," p. 420):—

"They enter the larva and apparently by unduly stimulating its appetite cause it to be fed excessively, so that it becomes unusually large at the time of pupation, and produces a gigantic worker form, with ocelli." This large form of worker he called a "mermithergate." It is not clear how it was ascertained that the worm actually entered the larva. Though it is fairly certain that the parasite enters its host in the larval stage, the results of my experiments so far do not show how and at what period this takes place. Wheeler goes on to say that the parasitized ants were in a constant state of hunger owing to the presence of the parasite. This I have also noticed in the case of *Lasius*. Emery had seen these mermithergates in 1890, but without realizing to what their increased size was due until later, and he then also recorded their presence in several other neotropical ants of different genera, and concluded that the worm must enter the larva.

Mrázek (1908) appears to have been the first to write in any detail of the parasitization of *Lasius* by *Mermis* in Europe, though I found the parasitized ants in 1898, and recorded them as brachypterous forms (1910). Mrázek showed that the wings of the host (in this case *Lasius alienus*), which are the most prominent secondary sexual characters in most female ants, only developed to about one-quarter or one-third of their normal size. Later, in 1910, Wheeler found small-winged females of *L. neoniger*, a closely related form from Colorado, some of which contained worms from 53 to 55 mm. in length.

My first discovery in England of female ants parasitized by *Mermis* (and known as mermithogynes) was in 1898 at Oddington near Oxford. Along a road bounded on each side by a deep ditch, which for the greater part of the year contained water, had occurred a marriage flight of the common yellow meadow ant, *Lasius flavus*. This was towards the end of August, and alate and dealate females were to be seen on the road for some days afterwards. Amongst these I picked up several short-winged forms, which some years later were found on dissection to contain *Mermis*. Two or three days later in the same place I found some mermithogynes of *Lasius alienus*, the species which formed the subject of Mrázek's paper ten years later. Again in 1900 and 1901 I found several more parasitized females of both these species in the same locality. These females are readily recognized by their abnormally small but otherwise perfectly formed wings. I tested their powers of

flight by throwing some of them into the air, but in no case were they able to fly at all.

It was not until 1916 that I again met with mermithogynes, this time in Somerset, in the marshes by the sea at Porlock, where examples of both *L. flavus* and *L. alienus* were abundant early in July (Crawley, 1916). The proportion of parasitized to normal females varied considerably according to the colony, but it was only in a small number of cases that the parasitized females outnumbered the others. The colonies were all large and flourishing in appearance.

Again, in July 1917, I came across many more mermithogynes of both the above species in the same locality, but in every case the normal females greatly outnumbered the mermithogynes, the average proportion not being more than 1 to 12, and in one nest only a single mermithogyne was found.

On my return home I placed these ants in "Janet" plaster nests with workers, males and pupæ.

At the end of the month two of the *L. flavus* mermithogynes became very restless, elevating their wings and curving their abdomens as if disturbed by the movement of the worms. One constantly bit the end of her gaster from which the head of the worm could be seen to protrude. At night one of the ants, presumably this one, was dead, and the worm had emerged and was lying dead among the worker ants, who were biting it. This seemed to indicate that in nature the worm would not emerge until the female had left the parent nest on the marriage flight. As stated above, the parasitized females do leave the nest at this period, though unable to fly, with the normal females. Within the next few days three more mermithogynes had died, without the parasites having emerged, and all had shown restless symptoms previously. The movements of the worms could be distinctly seen through the distended walls of the gasters of the dead ants. One day after the death of a female the parasite pierced the integument just below the anus and began to emerge. After attempting in vain to force its head under the soil, it succeeded in getting clear of its host's body in just over an hour. I then placed the worm on a piece of turf, but it was unable to pierce the turf, and eventually died.

By August 10 all the mermithogynes, except one *L. flavus*, were dead, but in only one case had the parasite completely emerged, and in one or two others it had partially done so. Sometimes the worm pushed its head through the anus itself, in other cases it was between two of the ventral plates of the gaster that the aperture was made by the parasite. It should be noted in passing that the thoraces of all the mermithogynes I examined were almost completely empty, and did not contain the large wing-muscles of the normal female which are later on used as

food to support the insect during the long period (often many months) occupied in rearing her new colony.

It now became clear that the worms could not satisfactorily emerge from their hosts and continue their existence if left on ordinary dry earth. I therefore varied the experiments as follows: I took a *L. alienus* mermithogyne that had been dead for twenty-four hours without the *Mermis* having emerged, and placed it in a saucer containing a little earth covered with water. In less than ten minutes the worm had emerged and was sluggishly lashing to and fro in the water, keeping up these movements all day.

In the evening I drained off the water in the saucer, and the

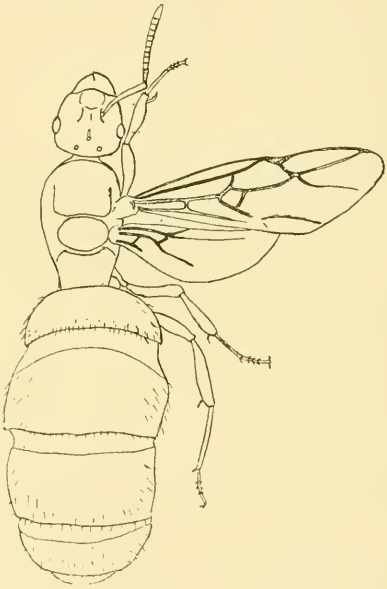

Fig. 1.—Mermithogyne of *Lasius alienus*.

worm then spent hours trying to bore into the wet earth, which was not deep enough to allow its whole body to be buried at one time.

When the earth dried up the worm became motionless, but flooding it with water was sufficient to arouse it to renewed activity. On August 13 the remaining *L. flavus* female died. I placed the body, as before, on earth barely covered with water, and the worm, a very small one, emerged with some rapidity, and at once began burrowing in the wet earth. From this time till the end of November, more than three months, this *Mermis* remained alive, increasing somewhat in size. After the first few

weeks it spent most of the time out of sight under the soil, only appearing when the earth became dry. War duties necessitated my leaving home for some months, and the *Mermis* in consequence died.

The size of the worms found in these two species of ant varied considerably (see description). In more than one case an ant contained no less than three worms. The illustrations show the relative size of the host and the parasite, also the manner in which the parasite is coiled up in its host.

My friend Dr. J. Bronté Gatenby very kindly cut a series of excellent sections of the abdomen of a *L. alienus* female with the

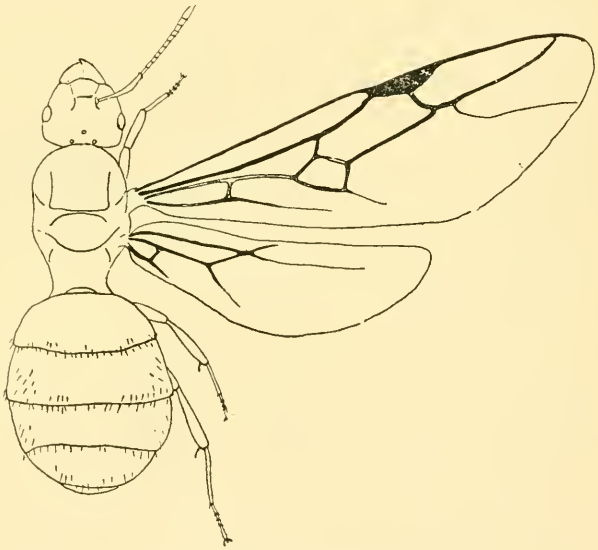

Fig. 2.—Normal female of *Lasius alienus*.

parasite *in situ*. These sections, and also the simple dissections of the abdomens of the hosts, show very clearly how considerably the ovaries are reduced in size compared with those of a normal female. The sections also distinctly show the beginning of degeneration of the nurse cells. Both these conditions are directly traceable to the starvation of the organ caused by the parasite. Other conditions pointed out by Gatenby as caused by the parasite are the hypertrophied tracheæ and the almost entire absence of fat-bodies in the host. The Malpighian tubules are normal.

A careful examination of the ant fails to reveal any external modification except the reduced wings and the distension of the abdomen caused by the presence of the worm. This distension

disappears after the emergence of the worm, and the ant has then a normal appearance except for the small wings. The size of the latter varies to a certain extent, a series of *L. flavus* showing a variation in the upper wing of 4·6 mm. to 5·3 mm., and one of *L. alienus* of 5·0 mm. to 6·2 mm., whereas the normal wing of the first species measures 9·0 mm. in length and that of the latter 10·0 mm. The variation in *L. niger* is 5·3 mm. to 6·0 mm., the normal wing being 10·0 mm.

Until 1920 the only two species of ant known as hosts of *Mermis* in this country were *L. flavus* and *L. alienus*, but in July 1920 my friend Mr. H. Donisthorpe found in Cornwall a colony of *L. niger* containing numerous mermithogynes (1921). The

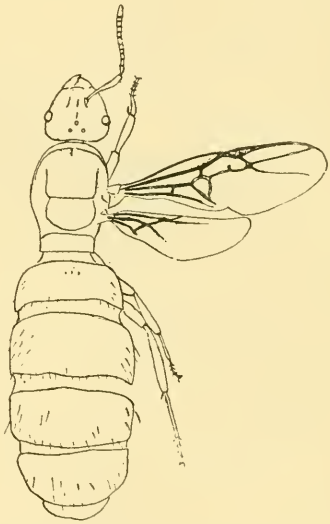

Fig. 3.—Mermithogyne of *Lasius flavus*.

habits of all three species are to a great extent similar. *L. flavus* throws up mounds which become covered with grass and may reach a diameter of over 2 ft. and a height of 1 ft., and these nests are generally in meadows. A certain amount of moisture is necessary for these ants, and nests are often found in damp situations, and stones, logs, etc., are often utilized as cover. *L. alienus*, though equally a hypogæic species, rarely throws up mounds, but is more fond of stones as shelter, and its nests are very frequently in damp situations. *L. niger* has habits similar to those of *alienus*, but lives more in the open air, and in damp places will erect earth mounds. All three species have the following important habits in common: they nest underground, preferably

in damp earth; they rarely have more than one fertile queen in each colony, the females are very much larger than the workers and are reared in large numbers every year, and are therefore specially suitable as hosts; and, finally, the larvæ hatched from eggs laid in spring and summer live through the winter and do not complete their metamorphosis till the following summer. Thus there are always larvæ in the nests of all three species all the year round. Every colony that I have found to contain *Mermis* (some 15 to 20 in all) was either in damp ground or near marshy ground or standing water, and it is interesting to note that Donisthorpe found his colony of *niger* near a stream running from a marsh into the sea. These facts support the conclusion arrived at from my experiments, viz. that water or marshy ground is necessary to the development of the worm after leaving its host. The behaviour of the worm when attempting to escape from the ant's body in water and on moist earth shows that the emergence is more easily effected in water. When the infected ant was placed on moist earth, the *Mermis* first protruded its head and attempted to burrow under the soil, but the movements of the ant, always very agitated, usually prevented this. After a time the worm succeeded in hooking itself round a projection of earth and held tight until the ant by pulling in all directions drew it clear from her body. This operation often took a considerable time, but when the ant was placed on the surface of the water the evacuation usually occupied but a few seconds, or at most a minute or two. The ant after getting free from the worm invariably performed a very complete toilet, and then seemed to take on a renewed lease of life, which, however, in the majority of cases only lasted a few days, and sometimes only twelve hours or so. A normal female of these species after fertilization lives from five to ten years and sometimes much longer.

It should be mentioned in passing that I brought back from Porlock in May 1920 (i.e. before the winged females were present) a colony of *L. flavus* containing two queens, and among the females when they eventually hatched was a single mermithogyne, proving that at least one larva had been infected, though I was unable to find any traces of the worms in numerous full-grown female larvæ that I dissected. This colony was used in a further experiment later on.

The infected colony of *L. niger* (the third species of this genus which is a host of *Mermis*) referred to above was very kindly handed over to me by Donisthorpe to enable me to continue the study of the further history of the worm. These mermithogynes are exactly similar, except for specific differences, to those of the other two species, but there is one structural anomaly not present in the former cases. In about nine-tenths of the *L. niger* mermithogynes there is a hole in the anterior border of the mesonotum

at its junction with the pronotum. On dissection this aperture is seen to consist of an invagination of the cuticle ending in a point inside the thoracic cavity. The hole in a typical specimen is situated 0·43 mm. from the anterior border of the mesonotum, with which it is connected by a shallow groove, rather narrower than the diameter of the hole itself. The actual aperture measures 0·21 mm. long by 0·12 mm. wide. Seen from the interior of the mesonotum, the funnel-shaped invagination measures 0·68 mm. from the border of the segment, and 0·32 mm. from the opposite edge of the hole to the point. The point itself is generally rounded. Several other specimens were examined and measured, the aperture

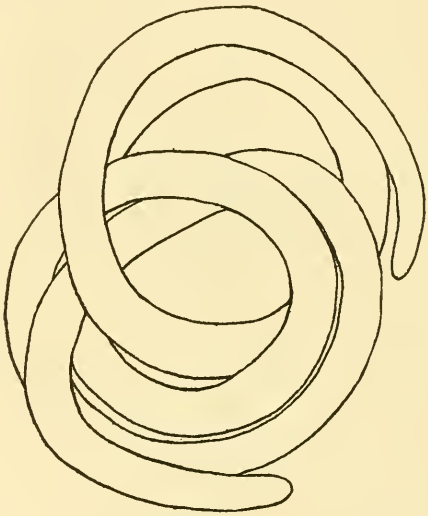

Fig. 4.—Worm *in situ* in abdomen of female ant.

and length of the point varying very slightly in different individuals according to their size.

This condition may be, and probably is, connected in some way with the parasitized state of the ant, but the hole is, at any rate immediately after the emergence of the ant from the pupa, large enough to admit a nearly full-grown larval *Mermis* which would have been obliged to pass through the minute aperture connecting the thorax with the abdomen in order to take up its position in the latter. The worm too would have been free in the nest previously, and, as has been seen, the worker ants kill an unprotected worm. Other reasons also compel one to seek for another cause for this aperture than the entrance of the worm, not the least of which is the fact that a proportion of the infected ants were with-

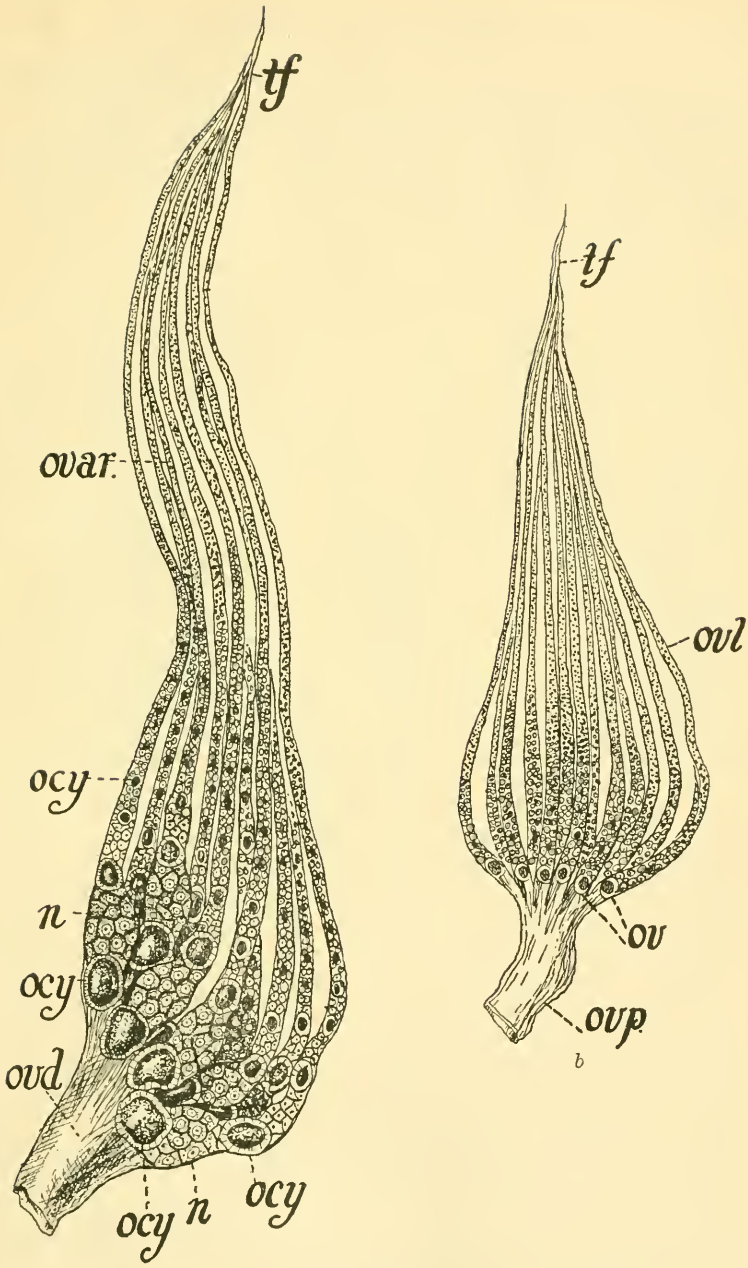


FIG. 5.

*a*, Ovary of normal female of *Lasius alienus*.
*b*, Ovary of parasitized female to same scale.
*ovd*, oviduct; *ocy*, oocyte; *n*, nurse cells.

out the hole, and it does not exist in any of the more numerous specimens from the other colonies previously examined.

There is another case of malformation in this colony, occurring in a normal female. It consists of a semicircular excision in the apical border of the third segment of the gaster, and is probably unconnected with the parasite.

I dissected a number of full-grown female larvæ and also several pupæ from this colony, but failed to find any trace of the worm. These mermithogynes were very active, often assisting callow ants to emerge from their cocoons, and were also very ravenous, devouring flies that I put into the nest, and also crippled and damaged pupæ and callows, besides always asking the workers for food. Occasionally one would be seized with a kind of paralysis, lie on its back with legs and antennæ extended and twitching, and a movement of the worm inside the gaster could be seen at the same time. Such ants usually recovered, but in one or two cases they died. After the emergence of the worms the ants became very active, but their death was only deferred a short time.

By constantly placing each mermithogyne, as soon as she became restless or died, on damp earth in a pan I succeeded in obtaining thirty-seven worms, which I transferred to a larger and deeper vessel with damp earth. At the beginning of November they were all still in the larval stage, the outer skin being very distinct, but the genital organs were beginning to develop. By Nov. 20 four had cast their larval skins, the operation consisting in piercing the skin a short distance from the head and then peeling off the skin by burrowing into the earth. When the earth became dry most of the worms came to the surface and remained motionless, with about a third of the body projecting in a coil in the air. A sprinkling of water invariably caused them to descend below the earth again. The first eggs were noticed in the uteri on Dec. 5. The problem of keeping them alive began to be acute about this time, mould making its appearance on the surface of the soil. Sand was tried in place of soil, but rapidly became matted with mould and destroyed the worms. Finally, the best method was found to be to keep them in small flower-pots with a layer of plaster of Paris at the bottom to close the hole. The terra-cotta being porous allowed drainage to take place, so that the earth remained very nearly free from mould, and the only drawback was the necessity of frequent watering to replace the evaporated moisture. Four or five worms had assumed a brown colour, but were quite healthy, though not so active as the others, and on casting their skins they were again white.

The process of egg-laying was easily observed under a low power. The eggs moved slowly down the vagina, and each egg became slightly compressed as it reached the orifice, where it halted

a moment and then shot out to a short distance, but still remained attached to the worm by a colourless gelatinous substance. When a sufficiently large group of eggs had in this manner collected round the orifice, it broke away by its own weight. When laid inside the larval skin, in which there appears to be no vulvar aperture, the eggs assumed the form of a flat ribbon as wide as

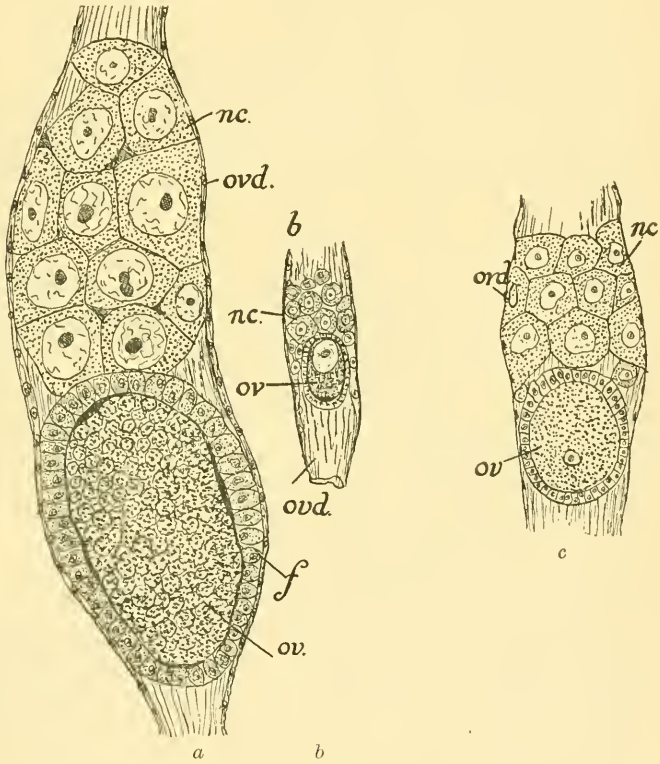


FIG. 6.

*a*, Largest oocyte of normal female of *Lasius alienis*.
*b*, Largest oocyte of worker of *Lasius alienus*.
*c*, Largest oocyte of parasitized female of *Lasius alienus*.
All to same scale.
*ov*, ovum ; *ovd*, oviduct ; *nc*, nurse cells.

the diameter of the skin, each egg being separated from its fellows by the gelatinous material. Almost all the cast skins were full of eggs, the egg-laying going on before, during and after the casting of the skin. It is possible that the skin forms a useful protection to the eggs, but the uterus after the casting of the skin contained

about as many eggs as were left in the skin. Some of the later eggs laid were already segmented.

I carefully counted the eggs in two typical cast skins. In the first there were over 6,560 eggs, and in the second over 5,900. Allowing for an equal number still in the uterus, this gives an average of about 12,000 eggs for each worm. Probably the number is even greater than this, as all the worms continued laying for some weeks after casting their skins.

By the beginning of May 1921 all but three or four worms had died, and I left them with their eggs in the flower-pots.

At the beginning of July I connected one of the pots with the nest of *L. flavus* referred to above, in the hope of tracing eventually the method of infection. The ants readily took up their quarters in the flower-pot.

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