Bull. ent. Res. (1968) **59**, 291–297
With Plates XII–XIII
Published 1969

The biology of *Pseudorhyssa sternata* Merrill (Hym., Ichneumonidae), a cleptoparasite of Siricid woodwasps

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Introduction

The cleptoparasitic * behaviour of *Pseudorhyssa sternata* Merrill was first described by Couturier (1949), who recorded that *P. sternata* females observed the primary Ichneumonid parasite, *Rhyssa persuasoria* (L.), drilling into Siricid-infested coniferous trees. When the primary parasite withdrew its ovipositor and departed, *P. sternata* found the oviposition shaft and inserted its ovipositor. No other details of the biology have been published, although the morphology of the immature stages is to be described by Spradbery (1970).

Materials and methods

Adults were reared from a variety of Siricid-infested logs of various species collected in Europe, and maintained under outdoor insectary conditions at Silwood Park. The females were mated shortly after emergence, and studied at 25°C or stored at 5°C in gauze-covered observation cages (30×30×30 cm). They were supplied with water, and with honey containing 1% protein hydrolysate. For adult behaviour studies, the females were offered *Pinus sylvestris* culture logs (19–25 cm long; 10–16 cm diameter) containing larvae of *Sirex juvencus* L., *S. cyaneus* F. or *S. noctilio* F.

Oviposition was secured and the immature stages reared by the technique of Spradbery (1968) which permits study of larval behaviour and development.

To study the factors involved in the detection of *R. persuasoria* oviposition shafts, a bioassay technique was developed employing "oviposition sheets": test substances were put into 20×7-mm cavities excavated 7 mm into 30×15-cm sheets of perspex, 1 cm thick. The cavities were covered with paper fixed with cellulose acetate tape. The bioassay sheets were put face downwards on the gauze-covered tops of the observation cages. The behaviour of the adults was observed at 25°C and 70% r.h. under ordinary laboratory lighting.

Life-history

The dates of emergence of adult *Pseudorhyssa sternata* and *R. persuasoria* from three European localities are given in Table I. The emergence periods of the two

* Cleptoparasitism is a form of multiparasitism in which access to and paralysis of a host by one parasite species are essential before the host is parasitised by a second parasite species (the cleptoparasite), which upon eclosion destroys the egg or larva of the first parasite before feeding on the paralysed, primary host.

TABLE I. *Emergence of* P. sternata *and* R. persuasoria *from timber maintained under outdoor conditions, Silwood Park, 1968*

Locality	*P. sternata*				*R. persuasoria*			
	♂ ♂		♁ ♁		♂ ♂		♀ ♀	
	No.	Dates	No.	Dates	No.	Dates	No.	Dates
Chatillon, Switzerland	29	25.iv.–27.v.	10	27.iv.–5.vi.	154	26.iii.–19.vi.	59	19.iv.–17.vi.
Lucelle, Switzerland	17	27.iv.–29.v.	24	2.v.–3.vi.	107	29.iii.–13.vi.	43	20.iv.–24.vi.
Winenne, Belgium	10	2.v.–22.v.	27	15.v.–3.vi.	99	11.v.–24.vi.	35	15.v.–25.vi.

species are rather similar, with a more extended period in *R. persuasoria.* The sex ratio in *P. sternata* was 1 ♀ : 1.1 ♂♂ and in *R. persuasoria* 1 ♀ : 2.6 ♂♂.

P. sternata females are responsive to males during the first two to three days following emergence, but do not mate very readily in the laboratory. The male mounts the female from behind, and strokes her antennae in a rowing action, pulling them backwards so that the male antennae slide over them. Pre-copulatory behaviour continues for a few seconds if the females are responsive, and more than a minute if they are not. Coupling occupies from a few seconds to more than a minute, during which the female's gaster jerks rhythmically. Multiple mating is common in both sexes.

The ovaries of the cleptoparasite mature rapidly, with an average of 2.3 mature eggs in females aged 0–1 day, and 6.0 eggs 1–2 days after emergence. The longevity of females was 28 days (range 17–41, $n = 15$).

When mature females of *P. sternata* and *R. persuasoria* are put on a Siricid-infested log, the primary parasite explores the surface of the log with its antennae, probing the superficial layers of the wood with the tip of the ovipositor and, when sufficiently stimulated, drills deeper into the wood in the vicinity of Siricid galleries and hosts. While the primary is drilling, the cleptoparasite often observes from a distance (1–8 cm), although the cleptoparasite frequently approaches the drilling primary parasite and strokes its legs and ovipositor with the antennae (Plate XII, fig. 1). Occasionally the cleptoparasite attempts to insert its ovipositor down the shaft being drilled by the primary. When the primary withdraws its ovipositor, the *P. sternata* female explores the surface with its antennae until the drill shaft is located. During exploratory behaviour, the distal ends of the antennae are curved back so that the dorsal surface of several segments are laid on the surface, in contrast with *R. persuasoria,* in which normally only the tips of the antennae are used.

When the drill shaft is found, the cleptoparasite raises its abdomen, and draws the ovipositor up under the body until it is in line with, and closely applied to, the ventral surface of the gaster. The tip of the ovipositor is manoeuvred forwards to the antennae, until the shaft is located. With the abdomen at an angle to the thorax, the ovipositor is inserted while supported by a groove along the sternites, and by the hind coxae (Plate XII, fig. 2). The mean duration of a drilling operation by *R. persuasoria* was 13.9 min (range 5–33, $n = 131$) compared with 6.2 min (range 3–18, $n = 19$) for *P. sternata.* Drilling by the cleptoparasite normally involved little more than occasionally clearing away detritus from the shaft, and its speed was facilitated by the smaller size of the ovipositor in cross section (Table II). The tips of the ovipositors of both species are morphologically similar, the valvulae being serrated terminally.

Although it is common for the cleptoparasites to observe ovipositing *R. persuasoria* before locating the shaft, they are also able to find the shafts several days after they have been drilled, and in the absence of *R. persuasoria* females.

After locating a host, *R. persuasoria* pierces its cuticle, injects venom and paralyses

TABLE II. *Dimensions* of ovipositors of* P. sternata *and* R. persuasoria *in relation to forewing length (as an index of body size)*

	Forewing length (mm)	Ovipositor dimensions (mm)		
		Length	Breadth	Thickness
P. sternata	15·2 (9–19)	29·5 (17–37)	0·15 (0·11–0·18)	0·046 (0·04–0·05)
R. persuasoria	16·8 (13–24)	28·5 (17–45)	0·21 (0·19–0·27)	0·079 (0·06–0·11)

Means of 20 females (ranges in parentheses)

it. After withdrawing the ovipositor from the host's body, an egg is deposited upon it. When *P. sternata* locates the host, it oviposits near the primary parasite egg (Plate XIII, fig. 1).

Oviposition by both species was readily obtained in oviposition cavities when host larvae were present, but unlike *R. persuasoria*, *P. sternata* also oviposited in cavities in the absence of hosts. *P. sternata* laid a maximum of three eggs on a single host in oviposition cavities. The cleptoparasite deposited approximately the same numbers of eggs on active Siricid larvae, paralysed larvae, and in cavities without larvae, and also laid eggs on wet synthetic sponge-pads placed on the cages to supply water. Both species also laid eggs on the undersurfaces of wooden shelves supporting their cages. When unparalysed, active Siricid larvae in oviposition cavities covered with paper drilled by *R. persuasoria* were offered to *P. sternata* alone, the larvae were apparently paralysed and the cuticle bore black patches of scar tissue surrounding the ovipositor punctures. The venom gland of *R. persuasoria* is composed of a long reservoir with branched glandular tissue at its free end, and in *P. sternata* there is a similar reservoir but without the branches.

Rarely, *P. sternata* drilled through untreated paper into frass-filled cavities containing larvae, in a manner similar to that of *R. persuasoria.*

The incubation period of the eggs of both species at 24°C and 100% r.h. was approximately two days. The first-instar larva of *P. sternata* is considerably larger than that of the primary parasite, and has a more heavily sclerotised head capsule with large falcate mandibles. After eclosion, the *P. sternata* larva moves over the surface of the host using a paired caudal appendage as a lever to assist locomotion. When contact is made with the primary larva, it is gripped by the mandibles, the cuticle is pierced, and the body mangled (Plate XIII, fig. 2). The primary larva attempts to retaliate and then *P. sternata* uses the caudal appendage as a balancing organ when rearing during combat. Some of the body contents of the primary are ingested before it is discarded and the cleptoparasite begins to feed on the host. If there is no *R. persuasoria* larva present, *P. sternata* behaves as a primary parasite feeding on the Siricid host shortly after eclosion. The first-instar cleptoparasite pierces the host cuticle with the mandibles and uses them to grip the host while it ingests the body contents. Except during the first instar and while moulting, the larva remains attached to the host, and occasionally the head and thorax are sunk into the host. Development from first to fifth (final) instar takes 12·5 days (range 12–14, $n = 10$) at 24°C. Second- to fifth-instar larvae of both species are very similar, with reduced cephalic sclerotisation, hypognathous heads, and small mandibles covered by the labrum, although the mandibles are moderately exposed in second-instar *P. sternata.* Larvae remain small until the early final instar when all but the cuticle, head capsule and terminal spine of the host is consumed. Feeding is normally completed 3–5 days after the parasite enters its final instar.

After two weeks, the *P. sternata* larva begins to spin a cocoon which closely lines the host chamber or rearing cavity. The final-instar larva overwinters, and pupates in the spring (March–April).

Experimental study of adult behaviour

To determine the ages of *R. persuasoria* oviposition shafts which *P. sternata* can detect, a log culture of *S. cyaneus* was established and exposed to *R. persuasoria* females. Ten drills were observed and marked daily for 28 days after exposure. Eight days after this, when the age of the drills ranged from 8 to 36 days, the log was exposed to five *P. sternata* females, and drilling activity recorded for eight days. The cleptoparasites made 31 drills into shafts aged 13–38 days (mean 25) at time of utilisation. However, dissection of the log showed that none of the *R. persuasoria* drills had resulted in the detection of hosts, and no oviposition was noted.

P. sternata also probed with its ovipositor into holes made in wood by 0·6-mm diameter pins, but no oviposition took place.

When paper drilled by *R. persuasoria* was offered to *P. sternata*, the cleptoparasite was attracted to it, located the holes, and inserted its ovipositor through them. Drills aged 1–12 days were attractive to *P. sternata* and elicited the ovipositor probing response.

To determine the relative attractiveness of paper drilled by *R. persuasoria*, Siricid frass, and the symbiotic fungus *Amylostereum* sp., the following experiment was made. Paper drilled by *R. persuasoria* or with similar-sized artificial holes, was used to cover cavities in bioassay sheets that contained frass or *S. juvencus* symbiont, or were empty. There were approximately the same number of drills or holes per cavity. The results of the bioassay are summarised in Table III (Experiment 1), and demonstrate the dominant attractiveness of paper drilled by *R. persuasoria*.

TABLE III. *Summary of experiments on the detection of* R. persuasoria *drill shafts by* P. sternata

Experimental details	Tested components: Contents of cavity	Tested components: Paper covering	No. of ovipositor probes by *P. sternata*
Experiment 1	Fungal symbiont	*R. persuasoria* drilled	14
9 replicates	Frass	*R. persuasoria* drilled	11
(36 ♀♀ used)	Empty	*R. persuasoria* drilled	10
	Fungus	Artificial holes	0
	Frass	Artificial holes	1
	Empty	Artificial holes	0
	Fungus	No holes	0
	Frass	No holes	0
	Empty	No holes	0
Experiment 2*	Frass	*R. persuasoria* drilled	128
12 replicates	Empty	*R. persuasoria* drilled	36
(48 ♀♀ used)	Frass	Artificial holes	13
	Empty	Artificial holes	6
Experiment 3	Filter paper discs		
12 replicates	i. Vaginal gland extract		64
(48 ♀♀ used)	ii. Venom gland extract		1
	iii. Water controls		4

* Frass was made wet by adding water.

In Experiment 2 (Table III), cavities containing wet frass and empty cavities were covered with paper drilled by *R. persuasoria*, and paper with artificial holes. Of the 183 ovipositor probes, 70% were made through *R. persuasoria* holes into frass, 20% through *R. persuasoria* holes into empty cavities, and 7% through artificial holes into frass, demonstrating that frass elicits the ovipositor probing response and that the combination of frass and *R. persuasoria* drills is more potent than either alone.

To determine whether *P. sternata* females might be attracted by a secretion with which *R. persuasoria* females line the oviposition shaft, water extracts were prepared of the venom gland and of the pair of well-developed accessory glands (vaginal gland pouches of Robertson, 1968) at the base of the paired oviducts. The glands of three individuals of *R. persuasoria* were macerated in 0·6 ml water, and the centrifuged extracts pipetted on to twelve 1·3-cm diameter filter-paper discs. Water was used for control discs. The impregnated discs were put on the clean gauze tops of the cages through which the parasite could probe with the ovipositor, with two discs of each substance per cage. The results of 12 replicates, each of 1·5 h duration, are summarised in Table III (Experiment 3) and suggest that secretions from the vaginal gland are largely responsible for the ovipositor probing response.

Behaviour of the immature stages

Under natural conditions, *P. sternata* oviposits shortly after *R. persuasoria* has parasitised the host, or up to a few days after the eclosion of the primary larva. The behaviour of newly emerged first-instar larvae of the two species is described above, but the following is a description of the responses of larvae to eggs and more advanced instars, as observed during the use of the artificial rearing techniques.

When eggs of either species were placed on hosts with first-instar *R. persuasoria* or *P. sternata*, the eggs were not attacked but were occasionally ruptured by accidental movements of the parasite larva. First-instar larvae of both species were the most active and, typically, they wandered over the host, feeding at various places on the body. That eggs are not usually attacked was confirmed when culture logs were dissected after exposure to the parasites, and first-instar larvae of either species were found with undamaged eggs on hosts. If eggs of *R. persuasoria* or *P. sternata* were held near first-instar larvae of either species and were moved when they came into contact, the eggs were immediately attacked and punctured. First-instar larvae of both species attacked any moving object, including the tips of forceps. Eggs of both species hatched normally when first-instar larvae of either species were present, but when the larvae came into physical contact with each other aggressive behaviour ensued. The first-instar cleptoparasite was always victorious, irrespective of the age of the first-instar primary and of the nature of its retaliatory behaviour. In cases of superparasitism by *P. sternata*, the first-instar larvae fight until one of them succeeds in killing the other.

When eggs of either species were present with second- to fifth-instar larvae of the primary or cleptoparasite, they did not elicit aggressive behaviour, although they were occasionally damaged by movements of the parasite larvae, particularly fourth and fifth instars. When first-instar *P. sternata* came into contact with second- to fifth-instar larvae of *R. persuasoria*, the cleptoparasite immediately gripped the primary with its mandibles and tore through the cuticle until the haemolymph oozed from the wound, and continued to lacerate the body until the primary ceased to move effectively. Occasionally, vigorous squirming movements by the primary dislodged the cleptoparasite, but *P. sternata* quickly seized the primary again. Under experimental conditions *P. sternata* was reared to larval maturity on fully-fed *R. persuasoria* larvae.

The duration of attacks by first-instar larvae of *P. sternata* was variable with conflicts of 1–5 min when primary first-instar larvae were attacked, and 15–60 min when advanced instars were encountered.

The mandibles of second-instar larvae of *P. sternata* are more exposed than those of *R. persuasoria*, and the cleptoparasite in this stage is able to kill first-instar larvae of the primary parasite. When a first-instar larva of *R. persuasoria* attacks second-instar *P. sternata*, the cleptoparasite bites the primary and wards off attack with rapid movements of the body. This includes rearing up on its bifurcate caudal appendage and twisting violently and with considerable agility to avoid the mandibles of the primary. Rarely the first-instar primary parasite inflicts sufficient damage on the second-instar cleptoparasite to ensure its own survival.

Discussion

P. sternata is shown to exhibit many adaptations in its morphology and biology which enable it to practice cleptoparasitism. For instance, the adult emergence period approximates to, but is overlapped by, that of the primary parasite, *R. persuasoria*. Likewise, the rapid maturation of the ovaries of *P. sternata* enables the females to take advantage of the ovipositing *R. persuasoria* soon after emergence.

The palpating action of the antennae is also different. The primary parasite uses the tips of the antennae during its search for the relatively large areas occupied by Siricid hosts, but *P. sternata*, during its search for the primary drill-shaft, uses several segments applied to the substrate, presumably providing a greater receptive surface.

Adaptation to cleptoparasitism is shown in the fact that, although the ovipositor of *P. sternata* is of similar length to that of the primary, it is much more slender, so enabling its possessor to penetrate the ready-make drills to their full depth with a minimum of effort.

The cleptoparasite was stimulated to intense ovipositor-probing activity by paper drilled by the primary parasite, and by extracts of *R. persuasoria* vaginal glands. It is probable that secretions from these glands are found in the drill shafts. Probing activity was also elicited by Siricid frass and the symbiotic fungus *Amylostereum* sp., which suggests that a more generalised, secondary attractant occurs in Siricid-infested timber. This secondary attractant could act as a host-habitat indicator, enabling the cleptoparasite to locate infested trees in the forest.

In a later paper, Spradbery (1970) will describe the long setae of the first-instar larvae of the cleptoparasite, which are doubtless an adaptation fitting them for the early detection of competitors, and also other anatomical features conferring superior fighting ability. In the present paper it has also been shown that the first-instar larvae of *P. sternata* are able to destroy all instars of *R. persuasoria*, an important capacity in a larva whose female parent exploits primary oviposition drills up to several weeks in age, and which may lead to Siricid cavities containing mature primary parasite larvae.

Summary

The life-history of *Pseudorhyssa sternata* Merrill was investigated under natural and artificial conditions.

When *P. sternata* and *Rhyssa persuasoria* (L.) females were present on Siricid-infested logs, *P. sternata* observed the primary parasite making drill shafts, and after the primary withdrew its ovipositor and moved away, *P. sternata* located the shaft and inserted its ovipositor to gain access to the host. *P. sternata* was able to locate *R. persuasoria* drill shafts aged 1–38 days.

P. sternata females were stimulated to oviposition behaviour when presented with paper drilled by *R. persuasoria*, and this response was enhanced by the presence of wet Siricid frass, or the symbiotic fungus of Siricids. Ovipositor probing was also made through artificial holes into frass. Bioassay of *R. persuasoria* vaginal and venom glands resulted in considerable probing into filter paper impregnated with vaginal gland extract.

It was concluded that *P. sternata* females probably locate Siricid-infested trees by responding to a generalised stimulus that is potent in larval frass, and which possibly derives from the symbiotic fungus. The cleptoparasite probably finds the drill-shaft by responding to a secretion of the vaginal gland of the primary parasite.

The eggs of both species hatched after two days at 24°C and the first-instar larva of *P. sternata* attacked the primary larva with its mandibles and killed it. First-instar larvae were not stimulated to aggressive behaviour in the presence of eggs of their own or the other parasite species, except when the eggs were made to move in their vicinity. The first-instar larva of *P. sternata* is eminently adapted for physical combat,

and the ability to kill primary parasite larvae is retained, at a much reduced level, in the second instar.

Development from first to final instar at 24°C was 12·5 days, feeding was completed 3–5 days later, and spinning of the cocoon began after a further 2 weeks. *P. sternata* overwintered in the final larval instar, pupated in March and April, and emerged during April–June. The longevity of adult females under experimental conditions was 28 days (range 17–41).

Acknowledgements

I wish to thank Dr. G. J. Kerrich (Commonwealth Institute of Entomology) for determining the adult material, Mr. Frank Wilson for his advice during the research and helpful criticism of the manuscript, and Mr. L. T. Woolcock for taking the photographs.

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(*Received 5 May 1969*)

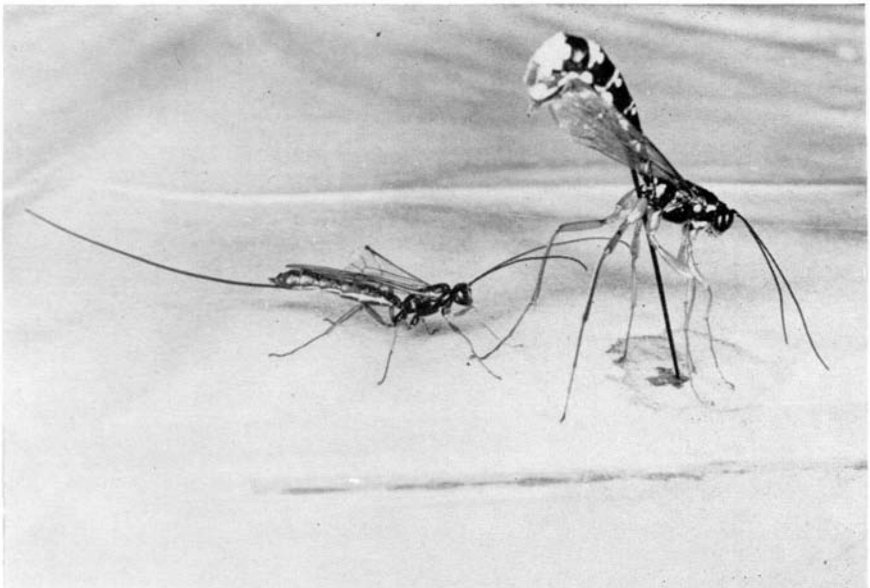

FIG. 1. *P. sternata* observing *R. persuasoria* drilling into the paper-covered cavity of an "oviposition sheet".

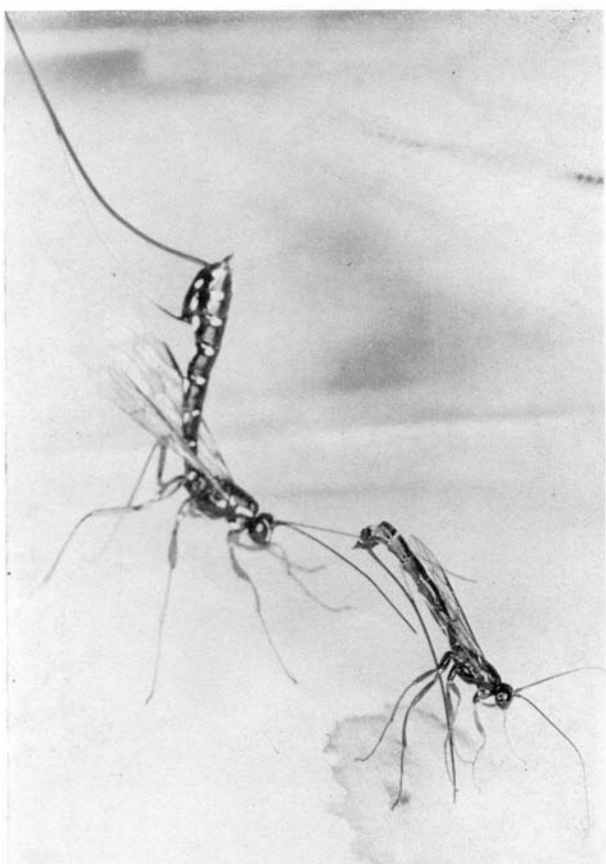

FIG. 2. *P. sternata* locating a hole previously made by

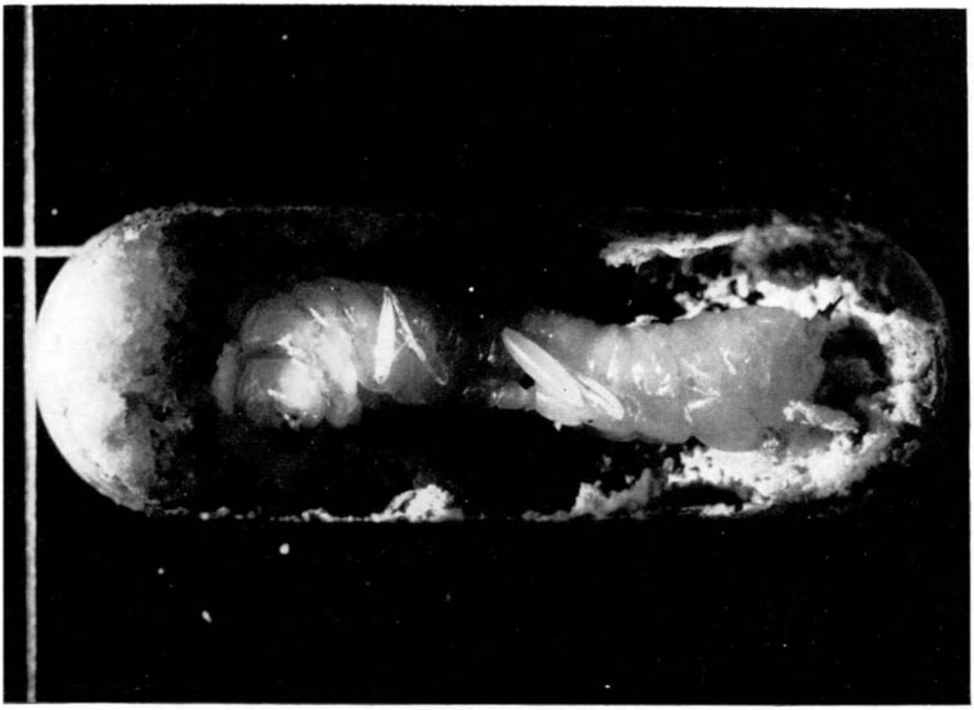

FIG. 1. Egg of *P. sternata* (right) and of *R. persuasoria* (left) on paralysed Siricid host in frass-filled cavity of "oviposition sheet".

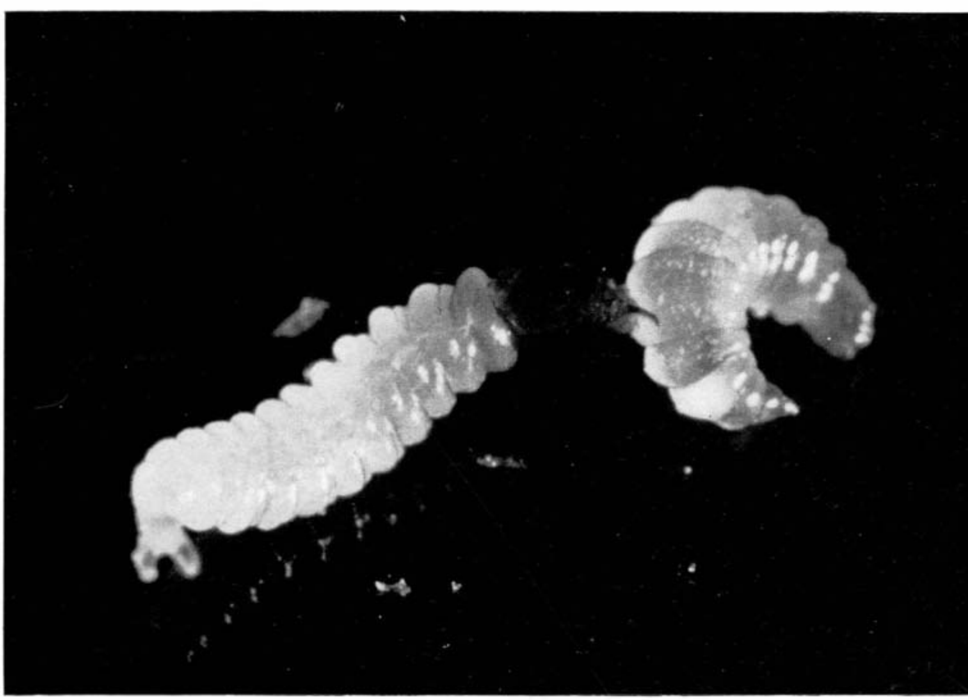

FIG. 2. First instar-larva of *P. sternata* (left) mangling *R. persuasoria* first-instar larva.