

**PSEUDOMETAGEA SCHWARZII (ASHM.) (EUCHARITIDAE:
HYMENOPTERA), A PARASITE OF LASIUS NEONIGER
EMERY (FORMICIDAE: HYMENOPTERA)¹**

G. L. AYRE

Abstract

In 1960 and 1961, studies were made on *Pseudometagea schwarzii* (Ashm.), a parasite of *Lasius neoniger* Emery in southern Ontario. The eggs are deposited in vegetation surrounding the ant nest and the first instar larvae (planidia) transfer to the ant larvae by attaching themselves to the worker ants. The larvae overwinter as internal parasites but complete their development as external parasites after the host has pupated in the spring. The adults emerge in June and oviposit immediately.

The adult parasites usually do not leave the area of the nest and, through the foraging activities of the ants, the planidia are returned to the colony that was originally parasitized. Hence the population is intensified and localized. Ninety percent parasitism of the overwintering brood may occur. The possible effects of this parasite on the host population are discussed.

Introduction

All eucharitids are parasitic on the mature larvae, prepupae, or pupae of ants and with minor exceptions all have similar life cycles. The only species for which the complete life cycle is known in detail is *Stilbula* (= *Schizaspidia*) *tenuicornis* (Ashm.) (2). However, detailed observations and studies on the behavior and various stages in the development of other known eucharitid (3, 4, 5, 8, 11) indicate that the habits of all species are remarkably similar. Large numbers of stalked eggs are deposited, usually in clusters, on or in vegetation that is not associated with the host. The first instar parasites are free-living planidia which are transferred to the host through the foraging activities of the worker ants. Early larval development may be internal or external on the immature ant but all species apparently complete their development as ectoparasites.

The eucharitid reported here was first discovered by the author when colonies of several species of ants common to southern Ontario were established in formicaria. Early in June, 1960, small adult Hymenoptera, later identified as *Pseudometagea schwarzii* (Ashm.), were observed in the foraging areas of colonies of *Lasius neoniger* Emery collected from the grounds of the Entomology Research Institute for Biological Control, Belleville, Ontario. Observations showed that they emerged from the ant cocoons and therefore were probably parasitic on the mature larvae or pupae. The following is an account of the life history and habits of this insect together with a description of the planidia and notes on the other immature stages.

Oviposition

Clausen (4) reported that the suitability of a plant for oviposition by eucharitids appeared to be governed by its physical qualities and not by a definite attraction. Such appeared to be true with *P. schwarzii*. Leaf and

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flower buds, bracts, or any area where leaves are appressed to the stem seem favorable. Those plants most commonly used in the area of study were the composite *Erigeron philadelphicus* L. (flower heads); plantain, *Plantago major* L. (flower spike); knot weed, *Polygonum achoreum* Blake (terminal and auxiliary buds); and lambs quarters, *Chenopodium album* L. (terminal and auxiliary buds). Though the parasites were often seen investigating, and apparently ovipositing in, the flower heads of the pineapple weed, *Matricaria chamomilla* L., no eggs were found in more than 25 flower heads examined.

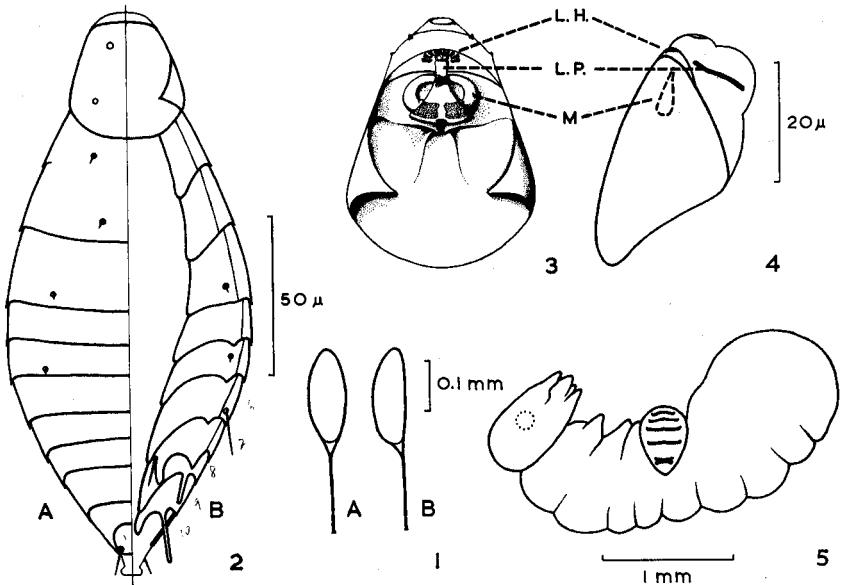
The females search for suitable oviposition sights only while travelling down the stem. Whenever a suitable cavity is found, eggs are laid. Because the female usually investigates many plants before oviposition is complete, and because these plants have frequently been visited by other females, it was not possible to determine the number of eggs actually deposited by each female under natural conditions. The eggs are laid in groups of from 10 to 200. Elongation of the plant cells often separates the larger groups into units of from 10 to 30 eggs each. The stalks of these units have a common center of attachment, indicating that eggs in any one unit were probably laid at the same time through a single puncture in the plant tissue.

In 1960, females of *P. schwarzii* began ovipositing during the latter part of June. Though the females lived only 1 or 2 days, adults were present and eggs were laid throughout July. Dissections showed that each newly emerged female contained approximately 450 fully developed eggs: the average number of ovarioles in 10 individuals examined was 31.2 ± 0.48 and the number of eggs in 20 ovarioles examined was 14.3 ± 0.47 . Dissections of field-collected material indicated that the full complement of eggs may be laid: many individuals were found with only one or two eggs remaining in the ovarioles and a few contained no eggs. An attempt to determine the actual number of eggs laid was made in the laboratory. Twenty pairs of males and females were placed in separate vials containing growing tips of *Erigeron* sp., at 24° C and 50% R.H. Sixteen of the females did not oviposit, three laid less than 50 eggs, and one laid 225 eggs. All died with eggs remaining in the ovarioles. This relatively poor egg lay was attributed to unsatisfactory environmental conditions and is not thought to indicate the full reproductive capacity of the females. For reasons mentioned earlier no accurate estimate of egg lay was obtained from egg counts made in the field.

Egg

The egg (Fig. 1A, B) is translucent white, approximately 0.19 mm long and 0.08 mm wide at its greatest diameter. It is ellipsoidal, slightly flattened on one side. The stalk is approximately 0.16 mm long and is apparently fully developed in ovarioles of the adult and does not elongate at the time of oviposition. This suggests that the stalk is an extension of the chorion as reported by Tripp (10) for the ichneumonid *Euceros frigidus* Cress and is not formed of secretory fluid which forms the stalk of chrysopid eggs (6).

Time from oviposition to eclosion was approximately 10 days under laboratory conditions (22° C and 45% R.H.). It was approximately 20 days in the field, though there was considerable variation. During development the eggs changed from a pure white through amber to dark brown. Frequently clusters



FIGS. 1-5. Immature stages of *Pseudometagea schwarzii* (Ashm.). (1) Eggs: A, dorsal view; B, lateral view. (2) Planidium: A, dorsal surface; B, ventral surface. (3) Ventral view of the head of the planidium: L.H., labral hooks; L.P., labial plate; M., mandibles. (4) Diagrammatic lateral view of the head of the planidium showing relative position of mouthparts. (5) Host immediately after pupation with fully distended planidia attached in characteristic position.

were found that contained eggs of all colors in this range. During this embryological development the plants have usually grown so that the buds or leaves have expanded and the eggs are fully exposed. If the eggs are exposed before the embryo is fully developed it may be assumed many are killed by desiccation: in the laboratory many newly deposited eggs dried out when exposed, though they were in Petri dishes with moist blotting paper. As the majority of eggs are laid in parts of the plant that are growing rapidly, it is not considered likely that many newly emerged larvae are lost through being trapped in a tightly closed bud. However, neither of these sources of mortality was investigated in detail.

Planidium

Figure 2 shows the arrangement of the sclerites, spines, and bristles. It was not determined if the caudal projection was a 12th segment or an unsclerotized portion of the 11th. The length of the planidium while in this position was 0.17 mm and the width at the fourth body segment was 0.07 mm.

The head capsule is approximately 0.03 mm in length and width. It bears two pair of lightly sclerotized discs and a lightly sclerotized rim (labrum) on the anterior margin. The extremely small mouthparts (Figs. 3 and 4) plus the heavy sclerotization of the head capsule made it impossible to determine the exact relationship of some of the parts. Ten "labral" hooks are arranged in a semicircle directly beneath the lightly sclerotized rim and

apparently attached to the heavily sclerotized portion of the capsule. It is assumed that these hooks are used as a rasping organ when the planidium enters the host or as an anchoring mechanism after the host has been penetrated. There is a flat plate completely separate from the head capsule and lying in a near-ventrodorsad plane in the ventral membranous portion of the head. (In mounted material this plate assumed a caudocephalic position and appeared to lie immediately beneath the mandibles, as shown in Fig. 3.) As this plate is the only visible structure ventrad to the mandibles, it is suggested that it is a lower-lip complex formed by the union of the maxillae, labium, and hypopharynx (9). The distal end of this plate bears two unsclerotized discs. This general arrangement of mouthparts is very similar to those of the planidia of *Orasema sixaolae* W. & W. and *O. costaricensis* W. & W. as described by Wheeler and Wheeler (11). *O. sixaolae*, however, has nine papillae in place of the labral hooks and in both species the labrum possesses papillae rather than the unsclerotized discs. The mouth opening was not found but stained planidia suggest it is situated in the normal position between the base of the mandibles. The stain entered through the sclerotized ring of the protractile sucker and outlined an ingestion tube leading to a preoral cavity located around the mandibles; from here the stain passed through the arch created by the two ventral projections of the sclerotized ridge that passed laterally immediately behind the base of the mandibles. The path of this stain suggests that the stomodaeum passes through this arch and that the mouth opening is immediately cephalad.

When the insect is disturbed the sucker mouth can be retracted and the whole head capsule bent forward to form a close union with the ventral surface of the thorax.

The planidia are very active on emergence but seldom move far from the original egg cluster. They assume an erect position on the leaf surface for a period of 2 to 3 days supported by the caudal segment and spines. During this time the slightest air current or movement of the plant will cause them to wave or twirl. At the end of 3 days the larvae either remain motionless or migrate. They are able to travel several inches by using a "humping" motion by anchoring themselves alternately with the caudal spines and oral sucker but generally do not leave the leaf or flower head. Those that migrate do not resume an upright position. In laboratory trials the planidia lived 6 to 7 days. Because of the difficulty in tracing individuals in the field no estimate was made of their natural life span. Whether active or not, they are capable of transferring to adult worker ants. At this stage they apparently are not host specific as in tests they would transfer to any insect or object with which they come in contact.

In laboratory tests, the planidia attached themselves to any part of the body of the worker ant and then migrated to the head. Most frequently they were found on the clypeus or labrum and from here transferred to the ant larvae. The planidium usually burrowed into the ant larva in the dorsal or pleural region of the second or third thoracic segment. Only occasionally were the parasites found embedded in the abdominal region of the host. Only large individuals were attacked but as one molt was observed in some ant larvae after parasitism, not all were in the last instar when attacked.

The planidium penetrates the larvae to a depth of 0.1 to 0.2 mm and then remains dormant until spring. The entrance hole in the host remains open. Wheeler and Wheeler (11) suggested that this is a respiratory funnel as is found with many of the Tachinidae (Diptera). Unlike the situation reported by these workers, the planidia of this species do not remain with the posterior end anchored in the integument; they are frequently found 0.5 mm or more from the point of entrance.

Development

The planidia begin their development when the ant larvae commence feeding in spring. The increase in size during the first instar is very great. Parker (7) reported that *Stilbula cyniformis* Rossi increase their volume by 1000 times before the first molt and Clausen (5) reported a similar increase in *Schizaspidia convergens* (Walk.). Though no volumetric measurements were taken for *P. schwarzii*, the increase in size during the first instar separated the sclerites by five to six times their own width.

The relationship of parasite and host during the winter and early developmental stages was not determined. When the ant has reached the prepupal stage, however, the fully distended first instar parasite lies between the cuticle and an invagination of the epidermal cells. Hence, when the prepupa molts, the parasite is left exposed, usually in the ventral region of the thorax (Fig. 5). At this stage, the degree to which the parasite has retarded the development of the host pupae is always similar: all appendages of the host are rudimentary, appearing as little more than stubs, and there is an apparent lack of development in the region of the petiole (Fig. 5).

Difficulty was experienced in rearing the external stages of the parasite after it had been removed from the host cocoon. Therefore, the following account of the subsequent development is based largely on information obtained by periodic dissections of parasitized material. The first molt of the parasite apparently occurs shortly after the last molt of the host larva. The cuticle splits ventrally but remains attached along one margin only. As the larva increases in size the cast cuticle is displaced laterally and in the mature second instar is found in the mid-ventral region. This form of ecdysis is common to most planidia of known species of eucharitids (3).

The second instar larva is creamy white with the yellowish contents of the digestive tract clearly visible. An anal lobe, which is characteristic of all species (3), is present. Other than the head, six poorly marked segments are visible on the dorsum. When larvae were prodded, feeble contractions were noted but the larvae were not capable of any ordered movement. There was no evidence of mandibles in either whole mounts or the second instar exuviae. The mouthparts were not examined in detail but this lack of mandibles suggests a sucker type as described by Clausen (2) for *Stilbula* (= *Schizaspidia*) *tenuicornis* Ashm. Ecdysis in the second instar occurs through a dorsal split in the cuticle. As with the first instar, however, this cuticle is not completely shed but is slowly drawn laterally and ventrally by the growth of the third instar.

The early third instar larvae is similar to the second but quickly assumes the short hunchback form of the prepupa. The anal lobe persists but all other

visible segmentation disappears. The integument is evenly covered by numerous uniform minute protrusions that are only distinguishable at 100 magnifications or more. At lesser magnifications the cuticle appears to be slightly roughened. There are no dorsolateral tubercles. Mandibles were not found.

Growth in the second and third instars is extremely rapid. As far as could be determined by dissections of the host cocoon the parasite larvae complete their development and pupate 4 to 5 days after the first molt. The exuviae of the first two instars are completely shed when the parasite pupates. The three resulting exuviae plus the remains of the host are found with the meconium of the host at the posterior end of the cocoon. The parasite apparently continues feeding until all food is exhausted as only the integument of the host remains. There may be some extraintestinal digestion to permit the parasite to drain the host so completely. Sections made of host material while *P. schwarzii* was in the late first instar larval stage showed a complete breakdown of host epithelial tissues at the point where the parasite was feeding. This observation would tend to support the supposition that extraintestinal digestion occurs. The duration of the pupal stage when reared in Petri dishes at 22° C after removal from the host cocoon was from 7 to 10 days.

Adults

The relatively large size of the host cocoon in relation to the size of the parasite permits the adult to clean and groom itself completely before it emerges. On emergence the adult makes its way directly to the soil surface. Its movement within the galleries of the nest is very rapid and usually no interference by the ants is encountered. More frequently, however, the initial movement of the adult within the cocoon attracts the worker ants, which react by assisting the parasite to open the cocoon, much as they do for their own pupae. Occasionally the ants opened the cocoon before any attempt to do so was made by the parasite. In such cases the ant hurriedly carried the adult parasite to the surface and placed it on the ground around the nest openings. These ants returned directly to the nest. Frequently other ants picked up those parasites closest to the nest openings and deposited them a foot or more away. This behavior pattern is identical with that observed in this and other species of ants when disposing of refuse from the nest. At no time did the workers show any hostility toward the parasite.

Mating occurred almost immediately on emergence. Both males and females mated several times. In one 10-minute period one female was observed to mate five times, twice with the same male. Matings usually lasted less than 5 seconds. Males were observed trying to mate with dead females on the ground and also with other males.

Parasite Population and Parasitism

Twenty-four collections totalling approximately 2500 ant larvae were either reared or examined microscopically for parasitism during the summer of 1960. Infestation by *P. schwarzii* appeared very localized. All collections from within a 25-ft radius of the apparent center of infestation contained over 80% parasitism, and two of these (approximately 800 individuals) had over 90%. In a collection (60 individuals) 120 ft from the center, para-

sitism had dropped to 35%, and beyond 200 ft no parasites were found in 18 nests examined. Clausen (5) reported that all eucharitid colonies are usually small and widely separated. He attributed this to the presence or absence of suitable oviposition places and not to host distribution or abundance. This is particularly true when the parasite oviposits in a specific plant. He further suggested distribution of the parasite is limited by the effects of ant colonies monopolizing certain areas and thus preventing other colonies from coming in contact with the planidia. However, as *P. schwarzii* is not specific in the choice of plants for oviposition the former reason given for the limited distribution is not justified for this species. The limited flight of the adult parasite and the foraging habits of the ant are considered the primary factors. On cloudy days the adults do not fly and usually deposit within 2 ft of the nest. If vegetation suitable for oviposition is present they will frequently oviposit within a few inches of the nest. On bright sunny days, when adult activity is greatest and frequent flights occur, they disperse more widely. However, they seldom fly more than 3 to 5 ft and the maximum flight observed was 10 ft. A large percentage of the eggs is therefore laid within the foraging area of the host ant nest and, through the foraging activities of the ants, the planidia are returned to the original center of infestation. Hence the population density of the parasite becomes increasingly more localized and intensified. In this respect, this species seems to differ from most other eucharitids for which population distributions and densities are known. Clausen (5) stated that parasitism by eucharitids is relatively low, even within the colony limits; the highest parasitism he recorded was 47% with *S. tenuicornis*, a parasite of *Camponotus* spp.

Though parasitism is very high within the centers of infestation, the influence of *P. schwarzii* on the population size of *L. neoneriger* is doubtful, even within these centers. The parasite only attacks the overwintering larvae. These are non-reproductive forms (workers) and as they do not emerge until June or July they do not contribute to the rearing of the early spring brood. This brood contains the reproductive forms (males and females), which have usually pupated before the winter brood emerges. The parasitized brood, however, does contribute to the rearing of secondary broods during mid and late summer. These include the last worker brood which again overwinters as larvae. They also contribute to the rearing of the early brood of the following year. The problem, then, is more one of the effect of brood: worker ratios on population growth rather than one of the direct influence of the parasite. Brian (1) showed that an optimum worker: brood ratio exists for colonies of *Myrmica rubra* L. Similar studies will have to be made with *L. neoneriger* before the influence of the parasite on the host population can be properly determined.

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