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GRADUATE COLLEGE

THE BIOLOGY OF GYMNOCARCELIA RICINORUM TOWNSEND, A TACHINID PARASITE OF THE SALT-MARSH CATERPILLAR

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

BY

THOMAS MERRILL GRAY

Norman, Oklahoma

1972

THE BIOLOGY OF GYMNOCARCELIA RICINORUM TOWNSEND, A TACHINID PARASITE OF THE SALT-MARSH CATERPILLAR

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The course of my graduate career at the University of Oklahoma has been influenced to a great degree by my association with Dr. Cluff E. Hopla. I wish to express my sincere thanks to him for the guidance he has given, for his encouragement, and his friendship.

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Mr. Ottis Ballard photographed and made prints of the fly anesthetizing apparatus. Mr. Jim Kennedy photographed and made prints of the adult fly Gymnocarcelia ricinorum.

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THE BIOLOGY OF GYMNOCARCELIA RICINORUM TOWNSEND, A TACHINID PARASITE OF THE SALT-MARSH CATERPILLAR

CHAPTER I

INTRODUCTION

Few biological control investigations have been concerned with the ecology of insect pests on host plants other than cultivated crops. In addition, little is known regarding the biology of Gymnocarcelia ricinorum Townsend 1919 (Diptera: Tachinidae), a parasite of the salt-marsh caterpillar, Estigmene acrea (Drury) 1773.

This fly species has several synonyms. Stone et al. (1965) lists Tachina noctuae Harris 1835 and Tachina albifrons Walker 1852, which is preoccupied by Tachina albifrons Walker 1836. Townsend (1919) made the original descriptions of both genus and species and lists Sturmia albifrons Coquillett 1897 as another synonym.

Known hosts of G. ricinorum include the following: Coquillett (1897) records Ecpantheria scribonia Stoll and the salt-marsh caterpillar, Estigmene (Leucarctia) acrea (Drury), as hosts of this species; Essig (1958), recording the fly as Sturmia albifrons Walker, lists its hosts as the

salt-marsh caterpillar, E. acrea (Drury), and the armyworm, Pseudaletia (Cirphis) unipuncta (Haworth).

Tachinid parasites of several species have been reared from E. acrea. Taylor's (1954) list includes Carcelia (Zenillia) reclinata (Aldrich and Webber), Compsilura (Tachina) concinnata (Meigen), Sisyropa eudryae (Townsend) (= Exorista eudryae /Townsend/, Zenillia eudryae /Townsend/, Oxexorista thompsoni Townsend), Gymnocarcelia ricinorum Townsend (= Sturmia albifrons Walker), Exorista mella (Walker) (= Tachina mella Walker, Tachina orgyiae LeBaron, Tachina clisiocampae Townsend, Achaetoneura fernaldi Williston, Tachina orgyiarum Townsend, Exorista larvarum, authors, not Linñaeus), Leschenaultia adusta (Loew) (= Blepharipeza adusta Loew, Rileymyia adusta /Loew/), Lespesia archippivora (Riley) (= Achaetoneura archippivora /Riley/, Tachina archippivora Riley, Meigenia websteri Townsend, Phorocera promiscua Townsend, Parafrontina apicalis Brauer and Bergenstamm, Masicera pauciseta Coquillett, Ypophaemyia malacosomae Townsend).

The purpose of this investigation was to study the morphology, life cycle, distribution, host-parasite interactions, and other ecological relationships of G. ricinorum in west-central Oklahoma.

CHAPTER II

MATERIALS AND METHODS

Investigations were conducted primarily in the environs of Weatherford, Oklahoma; all collections were made in the southeastern quarter of Custer County, Oklahoma. Field investigations were conducted during the summers of 1967, 1968, and 1970.

Field collections of late instar caterpillars were made by hand picking. Caterpillars were removed from the host plant, sweet clover (Melilotus spp.), either by pinching off a portion of the plant with a resting caterpillar or by touching the animal's posterior end and allowing it to crawl onto the author's hand. Collection containers consisted of wide mouth quart fruit jars. The center of the two piece metal lid was removed and a circle of aluminum wire screen substituted for it. Caterpillars were placed in jars with pieces of clover; care was exercised not to overcrowd the caterpillars in each jar. Jars were transported to the laboratory by car. In transit, the jars were placed in the shade with adequate ventilation to assure as little change in temperature, atmospheric gases, etc. as possible. Upon arrival at the laboratory, caterpillars were transferred to cages.

Adult fly and caterpillar holding cages consisted of a wooden frame made of one inch by one inch cypress pieces cut and nailed together. Outside dimensions were one foot by one foot by one foot. Aluminum wire screen was cut, fitted to the outside of the wooden frame, and stapled to it, thus forming the cage front, top, and two sides. A piece of rubber tire tube was cut, fitted to the back side of the wooden frame, and the edges stapled to it. A circular opening was cut in the center of the rubber sheet so that a one-piece jar lid, three inches in diameter, would fit securely when inserted in the opening. A piece of gutter tin was cut and folded; the result was a shallow tray, 12 inches by 12 inches, with each side one inch high. The cut edges of the screen wire, rubber sheet, and metal tray were covered with strips of plastic electrical tape. Onto the cage bottom, the metal tray was fitted, but not so securely that it could not easily be removed for cleaning purposes. After removing the metal jar lid, dry washed river sand was poured into the cage bottom to a level equal to the top of the wooden frame support. The lid was then replaced.

At any one time, caterpillars in cages were limited to approximately fifty per cage. Field collected caterpillars were supplied with cut sweet clover daily and the uneaten food removed the next day. Most of the caterpillar feces were removed at the same time as the uneaten food;

the remainder was mixed with dry sand in the cage bottom. For field parasitism studies, dead caterpillars were removed daily and placed in wide mouth pint fruit jars; cocoons were removed at the same time and placed in wide mouth quart fruit jars. Both jar types were equipped with lids identical to those used in field collections. Jar capacity was limited to a maximum of fifty hosts, either dead caterpillars or cocoons. After the dead caterpillars and cocoons were removed from the cages, additional field collections of hosts were sometimes added to the same cages, but not to exceed the maximum number stated above.

Host caterpillars, used for dissections, were collected in the field and placed in holding cages. No caterpillars, from these collections, were included in field parasitism data. Prior to dissection, caterpillars were killed by placing them in a vial of 70% ethyl alcohol. Immediately after killing, the caterpillars were dissected under water. The several minutes required to kill the host did not allow the parasite to migrate and often did not kill the fly larva. Each dissected caterpillar was examined for possible parasites. Numbers of parasites, locations in the host, and presence or absence of respiratory funnels were recorded for each dissected caterpillar. Parasites, respiratory funnels, and portions of the host's body to which the parasites were attached, were placed in vials containing 70% ethyl alcohol solution. The vials were labeled and retained for later fly morphology studies.

In earlier studies on the degrees of field parasitism of the host, some of the jars, containing either dead caterpillars or cocoons, were held at room temperature in the laboratory since a culturing chamber was not available.

Other jars, for later field parasitism studies, were placed in a culturing chamber. The chamber was model CTW-66 manufactured by Percival Refrigeration and Manufacturing Company. The chamber was maintained at a constant temperature of 80 $\pm$ 2 F and constant relative humidity of 50 $\pm$ 5%. Emerged flies and moths, held either at room temperature or at a constant temperature, were removed from the jars daily and the resulting adults either killed or utilized in other experiments. Numbers of adult flies and moths were recorded as they emerged. After a period of several months, dead caterpillars and cocoons in holding jars were examined for fly pupae and dead larvae; both were used in calculating parasites per hundred hosts. Each caterpillar, cocoon, and moth pupa was opened to assure that no parasite was left undetected.

As adult flies emerged from holding jars used in field parasitism studies, they were removed daily, as follows, and placed in holding cages in the culturing chamber, for studies of fly longevity and mating behavior. To remove the flies, an insect net was placed over the jar, the lid removed, and the flies were forced to fly up into

the apex of the net. Flies were then transferred to an empty quart jar with screen lid. The jar was inverted and placed in the anesthetizing apparatus funnel.

The anesthetizing apparatus is shown in figure 1 and was constructed of a ring stand and round jawed utility clamp supporting a polypropylene filtering flask. Using a one hole rubber stopper, a polypropylene Büchner funnel was inserted into the filtering flask. A gas regulator and cylinder of carbon dioxide were connected by rubber tubing to the filtering flask.

Using a minimal flow of carbon dioxide gas, the flies were anesthetized. Flies were removed individually by forceps, holding onto the wings, and marked on the notum, using a camel hair brush, with different colors of water base paint. For each longevity cage, flies that emerged on the first day were not marked and served as controls; on succeeding days, each group of flies was marked with a different color. Flies were transferred to cages for longevity studies and allowed to recover from anesthetization.

An aluminum foil food and water dish, one inch by three inches by three inches, was filled with absorbent cotton and placed on the cage floor. The cotton was saturated with tap water and a small amount of honey poured on approximately one-fourth of the cotton's top surface. The food and water dish was removed each day and cleaned prior

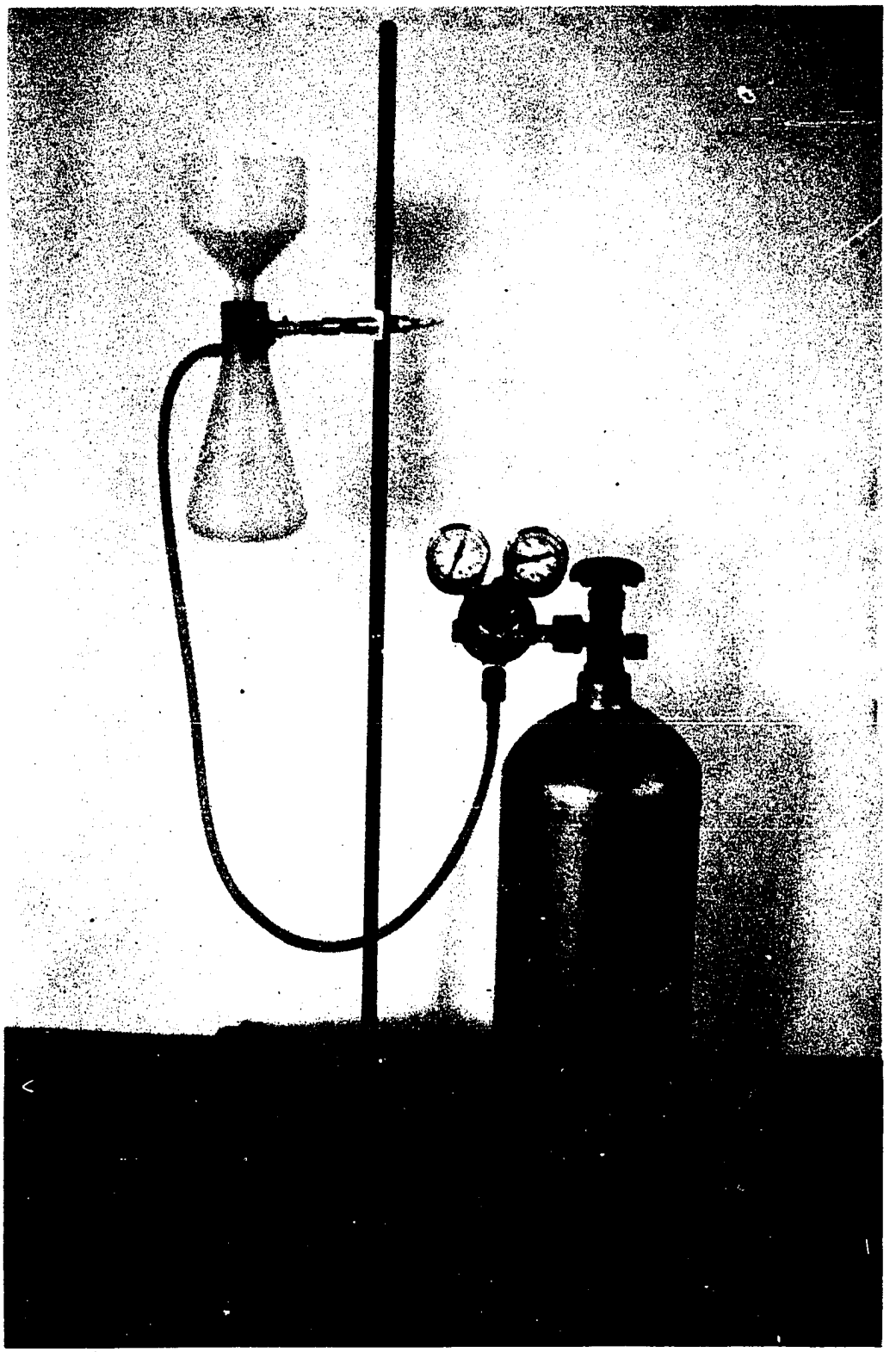


Figure 1. Fly Anesthetizing Apparatus.

to returning to the cage. The cotton was washed several times with tap water, returned to the dish, saturated with water, and honey poured on top of the cotton. Although the food and water were not sterile, this technique permitted only a limited growth of microorganisms. Perhaps these microorganisms provided certain nutrients lacking in the original honey and water solution.

Dead flies were removed daily from the cage, color markings recorded, and the flies pinned. Although some or most of the paint was lost, during the adult life of the fly, a sufficient amount remained on the specimen to identify the color marking by microscopic examination.

Since no color marking was repeated in any one longevity cage, the same flies were utilized in part of the fly mating behavior observations. Not only was the duration of copulation recorded, but, in addition, the age of each member of the mating pair. In addition, observations on the total mating time were also recorded for a few flies that were not part of a longevity study. When only a portion of the mating period was observed in longevity study flies, the ages of the flies were recorded, but not the total mating time or portion of it.

Flies used in longevity studies were also utilized in experiments to determine the duration of life cycle stages. Late instar caterpillars were collected in the field and held in cages approximately one week, to assure

they were not parasitized. Groups of five caterpillars were removed from the holding cages and placed in longevity cages for 30 minutes to be parasitized. Each group of five caterpillars, exposed to possible parasitism, was placed in a quart jar with screen lid and fed daily with sweet clover. Feces and uneaten food were removed each day from these jars.

As caterpillars in the jars either died or formed cocoons, each host was placed in an individual seven ounce styroform cup. A square piece of silk organza was placed over the opening and held in place with a rubber band. Silk organza is relatively transparent and, in addition, permits sufficient ventilation. In those caterpillars that formed a cocoon, after one day the cocoon was removed leaving the moth pupa exposed. Time of parasitization, fly pupa formation, and adult fly emergence were recorded. In some cases, the flies formed pupae inside the host caterpillar or moth pupa; therefore, only the total time from egg to adult was determined. In other situations, the flies did not emerge from pupae and only the time from egg to pupa stage was determined. Both sets of data were included in the final life cycle calculations.

CHAPTER III

RESULTS

Distribution of Host and Parasite

Known distribution of the salt-marsh caterpillar, E. acrea, is based on information supplied by E. L. Todd from specimens in the U. S. National Museum and from published records. Figure 2 shows the known distribution of this species in the United States. This species has been collected in the United States from the District of Columbia and 21 states. In Canada the distribution extends northward to Hudson Bay, Nova Scotia, Prince Edward Island and Newfoundland as well as westward along southern Canada to British Columbia. In addition, the species has been collected in Mexico, the Central American countries of Costa Rica and Guatemala, and Colombia in South America. In a personal communication to the author, E. L. Todd states, "All those from Guatemala to Colombia are the form with the white male. In Mexico both forms occur and it (white form) undoubtedly goes up into Arizona and Texas and beyond."

Known distribution of the tachinid fly, G. ricinorum, is based on information, in part supplied by C. W. Sabrosky, from specimens in the U. S. National

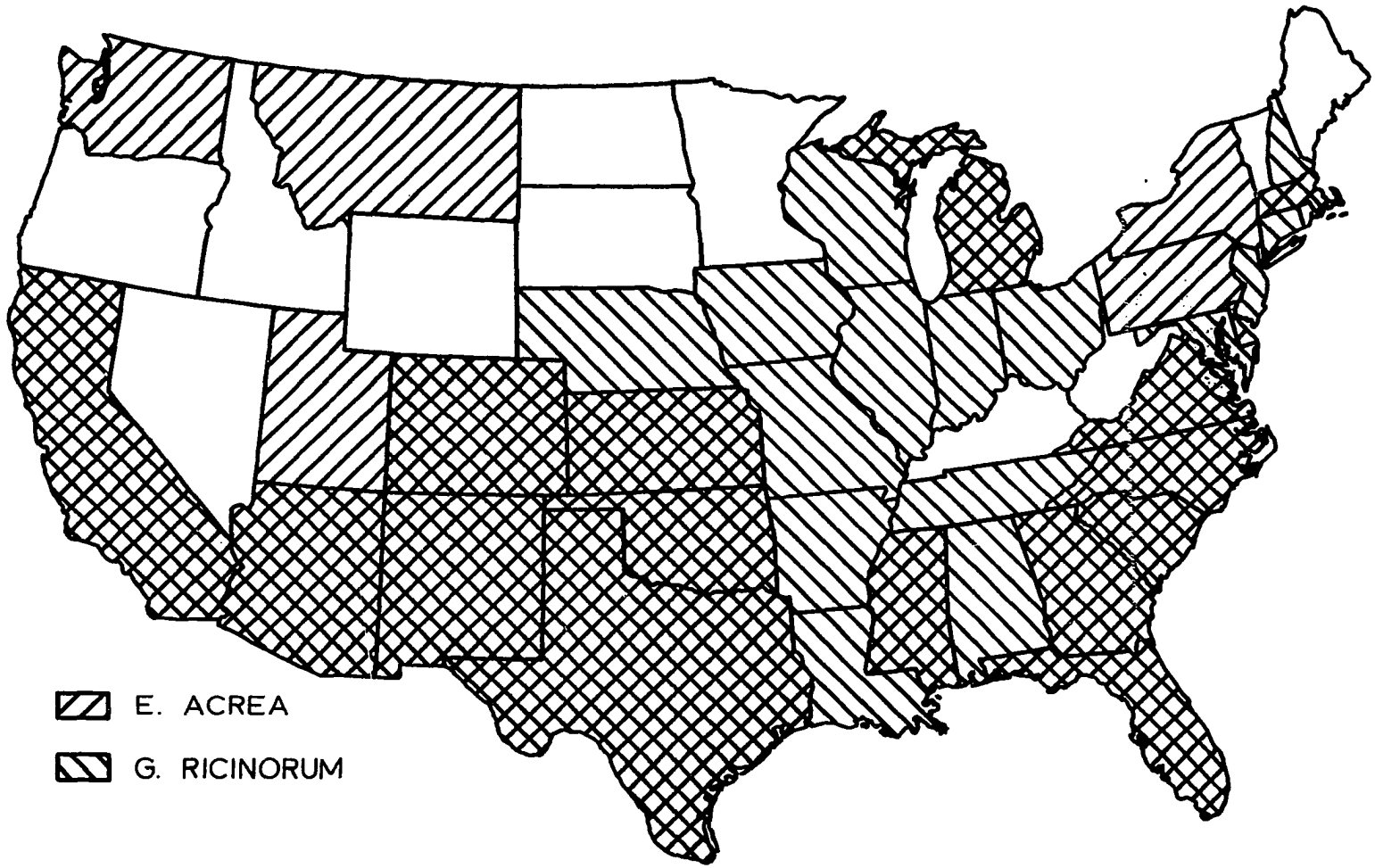


Figure 2. Known Distributions of the Salt-marsh Caterpillar, Estigmene acrea (Drury), and the Tachinid Fly, Gymnocarcelia ricinorum Townsend, in the United States.

Museum, records from elsewhere chiefly based on identifications by H. J. Reinhard, and published records. Additions were made from the author's own collections. Figure 2 also shows the known distribution of this fly species in the United States. This species has been collected in the United States from the District of Columbia and 30 states. In addition, the species has been collected from the Canadian provinces of Ontario and Saskatchewan, the Sonora of Mexico, and the Central American countries of El Salvador and Honduras.

Host Morphology

Descriptions of the host, E. acrea, are based on observations of local specimens. Description of the caterpillar is based, in part, on Peterson (1956) with additions by the author. Some variability in the host was observed, especially in coloration.

Caterpillar

Full grown larva: 40 to 50 mm in length; head capsule brownish-black with light yellow areas, a median broad irregular band over the epicranial suture and two lateral areas; labrum yellow; mandibles black; antennae yellow; palpi yellow-tan; two semicircles, each of six ocelli; thorax and abdomen pale yellow with mottled pigment areas occasionally tinged with orange, particularly in early instars; setae plumose arising from verrucae

encircling the middle of each segment except those bearing legs; secondary setae, simple and hairlike, borne only on head capsule, thoracic legs, and abdominal prolegs; setae either yellow, tan, reddish-brown, or black; spiracles large, elliptical, and bordered with black; abdominal prolegs present on segments three to six and ten; crochets on planta a heteroideous mesoseries.

Adult

White moth; antennae black with white bands; palpi orange, black, and white; sternum of prothorax with small patch of orange and two black dots; legs black and white with tops of femora broadly orange; both pair of wings with numerous small irregular black dots; most of abdominal dorsum with broad orange band; abdomen with one dorsal, two lateral, and three ventral longitudinal rows of small black dots; apex of abdomen white; hind wings of male usually orange, white in southern forms; male venter almost entirely orange and much more orange on legs.

Fly Morphology

Egg

Macrotype eggs of G. ricinorum are shown in figures 3A and 3B from dorsal and ventrolateral views. Eggs are oval in shape and appear almost hemispherical. They are slightly pointed at the anterior end, rounded dorsally, and flattened with a slight curvature on the ventral side.

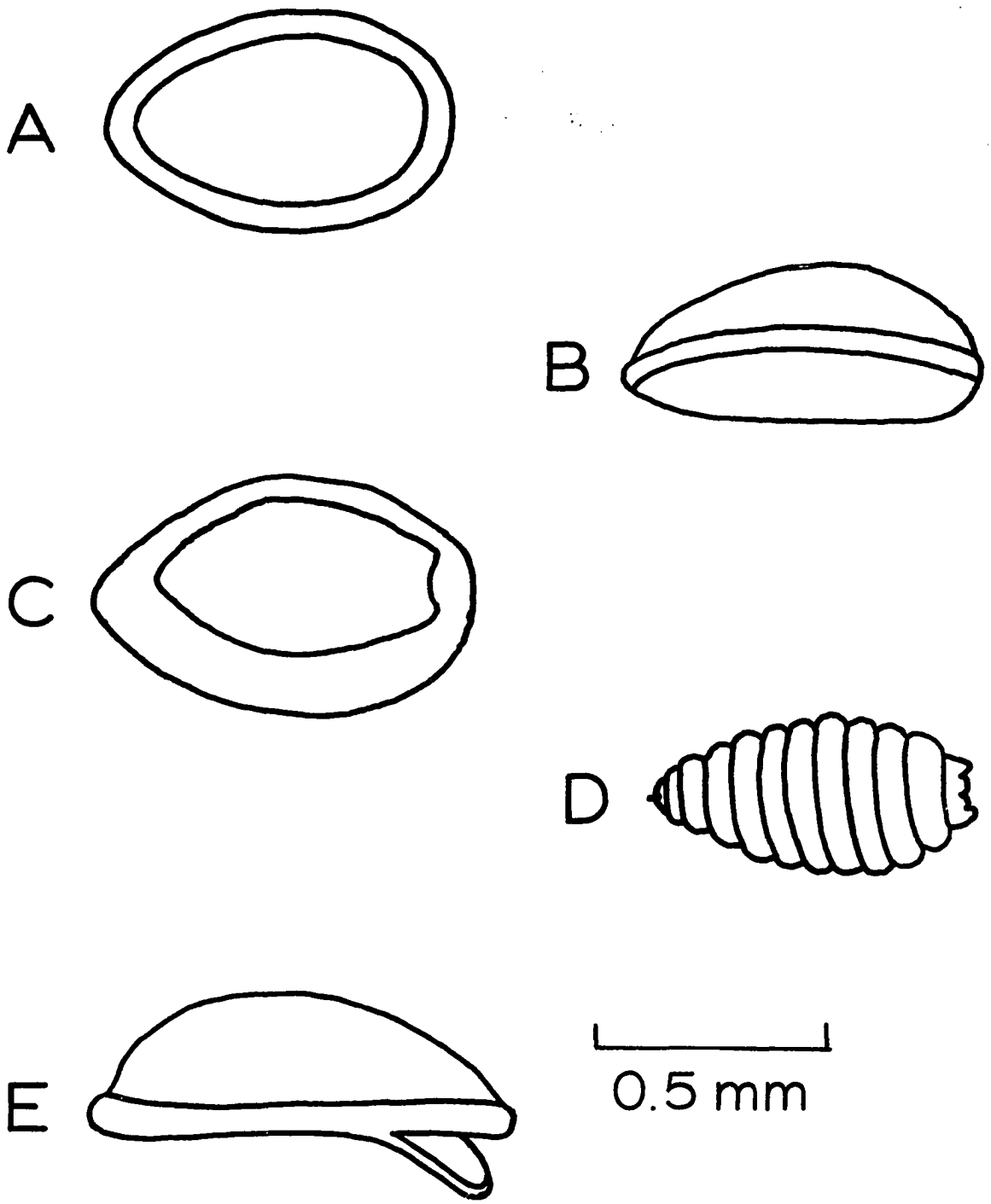


Figure 3. Gymnocarcelia ricinorum: A. Egg, Dorsal View; B. Egg, Ventrolateral View; C. Egg With a Fully Developed Embryo Inside the Chorion, Dorsal View; D. Fully Developed Embryo Removed From Its Egg Shell, Dorsal View; E. Discarded Chorion After Hatching, Lateral View.

Eggs of this species bear a slight marginal flange near the junction of the ventral and lateral areas. Color of the relatively heavy chorion is opaque white with a slight silver iridescence to the surface. Thickness of the ventral part of the egg shell is less than that of the rounded dorsal part. Dimensions are: length, 0.6 to 0.7 mm; width, 0.3 to 0.4 mm; and height, 0.2 to 0.3 mm.

Figure 3C shows an egg with a fully developed embryo inside the chorion. The egg shell had cleared, somewhat, after being preserved in a 70% ethyl alcohol solution for three years. The fully developed embryo was removed from its egg shell and is shown in Figure 3D. The embryo's length was 0.5 mm and the width was 0.3 mm.

The discarded chorion, after hatching, is shown in Figure 3E. Dehiscent eggs, the type found in this species, are provided with a fracture line across the somewhat pointed anterior end. This zone of weakness follows the edge of the flattened bottom for only a short distance. At hatching, the fracture line is broken and the dorsal portion of the chorion is forced upward, permitting the larva to emerge onto the surface of the host.

Larva

Larvae of this species have four stadia. Only one larval exuvia, from an early instar, was found in a respiratory funnel. Therefore, cast off exuviae could not be used in these studies to determine the exact numbers of

instars. Larvae of this species, particularly the later instars, cast off the larval skin over their anterior end. This method does not interfere with respiration as it would if the exuviae were matted into the respiratory funnel's base.

Dissections of larvae from hosts revealed at least four distinct larval instars, based mainly on the structure of the posterior pair of spiracles. Since there is a lack of apparent difference in sclerotization and sculpturing of spiracles of early instars, an additional instar may actually occur.

The first instar larva, a tachiniform type, is shown in Figures 4A and 4B illustrating lateral and posterior views. First instar larvae, utilized for these drawings, were recovered from the body surface of a dead fly. Eggs were laid on the dead fly by other caged flies as mentioned below. The eggs hatched and the dead first instar larvae were stuck to the surface of the fly.

Integument of the first instar varies from transparent to a light cream color. There are twelve obvious body segments, each bearing very narrow bands of dark minute spines on the margin of each segment. Each single row of spines completely encircles the body. Larvae are approximately 0.5 mm in length and 0.2 to 0.3 mm in width. All three parts of the unjointed buccopharyngeal apparatus are heavily sclerotized, with the mouth hooks or mandibles

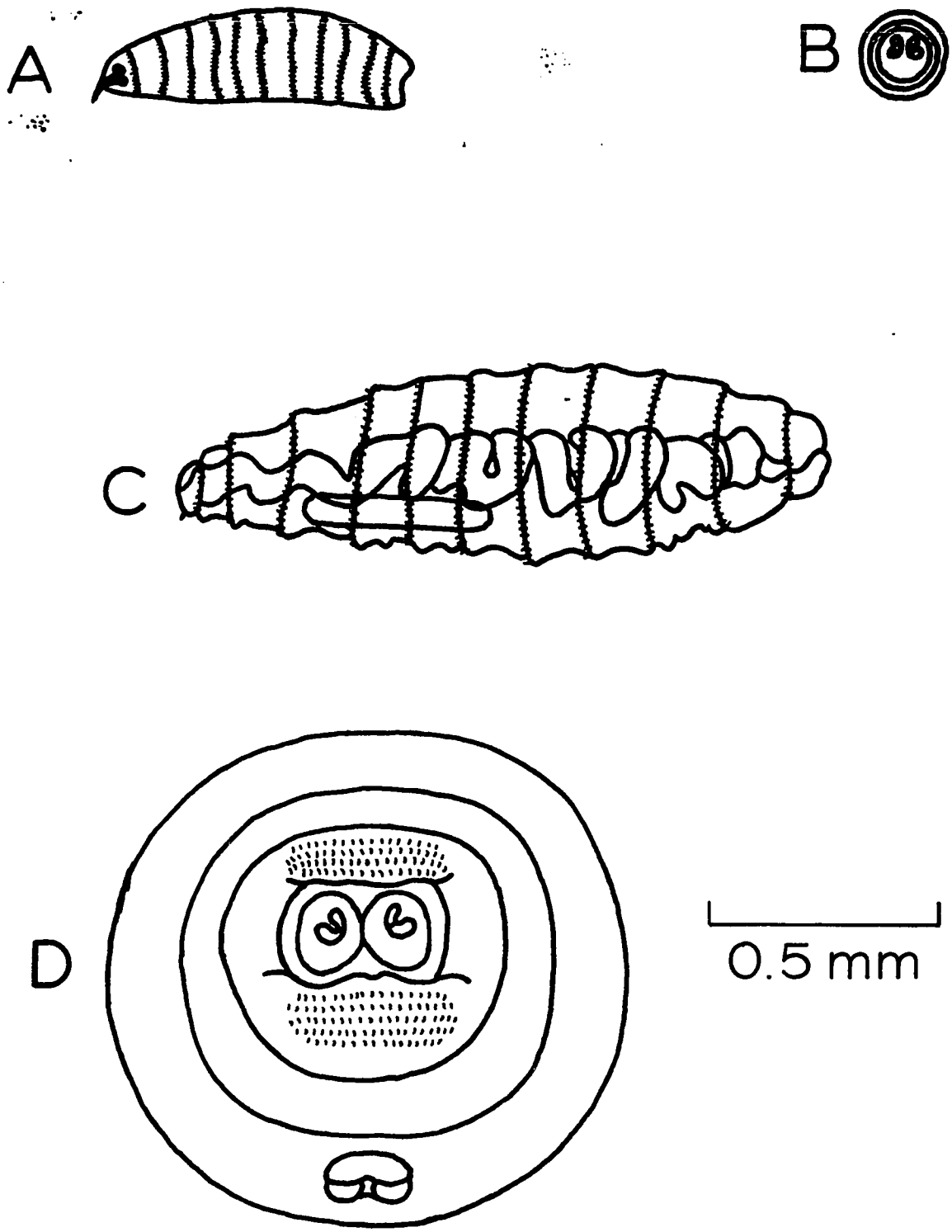


Figure 4. Gymnocarcelia ricinorum: A. First Instar Larva, Lateral View; B. First Instar Larva, Posterior View; C. Second Instar Larva, Lateral View; D. Second Instar Larva, Posterior View.

rather sharply pointed, arched, and deflected ventrally. The posterior pair of spiracles have kidney shaped openings and are only lightly sclerotized. Spiracular peritremes are transparent, not sclerotized, and their margins are not evident. This makes measurement difficult, but, since the spiracular slits are approximately 0.05 mm in length, peritreme diameters would be greater than this length.

A second instar larva is shown in lateral view in Figure 4C and posterior view in Figure 4D. In early stages of this instar, the integument is transparent and the internal organs may be seen vaguely through the body wall. In later stages of this instar, the body wall becomes opaque and more cream colored, leaving the internal organs no longer visible. The body length varies from one to two mm, the body width from 0.4 to 0.8 mm. Marginal segmental bands of spines remain very narrow, in this instar, and are quite delicate. In addition to the segmental bands, two broad patches of delicate spines, each consisting of four or more rows, are found on the dorsum and venter of the last abdominal segment with the posterior spiracles situated between them. The probable function of the spines is to hold the larva firmly in its respiratory funnel. Posterior spiracles, in this instar, have two evident spiracular slits for each spiracle. The two slits are more heavily sclerotized, slightly curved, and connected end to end forming the shape of the letter "C". The margin

of each spiracular peritreme is evident, they are not sclerotized, and they are almost circular in shape. Peritreme diameter is approximately 0.2 mm. The spiracles touch each other at one point along their margins. Only the tips of the recurved mouth hooks are evident from an external view. A structure not found in the first instar is three smooth, lightly sclerotized plates located on the ventral part of the tenth obvious body segment. It appears not to be a spiracle and may serve to secure the larva in its respiratory funnel. The plates do not bear hooks and in this instar do not have patches of minute spines in its proximity.

A ventral view of the third instar larva is shown in Figure 5A and a posterior view in Figure 5B. The integument remains cream colored and opaque, but the cuticular armature of this instar becomes more complex. In addition to the narrow marginal segmental bands of spines that completely encircle the body, there are additional narrow rows of spines on the venter adjacent to the marginal bands. The venter of the anterior end, particularly the first several segments, is provided with rather broad patches of spines in irregular and broken rows. On the dorsum and venter of the last abdominal segment are two patches of spines with the posterior spiracles between them. Body length varies from two to five mm, body width from one to two mm. The greatest body width occurs in the

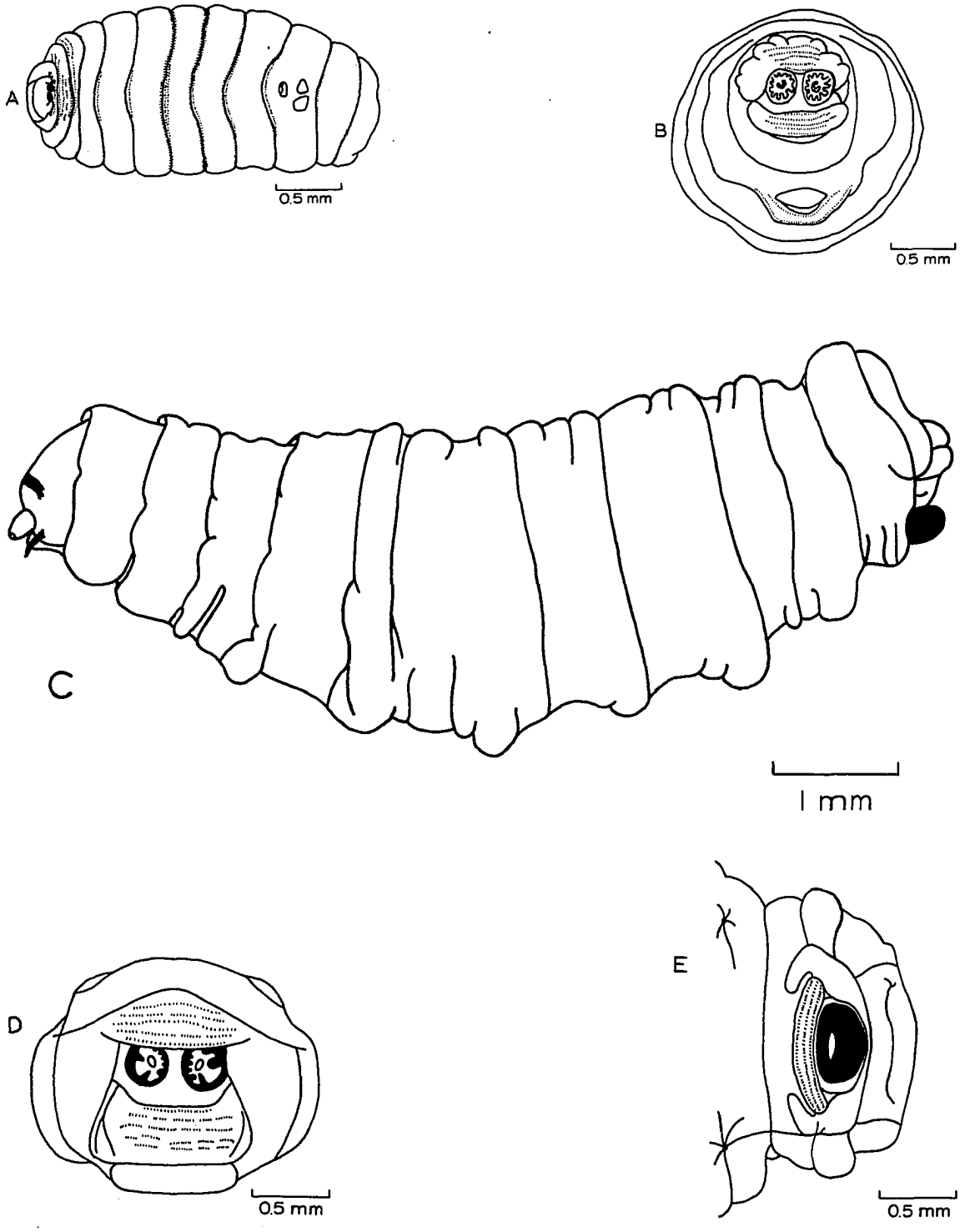


Figure 5. Gymnocarcelia ricinorum: A. Third Instar Larva, Ventral View; B. Third Instar Larva, Posterior View; C. Fourth Instar Larva, Lateral View; D. Fourth Instar Larva, Posterior View; E. Fourth Instar Larva, Posterior End From a Ventral View.

midsection. There is a slight tapering toward the posterior end and a much greater tapering toward the anterior end. The recurved mouth hooks are more robust than in the second instar and evident externally. The posterior spircales are similar in structure to those found in the previous instar except the spiracular slits and peritreme are more heavily sclerotized. Peritreme diameter is approximately 0.3 mm. Peritreme margins are separated by a short distance. The peritremes in this instar possess exceedingly long serpentine slits almost forming a complete circle about the two C-shaped central spiracular slits. Posterior spiracles of this instar gradually migrate to a slightly more dorsal position than that found in the second instar. In the third instar, the three ventral plates of the tenth obvious body segment migrate toward each other forming an elliptical, fused, two-part structure that is more heavily sclerotized than in the second instar. This ventral sclerotized button gradually migrates to a more posterior position. Anterior to the ventral button, in later stages of the third instar, two or three slightly U-shaped rows of spines become associated with the button.

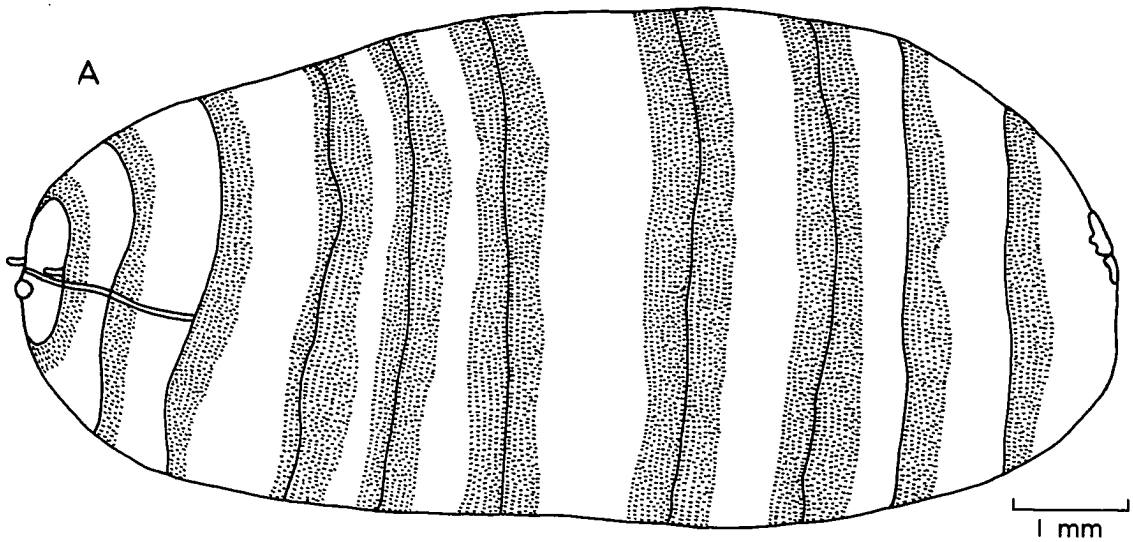
A lateral view of the fourth instar larva is shown in Figure 5C, a posterior view in Figure 5D, and the posterior end from a ventral view in Figure 5E. In this instar, the marginal segmental bands of spines become broader and each consists of several irregular rows of spines completely encircling the body. In addition to the dorsal

and ventral patches of spines associated with the posterior spiracles, there is a narrow elongated patch of rather heavy spines anterior to the ventral button. Body length of mature larvae varies from five to ten mm, body width from two to four mm. The posterior segment is approximately the same width as those preceding it, but caudad there is some tapering. Although segmentation is distinct, as in previous instars, it is somewhat obscured by segmental folds. Larvae of this species appear to have distinct ventral "pseudopodia" located on abdominal segments near intersegmental sutures. Paired mouth hooks of the fourth instar are robust and distinctly hooked. Posterior spiracles of this instar are distinctly different than those of earlier instars. There appear to be three spiracular slits, but the spiracular openings are not obvious. Each spiracular slit is located in one of the three lateral lobes of a median cream colored design resembling a three fingered hand. Medially the design bears four minute lobes and a spiracular button is located in its center. Peritremes are complete, dark, heavily sclerotized, and project between the middle and outer slits. Peritreme diameter is approximately 0.4 mm. Spiracles of the fourth instar are separated by a greater distance than the spiracles of the third instar, are situated above the transverse axis, and are only slightly dorsal. The ventral button in the mature larva is quite prominent from a lateral view. The flat

plates of the third instar have migrated and fused, in the fourth instar, to form an almost elliptical structure when viewed ventrally. From a lateral aspect, this very dark, heavily sclerotized button protrudes posteriorly. Its deep central slit, which extends laterally, may cause one to conclude that it serves some respiratory function. Since no tracheal connections were observed, it does not function as a spiracle.

Pupa

A lateral view of the pupa is shown in Figure 6A, an anterior view in Figure 6B, and a posterior view in Figure 6C. Pupae are subelliptical, wider in the mid-region, with anterior end narrower than posterior end, and rounded at both ends. The longitudinal axis is straight. Pupal color ranges from light reddish-brown to dark brown; some may appear almost black. The surface may be dull or appears to have a slight luster due to an armature of bands of spines completely encircling each body segment. Inter-segmental constrictions are distinct on the surface. Normal pupal length varies from approximately eight to nine mm and approximate width from three to four mm. When larvae are forced to pupate, due to a shortage of food remaining in the host, they may form pupae of a much smaller size. There are two projections through the puparial wall at the anterior end near the first intersegmental suture. These may be the remains of the mouth hooks, but they are not



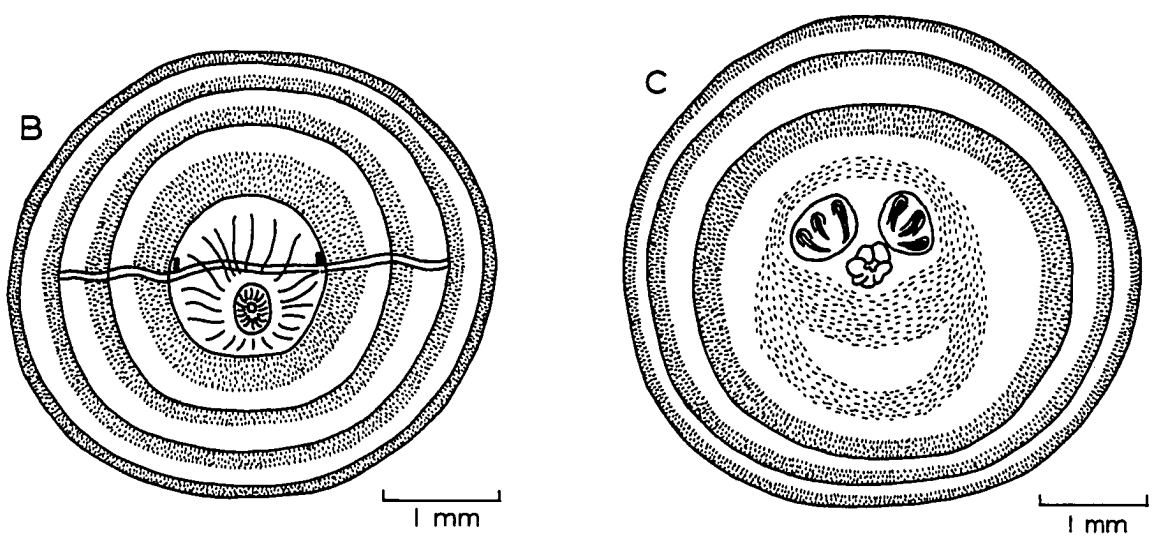


Figure 6. Gymnocarcelia ricinorum: A. Pupa, Lateral View; B. Pupa, Anterior View; C. Pupa, Posterior View.

curved or pointed. The larval oral opening is represented by a distinct anterior pore in the center of a slightly raised, wrinkled dome located slightly ventrad to the transverse axis. On the posterior end of the pupa the spiracles are quite evident. The spiracles are slightly raised and somewhat dorsad to the transverse axis. Peritreme margins are distinct as are the three slightly curved slits of each spiracle. The slits are incompletely bordered by rounded ridges. Spiracular buttons are no longer evident and the entire spiracle is almost the same color as the rest of the pupa. The anal opening appears as a distinct posterior pore in the center of a slightly raised sphincter-like dome. It is located slightly dorsad to the transverse axis and near the ventral margins of the posterior spiracles. The prominent ventral button, found in the fourth instar, is no longer present. This observation may tend to confirm its function to be other than a spiracle. The two halves of the puparial cap separate from each other and from the remainder of the puparial wall at the time of emergence of the adult fly. Both halves break away from each other, but commonly remain incompletely separated from the remainder of the puparial wall. There are both horizontal and vertical lines of cleavage. The horizontal cleavage line extends from a posterior point on each side, at the intersegmental suture between the third and fourth segments, anteriorly across the front of the pupa. Mouth

hooks are dorsad to the horizontal cleavage line and the mouth is ventrad. The horizontal line of cleavage appears as a slightly raised ridge. The vertical cleavage line passes completely around the pupa and follows the intersegmental suture, between the third and fourth segments, as a deep groove.

Adult

The description of the adult fly includes material from original descriptions of Townsend 1919 and Coquillett 1897. Additional parts of the description are added from the author's observations. Males and females are morphologically similar. The adult female fly is shown in Figure 7.

Length, 9 to 11 mm; eyes bare; head silver white; broad brown band from base of antennae generally fading near ocelli; ocellar bristles directed obliquely forward; lowest frontal bristles beneath the middle of second antennal joint; sides of face on lower half bare; oral vibrissae at most only one-half the length of second antennal joint above the level of front edge of oral margin; oral vibrissae on a level with front edge of oral margin; single row of short bristles between outer vertical bristles and bristly lower part of gena; bristles of gena covering at least the lower three-fourths; facial ridges bristly on less than the lowest fourth; collar of fine white setae covering the entire posterior part of the

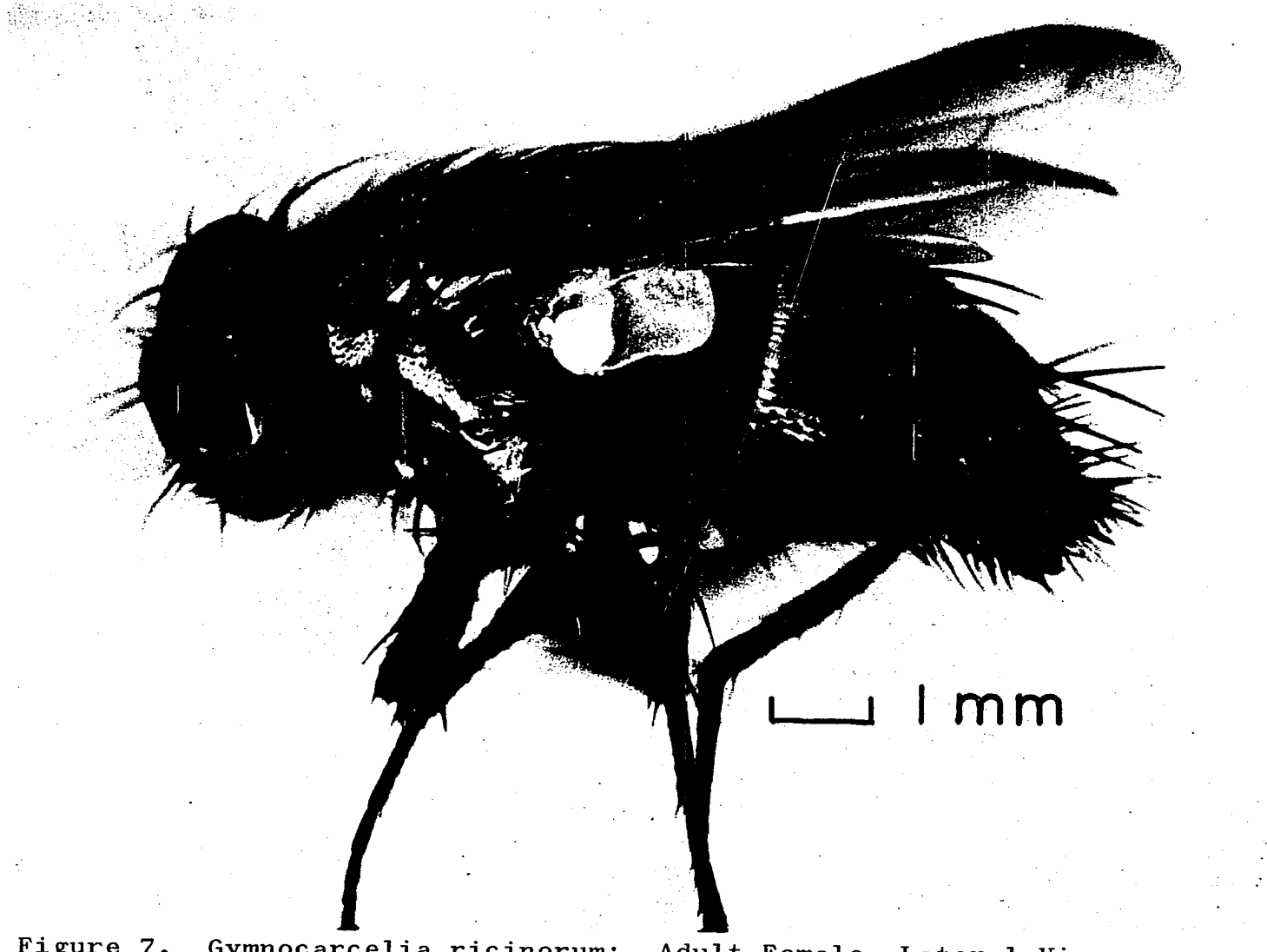


Figure 7. Gymnocarcelia ricinorum: Adult Female, Lateral View.

head; palpi yellow; head length at oral vibrissae much shorter than at base of antennae; antennae reaching at least the lowest fourth of the face; proboscis short, robust, fleshy, the labella soft.

Thorax gray-white with some black markings; mesonotum with two mesal narrow black bands beginning at anterior margin and fading beyond transverse suture; apex of scutellum broadly yellow; four postsutural macrochaetae; three sternopleural bristles; legs black; posterior side of front femur broadly gray-white; middle tibiae each bearing three or more macrochaetae on front side near middle; hind tibiae outwardly ciliate with bristles; apical cell ending far before extreme tip of wing; first vein, R_1, bare; third vein, R_{4+5}, bearing two bristles at its base; last section of fifth vein, Cu, less than one-third as long as preceding section.

Abdomen black; anterior margin of second, third, and fourth abdominal segments gray-white fading to black at posterior margin; apex of abdomen black; no discal macrochaetae on second and third abdominal segments, fourth covered except on base with none of the macrochaetae on this segment more than three-fourths as long as those on the third; first segment of abdomen with two dorsal marginal macrochaetae, second segment bearing two dorsal and two lateral marginal macrochaetae, third segment with marginal macrochaetae continuous on sides and dorsum.

Locations of Larvae in the Host

Of fifteen host caterpillars that were parasitized in the field and dissected, each of four hosts contained one fly larva, four contained two fly larvae, five contained three fly larvae, one contained four fly larvae, and one contained five fly larvae. On the basis of the above observations and other extensive field parasitism studies, it appears that five is the maximum number of fly larvae of this species that can successfully parasitize an individual salt-marsh caterpillar.

Early first instar fly larvae, obtained from a caterpillar observed to be parasitized by several caged adult flies in the laboratory and containing an abnormally large number of parasites, were found in the following locations: several fly larvae were embedded in the host's fat body in small nonsclerotized respiratory funnels, several were moving freely in the host's hemocoel, one was found with the posterior end in a torn trachea, one was in the salivary gland, and one was in the malpighian tubule. This shows there is considerable migration in the host's body before the larva forms a respiratory funnel.

It seems logical that while the first instar larva is migrating in the host's body the only way the larva can obtain its oxygen requirements would be by cutaneous respiration. Older first instar larvae may find this oxygen supply inadequate and begin, at least, to form a

temporary respiratory funnel. Clausen (1962) states that the tracheal funnel represents a defensive reaction on the part of the host to irritation incident to the making of the perforation in the integument or the tracheal wall by the parasite and to the persistence of the posterior end of the body of the latter in the wound. The larval respiratory funnel, in which the posterior end of the body, with the functional spiracles, is fixed, is an adaptation of very general occurrence in the Tachinidae; but, strangely enough, it is found elsewhere in only a very few highly specialized parasitic species of the closely related Sarcophagidae and in no other families of parasitic Diptera.

After the initial migration of early first instar larvae, they were observed to embed in the longitudinal muscle or fat body of the host. Five first instar larvae were located in the host's muscle and two in the fat body. Figure 8A shows a larva in muscle and Figure 8B a larva in the fat body. In both instances, there was little or no sclerotization of the delicate and loose host tissue surrounding the larvae. It should be noted in Figure 8A that no connections with tracheae are evident, but in Figure 8B a small trachea makes a connection with the fat body mass. Other larvae embedded in fat body tissue show no nearby connection with the tracheal system. The last situation appears to be the most common.

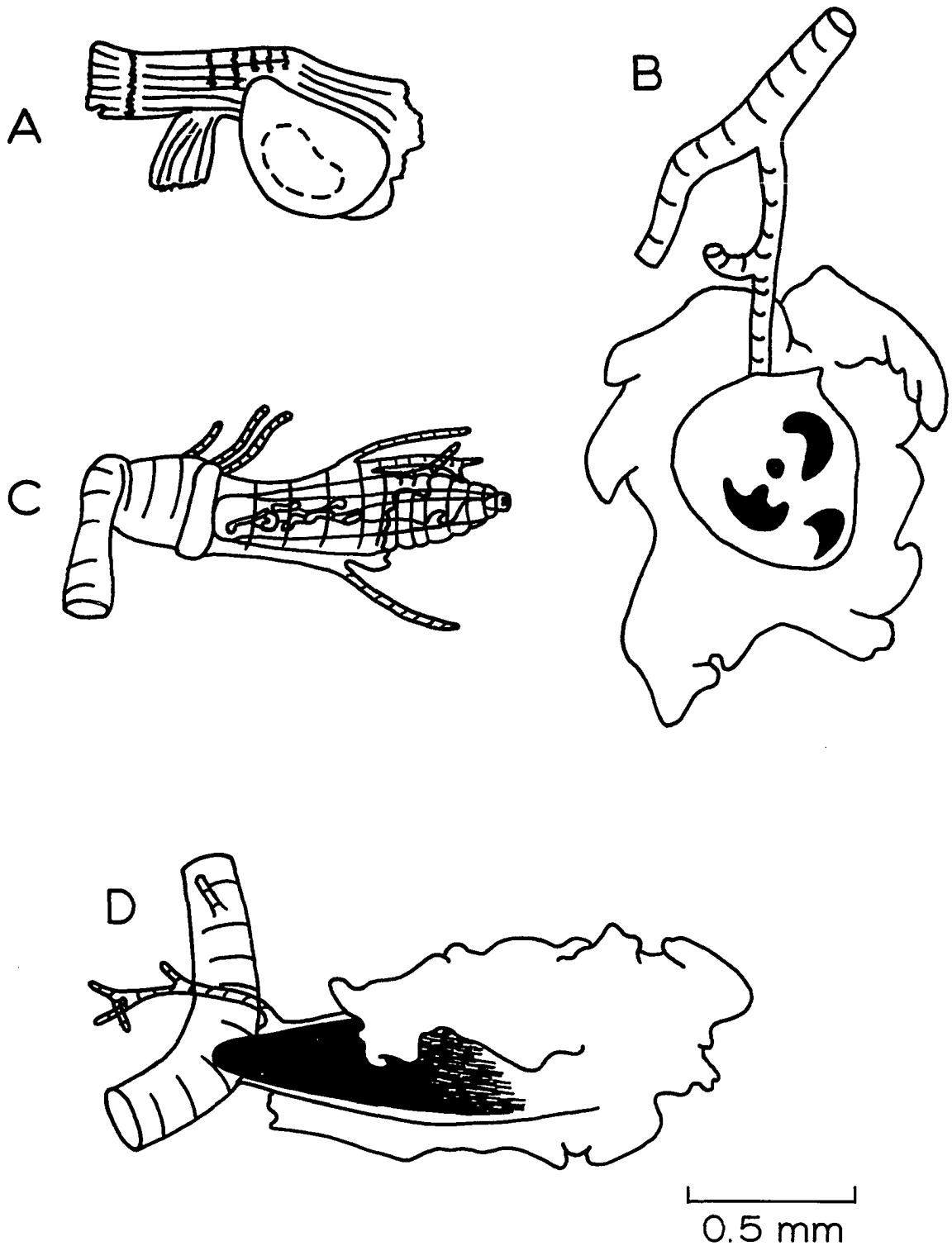


Figure 8. Gymnocarcelia ricinorum: A. First Instar Larva Embedded in Host's Muscle; B. First Instar Larva Embedded in Host's Fat Body; C. First Instar Larva, Posterior End in Torn Host's Trachea; D. Respiratory Funnel Containing Late First Instar Larva.

Figure 8C shows an early first instar larva with its posterior end in a torn host trachea. The larva appears to enter the torn trachea posterior end first and exerts some pressure as it forces its body into the tracheal opening. Evidence for this is seen in that the host's trachea is folded somewhat posterior to the larva. One might assume that the initial perforation of the trachea is made by the larval mouth hooks, but this does not appear to be the case. Clausen (1962) states that several authors have corroborated the conclusion that in several species the perforation is accomplished by the use of the posterior end of the body.

From the above discussion it should be evident that it is during the later part of the first stadium that the larva forms its respiratory funnel. Figure 8D shows a respiratory funnel for a late first instar larva. Table 1 shows the locations of fly respiratory funnels in nine caterpillar hosts. The most anterior respiratory funnel was located between the prothoracic and mesothoracic spiracles. No respiratory funnel was located posterior to the sixth abdominal spiracles. There appears to be a somewhat random distribution of respiratory funnels between these two locations in host caterpillars. Respiratory funnels in individual caterpillars seem to have a somewhat clumped distribution that may be due to the limited area of the host's body selected by a fly as an oviposition

Table 1: Locations of fly larval respiratory funnels in nine caterpillar hosts.

Host	Larval Instar	Location in Host
1	First	First abdominal spiracle; in muscle.
	First	Third abdominal spiracle; in fat body (See Fig. 8B).
2	First	Fourth abdominal spiracle.
	Second	Second abdominal spiracle; near gonads.
	Second	Between mesothoracic and metathoracic spiracles.
3	First	Sixth abdominal spiracle.
	Second	First abdominal spiracle (See Fig. 4C).
	Second	Third abdominal spiracle.
	Second	Fourth abdominal spiracle.
	Second	Fourth abdominal spiracle; opposite side.
4	Second	Fifth abdominal spiracle.
	Second	Sixth abdominal spiracle; opposite side.
5	Second	Third abdominal spiracle.
	Second	Third abdominal spiracle; same side.
	Second	Between prothoracic and mesothoracic spiracles (See Fig. 9A).
6	Second	Third abdominal spiracle; anterior end of larva near heart.

Table 1: (Cont.)

Host	Larval Instar	Location in Host
7	Second	On dorsum in region of fifth abdominal spiracles.
8	Second	Metathoracic spiracle (See Fig. 4D).
	Second	Metathoracic spiracle.
	Third	Sixth abdominal spiracle; anterior end of larva dorsal to gut and overlying it (See Fig. 9B).
9	Third	On dorsum in region of metathoracic spiracles (See Fig. 5A).
	Third	On dorsum in region of metathoracic spiracles.
	Third	On dorsum in region of metathoracic spiracles.

site. Even though the first instar fly larva migrates, the range of migration may be quite limited. Therefore, the locations of respiratory funnels may be near the point of penetration of the host's integument by the first instar larva. Respiratory funnels that were in close proximity to each other commonly were separated by at least the distance of one host spiracle. Funnels commonly were on opposite sides, at a pair of host spiracles, but in two instances two funnels were attached in the same region of a single spiracle. The most common locations for respiratory funnels were in the regions of the metathoracic and third abdominal spiracles in this limited number of host dissections. References to figure numbers in Table 1 refer to illustrations of larvae and respiratory funnels removed from those host caterpillars.

Clausen (1962) states that the respiratory funnel increases gradually in size with the growth of the larva, and the basal portion may eventually appear as a more or less slender stalk. Usually the funnel is greatly darkened in color, this being most pronounced near the point of attachment, where the wall is thickest, and fades out toward the rim. In a very few species, the funnel is almost colorless. Occasionally, it has a distinctly "segmented" appearance due to a marked difference in size and form to accommodate the successive instars.

There are several exceptions to Clausen's statements in regard to this species. In its initial formation, the respiratory funnel is rather conical in shape and only the basal portion is greatly darkened in color. The color gradually fades out rather quickly toward the open anterior half of the funnel. This species of host caterpillar possesses a very heavy fat deposit in the fat body and, even during the early stages of respiratory funnel formation, the anterior end of the funnel becomes covered by a dense fat deposit. In later stages of funnel formation, the darkly sclerotized areas either become obscured or totally covered by fat body deposits. This situation is evident from Figure 9A which shows the respiratory funnel for a second instar larva, Figure 9B showing the funnel for an early third instar, and Figure 9C which shows a funnel for a late third instar. In the latter figure, connections with two spiracles on the same side of the host were made by this larva in its funnel formation. This does not appear to be the usual situation.

In general, a single respiratory attachment is made during the life of the larva, and its position remains fixed in the host body from the time of formation of the funnel until it is abandoned for gross feeding (Clausen 1962). This appears generally to be the case as, at least up to and including the early fourth instar larva, it is almost totally surrounded by a respiratory funnel (See

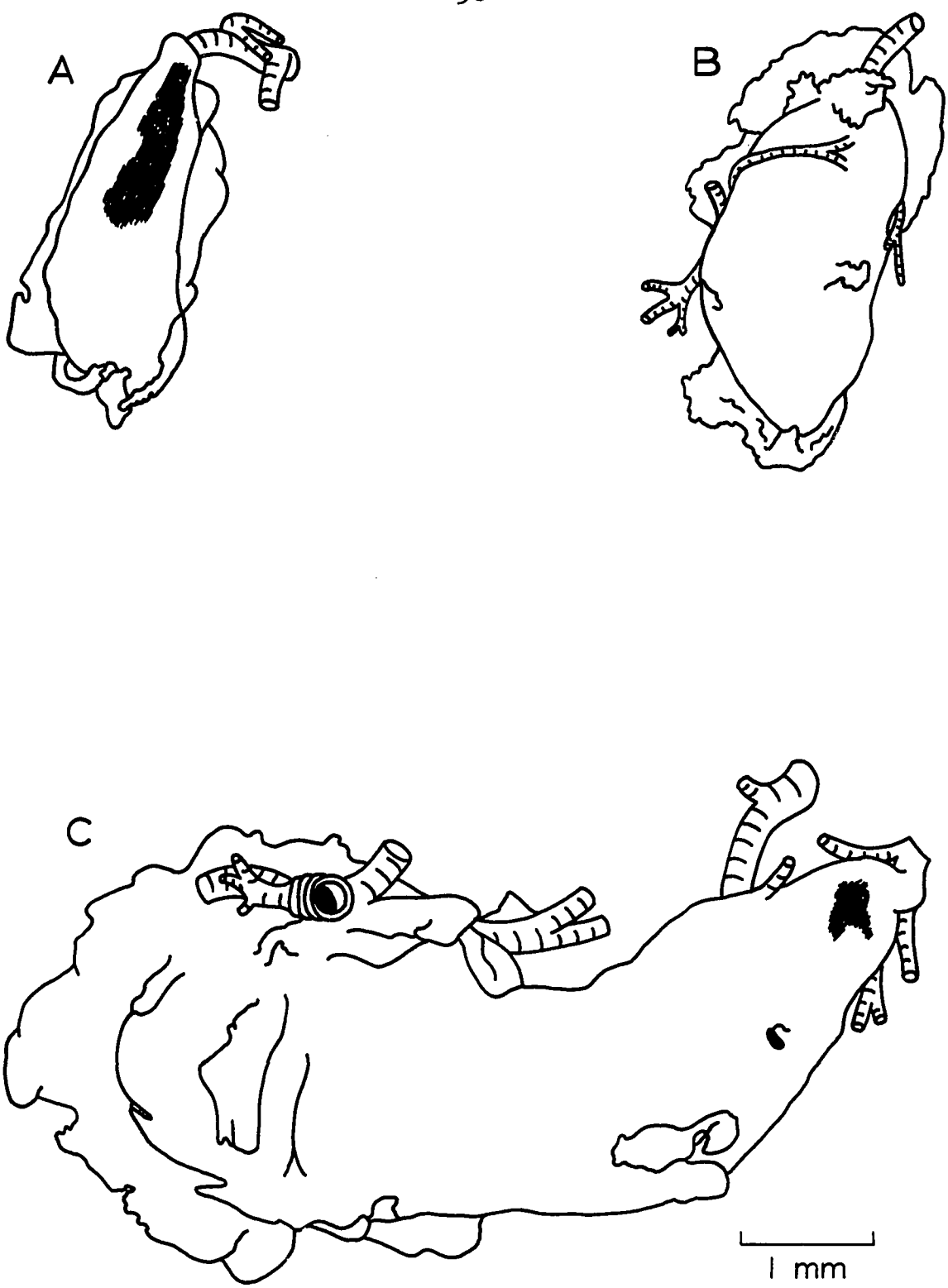


Figure 9. Gymnocarcelia ricinorum: Respiratory Funnels; A. Containing Second Instar Larva; B. Containing Early Third Instar Larva; C. Containing Late Third Instar Larva.

larvae in Figures 5C, 5D, and 5E). One exception to this statement was found in the dissection of host caterpillar number 2 (See Table 1) where one very small empty respiratory funnel embedded in fat body was observed. One possible explanation for this observation is that the tracheal connections to the fat body at this location provided an inadequate respiratory supply. The larva then abandoned this funnel, made another connection with the host's tracheal system, and formed a new funnel.

External evidence of the respiratory funnel in parasitized caterpillars was not found in this fly species. Although this is not uncommon in fly species that make a direct connection with the tracheal system of the host, the massive fat body of the caterpillar would, as well, tend to mask the presence of the funnel in the host.

Larvae of this fly species may undergo several molts while partially enclosed in their respiratory funnels. In all dissections of respiratory funnels, an attempt was made to find the larval exuviae as a possible aid in determination of individual instars. With one exception, no exuviae were found. In the only respiratory funnel that contained a single exuvia, the exuvia was folded and pressed against the inner wall near the open end of the funnel (See Figures 5B and 9C). In addition, no larval exuviae were found in the host's hemocoel.

Larval Free Feeding Period, Pupation, and Emergence

The time at which the respiratory funnel connection is normally broken appears to be in the later portion of the fourth stadium. If the fourth instar larva can no longer reach a food source or when the host dies, the larva may begin a period of free feeding in the host. During this free feeding period, the larvae consume almost all of the host's internal organs. Larval parasite respiration may involve contact with air spaces created by removal of the host's internal organs. These air spaces, in turn, either have direct contact with spiracles or torn ends of tracheal branches. On numerous occasions, the host's integument was observed to be torn in one or more places, which would provide additional access to atmospheric air. Torn areas in the host's integument are made sometime before the larvae leave the host.

Pupation commonly occurs outside the host, although, in several instances, one or more of the larvae remained in the host and pupation occurred there. Pupation normally occurs inside the host's cocoon, if it has formed a cocoon prior to its death, but one or more larvae may leave the host's cocoon while the remainder stay behind. In certain situations, however, all the larvae may leave both the host and the cocoon. When the host dies before cocoon formation, the fly larvae commonly leave the host and pupate in the soil. This also occurs in larvae that leave the cocoon.

If a host pupates in its cocoon, fly larvae cut a small hole for exit from the host's pupa case. The majority of hosts died after cocoon formation, before pupation, and remained in the larval state inside their cocoons. This weakened condition is probably due to the parasite's presence. Less than one-half of the parasitized hosts died as late instar caterpillars and the remainder died in their cocoons. Host cocoons are constructed of an outer layer of cemented setae, broken from the bodies of caterpillars, and an inner layer of silk.

As flies emerge from pupae, either inside their hosts or outside their hosts but inside the cocoons, they usually do not experience difficulty leaving the hard, dry host integuments, if holes are present, or the loosely woven host cocoons. This loose construction of the cocoon permits easy exit by the fly soon after emergence. Only a very few flies were found inside cocoons and these were small and poorly formed. A small number of adult flies were found inside their pupa cases and inside the integument of the host. This occurred when the host's integument had folded around them or when the pupa case was partially embedded in hardened host internal tissue, thus preventing escape by the flies.

Duration of Life Cycle Stages

Figure 10 shows the duration of life cycle stages of the fly for 35 hosts parasitized in the laboratory. Some

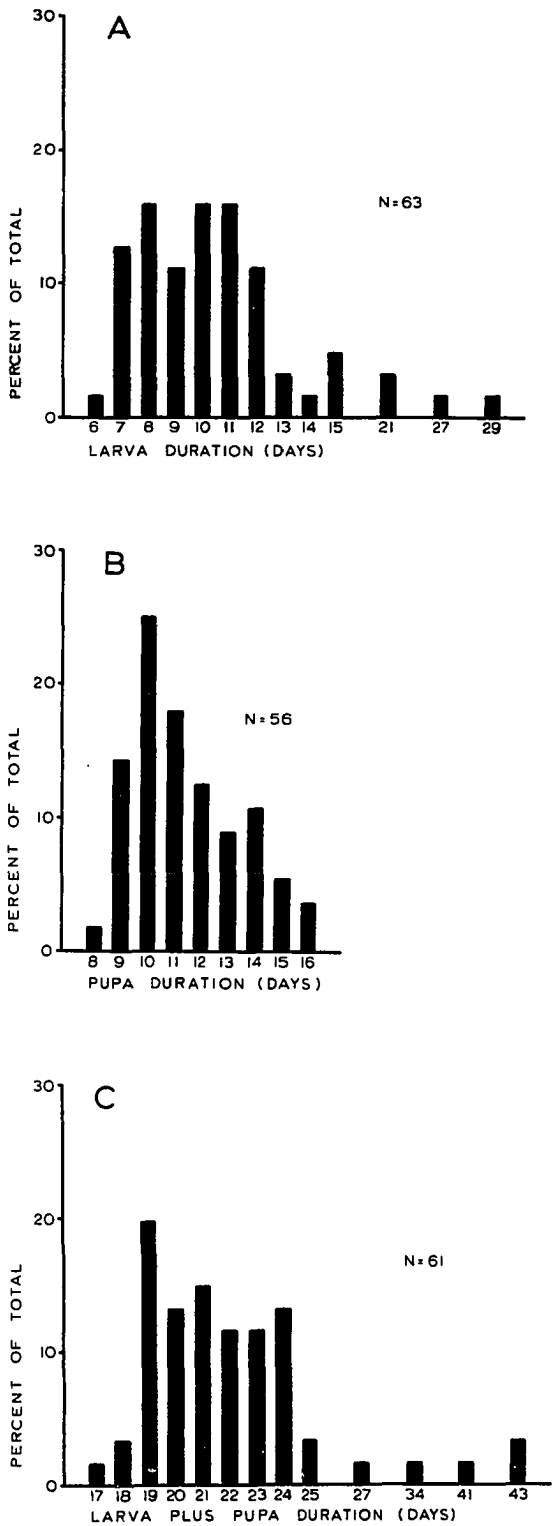


Figure 10. Fly Life Cycle Durations in Days: A. Percent of Total for Each Larva Duration; B. Percent of Total for Each Pupa Duration; C. Percent of Total for Each Larva Plus Pupa Duration.

flies died in the pupa stage; therefore, durations of the pupa stage and larva plus pupa stages were not recorded. In other situations, the flies pupated inside the host; durations of larva and pupa stages were not observed, but the duration of larva plus pupa stages were recorded when the adult fly emerged.

In this fly species, the time required to pass through the larval stage ranged from 6 to 29 days with an average of 10.8 days. Percent of the total 63 flies for each larva duration in days is shown in Figure 10A. Duration of the pupa stage ranged from 8 to 16 days with an average of 11.4 days. Figure 10B shows the percent of the total 56 flies for each pupa duration in days. The total developmental period after hatching, larva plus pupa stages, ranged from 17 to 43 days with an average of 22.5 days. Percent of the total 61 flies is shown in Figure 10C for each larva plus pupa duration in days.

No significant differences were observed in the length of the larval and pupal stages when a comparison was made between hosts that died as caterpillars and those that died after cocoon formation. There was a slight tendency for the larval stage to be shorter in hosts that died as caterpillars which may be due to a shortage of food available to the parasites. Duration of both life cycle stages for this fly species compares favorably with general averages for multiple generation flies in the

family Tachinidae. Ranges for larval and pupal stages may appear to be somewhat large, but, in addition, it should be noted that the range of variability among individuals from the same host, is quite small or zero. Therefore, these differences are probably due to genetic variability in this species.

Table 2 shows both adult fly longevity ranges and average longevities for both sexes by cages. Also, total flies per cage is given. These flies were laboratory reared during the summers of 1967 and 1968. Totals for longevity averages and ranges for 1967, 1968, and both years are also presented.

Data for individual cages and totals for individual years do not show many definite patterns. With two exceptions, 67-1 and 68-3, the upper limit of the longevity range for females was greater than for males. In one-half the cages for both years, the average longevity of females was greater than for males, and in the other one-half the pattern was reversed. This inconsistency in pattern is to be expected when small numbers of individuals are considered. In regard to longevity for all cages for each year, the total range and upper limit of the range for females was greater than for males. Average fly longevity for each year was greater for females than males or approximately equal. Longevity range and upper limits of the range, for all fly cages and both years, was greater in females than

Table 2: Adult fly longevity for both sexes by cages for the years 1967 and 1968.

Cage Number	Total Flies per Cage		Longevity Range in Days		Average Longevity in Days	
	Males	Females	Males	Females	Males	Females
67-1	9	11	6-20	2-13	11.4	8.6
67-2	12	17	2-23	2-27	13.3	16.0
67-3	10	9	5-26	7-43	16.0	25.7
All Cages 1967	31	37	2-26	2-43	13.7	16.1
68-1	13	12	8-31	7-38	20.5	24.1
68-2	21	23	8-26	2-28	17.3	16.6
68-3	29	32	1-24	3-22	12.9	12.3
All Cages 1968	63	67	1-31	2-38	16.0	15.9
Total Both Years	94	104	1-31	2-43	15.2	16.0

males. Also, the average longevity of females was greater than for males.

Since female flies mated with males in their cages, it is probable that they would have lived longer if they had remained unmated. Unmated female flies commonly live longer than mated flies. This situation does not normally occur in the field and, therefore, was ignored in these experiments.

Mating Behavior

Observations were made of mating behavior of caged flies in the laboratory. Some flies were used both in longevity studies and for observations of mating behavior, therefore, the ages of some flies were known. Adult flies were held in jars no longer than 24 hours after emergence, and copulation often occurred almost immediately after the flies were placed together in cages. When flies were used as part of longevity studies, mating behavior was delayed until the flies, particularly the males, were fully recovered from carbon dioxide anesthetization.

In usual premating behavior, the male flew to a stationary female and landed on her back. The female would resist and attempt to fly away, but the male would make a determined effort to hold onto the female. This usually resulted in both members of the pair falling to the floor of the cage. The pair of flies would roll around on the

cage floor until the male was in the proper position to insert the copulatory organ.

At the approach of another fly or a caterpillar, the flies in copula would move in unison to get out of the way. Neither strong air pressure directed at the mating pair nor movements of the author's hand, back and forth a few inches above them, induced the flies to stop mating, although they would change position slightly on the cage floor or sides. At no time was mating observed when the ambient room temperature was below 75 F. The upper temperature limit for mating was not determined.

Unsuccessful attempts by males to mate with copulating females were observed. In one case, a second male approached the female and hit the female's head, thorax, and legs with his prothoracic legs, but the mating pair remained in copula. In another situation, the mating pair were changing position. The mating male was partially hidden by sweet clover on the cage floor, and was positioned at a 90 degree angle to the long axis of the female. A second male approached the female, jumped on her back, moved off her, jumped on her right side, and gradually moved onto her back. When the second male found he could not mate with her because of the first male, he flew away.

On numerous occasions, male flies were observed in copula with their prothoracic tarsi resting on the female's eyes, i.e., the right tarsus on the right eye and the left

tarsus on the left eye. The male fly's mesothoracic and metathoracic legs held the female fly's thorax and abdomen. Flies, while mating on the sides of the cage, would mate with their heads pointing down, shift position so their heads would point up, and then back again to the head down position. There seemed to be no preference as to body position during copulation.

Table 3 shows the total mating time and ages of flies in copula for several mating fly pairs. Total mating time ranged from the minimum of 40 ± 5 minutes to a maximum of 145 ± 5 minutes. Most total mating times were 75 minutes or less; however, four of the observations were over two hours in duration. Of the 13 total mating times, the average was 83 minutes. Ages of male flies in copula ranged from 1 to 23 days with most flies 4 days old or less, while ages of female flies ranged from 1 to 23 days with most flies 4 days old or less.

Several postmating behavior observations were made, which showed uniform behavior among members of each sex. All males after breaking copula would make a short flight of a few minutes, locate the food source, and feed for a very short period. After breaking copula, a female would remain in the same spot, rub the tip of her abdomen with her metathoracic legs, and occasionally rub her wings. The female, after several minutes of grooming behavior, would fly for a few minutes, locate the food source, and feed for

Table 3: Total mating time and ages of flies in copula.

Total Mating Time in Minutes	Ages of Flies in Days	
	Males	Females
40 ± 5	2	1
40 ± 5	--	--
55 ± 5	1	4
55 ± 5	--	--
55 ± 5	--	--
65 ± 5	--	--
75 ± 5	3	1
75 ± 5	1	10
75 ± 5	3	7
125 ± 5	23	23
130 ± 5	4	1
140 ± 5	2	3
145 ± 5	2	1
--	1	1
--	9	2
--	11	13

a short period. Periodically after feeding, a female would continue to rub the tip of her abdomen with her legs.

Oviposition Behavior

Oviposition by flies on late instar salt-marsh caterpillars was observed both in the field and in the laboratory. Field observations confirmed those made in the laboratory.

A female fly would land near a caterpillar and walk or make short flights to get closer to the host. The fly would approach the caterpillar from the front, sides, or rear and hit at or touch the caterpillar's setae with either or both prothoracic legs. This behavior pattern would continue until a response was elicited in the caterpillar. The typical host response was a rearing back of the caterpillar's head and thoracic regions and a waving to the right and left by the front part of its body. When a caterpillar encountered another caterpillar and periodically as a caterpillar was moving into unfamiliar territory, this same response was observed. The typical host response appears to be required before the fly will oviposit. It may be necessary for the fly to identify the host's anterior end or to determine if the caterpillar is alive or not. The fly would then oviposit by curving her abdomen under her, extending her ovipositor, and quickly touching it to the ventrolateral side of the thoracic region or the anterior portion of the host's abdomen. Fly

eggs easily adhere to the outside of the host's body wall.

A typical number of eggs laid on a single caterpillar is two or three. Sometimes flies lay only a single egg and even more rarely four eggs.

Usually the caterpillar's response to attachment of the egg to its body wall was a minimal body movement. Sometimes the host would rear back the front part of its body in a vain attempt to drive off the fly. In a few observations, particularly when mated females had been denied hosts for several days, the caterpillar's response to fly oviposition was violent. Within a few seconds after the egg was cemented to the host's body, the caterpillar would start twisting and turning its entire body as if in great pain. The host would often fall to the bottom of the cage and roll over and over in the sand in the cage bottom, trying to dislodge the parasite. At this time, it appears that the first instar larvae had hatched and were penetrating the host's body wall. After about 30 seconds of violent behavior, the caterpillars resumed their normal activities.

If mated female flies were totally denied a normal host, they would not oviposit on cage surfaces or on sweetclover cuttings placed in the cage bottoms. The flies did, however, lay large numbers of eggs on the dead bodies of other flies in the cages. When late instar arctiid caterpillars of a different species, Diacrisia virginica (F.),

were placed in the same cage with the flies, they did not oviposit on them.

Degree of Field Parasitism

As stated above, the number of parasites per host varied from one to a maximum of five in field collections of hosts. Because field collections of hosts were extensive during the summers of 1967 and 1968, and because of the variability in parasite numbers per host, the data in Table 4 are expressed as parasites per hundred hosts. Field collections were made in the southeastern quarter of Custer County, Oklahoma near the cities of Weatherford and Arapaho. Collection dates, number of hosts, and number of parasites are also given in the table.

The number of parasites per hundred hosts during the summer months of 1967, June 22 to October 16, remained fairly constant and ranged from a low of 18.1 to a high of 33.3 with an average of 24.1 for the entire period. In collections made between June 4 and July 9 of 1968, the number of parasites per hundred hosts ranged from a low of 28.0 to a high of 89.3 with the latter occurring in the first collection for the first 1968 period. In the second 1968 collection period, July 29 to October 12, parasitism ranged from a low of 111.8 parasites per hundred hosts to a high of 203.9 which is a noticeable increase. The average for the first 1968 collection period was 56.1 parasites per hundred hosts, while the average for the second period was

Table 4: Degree of fly parasitism of host caterpillars in field collections made during the summers of 1967 and 1968 in Custer County, Oklahoma.

Cage Number	Collection Dates	Number of Hosts	Number of Parasites	Parasites per Hundred Hosts
67-1	June 22-24	108	27	25.0
67-2	Aug. 9-10	112	24	21.4
67-3	Aug. 14-18	90	23	25.6
67-4	Aug. 30	72	13	18.1
67-5	Sept. 5	47	14	29.8
67-6	Sept. 11	36	12	33.3
67-6	Sept. 14-Oct. 16	402	96	23.9
67-1 to 67-7	1967 Total	867	209	24.1
68-1	June 4-8	112	100	89.3
68-2	June 8-11	89	40	44.9
68-3	June 17-20	114	75	65.8
68-4	June 25-28	135	66	48.9
68-5	June 29	143	40	28.0
68-6	July 4-9	111	74	66.7
68-7	July 29-Aug. 1	27	36	133.3
68-8	Aug. 1-2	26	53	203.9
68-9	Oct. 12	127	142	111.8

Table 4: (Cont.)

Cage Number	Collection Dates	Number of Hosts	Number of Parasites	Parasites per Hundred Hosts
68-1 to 68-6	1968: Subtotal 1	704	395	56.1
68-7 to 68-9	1968: Subtotal 2	180	231	128.3
68-1 to 68-9	1968 Total	884	626	70.8
All Cages	1967 and 1968: Grand Total	1751	835	47.7

128.3 parasites. There was an increase in parasitism greater than 100% when the first 1968 collection period is compared with the 1967 period. This greater than doubling phenomenon is again seen when the first 1968 collection period is compared with the second 1968 period. Average parasitism in 1968 was 70.8 parasites per hundred hosts or nearly three times the average parasitism for 1967. Total number of hosts collected during the two years, 867 hosts for 1967 and 884 in 1968, is almost the same. For both years, 1967 and 1968, the average number of parasites per hundred hosts was 47.7.

Table 5 shows the monthly rainfall, monthly mean high temperature, and number of days with high temperatures 100 F and over. The data cover portions of the years 1967, 1968, and 1970. Information was obtained from official weather data gathered at Weatherford, Custer County, Oklahoma.

The summers of 1967 and 1968 were particularly favorable for both host and parasite population increases as the maximum daily temperatures were lower than normal and the total monthly rainfalls were greater than normal, particularly during July and August. Abundant rainfall and mild temperatures permitted the principal host food plant, white sweet clover, to stay green and grow until the first killing frost.

Table 5: Monthly rainfall and temperatures for portions of the years 1967, 1968, and 1970 at Weatherford, Custer County, Oklahoma.

Year	Month	Rainfall in Inches	Mean High Temperature in Degrees F	Number of Days with High Temperatures 100 F and Over
1967	June	5.48	89.5	2
	July	2.13	90.7	4
	Aug.	2.24	90.7	5
	Sept.	5.12	80.2	0
	Oct.	1.29	75.6	0
1968	June	1.80	89.2	0
	July	3.91	91.4	1
	Aug.	7.50	92.0	4
	Sept.	2.08	83.2	0
	Oct.	2.99	76.5	0
1970	June	1.06	91.7	6
	July	3.63	97.2	12
	Aug.	0.42	97.0	11

Data for the three summer months of 1970 are included as an example of a year that was quite unfavorable for host and parasite population buildups. Between June 11 and July 3, there was a period of 21 days without any rainfall. During this period, sweet clover dried out and died. No host caterpillars were collected after June 27 as the species remained in a dormant state in their cocoons and no new generations were produced during the rest of the year. It appears that many days with high temperatures of 100 F or over and scarcity of rainfall is inhibitive of repetitive generations of both host and parasite species.

Other Ecological Relationships

Caterpillars of *E. acrea* were collected primarily along roadsides and in uncultivated pastures. The preferred host plant in these habitats appeared to be white sweet clover, *Melilotus alba* Desr., although the caterpillars occasionally would be found on yellow sweet clover, *Melilotus officinalis* (L.) Lam. Another species of arctiid caterpillar, the yellow woollybear *Diacrisia virginica* (F.), was also found in these habitats in nearly as great a number. In situations where the two species were in competition with each other, there seemed to be some degree of restriction to one host plant by each moth species. Although both species fed readily on either host plant, *E. acrea* was found mainly on white sweet clover and *D. virginica* on yellow sweet clover. White sweet clover,

in collecting areas, was more abundant in more moist soils, while yellow sweet clover was more common in drier situations. Uncultivated Melilotus spp. in collecting areas are not natives. Seeds of host plants probably were transported to these habitats by water, gravity, animals, and accidentally by man from cultivated areas.

While collecting E. acrea, separate collections of D. virginica were made in an attempt to determine if G. ricinorum was parasitizing both hosts. Large numbers of two species of Tachinidae, mainly Lespesia archippivora (Riley) and a few Lespesia aletiae (Riley), were reared from field parasitized D. virginica. Collections of E. acrea, parasitized in the field, did not yield Lespesia spp. parasites. Nonparasitized field collected caterpillars of D. virginica were placed in cages with ovipositing flies of G. ricinorum, the caterpillars were placed in jars with food, and were allowed to progress toward maturity. Attempts to artificially parasitize D. virginica were unsuccessful even though flies occasionally would oviposit on this caterpillar species. As was stated above, caged flies hindered from ovipositing sometimes would oviposit on dead flies on the bottom of cages. These behavior patterns appear to be directed by a need to oviposit rather than by stimuli provided by similar substitute hosts.

The salt-marsh caterpillar feeds on a number of cultivated and wild plants. Peterson (1956) states that this insect is found on many garden crops. Taylor (1954) reports that E. acrea occasionally threatens destruction of fall plantings of vegetables in the Salt River Valley of Arizona. Large numbers develop on cotton, which is one of this caterpillar's principal host plants. When their preferred food becomes scarce, the larvae migrate to lettuce and miscellaneous other crops. Young and Sifuentes (1959) list as host plants of the salt-marsh caterpillar: amaranth, Amaranthus palmeri S. Wats., the preferred native host; others, in order of preference, include ground cherry, Physalis angulata L., angle-pod, Gonolobus sp., and malva, Anoda pentaschista Gray. They report that the first three species are more suitable hosts, for development of the caterpillar, than either cotton or corn, cultivated host plants, in the Yaqui Valley, Sonora, Mexico.

As stated above, large numbers of L. archippivora and L. aletiae (= Tachina aletiae Riley, Tachina fraterna Comstock) were reared from D. virginica feeding on sweet clover in west-central Oklahoma, but Lespesia spp. were not found parasitizing the salt-marsh caterpillar in the same habitats. Butler (1958) states that E. acrea is the host of Lespesia (Achaetoneura) archippivora (Riley) throughout southern Arizona, but the fly was not found in samples from northern Arizona. Bottrell et al. (1968) report that in

collections made in Oklahoma during 1965 and 1966, L. archippivora was the second most common tachinid reared from both the bollworm, Heliothis zea (Boddie) and tobacco budworm, Heliothis virescens (Fabricius) on alfalfa and cotton. Bottrell (1969) collected L. archippivora and a single record of L. aletiae from the larvae of the yellow-striped armyworm, Prodenia orithogalli Guenée, which feeds on many cultivated and wild plants in Oklahoma. Host plants of the caterpillar were alfalfa, Amaranthus sp., and Russian thistle, Salsola kali L. About 20% of the caterpillars collected in September were parasitized by L. archippivora, which was the most common parasite, of seven tachinid species, recovered from host larvae. Bryan, Jackson, and Patana (1968) report that when female flies were presented with one host, in tests with L. archippivora, they readily oviposited. Hosts were the bollworm; the salt-marsh caterpillar; the cabbage looper, Trichoplusia ni (Hübner); and the beet armyworm, Spodoptera exigua (Hübner). In a second test, these flies were then given a choice of four host larvae of each species. Beet armyworms and salt-marsh caterpillars appeared to be preferred based on the number of parasitized host larvae and the number of fly puparia produced. The result was not a true picture of host preference, but in reality, it was a combination of host preference and efficiency in parasitization.

It appears that even though L. archippivora is a known parasite of the salt-marsh caterpillar in other localities, in collections made in Custer County, Lespesia spp. exhibited a marked preference for and restriction to D. virginica rather than parasitizing the salt-marsh caterpillar. The literature reveals a large number of potential host species for parasitization by Lespesia spp. A combination of certain ecological conditions, host preference, and possible competition with G. ricinorum may have resulted in the absence of parasitization of the salt-marsh caterpillar during the period of observation.

Taylor (1954) reports the ichneumonid Enicospilus glabratus (Say) (= Eremotyles arctiae Ashmead) as a species of Hymenoptera parasitizing the salt-marsh caterpillar. In collections of the caterpillar in Oklahoma, very few ichneumonid parasites were found. A single record of Barylypa sp. was recovered from a caterpillar collected on sweet clover in 1967. In a collection of 103 hosts in 1967, two Enicospilus sp. parasites were recovered, but in another collection of 402 hosts a single record of the parasite and a dead ichneumonid larva of unknown species were recovered. In two collections in 1967, single records of dead ichneumonid pupae were recovered; one collection contained 90 hosts and another contained 72 hosts. A single record of Enicospilus sp. was recovered from a collection of 441 D. virginica hosts made in 1967. No ichneumonid parasites

were recovered from collections of both species of caterpillar hosts during 1968. The very low degree of parasitism suggests these ichneumonid species may be secondary parasites.

CHAPTER IV

DISCUSSION

Undoubtedly, there are many gaps in the known distribution of both E. acrea and G. ricinorum, which are due either to failure to collect in those localities or to inaccessibility of collections to the author. Based on the known distribution of the salt-marsh caterpillar, it appears to be rather widely distributed on the North American continent. There is a greater number of recorded states in which the fly has been collected than for the salt-marsh caterpillar, but many of these are in the eastern part of the United States. Since the fly is not restricted to one species of host, it utilizes other hosts in those eastern localities. Known collections of G. ricinorum do not include a very large area of the northwestern United States, north and west of Colorado. There may be any number of reasons for the fly's absence in that area, one of which may be the altitude of the Rocky Mountains. It appears the fly's limits of tolerance to temperature and moisture are very wide, considering its distribution into Canada and Central America. Therefore, the latter two physical factors probably are not limiting.

Since a lack of tracheal connections to the larval ventral button eliminates the possibility of a respiratory function, the true function of this structure remains obscure. A search of the literature did not reveal the presence of a ventral button in other tachinid fly larvae. One possible function is that it may be used to break through the host's tracheae. As the larva increases in size, the respiratory funnel also grows larger. New connections with the host's tracheae may be required with greater demands for gas exchange. Another more probable function is to hold the larva in its respiratory funnel. With time the food supply for the developing larva is reduced and the food is a greater distance from it. Both of these would require the larva to leave less and less of its posterior end in its respiratory funnel. This latter possible function tends to be supported by the fact that the ventral button does not begin to protrude until the third instar and only becomes fully developed in the fourth instar.

It is highly probable that the usual pattern of ecdysis involves the ejection of exuviae from the larval respiratory funnel mouth. If exuviae were cast off the posterior end of the larva, rather than the anterior end, the exuviae would be matted into the funnel's base where they would interfere with larval respiration.

Deviations from the usual number of two or three fly eggs laid may be either due to some distracting environmental factor, in the case of a single egg, or perhaps a shortage of hosts, in the case of four eggs. Genetic variability in this species may be another possibility.

With favorable temperatures and rainfall, during the summer months of 1967 and 1968 in Custer County, Oklahoma, host and parasite populations increased. There appears no direct correlation between either rainfall or temperature and the rather sudden increases in the degree of field parasitism, but these increases may be due to the combined effects of both environmental factors. The doubling phenomena of the parasitic fly, mentioned above, may also involve greater parasite biotic potential than that found in the host under these environmental conditions.

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