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Jan 15, 1934

ZENILLIA LIBATRIX PANZER, A TACHINID PARASITE OF THE GYPSY MOTH AND THE BROWN-TAIL MOTH^{1,2}

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INTRODUCTION

Early European rearings of the gypsy moth (*Porthetria dispar* L.) and the brown-tail moth (*Nygmia phaeorrhoea* Don.) for the purpose of obtaining natural enemies of these pests for liberation in the United States showed that *Zenillia libatrix* Panzer was a parasite of minor importance on both these insects. Later it was also reared in small numbers from the satin moth (*Stilpnotia salicis* L.). In 1928 a fairly large number of *Z. libatrix* were recovered from *P. dispar* reared at Vecs, Hungary, and study on the biology of the species was begun at the sublaboratory of the Bureau of Entomology, United States Department of Agriculture, in Budapest. This paper gives the results of the study and briefly discusses the attempts that have been made to establish the parasite in New England and the probability of its establishment.

REVIEW OF LITERATURE

References to *Zenillia libatrix* are fairly common. In 1908 Townsend (17)⁴ briefly noted its habit of leaf oviposition and the fact that it is double-brooded. Pantel (11, pp. 46, 48) in 1910 placed it (under the genus *Myxexorista*) in his group II of leaf-ovipositing tachinids and figured the egg and an ovariole. Howard and Fiske (8, pp. 90-91) in 1911 and Burgess and Crossman (5, p. 115) in 1929 recorded it as a parasite of both the gypsy moth and the brown-tail moth and noted the number of flies liberated in the United States. In 1920 Baer (1, p. 153) gave a list of lepidopterous hosts attacked by *Z. libatrix*. Eidmann (7) in 1926 mentioned the fact that it is very polyphagous and its mode of gaining entrance into the host. Finally, in 1931, Brown (4) recorded it as a parasite of the satin moth and briefly indicated its life cycle.

DISTRIBUTION AND HOST RELATIONSHIPS

Zenillia libatrix is common throughout Europe. Rearings of gypsy and brown-tail moth material in connection with the work of the United States Bureau of Entomology show recoveries from

¹ Received for publication Oct. 2, 1933; issued March, 1934.

² This study was conducted under the direction of C. W. Collins, in charge of the Bureau of Entomology field laboratory, Melrose Highlands, Mass., at its European sublaboratory at Budapest, Hungary, during 1929, 1930, and 1931, and at Melrose Highlands in 1932.

³ The writer expresses his gratitude to R. T. Webber for the use of his notes on *Zenillia libatrix* and for many helpful suggestions; to D. W. Farquhar for laboratory assistance at Melrose Highlands; to Ferenc Mihalyi for laboratory assistance at Budapest; and to W. F. Sellers, W. E. Ripper, R. C. Brown, and Josef Ujhelyi for help in making collections in Europe.

⁴ Reference is made by number (italic) to Literature Cited, p. 113

Spain, France, Germany, Austria, Czechoslovakia, Hungary, Italy, Yugoslavia, and Russia. Wainwright (18) records it from England, and Lundbeck (9) from Denmark, Sweden, and Finland. Howard and Fiske (8, p. 302), Baer (1, p. 153), and Brown (4) state that the species is principally a southern form, but the largest collections made of it in gypsy-moth work were in Hungary, while in rather extensive rearings in Spain, Portugal, and Morocco only a single specimen (from Spain) was reared.

Zenillia libatrix is very polyphagous. A list of hosts recorded in European literature follows. Those starred (*) are species from which, during this study, the parasite has also been reared from field-collected material.

LEPIDOPTEROUS HOSTS OF ZENILLIA LIBATRIX RECORDED IN EUROPEAN LITERATURE AND REARED FROM FIELD-COLLECTED MATERIAL IN HUNGARY

<i>Abrostola asclepiadis</i> Schiff. (1, 3, 8, 9)	* <i>Oxycesta geographica</i> Fab. ⁵
<i>Acrionicta auricomica</i> Fab. (9)	<i>Phlyctenodes verticalis</i> L. (1, 9)
<i>Brephos nothum</i> Hbn. (1, 3, 8, 9)	<i>Porthesia similis</i> Fuess. (1, 9)
<i>Bupalus piniarius</i> L. (1, 7, 9)	<i>Pygaera anachoreta</i> F. (1, 9)
<i>Dasychira pudibunda</i> L. (1, 3, 8, 9)	* <i>Pygaera pigra</i> Hufn. (1, 3, 8, 9)
<i>Drepana cultraria</i> Fab. (18)	<i>Salebria marmorata</i> Alph. (13)
* <i>Euproctis chrysoorrhoea</i> L. (= <i>Nygmia phaeorrhoea</i> Don.) (1, 9)	* <i>Stilpnotia salicis</i> L. (4)
<i>Larentia autumnalis</i> Strom. (1, 3, 8, 9)	<i>Sylepta ruralis</i> Sc. (1, 9)
<i>Liparis monacha</i> L. (2)	<i>Thaumetopoea processionea</i> L. (1, 3, 8, 9)
<i>Loxostege sticticalis</i> L. (10)	<i>Yponomeuta cognatella</i> Hbn. (9)
* <i>Lymantria</i> (= <i>Porthetria</i>) <i>dispar</i> L. (1, 3, 8, 9)	<i>Yponomeuta evonymella</i> L. (1, 3, 8, 9)
<i>Malacosoma neustria</i> L. (1, 3, 8, 9)	<i>Yponomeuta padella</i> L. (1, 3, 8, 9)
	<i>Yponomeuta rorella</i> Hbn. (1, 9)

Although *Pygaera pigra* was the only field-collected host in which *Zenillia libatrix* overwintered, the species also passed the winter successfully in *Oxycesta geographica*, *Calocasia coryli* L., and *Acrionicta rumicis* L. attacked at the Budapest laboratory.

In the United States at the Melrose Highlands (Mass.) laboratory, D. W. Farquhar and R. M. Seeley, under the direction of R. T. Webber, successfully used the silkworm (*Bombyx mori* L.) to rear a summer generation of the flies, and they had a large number of native lepidopteran larvae, representing 23 species, attacked by *Zenillia libatrix* in an attempt to determine whether there was a suitable alternate host for the species in New England. They found that the parasite was capable of completing a summer generation in at least two species, *Euchaetias egle* Drury and *Melalopha inclusa* Hbn., and the writer, on returning to Melrose Highlands, successfully brought it through the winter on *M. inclusa*.

ECONOMIC IMPORTANCE

From 1906 to 1910 only 177 adults of *Zenillia libatrix* were liberated in New England. They were obtained from brown-tail-moth caterpillars collected in Europe. In 1923 the Bureau of Entomology resumed the importation of enemies of the gypsy moth and the brown-tail moth from Europe, but since that time no heavy infestations of *Nygmia phaeorrhoea* have been investigated there and collections of these two species have been confined almost entirely to *Porthetria dispar*. Recoveries of *Z. libatrix* were negligible until 1927, when 407

⁵ Not recorded in literature but reared during this study.

puparia were reared from the gypsy moth at Moscenica, Yugoslavia. In 1928, 1,690 puparia were obtained from 230,000 *P. dispar* collected at Vecs, Hungary. Since that time recoveries have been small, exceeding 100 only twice; 163 were reared from 330,000 *P. dispar* collected at Galgamacs, Hungary, in 1931, and 109 were reared from 320,000 *P. dispar* collected at Jánk, Hungary, in 1930.

Collections of satin-moth larvae were made in Vienna, Austria, from 1928 to 1930. In 1928, 40 *Zenillia libatrix* were recovered from 50,000 *Stilpnotia salicis*; in 1929, 124 were recovered from 90,000 larvae; and in 1930, 26 were reared from 90,000 larvae.

In 1930 about 6,000 brown-tail-moth larvae were collected in Hungary, but no *Zenillia libatrix* were reared. In 1931 no puparia of this species were reared from 1,500 *Nygmia phaeorrhoea* collected near Budapest, Hungary, but 22 puparia were reared from about 1,000 larvae collected at Oberpullendorf, Austria. In 1932, 186 *Z. libatrix* were reared from 5,600 larvae collected at the same place.

This summary shows rather conclusively that *Zenillia libatrix* is usually of slight economic importance as a parasite of the gypsy moth, the brown-tail moth, or the satin moth. Nevertheless, the fact that a large number of puparia were recovered at Vecs, Hungary, in 1928 indicates that the species may become important under favorable conditions. At times it may also be a valuable parasite of other host species which it attacks. Pustovoit (13) has recorded a parasitization by *Z. libatrix* of 10.5 percent on the procession moth (*Thaumetopoea processionea* L.).

TECHNICAL DESCRIPTION

ADULT

The adult fly was originally described as *Musca libatrix* by Panzer (12) in 1798. The original Latin description is very brief, but Lundbeck (9, pt. 7, pp. 338-339) has written the excellent redescription and synonymy which follow. Lundbeck calls the visible segments 2-5; the present writer calls them 1-4. Lundbeck omits the last segment entirely (his fifth, the writer's fourth).

1. *Z. libatrix* Panz.

1798. Panz. Faun. Germ. LIV, 12 (*Musca*)—1824. Meig. Syst. Besch. IV, 400, 281 (*Tachina*) et 1838. VII, 256, 46 (*Exorista*)—1844. Zett. Dipt. Scand. III, 1163, 164 (*Tachina*)—1862. Schin. F. A. I, 464 (*Exorista*)—1891. B. B. Denkschr. Akad. Wiss. Wien, LVIII, 333 (*Myxexorista*)—1907. Kat. paläarkt. Dipt. III, 278—1907. Villen. Wien. Ent. Zeitg. XXVI, 254, 42—1921. Baer, Zeitschr. f. angew. Ent. VII, 153—1924. Stein, Arch. f. Naturgesch. 90, 6, 77, 14 (*Exorista*)—*Tachina fauna* Meig. 1824. 1 c. IV, 393, 268 et 1830. VI, 368 et 1838. VII, 256, 34 (*Exorista*)—1862. Schin. F. A. I, 464 (*Exorista*)—1900. Villen. Bull. Soc. Ent. de Fr. 159, 11, 12 et 1907. Wien. Ent. Zeitg. XXVI, 248, 5—1907. Kat. paläarkt. Dipt. III, 278.

All brownish-yellow pruinose species. Male. Frons above a little narrower than the eye, somewhat protruding. Orbits much broader than frontal stripe, yellow or almost golden; cheeks yellow above, silvery whitish below; jowls grey, nearly one third of the height of the eye; frontal stripe narrow, widening downwards, velvet black or brownish black. Weak outer vertical bristles present. Frontal bristles descending fully to the end of second antennal joint, two uppermost reclinate. Vibrissae ascending fully to the middle, the upper ones small. Orbits and jowls with black hairs. Occiput yellowish grey, with yellowish hairs, and black hairs behind postocular bristles. Eyes pale-hairy. Antennae black,

third joint about four times as long as second; arista as long or fully as long as antennae, thickened in basal half. Palpi yellow. Thorax yellow pruinose, with four narrow black stripes, the median abbreviated behind, the lateral interrupted at the suture into two elongated spots; scutellum bright yellow. Thorax black-haired. Three sternopleural bristles. Abdomen quite yellowish or brownish yellow pruinose, basal segment a little darker; it is black-haired, with a pair of marginal bristles on second segment, a pair of discal and marginal on third and a pair of discal and a row of marginal on fourth segment. Legs black, a little greyish pruinose. Wings yellow at base and anterior margin, outwards slightly tinged; veins brown; first posterior cell narrowly open, ending near apex of wing; discal angle obtuse; apical cross-vein about straight. Squamulae yellow or deep yellow. Halteres yellow.

Female. Similar; frons a little broader, as broad as the eye.

Length 6.5–8 mm.

* * * * *

Remarks: The species is known to vary in colour, being sometimes greyish, but our specimens are all brownish yellow. On account of its varying it has been described under several names; to the above synonymy still can be added: *Tachina dolosa* Meig., *Exorista ancilla* Meig., *Myxexorista macrops* B. B., *M. grisella* B. B., *Zenillia perplexa* Pand., *Z. discerpta* Pand., *Z. fulva* Pand., of these *fauna* Meig., *ancilla* Meig., and *grisella* B. B. belong to the greyish variety.

IMMATURE STAGES

Egg

The egg (fig. 1, *A*) is microtype, about 0.15 mm wide and 0.20 mm long. It is ovoid in shape, and there is a distinct micropyle at the cephalic extremity. The thick upper surface of the chorion is rounded and heavily pigmented with conspicuous reticulations; the lower surface is thin, flat, and transparent. Beneath the chorion there is a thin but strong vitelline membrane enclosing the embryo. A thin layer of gelatinous material sticks the egg to the foliage and may be seen protruding slightly around the ventral margin of the egg.

FIRST-INSTAR LARVA

The larva (fig. 1, *B*) increases greatly in size during the first instar. A specimen removed from the egg is 0.23 mm long and 0.10 mm wide. The 5-day-old specimen figured is 0.45 mm long and 0.16 mm wide. Maximum growth attained in this instar is about 2 mm in length and 0.56 mm in width. The larva is cylindrical, tapering anteriorly and rounded posteriorly. It is composed of the pseudocephalon, bearing the antennal and sensorial organs, and 11 body segments. The pseudocephalon is unarmed, but on all the other segments except the eleventh the colorless cuticle bears rows of minute spines. The first three anterior (thoracic) segments are completely encircled with spines anteriorly. On the fourth (first abdominal) segment the band of spines is broken in the pleural region. The fifth, sixth, and seventh segments have small groups of spines on their anterior margins in the ventral region. The eighth, ninth, and tenth segments have small anterior groups and also small posterior groups in the ventral region. The eleventh segment is unarmed. The arrangement of the spines in rows and their comparative sizes are indicated in the figure. Those on the anterior margins of the segments are directed backward, those on the posterior margins are directed forward. In a small, young larva the spines are very conspicuous, but as the larva grows they become widespread and less prominent.

The buccopharyngeal armature of the freshly emerged larva is shown in figure 1, *D*. It has no articulations. The median tooth is well developed and the basal lobes are very lightly pigmented. There is a pair of lateral plates at the anterior end of the median tooth, and a single salivary-gland plate ventrad of the basal region. When the salivary-gland plate is turned on its side, a pair of minute openings can be seen at the anterior extremity. In fully developed first-instar larvae the buccopharyngeal armature presents a different appearance on account of the further sclerotization of the basal lobes (fig. 1, *E*).

The larva is metapneustic. The two posterior spiracles open on the dorso-pleural portion of the last abdominal segment. The spiracular chambers (fig. 1, *C*) are about twice as long as broad.

The only sensory organs observed are the minute antennal and maxillary organs on each side of the mouth opening. The antennal organs are circular in outline

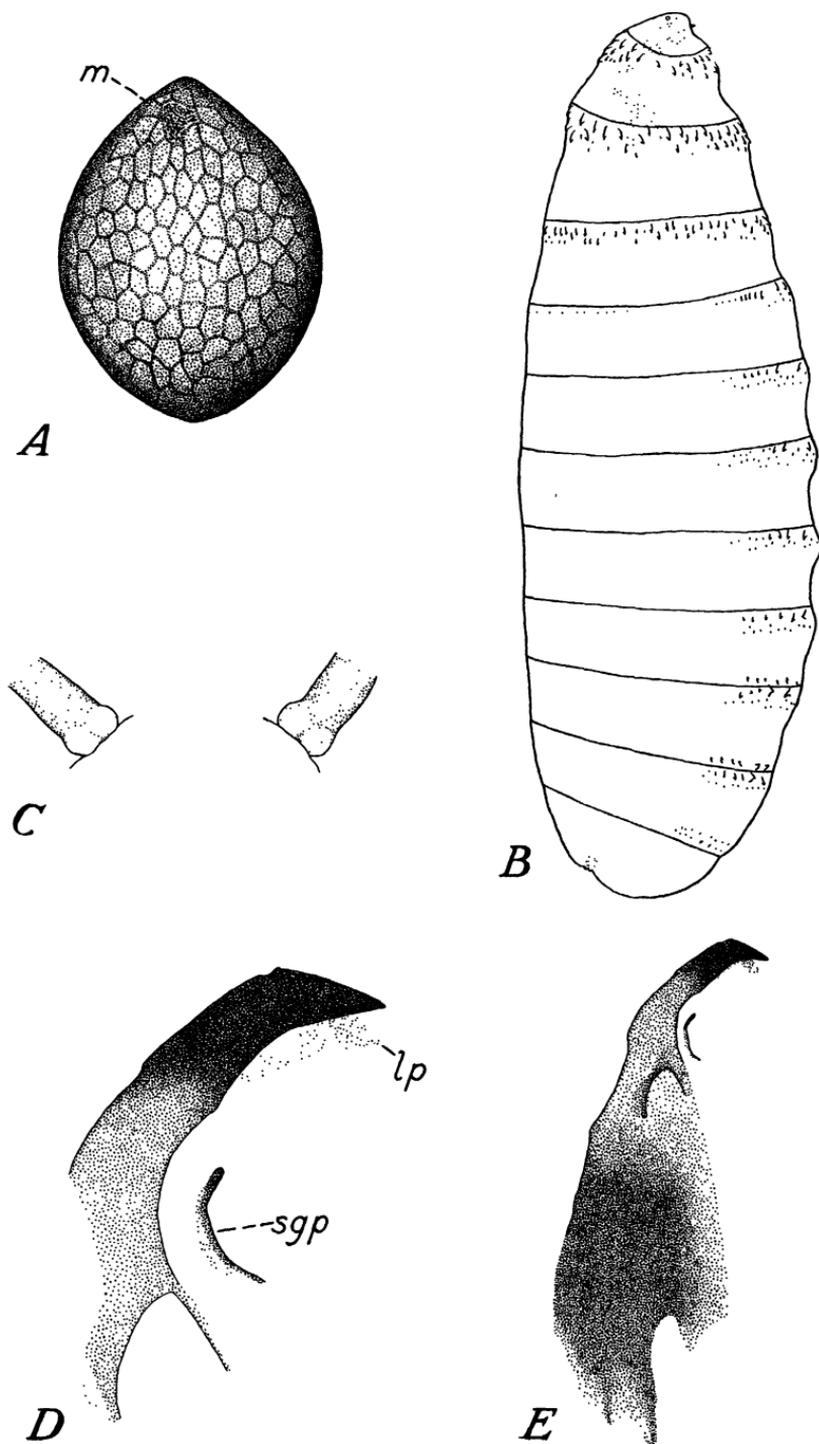


FIGURE 1.—*Zenillia libatrix*, egg and first larval instar: *A*, Egg, dorsal view, showing micropyle, *m* ($\times 220$); *B*, larva, lateral aspect ($\times 250$); *C*, posterior spiracular chambers ($\times 1,300$); *D*, buccopharyngeal armature of freshly emerged larva, showing lateral plates, *lp*, and salivary-gland plate, *sgp* ($\times 1,000$); *E*, buccopharyngeal armature of fully developed first-instar larva ($\times 320$).

and convexly protuberant, measuring 0.0025 mm in both height and breadth. Just below them are the maxillary organs, each composed of a group of minute points raised very slightly above the surface of the cuticle. Each group has 2 rather prominent points and above them 2 and below them 4 or 5 tiny points.

SECOND-INSTAR LARVA

The second-instar larva (fig. 2, *A*) is about 3.3 mm long and 0.9 mm wide when first formed. A larva just about to molt to the third instar was found to be 6.25 mm long and 2 mm wide. It is more robust than the first-instar larva, and the posterior extremity is truncate rather than rounded. The cuticle is still colorless. Although the cuticular spines are much more numerous than in the first instar, they are smaller and weakly pigmented, and therefore far less conspicuous. The pseudocephalon is unarmed. There are completely encircling bands of spines on the anterior margins of the first three segments. Segments 4 to 10, inclusive, have only very small groups of spines on their anterior margins, and these are all in the ventral region. The posterior margins of these segments, on the contrary, are well armed. Segments 4 and 5 are not completely encircled, for there are no spines in the dorsal region. Segments 6 to 10, however, have completely encircling bands on their posterior margins. Segment 11 has no spines on the anterior margin, but on the posterior margin there are from 15 to 20 rows. Below the spiracles of this segment there are several rows of spines directed away from the spiracles in a dorsoventral direction. The other spines are directed anteriorly. Figure 2, *A*, shows the arrangement of the spines, but there is considerable variation in the number of rows in different specimens. The spines on the anterior margins of the segments are pointed backward and those on the posterior border are pointed forward, as in the first instar.

In this instar the buccopharyngeal armature (fig. 2, *B*) terminates in a pair of lateral hooks. There are no articulations. The dorsal wing of the ventral plate is much longer than the ventral wing, but there is no progressive sclerotization of the basal wings as in the first instar. At the base of the lateral hooks there is a small sclerite, the hypopharyngeal plate, and dorsad of it the epipharyngeal plate. These sclerites are essentially the same in the second and third instars. They will be described in connection with the description of the third-instar larva.

The second-instar larva is amphipneustic. The anterior pair of spiracles (fig. 2, *C*) present two minute papillae, which open on the posterior border of the first body segment. There are no pigmented spiracular chambers connecting them with the tracheae, although the faint suggestion of an unpigmented tube may be found in prepared specimens. The posterior pair of spiracles (fig. 2, *D*) are well developed. Each has two papillae and often one of them is branched, as in the figure. The heavy spiracular chambers are about one and one half times as long as broad. The scar formed from the first-instar spiracles is prominent at the base of the spiracular openings.

The sensorial organs on the pseudocephalon are practically the same as in the first instar. The only difference is that they are raised a little higher. In this instar 4 pairs of small sensorial organs, having the form of fingerlike projections, were noted on the last abdominal segment, 2 pairs above the spiracles and 2 below.

THIRD-INSTAR LARVA

The third-instar larva (fig. 3, *A*) has the same form as the preceding instar. It is much larger, measuring 7.5 mm long and 2.5 mm wide to 11 mm long and 3.5 mm wide. The cuticle is colorless and transparent and armed as before with tiny spines, but in this instar the spines are relatively so small that it is hard to see them. The pseudocephalon is armed, bearing 3 or 4 short rows of spines on each side of the mouth opening. Segments 1 to 9, inclusive, have completely encircling bands of spines on their anterior margins. On segment 10 this band is incomplete, there being no spines in the dorsal region. Segment 11 has no spines on its anterior margin. The anterior bands on the first three segments are of nearly uniform width throughout, but the bands on the abdominal segments are much wider on the venter where they cover the pseudopodia. Proceeding posteriorly there is a diminution of spines on the dorsal region on the anterior margins of the segments. The first three segments have no spines on their posterior borders. Segment 4 has a few, and the number on each segment increases proceeding posteriorly. On the posterior margins of segments 7 to 11 there are completely encircling bands of spines. On segment 11 there may be as many as 20 rows directed anteriorly, and several rows below the spiracles have a dorsoventral

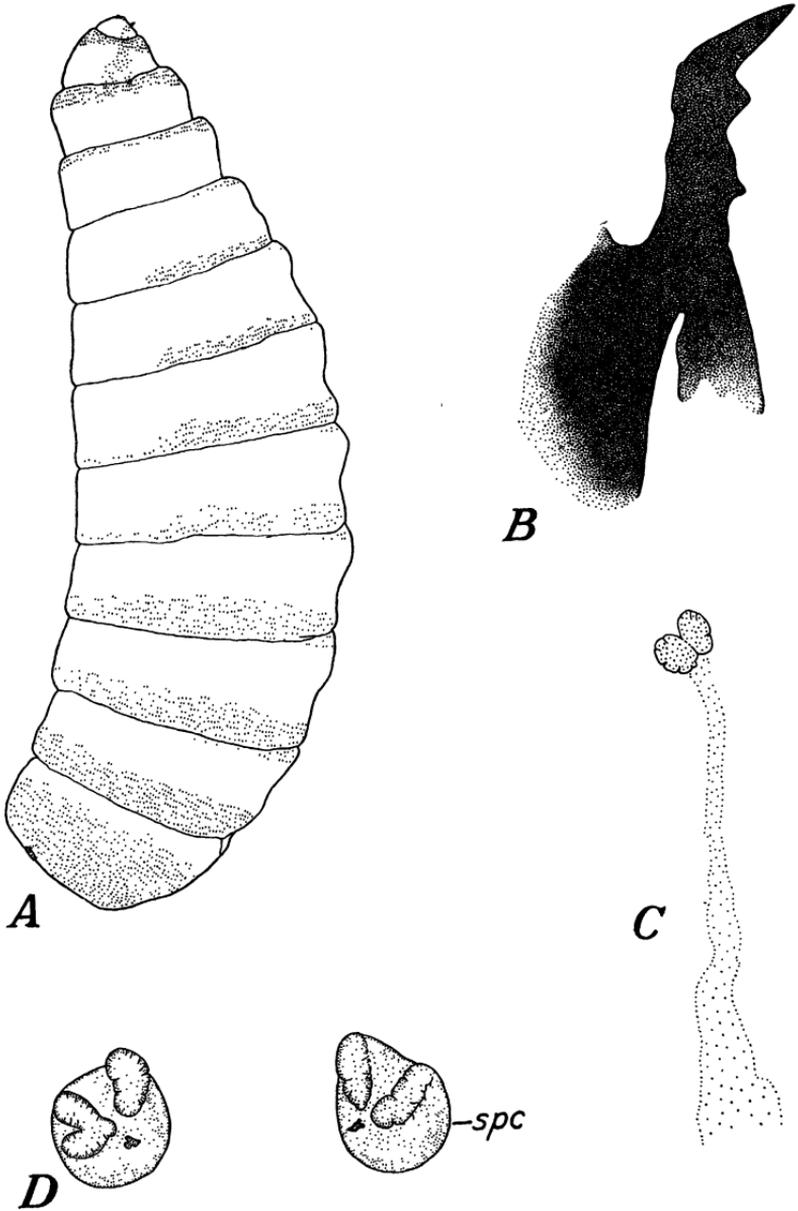


FIGURE 2.—*Zenillia libatrix*, second larval instar; A, Larva, lateral aspect ($\times 21$); B, buccopharyngeal armature ($\times 160$); C, anterior spiracles ($\times 600$); D, posterior spiracles, showing spiracular chambers, *spc* ($\times 200$).

direction. Figure 3, *A*, shows the disposition of the spines, but they are actually by no means as prominent as here indicated. The spines on the anterior margins of the segments point backward, and those on the posterior margins point forward as before.

The buccopharyngeal armature (fig. 3, *B*) is quite different from that of the second-instar larva. The lateral hooks are much straighter, there is an articulation between the intermediate region and the basal region, the dorsoanterior angle of the dorsal wing of the basal plate is strongly produced anteriorly, and there is a weakly sclerotized connection between it and the lower portion of the lateral hook. In many specimens a small opening is seen in the lateral hooks at the base of the ventral projection. It is believed that this is formed by the cells which generate the anterior hooks, as shown by Thompson (16, p. 39, pl. IX, fig. 23) in the larva of *Miltogramma punctatum* Meig., for in freshly molted third-instar larvae this opening is quite large. In many specimens the ventral projection of the lateral hooks seems to have a well-developed spine at its apex. This spine, though, is actually attached to the cuticle. Just above the intermediate region between the lateral hooks, the hypopharyngeal plate (fig. 3, *E*) may be distinguished. This is a small, irregularly shaped sclerite having two unsclerotized areas in the center of which are minute sensoria. The hypopharyngeal plate is attached basally to the intermediate region and anteriorly to the labium. The labium is a tough membrane armed with a varying number of well-developed spines. Just dorsad of the hypopharyngeal plate is the minute epipharyngeal plate (fig. 3, *F*). This plate varies considerably in shape. Often it is deeply emarginate. It has several unsclerotized areas bearing sensoria, as indicated in the figure.

The larva is amphipneustic in the third instar. The anterior spiracles (fig. 3, *C*) are well developed; they usually bear two papillae, and one specimen has been observed with three. The spiracular chamber is broad, and it widens abruptly into a cap fitting over the trachea. The posterior spiracles (fig. 3, *D*) are large, heavily sclerotized, and strongly raised. They are almost half as high as broad. Each spiracular plate has three respiratory slits. The molting scar is rather inconspicuous. The specimen figured was taken from a fairly young third-instar larva in order to show the respiratory slits well, but in an older larva almost the entire surface of the spiracle, with the exception of the slits and a small area around the molting scar, is pigmented to a deep black color.

The sensory organs on the pseudocephalon, antennal and maxillary, as well as the four pairs of fingerlike sensory organs on the eleventh segment, are the same as in the second instar, but they are even more prominently raised from the surrounding cuticle. No other sensory organs have been distinguished.

THE PUPARIUM

The puparia average about 8 mm long and 3 mm wide at the center. They are dull red. Both the anterior and posterior ends of the puparium are rounded. The posterior spiracles are situated a little above the longitudinal axis and just anterior to the apex. The spiracles are shiny black and raised almost half as high as their width. The anal opening is on the under side on the anterior margin of the eleventh segment. The anterior spiracles are very small but distinct.

The pupal respiratory apparatus (fig. 3, *G*) is of the reduced type, the prothoracic cornicles being absent. The tubes that usually connect them with the internal spiracles are present, and there is a small, slightly roughened, yellowish area in the cuticle of the prepupa where the apex of this tube comes in contact with the puparial shell. The internal spiracles are well developed. They bear about 200 respiratory papillae arranged along 5 or 6 radiating branches.

BIOLOGY AND HABITS

SEASONAL HISTORY

Zenillia libatrix passes the winter as a first-instar or second-instar larva within the host pupa and completes its development early in the spring. In the laboratory the first flies appeared April 6, 1928, May 18, 1929, and May 16, 1931. An adult male was taken in the field at Vecs, Hungary, on May 18, 1929.

The first adults of *Zenillia libatrix*, therefore, attack *Porthetria dispar* or some other host larva from about the middle of May until

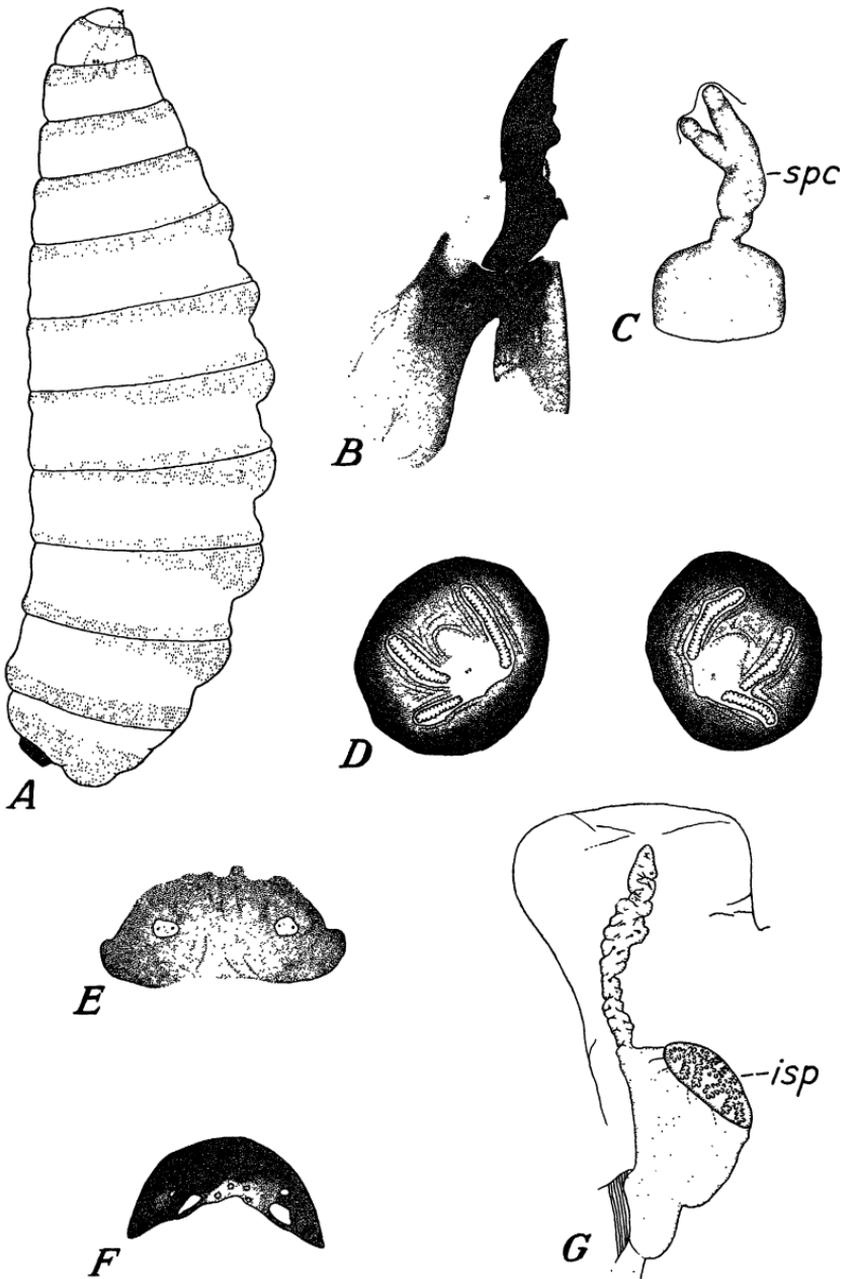


FIGURE 3.—*Zenillia libatrix*, third larval instar and pupa: *A*, Larva, lateral aspect ($\times 13$); *B*, buccopharyngeal armature ($\times 75$); *C*, anterior spiracles, showing spiracular chambers, *spc* ($\times 160$); *D*, posterior spiracles, dorsal view ($\times 60$); *E*, hypopharyngeal plate ($\times 425$); *F*, epipharyngeal plate ($\times 500$); *G* pupal respiratory apparatus, showing internal spiracle, *isp* ($\times 66$).

the first of June or later. Puparia of *Z. libatrix* were recovered from field-collected *P. dispar* between June 22 and July 20 in Hungary. Adults issued between July 6 and August 6 in the laboratory, but probably somewhat later in the cooler forest. It is questionable whether another complete generation of *Z. libatrix* develops in nature. There is probably time, for a second summer generation is easily reared in the laboratory. Nevertheless, it seems doubtful, because of the scarcity of host material late in July and early in August and because flies issuing at that time could live long enough to attack larvae in which their progeny would overwinter. One female of *Z. libatrix* was taken at Vecs on August 25, 1928. The only field-collected larvae in which this parasite overwintered were *Pygaera pigra* Hufn. collected on October 6 and 10 near Budapest, Hungary.

In Hungary, therefore, *Zenillia libatrix* has at least two generations a year and possibly a partial third, while farther south it may have three regularly.

LENGTH OF LIFE

Zenillia libatrix adults live a considerable time under laboratory conditions. As many as five flies were held in glass-covered wooden boxes 5.9 by 7.9 by 3.9 inches (15 by 20 by 10 cm). They were fed lump sugar and honey solution (1 part of honey to 5 parts of water) held on sponges. When the flies were not being used, they were kept in a dark, cool place.

The average length of life of 18 mated females was 49.7 days, with a minimum of 27 and a maximum of 65 days; 21 males averaged 29.4 days, with a minimum of 8 and a maximum of 49 days; and 6 unmated females averaged 47.1 days, with a minimum of 34 and a maximum of 56 days. Of 4 males and 2 females issuing on July 12 which were given neither food nor water, 2 of the males lived 4 days, the other 2 males lived 5 days, and both females lived 5 days.

MATING

Zenillia libatrix adults mate readily in cloth-covered cages held in the light, but not in the direct sunlight. They prefer the morning hours. Temperatures from 64.4° to 77° F. (18° to 25° C.) are favorable. The male flies are particularly attracted by flying females. The average time in coitus, for 16 pairs, was 85 minutes, with a minimum of 35 and a maximum of 130. Although females up to 3 or 4 days old mate fairly readily, freshly emerged females and males from 2 to several days old mate best.

Female flies never mated more than once, but experimentation indicated that 1 male can fertilize about 8 females. One hundred eggs were examined from each of 8 females fertilized by a single male, and at least 93 percent of the eggs from each female were fertile. A similar examination of the eggs of 8 females fertilized by another male showed that the eggs of each of the first 7 females were at least 92 percent fertile, while the eighth female had only 3 percent of her eggs fertilized.

PREOVIPOSITION PERIOD AND REPRODUCTIVE ORGANS

The reproductive organs of a freshly emerged *Zenillia libatrix* female are shown in figure 4, A. Each ovary consists of a number of ovarioles (fig. 4, B). Dissections showed that in some small flies there were only 61, while in one very large fly there were 92 in one

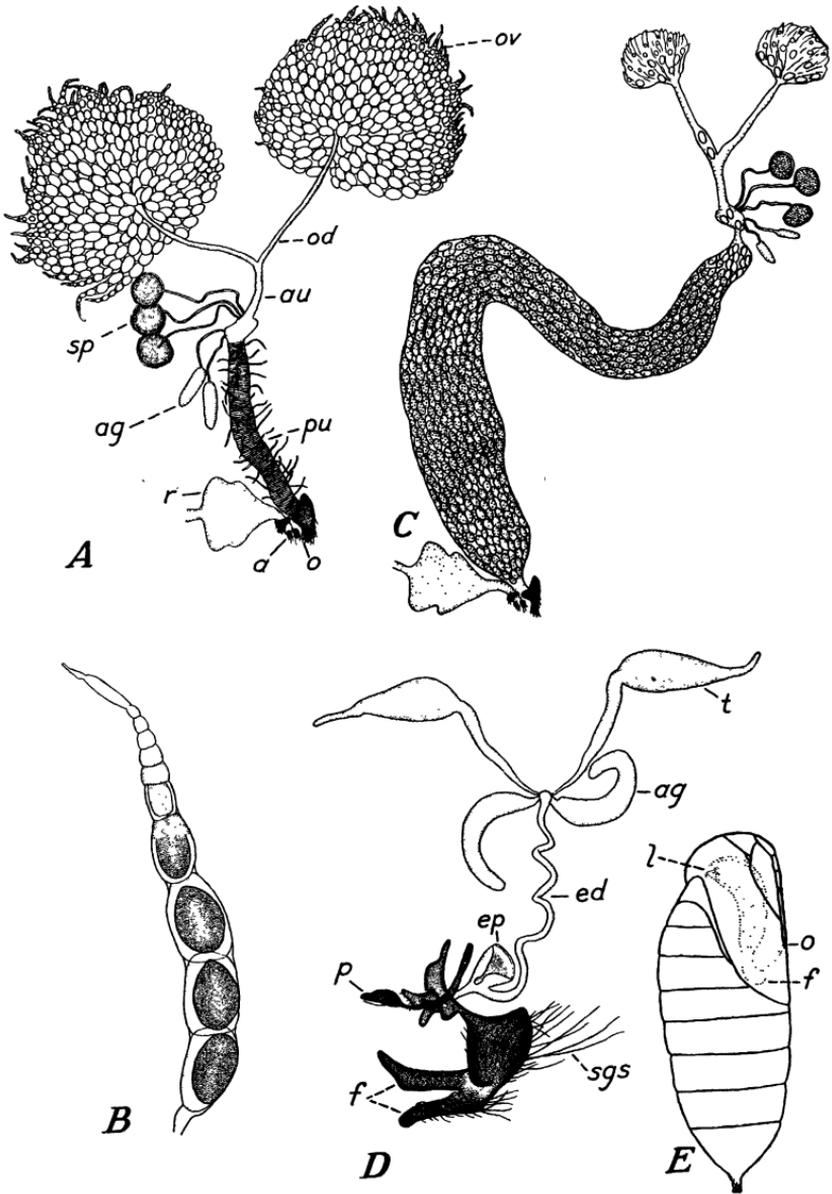


FIGURE 4.—*Zenillia libatrix*; A, Reproductive organs of freshly emerged unmated female; *ov*, ovary; *od* oviduct; *au*, anterior uterus; *sp*, spermatheca; *ag*, accessory gland; *pu*, posterior uterus; *r*, rectum; *a*, anus; *o*, ovipositor ($\times 13$). B, Ovariole ($\times 38$). C, Reproductive organs of mated ovipositing female ($\times 10$). D, Male reproductive organs: *t*, testis; *ag*, accessory gland; *ed*, ejaculatory duct; *ep*, ejaculatory pump; *sgs*, second genital segment; *p*, penis; *f*, forceps ($\times 17$). E, Host pupa with *Z. libatrix* larva in situ; *o*, opening to outside air; *f*, tegumental funnel; *l*, parasite larva ($\times 2$).

ovary and 107 in the other. In a freshly emerged female about 10 developing eggs can be seen in each ovariole. If the fly is held several days before mating, all the eggs that will develop can be distinguished. Dissection showed that 14 is the usual number in an ovariole.

After the fly is mated, the eggs develop rapidly. The mature eggs are pushed into the oviducts and pass the spermathecal opening, where they are fertilized, and from there descend to the posterior uterus. The posterior uterus, which is quite short in the unmated female, enlarges enormously as the eggs descend into it until it forms a complete coil, taking up most of the fly's abdomen. Figure 4, C, shows the organs of a fertilized female extended in order to show the various parts.

Oviposition does not begin until practically all the eggs are in the posterior uterus. Six females were mated and isolated on July 15. One of them started ovipositing in 8 days, 3 in 9, and 2 in 10 days; but it was not until a few days later that they oviposited eagerly.

The male reproductive organs are shown in figure 4, D.

OVIPOSITION

The fact that *Zenillia libatrix* females deposit their eggs on foliage has already been noted. The object of this peculiar habit is to effect entrance into a host larva with the eaten foliage. In confinement the flies oviposit readily on almost any type of leaf, usually along the leaf margin. The fly bends the abdomen forward between its legs and deposits the egg by touching the surface of the leaf. A bit of gelatinous substance on the ventral surface of the egg sticks it to the leaf. The presence of a host larva undoubtedly stimulates oviposition, and if the edges of the leaf are cut the flies will oviposit along these cuts very readily, whether host larvae are present or not. Evidently the flies can sense that a feeding larva is probably responsible for fresh cuts in a leaf.

REPRODUCTIVE CAPACITY

Dissection of several female flies showed that their reproductive capacity varied considerably with the size of the fly. One very small fly had only 820 eggs, while the greatest number found was 2,439. The average number of eggs from 10 flies reared from *Porthetria dispar* was 1,820.

VIABILITY OF EGGS

When *Zenillia libatrix* eggs are laid, the embryos are completely developed, and upon examination distinct movement can be seen. Observations were made to determine how long the eggs that are not eaten remain viable after deposition. Environmental factors affect the eggs so much that it seemed to be impossible to determine the percentage which lived a specific number of days or even their average length of life. Eggs laid on the upper surface of the leaf and exposed to sunlight lost their viability more quickly than those laid on the under surface of the leaf. It was therefore decided simply to try to find the maximum number of days after deposition that eggs would remain so virile that host larvae eating them would become parasitized. For this purpose flies were induced to oviposit on the foliage of trees by confining them for several hours, in small cages, over a few of the leaves. The leaves were then left exposed on the

trees and on successive days were cut and fed to host larvae. In 1931, at Budapest, Hungary, when *Porthetria dispar* larvae were fed *Z. libatrix* eggs from 1 to 12 days old, larvae that ate eggs from 1 to 7 days old were killed by the parasite. In 1932, at Melrose Highlands, when larvae of *Bombyx mori* L. were fed eggs from 8 to 22 days old, the larvae that ate eggs from 8 to 15 days old produced *Z. libatrix*. It is therefore apparent that some of the eggs remain viable at least 15 days. Another fact brought out by these observations was that, although the eggs are scraped off the foliage rather easily when a drop of water is applied, they stick on very well during heavy rains.

MODE OF ENTRANCE INTO HOST

The following observations on the entrance of the parasite into its host were made for the writer by D. W. Farquhar:

By means of the binocular microscope, larvae of *Euchaetias egle* Drury were observed feeding on foliage bearing *Zenillia* eggs. The larvae assumed a position along the edge of the leaf, parallel to its axis, biting off areas of the margin with their laterally operating mandibles. Since the areas bitten off are considerably larger than the eggs, most of the latter are entirely engulfed. However, if the mandibles strike the eggs a glancing blow, the eggs are forced either into the mouth or back onto the leaf to be consumed later. If the mandibles strike the eggs a direct blow, the maggot is ejected from the egg and either enters the mouth of the host or adheres to the foliage until subsequently retaken. Although not observed in the laboratory, it is probable that some eggs or maggots, when struck by the jaws of the host caterpillar, drop to the ground and are lost.

An effort was made to locate the portion of the alimentary tract in which the eggs hatched. Dissection of a *Euchaetias egle* larva 5 minutes after it had fed on foliage bearing *Zenillia* eggs showed both maggots and unhatched eggs distributed from the anterior end of the alimentary tract to the large intestine. The maggots were crawling about in the lumen of the canal, none having penetrated the wall. Those eggs that had not hatched yielded maggots readily when lightly compressed with the forceps. An examination of the excrement of parasitized caterpillars showed many empty eggshells but no unhatched eggs. To determine whether the digestive fluids alone were the direct cause of hatching, the entire digestive tract of caterpillars was dissected out, dried externally to remove all blood, slit open, and eggs were introduced. A pronounced swelling of eggs ensued, owing to imbibition of the digestive juices, but none of them hatched.

From these experiments it appears that (1) hatching is not limited to any one part of the alimentary tract but occurs generally throughout its length, and (2) the digestive juices do not alone cause the eggs to hatch, but they induce a swelling of the eggs which renders them more susceptible to rupture due to the variations in pressure caused by motions of the digestive tract and of the caterpillar as a whole. It is probable that the absorption of the digestive fluids is followed by increased activity of the maggot, which assists in the hatching, particularly in the rupture of the vitelline membrane.

The writer also found that *Zenillia* eggs failed to hatch when immersed in fluids removed from the digestive tract of *Porthetria dispar*, but Severin, Severin, and Hartung (15) observed that the microtype eggs of *Chaetogaedia monticola* Bigot hatched very well when placed in the alkaline juices emitted from the mouths of several species of host larvae.

LARVAL DEVELOPMENT

The time required for *Zenillia libatrix* to complete its larval development depends more on the development of the host than on the parasite itself. The parasite larva hatches very soon after the egg is eaten and bores through the wall of the alimentary tract into the body cavity. It then enters one of the large abdominal muscles, the

silk glands, or occasionally a histoblast. Dissections have shown 46 in silk glands, 37 in muscle fibers, 2 in histoblasts, and 35 "floating free." Those found floating free were probably in muscle fibers that were ruptured by dissection. Larvae have been found in the silk gland 48 hours after the egg was eaten, and it is probable that they reached there some time before that.

The tiny first-instar larva remains in one of these three locations, developing slowly until the host larva starts to pupate. During this period it has no connection with the air and must obtain its supply of oxygen through its body wall or from ingested blood. When the host larva starts to pupate, the parasite larva migrates to the anterior portion of the forming pupa. At this time it starts to grow rapidly, and the basal lobes of the buccopharyngeal armature become sclerotized, as shown in figure 1, *E*. The parasite now forces a small opening in the host pupa between any of the ventral plates of the head sclerites. The irritation set up at this point results in an ingrowth from the host pupa, which rapidly turns dark brown and forms around the parasite larva in the shape of a funnel with the narrow end open to the outside air. This peculiar formation, which is common among the Tachinidae, assures the parasite of a constant supply of air. In *Zenillia* the funnel tube is long and narrow and sharply angled where it widens out (fig. 4, *E*). The wide part of the funnel rests against the inside of the host pupal shell. The rest of the parasite's larval life is completed rapidly. It molts to the second instar soon after the funnel is formed. As it grows the funnel also increases in size. After it molts to the third instar, it rapidly devours most of the contents of the host pupa and issues by cutting an opening between the abdominal segments. Occasionally it forms its puparium inside the host pupa, and the fly issues by breaking the pupal shell.

Because larvae of *Zenillia libatrix* do not begin to develop rapidly until the host larva pupates, the time required for development is variable. Often, when two host larvae are attacked on the same date, one will pupate within a few days while the other may require as long as 2 weeks or more. In such cases the *Zenillia* maggot in the host that pupated may issue and form its puparium while the *Zenillia* maggot in the host larva that did not pupate is still in the first instar. In laboratory rearings 2 *Porthetria dispar* pupae, the larvae of which were fed eggs on August 8, produced *Z. libatrix* puparia 15 and 16 days after attack, and 19 *Stilpnotia salicis* larvae that were fed eggs on August 2 pupated and produced 6 *Z. libatrix* puparia 19 days after attack. In most of the laboratory rearings, though, development was much slower. On August 6, 123 fourth-instar *P. dispar* larvae were attacked, and from them 103 *Zenillia* puparia and 11 *P. dispar* moths were reared. The first puparia were formed on September 1 and the last on September 17. Maximum formation of puparia occurred September 10 and 11, 35 and 36 days after attack.

Zenillia libatrix larvae overwinter in the first or second instar within the funnel formed in their host pupae. Most of the overwintering larvae are in the second instar, but evidently their development is sometimes arrested by cold temperatures before they molt to this instar.

Zenillia libatrix larvae are so tiny (0.23 mm long and 0.10 mm wide) when first hatched that Townsend (17) considered it probable that there were 4 larval instars in *Zenillia* and other tachinids laying microtype eggs, as compared with 3 in other tachinids. First-instar *Zenillia* larvae at all stages of development were therefore examined. By comparing the number and arrangement of the cuticular spines, and the size of the anal spiracles and spiracular chambers, it was definitely determined that *Zenillia* has only 3 larval instars. The enormous growth in the first instar is, nevertheless, very striking. Larvae only 0.23 mm long when hatched regularly increase to 10 times this size, or about 2 mm, without molting. Such an increase may, however, be more common than was formerly supposed. Cushman (6) found that the ichneumonid *Thersilochus conotracheli* Riley also increases enormously in size during the first instar. He does not give dimensions of freshly emerged larvae, but the egg is only 0.33 mm long and a full-grown first-instar larva is 2.00 mm long.

PERIOD SPENT AS A PUPARIUM

After issuing from the host pupa, the full-grown *Zenillia* maggot burrows into the ground a short distance and forms its puparium. No records of the time between the formation of the puparium and the issuance of the adult flies were made under natural conditions. Table 1 shows the time required when the puparia were held in the laboratory. Records were made in September.

TABLE 1.—Time spent by *Zenillia libatrix* in the puparium when held in laboratory

Time after formation of puparium (days)	Adult males issuing	Adult females issuing	Time after formation of puparium (days)	Adult males issuing	Adult females issuing
	<i>Number</i>	<i>Number</i>		<i>Number</i>	<i>Number</i>
11.....	4	1	15.....	0	19
12.....	7	2	16.....	0	4
13.....	18	1	17.....	0	1
14.....	16	15			

As is common among the Tachinidae, the majority of female *Zenillia* issued about 2 days later than the majority of the males. This is an important factor in mating, for the best mating is obtained between freshly emerged females and males from 1 to several days old.

LABORATORY REARING

Zenillia libatrix did not hibernate readily in laboratory-reared material. At Budapest and also at Melrose Highlands, Mass., a large number of host larvae, in which the species develops a summer generation, and which overwinter as pupae, were attacked late in September and early in October. A few of the parasite larvae hibernated, but the majority completed development and the flies issued so late that they could not possibly have found host larvae to parasitize.

Observations were made on the number of *Zenillia libatrix* that could complete development in a single *Porthetria dispar*. Sixty-three host larvae that ate *Zenillia* eggs pupated, and the pupae were isolated. Thirty-seven produced no parasites, 20 produced 1 puparium, 4 produced 2 puparia, 1 produced 3, and 1 produced 5 puparia.

At Melrose Highlands 8 puparia were recovered from a single pupa of *Bombyx mori*.

Fifty *Porthetria dispar* larvae that ate different numbers of eggs of *Zenillia libatrix* were isolated and reared for parasites. In this small number of examples there seemed to be no correlation between the number of *Zenillia libatrix* eggs eaten and the probability that a parasite would develop. One larva that ate 2 eggs pupated, and from these eggs 2 *Zenillia libatrix* completed development; but in a number of instances no parasite developed even when from 10 to 30 eggs were eaten. No superparasitism was detected in these specimens.

It was at first believed that, unless host larvae eating *Zenillia* eggs were fairly large, the eggs would be crushed. It was found, however, that a large percentage of *Zenillia libatrix* completed development in *Porthetria dispar* that were fed eggs when they were small third-instar larvae.

FACTORS LIMITING THE EFFECTIVENESS OF ZENILLIA LIBATRIX AS A PARASITE

The fact that *Zenillia libatrix* has never been reared in large numbers from *Porthetria dispar*, *Nygmia phaeorrhoea*, or *Stilpnotia salicis*, although some puparia are usually recovered from large-scale rearings of each of these hosts, indicates that there must be factors seriously limiting the effectiveness of the species as a parasite. It surely is not the fly's habit of ovipositing on leaves, for *Sturmia scutellata* R.D., one of the most effective of all *Porthetria dispar* parasites, gains entrance into the host in the same manner. Climatic conditions can also hardly be responsible, for *Zenillia* has a wide distribution. *Zenillia* may not be entirely suited to these hosts, but that also hardly seems likely, for when the eggs are eaten under laboratory conditions a fairly large percentage of attacked larvae produce the parasite. No natural enemies of *Zenillia libatrix* were observed, and in *Porthetria dispar* no maggots killed by phagocytes were noted.

A few facts have been noted in rearing work, however, which might be partly responsible for the parasite's low effectiveness. The fact that the species is very polyphagous would seem to limit its effectiveness on any one species. Since *Zenillia libatrix* is double-brooded, a great many individuals complete a generation in the fall after suitable host larvae have gone into hibernation. As these flies perish without reproducing, a small number of flies issue in the spring. Probably the most important limiting factor, though, is that the species must be severely handicapped by parasitic competitors. It requires a long period of development, and host larvae containing small *Zenillia* maggots might be attacked by other parasites, such as *Phorocera agilis* R.D., which would complete development and issue from the host larvae before *Zenillia libatrix* even molted to the second instar. It seems to be just as readily defeated in competition by *Sturmia scutellata*, which usually issues from the host pupa, for this species develops beyond the first instar in the host larva, and therefore when the host pupates it is considerably further developed than *Zenillia*. At Vecs, Hungary, so many puparia of *Zenillia libatrix* were recovered in 1928 that a fair recovery was expected in 1929. As a matter of fact, the species practically disappeared. Apparently it had overwintered successfully, for a male adult was taken in the field that spring. That summer parasitization by *Sturmia scutella* increased enormously.

PROBABILITY OF ESTABLISHMENT

From 1906 to 1910 only 177 adult *Zenillia libatrix* were liberated in New England. In 1927, 327 adults were liberated, in 1928, 1,004 adults, and from 1929 to 1932 only 129 adults were liberated. This is a small number, but, since laboratory work has indicated that the species can hibernate in at least one common native lepidopterous larva, it is quite possible that it has been able to survive. It has never been recovered from collections of *Porthetria dispar*, *Nygmia phaeorrhoea*, and *Stilpnotia salicis* in New England, but perhaps further collections will show that it is actually established.

SUMMARY

Zenillia libatrix is a leaf-ovipositing tachinid, common throughout Europe. It is a parasite of minor importance on the gypsy moth, brown-tail moth, and satin moth and attacks many other species of lepidopterous larvae. It has been liberated in New England but has not yet been recovered.

The various stages of the parasite have been described in detail.

A study of the life history of *Zenillia libatrix* has shown that it has two generations a year and possibly a partial third. The winter is spent as a first-instar or a second-instar larva within the host pupa. The first generation is completed on *Porthetria dispar* or some other host available during May, June, and early July. A second generation may be completed in August, but probably larvae of the second generation hibernate. The parasite has been reared in the spring from larvae of *Pygaera pigra* collected in the field in October.

The adult flies live and mate well in confinement. The females oviposit readily on leaves that have been fed upon or cut. The average number of eggs produced by one female is about 1,800. The eggs may remain viable for as long as 15 days after oviposition. The eggs are eaten by host larvae as they feed upon foliage, and the tiny *Zenillia* larvae hatch and bore their way through the alimentary tract. They enter the silk gland, one of the abdominal muscles, or a histoblast and develop very slowly until the host pupates. They then migrate to the anterior portion of the host pupa, form an integumental breathing funnel, and rapidly finish development. The full-grown larva issues from the host pupa and forms its puparium in the ground. The male usually spends 13 or 14 days in the puparium, the female 14 or 15 days.

As many as 5 *Zenillia* larvae may complete development in a single specimen of *P. dispar*, although usually only 1 parasite issues from a host.

The effectiveness of the parasite seems to be limited by its polyphagous habits, the fact that it is double-brooded, and its slow larval development, which makes it a poor competitor of other larval parasites.

It may be established in the United States, for although only small numbers have been liberated, it has been found to overwinter in a common native species, *Melalopha inclusa*, attacked at the laboratory.

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