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Paradexodes epilachnae, a Tachinid Parasite of the Mexican Bean Beetle [1]

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INTRODUCTION

The Mexican bean beetle (*Epilachna varivestis* Muls.) has been known from the Southwest for about 85 years and appears to have migrated from Mexico, where it is widely distributed.[3] In 1918 it appeared in Alabama and spread rapidly over the central and eastern parts of the United States. Its insect parasites and predators, however, did not follow the bean beetle into the new territory, and few of the parasitic and predacious insects occurring in the United States appear to be of value in the control of this insect.[4] Therefore, after the chance discovery of a dipterous puparium in a quantity of larvae of *Epilachna varivestis* collected near Mexico City in 1921 by H. F. Wickham, who was detailed to search for parasites of the beetle in Mexico, a considerable search was made, chiefly in Mexico, for natural enemies of this insect. E. G. Smyth was engaged by the Bureau of Entomology to conduct this search. In 1922 he found a tachinid parasite of the larval stages of the bean beetle abundant at Mexico City and shipped several hundred parasitized hosts and puparia to the junior author at Birmingham, Ala. Adults were

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[2] The authors are indebted to Alvah Peterson, of the Ohio State University, and C. C. Plummer, R. W. Brubaker, G. V. Johnson, J. W. Apple, and others of the Bureau of Entomology and Plant Quarantine for assistance in handling and colonization work. All the drawings were made by the senior author.

[3] Landis, B. J., and Plummer, C. C. THE MEXICAN BEAN BEETLE IN MEXICO. Jour. Agr. Res. 50: 989–1001, illus. 1935.

[4] Howard, N. F., and Landis, B. J. PARASITES AND PREDATORS OF THE MEXICAN BEAN BEETLE IN THE UNITED STATES. U. S. Dept. Agr. Cir. 418, 12 pp., illus. 1936.

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reared and submitted to the late J. M. Aldrich, who recognized them as new and described the species in 1923 [5] as *Paradexodes epilachnae*. In 1923 Smyth again collected and shipped parasitized hosts and puparia to Birmingham. As had been the case the previous year, the parasite did not survive the winter or become established after liberation, and the project was discontinued. It was later thought that a more intensive study of the parasite and its hosts in Mexico might yield sufficient knowledge to make its successful introduction into the United States possible. In 1929 and 1930 the senior author was detailed to make such a study, and the work was carried on at Mexico City.

During the period 1931–36 the parasite was reared at Columbus, Ohio, by the authors. Some of the results of these studies are recorded herein.

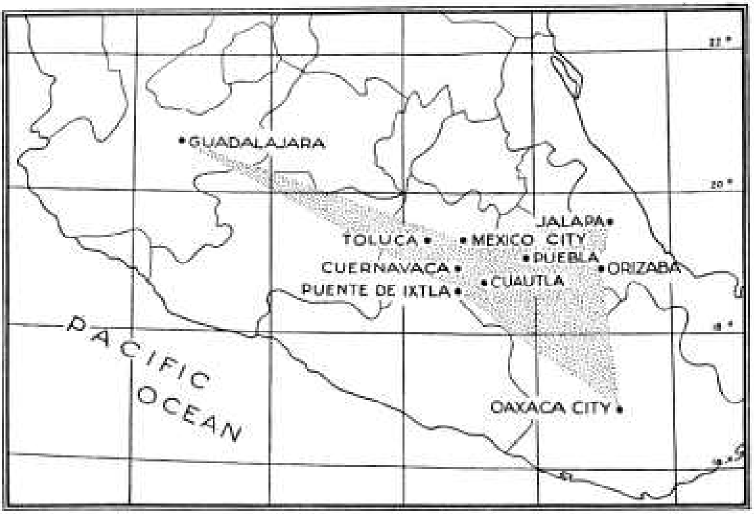

FIGURE 1.—Map of central Mexico showing the area in which *Paradexodes epilachnae* was collected.

The parasite was found abundantly at Mexico City and its presence was also established within the area from Jalapa, Vera Cruz, west to Guadalajara, Jalisco, and south to Oaxaca, Oaxaca (fig. 1).

HOSTS OF PARADEXODES EPILACHNAE ALDRICH

The known hosts of *Paradexodes epilachnae* in Mexico are *Epilachna varivestis* Muls., *E. mexicana* Muls., *E. defecta* Muls., *E. obscurella* Muls., and *E. virgata* Muls. In 1923 Smyth reared puparia, apparently of *P. epilachnae*, from larvae of *E. defecta* Muls. which he collected at Quetzal, Guatemala. The squash beetle (*E. borealis* (F.) was found to be a suitable host under insectary conditions at Columbus. It is assumed that *E. borealis* and perhaps other epilachnids not observed in Mexico are hosts of this parasite.

[5] ALDRICH, J. M. A NEW PARASITIC FLY BRED FROM THE BEAN BEETLE. Ent. Soc. Wash. Proc. 25: 95–97. 1923.

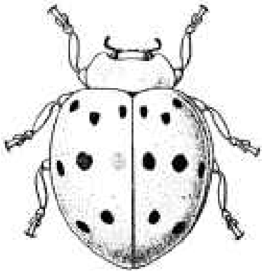

FIGURE 2.—*Epilachna varivestis:* Adult, × 5.

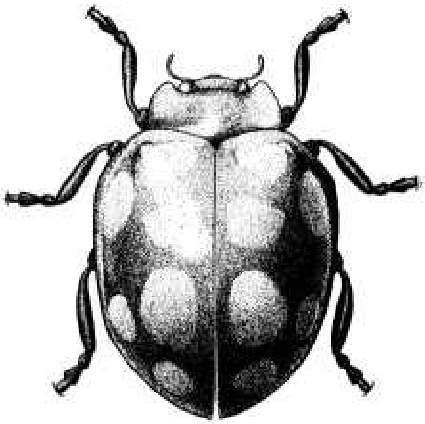

FIGURE 3.—*Epilachna mexicana:* Adult, × 5.

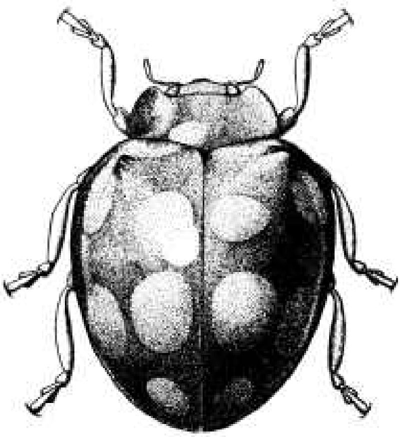

FIGURE 4.—*Epilachna defecta:* Adult, × 5.

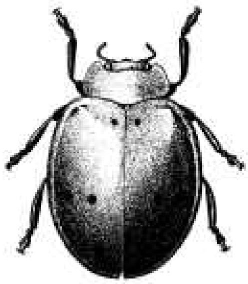

FIGURE 5.—*Epilachna obscurella:* Adult, × 5.

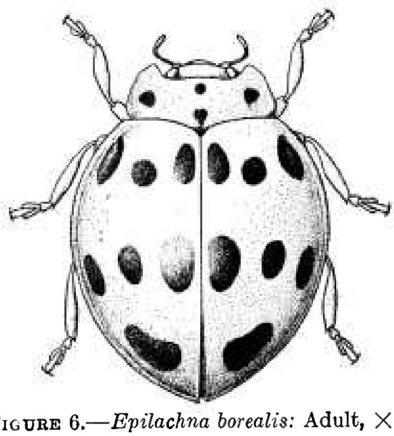

FIGURE 6.—*Epilachna borealis:* Adult, × 5.

Epilachna varivestis (fig. 2) feeds on cultivated and wild beans (*Phaseolus* spp.), beggarweed (*Meibomia* spp.), and occasionally other legumes. At Mexico City, where there is one generation a year, larvae are present from the latter part of June until some time in October (fig. 7). In more tropical areas of Mexico two or more generations of *E. varivestis* occur, but the period during which larvae are present is nearly the same.

Epilachna mexicana (fig. 3) feeds on *Cestrum aurantiacum*, *C. nocturnum*, *Echinocystus* sp., *Sicyos laciniata*, *Solanum bicolor*, *S. nigrum*, and probably *C. lanatum*.[6] The adult is 8.5 mm. in length. The larval, pupal, and adult stages are black, except for 12 large yellow or brick-red spots on the elytra of the adult. Large numbers of eggs are laid in elongate masses on the midribs of the undersides of leaves. At Cuernavaca, Morelos, where there are two generations a year, adults were found on foliage along the banks of streams from June 2 until October. Mature larvae of the first generation were most abundant July 20. Adults were collected at Puente de Ixtla, Morelos, June 11 and July 25; at Xochimilco, Federal District, June 28; at Taxco, Guerrero, July 10; at Oaxaca, Oaxaca, August 22; and at Mexico City, Federal District, August 29.

Epilachna defecta (fig. 4) feeds on *Cestrum aurantiacum*, *C. lanatum*, *C. nocturnum*, *Solanum bicolor*, and *S. nigrum*.[7] The adult is 8.5 mm. in length. The legs, ventral sclerites, and mouth parts are dull orange, and 10 large brick-red spots occur on the black elytra. Two egg masses along the midrib on the underside of leaves contained 82 and 89 eggs, respectively. The larvae and pupae are black. Larvae and adults were present at Jalapa and Cordoba, Vera Cruz, on June 7 and July 2, respectively; adults were present at Guadalajara, Jalisco, on August 8.

Epilachna obscurella (fig. 5) feeds on beans, squash, and wild cucurbits. The adult is 6.3 mm. in length, is black, and covered with a gray-green pilosity, except for 14 or fewer small spots on the elytra. The larvae are black, except immediately after molting, when the spines are white to the tips. The pupae are gray with black stripes or patches and resemble pupae of *E. varivestis* reared at low temperature. This species is less prolific than *Epilachna varivestis*. Larvae leaving the egg mass scatter so that two or more larvae rarely are found feeding on the same leaf. On squash the adults feed at the margins of the leaves similarly to *E. borealis*, but areas are not "ringed" and wilted prior to feeding. Adults and larvae were found at Chalco and Xochimilco, Federal District, and at Cuautla, Morelos, from June 11 through September, where they were associated with *Epilachna varivestis* in mixed plantings of corn, beans, and squash.

Epilachna borealis (fig. 6) feeds on wild and cultivated cucurbits. The adult is 8 mm. in length. The larval and pupal stages closely resemble those of *E. varivestis*. The adults differ in that *E. borealis* has 14 rather large black spots on the elytra and *E. varivestis* has 16 rather small black spots on the elytra. Adults were collected at Puente de Ixtla, Morelos, June 11 and July 24; at Vera Cruz and Cordoba, Vera Cruz, June 5 and July 3, respectively, and at Guadalajara, Jalisco, August 8.

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[6] Records obtained from the following: GORHAM, HENRY STEPHEN. EPILACHNA MEXICANA. Biologia Centrali-Americana 7: 240. 1899. Also from correspondence of E. G. Smyth.

[7] See footnote 6.

Epilachna virgata was collected near Cuernavaca, Morelos, in December 1931, by C. C. Plummer. Adults reared from pupae were approximately 5 mm. in length. The head and thorax are dull red, and the elytra are orange with eight irregular brown spots.

Larvae of species of *Epilachna* parasitized by *Paradexodes epilachnae* in Mexico were found in the field from June 7 to December 3 (fig. 7). Life-history studies in the laboratory showed no indication of a diapause or resting stage sufficiently long to carry the parasite through the dry winter months without some reproduction. It seems probable that certain host larvae are present in some regions in Mexico less affected by seasonal drought and that these sustain a small population of the parasite throughout the year.

The percentage of parasitization of the first mature host larvae occurring on the Central Plateau of Mexico at the beginning of the rainy season is very low, and the increase is gradual until the host populations have reached their greatest abundance in August and

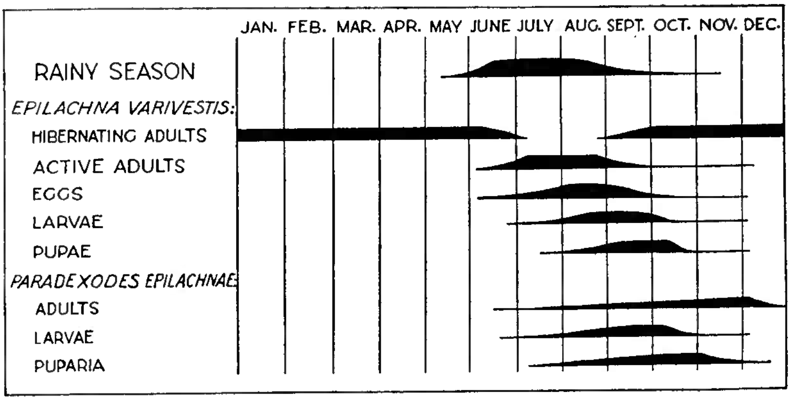

FIGURE 7.—Seasonal activities of *Epilachna varivestis* and its parasite, *Paradexodes epilachnae*, as determined by field observations associated with laboratory rearings at Mexico City. The extremes of each area represent approximately the earliest and latest activities, while the apex represents the peak of such activities.

September (fig. 8). With the decline of host abundance due to lower temperature and less frequent rains the percentage of parasitization increases rapidly and the highest parasitization occurs late in the season.

In the vicinity of Mexico City *Paradexodes epilachnae* occurs in greatest abundance in larvae of *Epilachna varivestis* and *E. obscurella*. Parasitized hosts were collected from the middle of July until December 3. In 1929 the maximum parasitization of 81.4 percent occurred in larvae collected November 4. In 1929 and 1930 the most severe infestation of *E. varivestis* was found near Chalco, Federal District, 33 miles southeast of Mexico City. Here the parasitization averaged nearly 45 percent for a period of 15 days during the latter part of September. Early in October frosts killed the bean plants, and the terrain was gradually leveled by wind. In February soil was sifted in this locality, and although great quantities of puparia of *P. epilachnae* were found, all were either empty or contained dead specimens.

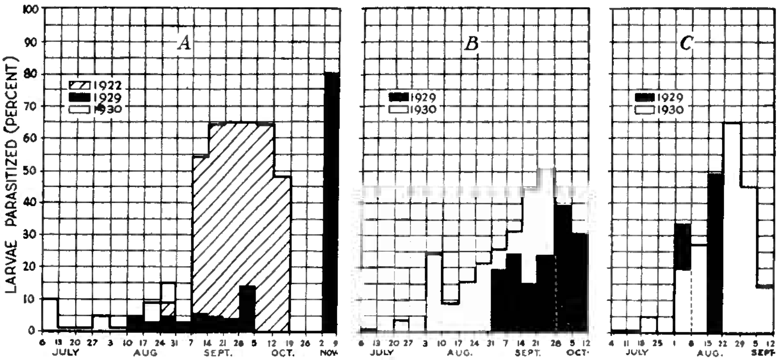

FIGURE 8.—Percentage of larvae of *Epilachna varivestis* parasitized by *Paradexodes epilachnae* in three localities in central Mexico during 1922, 1929, and 1930: *A*, Mexico City, Federal District; *B*, Chalco, Federal District; *C*, Cuernavaca, Morelos.

The average parasitization for the seasonal periods of 3 years during which larvae of *Epilachna varivestis* were collected in the vicinity of Mexico City ranged between 16.3 and 54.0 percent (table 1).

TABLE 1.—*Percentages of Epilachna varivestis parasitized by Paradexodes epilachnae at Mexico City, Federal District, during 1922, 1929, and 1930*

Year	Period	Hosts collected	Rate of parasitization
		Number	*Percent*
1922	Aug. 25 to Oct. 13	2,520	54.0
1929	Aug. 26 to Oct. 9	21,831	16.3
1930	Aug. 25 to Sept. 24	41,822	34.1

In the vicinity of Cuernavaca, Morelos, *Paradexodes epilachnae* occurs in larvae of *Epilachna varivestis* and *E. mexicana*. The larvae of *E. mexicana* are present both before and after the seasonal occurrence of larvae of *E. varivestis*. The parasite was present in one or both hosts from July 4 until September 7. Parasitization was less than 5 percent throughout July, reached a maximum of 65 percent on August 24, and declined to 13 percent on September 6. The small amount of parasitization occurring late in the summer appeared to be due to the high temperature of the soil in which puparia occur and to the great amount of hyperparasitization.

At various times during the growing season of 1930 a few localities other than the Federal District and Cuernavaca, Morelos, were visited in order that the parasite situation might be ascertained. The results of these visits are summarized in table 2.

TABLE 2.—*Abundance of Paradexodes epilachnae in various localities in Mexico on different dates in 1930*

Date	Place	Elevation	Host	Rate of parasitization
		Feet		*Percent*
June 7	Jalapa, Vera Cruz	4,681	*Epilachna defecta*	35.0
July 2	Cordoba, Vera Cruz	2,756	*E. mexicana*	1.0
July 16	Atlixco, Puebla	6,171	*E. varivestis*	(1)
Aug. 8	Guadalajara, Jalisco	4,987	do	35.0
Aug. 22	Oaxaca, Oaxaca	5,068	do	(1)

[1] Trace.

HYPERPARASITES OF PARADEXODES EPILACHNAE

A large solitary chalcid (*Brachymeria carinatifrons* Gahan)[8] was present in a large proportion of the puparia of *Paradexodes epilachnae* reared from larvae of *Epilachna varivestis* collected by E. G. Smyth at Coapa, Federal District, Mexico, in 1922. This hyperparasite was not found in that locality in 1929 and 1930 but emerged in large numbers from puparia of *P. epilachnae* obtained from larvae of *E. varivestis* and *E. mexicana* collected at Cuernavaca, Morelos, in 1930. In puparia of individuals reared from *E. mexicana* the parasitization was 12.5 percent on July 2, 31 on July 4, and 26 on July 12. In puparia of individuals reared from *E. varivestis* the parasitization was 43.8 percent on August 1 and 21 on August 24. In puparia of individuals reared from larvae of *E. mexicana* collected at Cordoba, Vera Cruz, July 2, the parasitization by *B. carinatifrons* was 13 percent. One adult *B. carinatifrons* was picked from foliage on which adults of *E. mexicana* were feeding at Oaxaca, Oaxaca, August 22.

The hyperparasite oviposits in the epilachnid larva, and the hymenopterous larva enters the maggot of the dipterous primary parasite. The development of the chalcid is retarded until the dipterous host has completed larval development and pupated. At 80° F. puparia of *Paradexodes epilachnae* produced adults of *P. epilachnae* after a developmental period of 10 days or adults of *Brachymeria carinatifrons* after 18.8 days.

Six chalcids, representing an undescribed species of *Tetrastichus*, were reared by C. C. Plummer from a pupa of *Epilachna mitis* Muls., collected at Simojovel, Chiapas, in December 1932. One larval skin of this epilachnid was also found from which a dipterous parasite had emerged.

Of a collection of 37 puparia of *Paradexodes epilachnae* sifted from soil at Columbus, March 30, 1935, 7 puparia each produced an ichneumonid, *Phygadeuon subfuscus* Cress. (fig. 9). During April, May, and June more than 100 of these hyperparasites were bred in the laboratory on puparia of *Paradexodes epilachnae*.

[8] GAHAN, A. B. BRACHYMERIA CARINATIFRONS, NEW SPECIES (HYMENOPTERA: CHALCIDIDAE). Ent. Soc. Wash. Proc. 37: 165-167. 1935.

The female *Phygadeuon subfuscus* (fig. 10) climbs upon the puparium and tests the surface with the antennae and ovipositor. When a depression is found, considerable pressure is applied to the ovipositor, and as the puparium is pierced, the ovipositor is sent far into the

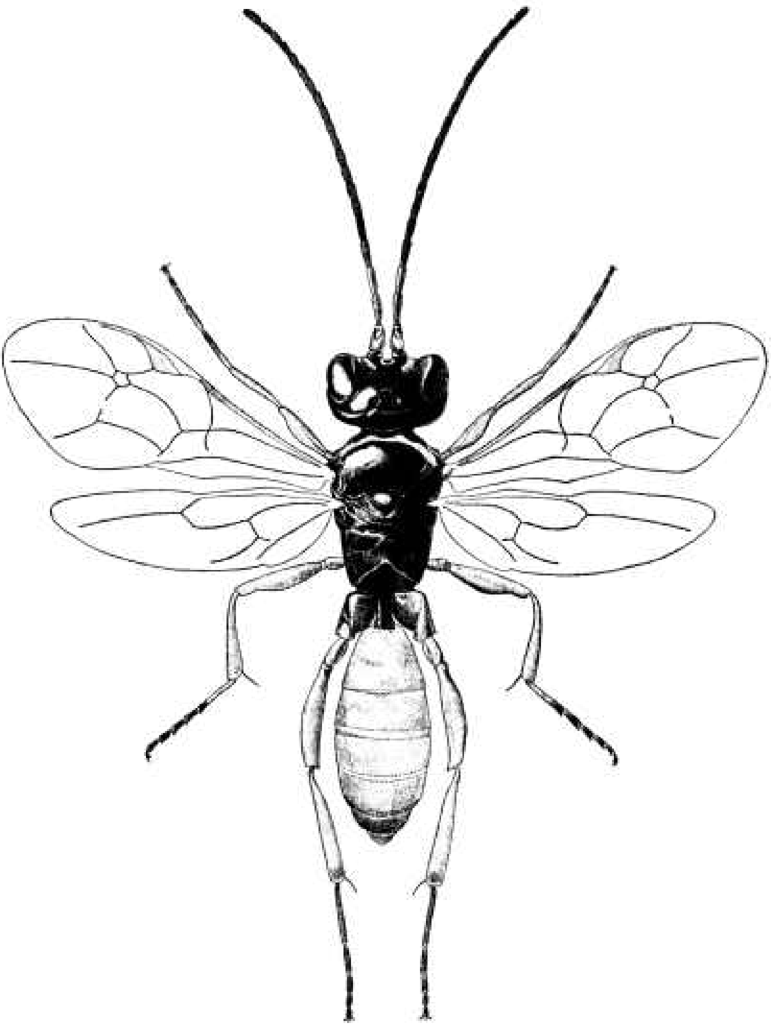

FIGURE 9.—*Phygadeuon subfuscus:* Adult male, ×10.

interior of the host. The tip of the ovipositor is then withdrawn to the cuticula of the larva and an egg is deposited.

The egg is transparent and narrowly elliptical. Although several eggs have been found in one puparium, only one parasite completes development. The egg stage lasts approximately 2 days. There appear to be three larval instars, all of which feed externally on the host within the puparium.

The average length of the developmental period, egg to adult, for 13 individuals held at room temperature was 24.5 days; for 38 individuals at 70° F., 24.6 days; and for 33 individuals at 80°, 19.3 days.

Five individuals of an undescribed species of *Myrmecopia* appeared in a collection of puparia of *Paradexodes epilachnae* sifted from soil at Columbus, September 9, 1935. Several adults of *Phygadeuon subfuscus* also emerged from this collection, so it is difficult to determine whether *Myrmecopia* is parasitic on *Phygadeuon* or on *Paradexodes*.

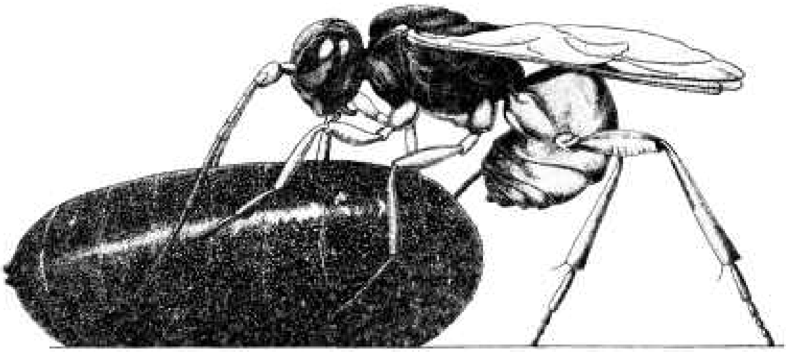

FIGURE 10.—Parasitization of puparium of *Paradexodes epilachnae* by female *Phygadeuon subfuscus*.

Because of the time which elapsed between the emergence of *Phygadeuon* and *Myrmecopia*, it appears that *Myrmecopia* is a tertiary parasite of *Epilachna varivestis*.

ATTEMPTS TO INTRODUCE PARADEXODES EPILACHNAE INTO THE UNITED STATES

During September and October of 1922 and 1923 shipments of puparia of *Paradexodes epilachnae* from the Federal District and Cuernavaca, Morelos, Mexico, totaling approximately 2,400 individuals were received at Birmingham. Some of the puparia were stored at a temperature near 50° F., and the adult parasites issuing from the remainder either were liberated in the field or used in biological studies. At least one complete generation of the parasite was bred in the greenhouse, but the stock died out before spring. With the exception of a few adults that emerged and died in the storage boxes, all the stored puparia were found dead in the spring.

Between July 20 and October 12 of 1929 and 1930 shipments of parasite material yielding approximately 60,000 puparia were received from the Federal District and Cuernavaca, Morelos, Mexico, in an especially constructed insectary at Columbus. No parasites were released during 1929 and 1930, and some of the material was stored, some was used for rearing stock, and the balance was used in determining the specificity of the parasite to native phytophagous and carnivorous coccinellids.

In the fall of 1929 attempts to store 2,000 puparia by several methods were unsuccessful. None of the puparia survived when in a fruit-storage vault, where the temperature fluctuated between 40° and 50° F., in a laboratory refrigerator, or in cages at various depths below the surface of the soil. Again in 1930 approximately 12,000 puparia were placed in storage at various temperatures but without success. No temperature was found at which the puparial stage of the parasite entered a diapause. Examination of the stored material at weekly intervals showed that the lower the temperature the more rapidly the puparia succumbed. Although a few malformed adults emerged from puparia stored for 72 days at 50°, samples of puparia removed at intervals showed a gradual increase in the percentage of mortality up to the time of adult emergence in storage (fig. 11). The greatest length of time puparia could be stored without deleterious effect was 44 days at 53.6°.

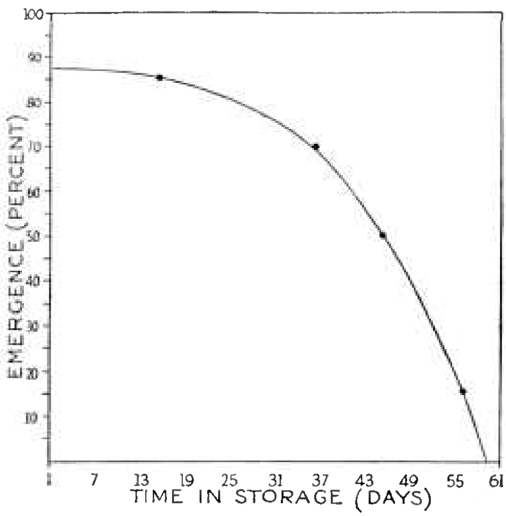

FIGURE 11.—The lethal effect of storage at 50° F. on 1,027 puparia of *Paradexodes epilachnae* as measured by the percentage of mortality in samples of puparia removed at intervals.

As storage of the puparia had failed, it was necessary to breed the parasite without interruption throughout the winter months. Beginning in August 1930, the parasite was bred continuously either in a heated laboratory or in a field insectary for more than 60 months. During this time approximately 60 generations of the parasite were bred.

The rearing of sufficient numbers of host larvae during the periods they were not present in the field was the most difficult problem encountered in the continuous breeding of the parasite. From June until October, except for a short period usually occurring between the two summer generations, the parasite was bred on hosts collected from the field. During the midsummer period of scarcity and the remainder of the year when hosts were not present in the field they were reared under controlled conditions.

Adults of *Epilachna varivestis* were taken from winter hibernation quarters to a heated laboratory, where eggs were laid after 3 weeks. The beetles were confined in wire-screen cages on bean plants grown in earthenware flowerpots. Egg masses were clipped from the bean leaves as laid and placed in Petri dishes on blotting paper moistened with cupric chloride solution. The larvae were reared in wire-screen cages covering bean plants until they were exposed to the parasites. The mortality among laboratory-reared larvae was highest during February because of the poor condition of the bean foilage.

METHODS USED IN BREEDING THE PARASITE

The breeding cages that were found to be most satisfactory for containing the adult parasites measured 12 by 12 by 6 inches. The cage consisted of a one-piece bottom and 1-inch frames of white pine, covered on three sides with thin muslin and on the fourth side with a muslin sleeve 12 inches long. The removable top consisted of a piece of heavy glass. Each cage accommodated approximately 100 adult parasites.

A capillary water fountain, consisting of a wide-mouth bottle 2½ by 2 inches and fitted with folded strips of white blotting paper held loosely by a cotton plug, was placed in each cage. The food consisted of raisins and loaf sugar fastened by black-enameled insect pins.

Electric desk lights containing frosted bulbs provided light on cloudy days and heat on cool nights. Fans placed close to the cages increased the rate of evaporation when the temperature-humidity ratio was unfavorable.

CARE OF PARASITIZED HOSTS

Mature fourth-instar larvae of *Epilachna varivestis* only were used in the breeding work. They were rugged, relatively inactive, and required little food during the time they were exposed to the parasites.

Reared or field-collected larvae were counted into lots of 50 and placed in bottoms of Petri dishes lined with bean leaves. The larvae remained in the parasite cages for 24 hours. The uneaten foliage was then removed from the dishes, and the larvae were placed in flowerpot saucers moistened and lined with fresh bean foliage. Glass plates were placed over the saucers, and all the sets of larvae exposed to parasites on the same day were stacked together. Normal puparia were formed when the proper humidity was maintained.

Puparia were placed in Petri dishes in lots of 100 each on blotting paper disks moistened with cupric chloride solution. Previously the disks had been placed in a mold which gave them an extremely irregular surface. This irregularity reduced the amount of sweating in the dishes and also provided roughened surfaces suitable for parasite emergence.

During the summer months dishes containing puparia occasionally were contaminated with a small dipteron (*Sciara* sp.) and as many as four larvae of this predator were found in one puparium. A covering of finely screened sphagnum moss stopped the breeding of this fly.

DESCRIPTION OF PARADEXODES EPILACHNAE

THE ADULT

Paradexodes epilachnae (fig. 12) was described by Aldrich [9] from many specimens reared by E. G. Smyth from larvae of *Epilachna varivestis* collected at Coapa, Federal District, Mexico, in 1922. Aldrich states that there is no generic difference between *P. epilachnae* and *Urodexodes charapensis* Towns. from Peru.

Aldrich found males from Mexico to be from 5.5 to 6 mm. in length and females from 5 to 5.5 mm. in length. One male, with unusual

[9] See footnote 5, p. 2.

markings, collected at Cholula, Puebla, July 16, 1930, was 8 mm. in length. The average length of 50 males reared by the writers at Columbus was 6.1 mm., and the average length of 66 females was 5.6 mm.

The body and legs are entirely black; the thorax has four black stripes anteriorly when viewed from behind, and the posterior half or more is shining in most lights.

Certain tertiary sexual characters are of value in separating the sexes. In the male the vertex and front are narrow, the parafrontals

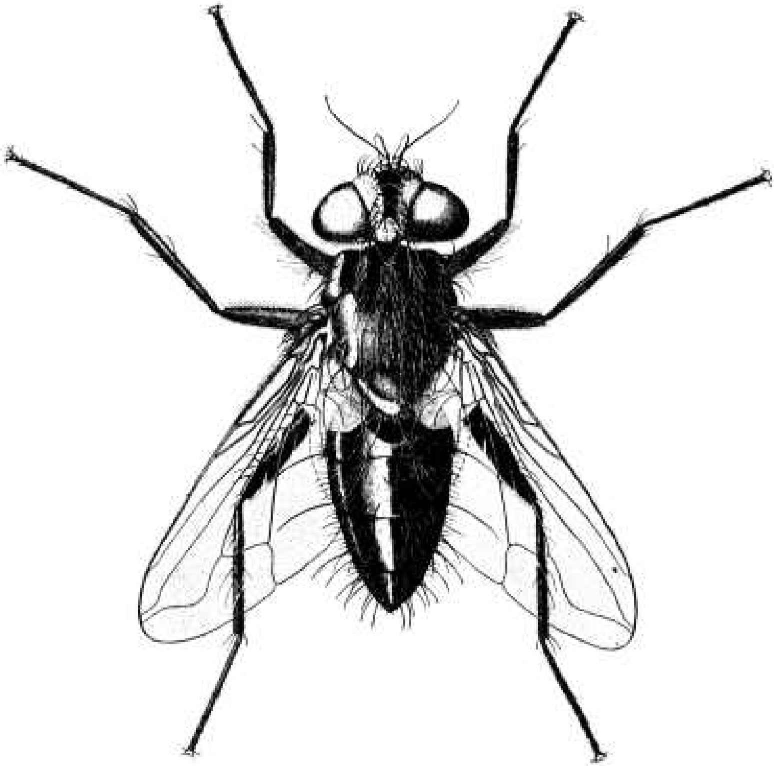

FIGURE 12.—Adult male of *Paradexodes epilachnae*, × 10.

are usually yellowish or golden, the orbital bristles are lacking, and the claws and pulvillae (fig. 13), as well as the wings, are longer than in the female. The abdomen is conical and usually longer than that of the female.

THE EGG

The egg (fig. 14) is subcylindrical and unpedicelled and is 0.4 mm. long at the time of oviposition. A small micropyle is present. The chorion is thin, membranous, minutely pitted, and devoid of color. The chorion is ruptured in most cases by the deposition process. Infertile eggs are slightly larger than fertile eggs of the same age.

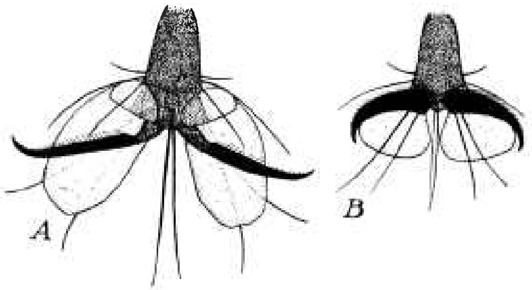

FIGURE 13.—Claws and pulvillae of male (*A*) and female (*B*) *Paradexodes epilachnae.*

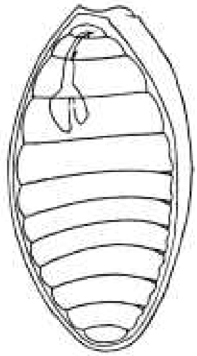

FIGURE 14.—Mature egg of *Paradexodes epilachnae* dissected from the body of a female, × 100.

THE LARVA

Larvae at time of hatching are 0.6 mm. in length and reach a maximum length in the first instar of 1.1 mm. The first-instar larva (fig. 15, *A*) is cylindrical and tapers at the ends. It consists of a rectractile pseudocephalon and 11 distinguishable body segments, all of which are opaque white.

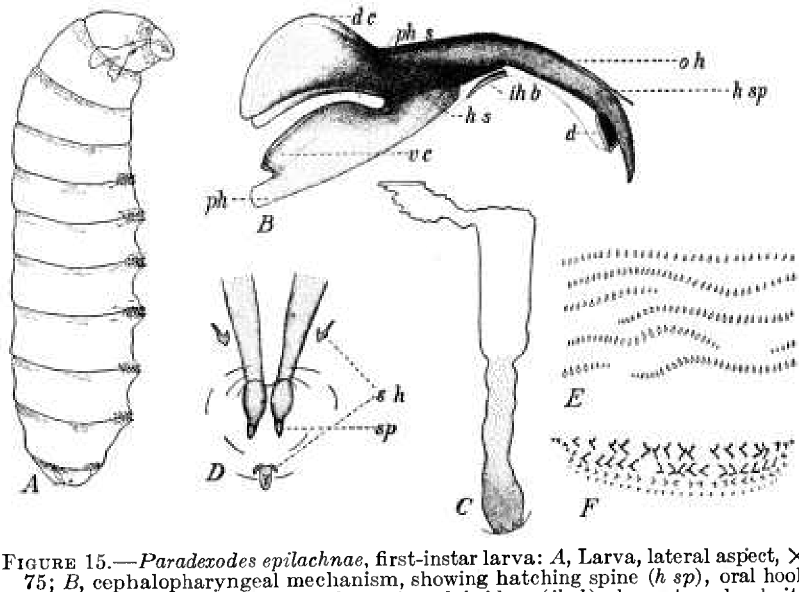

FIGURE 15.—*Paradexodes epilachnae*, first-instar larva: *A*, Larva, lateral aspect, × 75; *B*, cephalopharyngeal mechanism, showing hatching spine (*h sp*), oral hook (*o h*), dental plates (*d*), infrahypostomal bridge (*ih b*), hypostomal sclerite (*h s*), pharyngeal sclerite (*ph s*), dorsal cornu (*d c*), ventral cornu (*v c*), and pharynx (*ph*); *C*, anterior spiracular chamber; *D*, posterior spiracles, showing spiracular opening (*sp*) and stigmatic hooks (*s h*); *E*, segmental cuticular armature; *F*, cuticular armature of ventral fusiform areas.

On each anterior angle of the pseudocephalon is a disklike antennal papilla and a group of approximately six small, circular points slightly raised from the surface of the cuticle. There are no spines on the pseudocephalon, but each body segment bears between four and six rows of spines (*E*), chiefly at the anterior margins. The rows of spines are more pronounced on segments 1, 2, and 10. Ventrally at the union of segments 4 and 5 and continuing through the union of segments 9 and 10 are small fusiform areas each bearing two rows of heavily sclerotized ambulatory spines (*F*). These spines have widely separated, bilobed bases set in the cuticle parallel to the long axis of the larva.

The cephalopharyngeal mechanism (*B*) is not completely sclerotized at the time of hatching. The single narrow oral hook (*o h*) bears

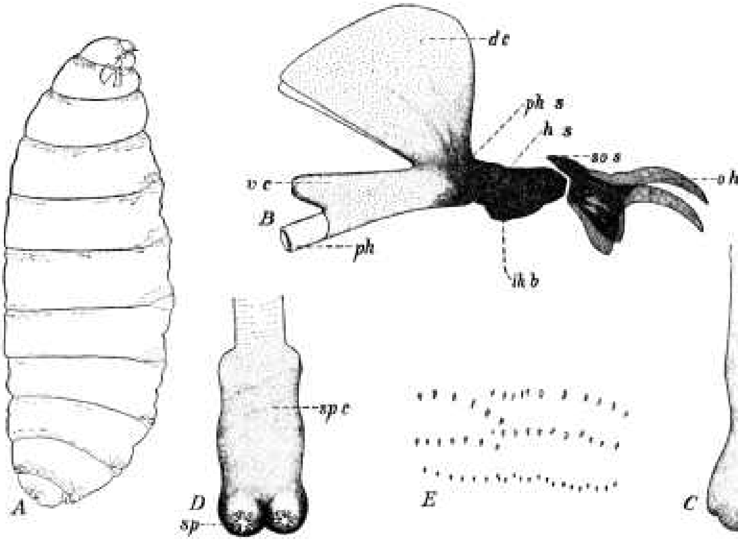

FIGURE 16.—*Paradexodes epilachnae*, second-instar larva: *A*, Larva, lateral aspect, × 20; *B*, cephalopharyngeal mechanism, showing oral hooks (*o h*), supraoral sclerites (*so s*), infrahypostomal bridge (*ih b*), hypostomal sclerite (*h s*), pharyngeal sclerites (*ph s*), dorsal cornu (*d c*), ventral cornu (*v c*), and pharynx (*ph*); *C*, anterior spiracle; *D*, posterior spiracles (*sp*), showing spiracular chamber (*sp c*); *E*, cuticular armature.

approximately 15 minute notches on the anterodorsal surface. In the roof of the oral cavity and above the oral hook is a narrow, partly sclerotized hatching spine (*h sp*). Laterally and somewhat ventral to the oral hook are the two prominent dental sclerites (*d*). Posterior to the fused hypostomal sclerites (*h s*) is the infrahypostomal bridge (*ih b*). The pharyngeal sclerites (*ph s*) consist of 2 dorsal cornua (*d c*) and a fused ventral cornu (*v c*), which enclose the pharynx. The ventral cornu is not striated longitudinally.

Anterior spiracles, present at the time of hatching but largest in the full-grown first-instar larva (*C*), may not function. The two posterior spiracles (*D*) open on the dorsopleural portion of the cuticle of the last body segment. The conical anal stigmata contain irregular spiracular openings (*sp*). The three stigmatic hooks (*s h*) consist of two simple sclerotized hooks anterodorsal to the anal stigmata and a heavy three-barbed hook lying in the midline ventrad.

The second-instar larva is approximately 3.8 mm. in length (fig. 16, *A*). The number of rows and the arrangement of the cuticular spines are essentially the same as in the first-instar larva, but the spines are smaller. The spines covering the ventral fusiform areas are similar to those circling the segments (*E*).

The cephalopharyngeal mechanism is well developed. The oral hooks (*o h*) consist of two narrow, slightly curved sclerites and are broad basally where they articulate with the hypostomal sclerites (*h s*). Two sharp supraoral sclerites (*so s*) are fused with the posterior bases of the oral hooks. There is no articulation between the hypostomal sclerites and the two pharyngeal sclerites. The pharyngeal sclerites consist of two dorsal cornua and a fused ventral cornu. The ventral cornu is not striated longitudinally.

The second-instar larva is amphipneustic. The anterior spiracles (*C*) each have three respiratory papillae. The posterior spiracles (*D*) are functional and protrude slightly above the cuticle.

The sensory papillae are essentially the same as in the third-instar larva.

The third-instar larva (fig. 17, *A*) is approximately 6.4 mm. long. The cuticular armature (*F*) circling the segments is heavier than in the second-instar larva. The ventral fusiform areas are large and appear to aid the larva in locomotion after it has left the host. On the pseudocephalon laterad of each oral hook is a sclerotized integumental area, the oral guard (*H, o g*). Posterior to the oral guards is a series of four or more sclerotized toothed folds, the transverse channels (*I, tr c*), through which food materials enter the oral cavity.

The cephalopharyngeal mechanism (*B*) is similar to that of the second-instar larva. On the convex ventral surface of each oral hook are four ridges, on one of which are a number of oral teeth (*C, o t*). The hypostomal sclerites articulate anteriorly with the oral hooks and posteriorly with the pharyngeal sclerites. The hypostomal sclerites are joined ventrally by the infrahypostomal bridge (*ih b*). Lying free between the hypostomal plates is a small epipharyngeal plate of uncertain shape. Partly fused to the dorsal surface of the hypostomal sclerites are the suprahypostomal sclerites. The pharyngeal arch (*ph a*) unites the dorsal cornu and articulates with the hypostomal sclerites. The ventral cornu is not striated longitudinally.

Four pairs of sensory papillae are present on the pseudocephalon, one element of each lying on opposite sides of the mouth. On the anterior angles of the pseudocephalon are two groups of sensory papillae consisting of one anterior sense papilla (*G, a s p*) and one posterior sense papilla (*p s p*) on each side. Two retractile peglike structures occur on the posterior papilla. Laterad of each oral guard (*H, o g*) is an oral papilla (*o p*). Between the oral guard and the posterior border of the pseudocephalon is a peglike sensory papilla shown in *H*.

The third-instar larva is amphipneustic. The anterior spiracles (*D*) each contain three or four respiratory papillae, the number varying sometimes in the same larva. Each papilla has a feathery slitlike opening. The long sclerotized stigmatic chamber is yellow. The two posterior spiracles open on short, thick, semicircular anal stigmata (*E*), the two flattened sides of which are opposed. Figure 17, *E*, shows the posterior larval spiracles of the third-instar larva formed around the second-instar larval spiracles prior to the molt of the larva. Molting of the larval integument causes the old spiracular system to pull out, leaving a scar which is known as the button (*b*) of the third-instar spiracle. Two of the three sublinelike spiracles (fig.

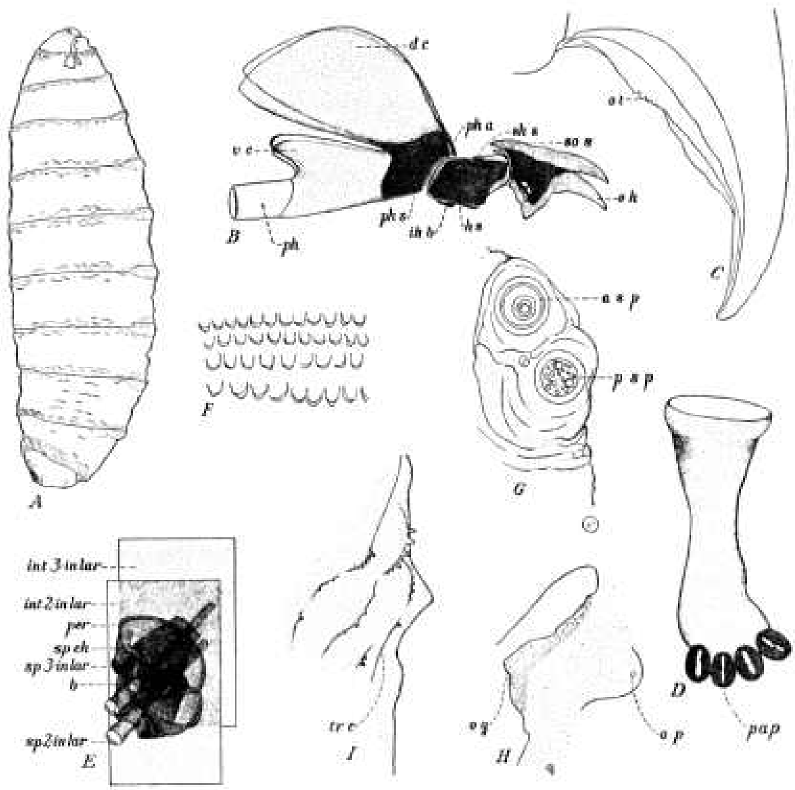

FIGURE 17.—*Paradexodes epilachnae*, third-instar larva: *A*, Larva, lateral aspect, ×10; *B*, cephalopharyngeal mechanism, showing oral hooks (*o h*), supraoral sclerites (*so s*), hypostomal sclerites (*h s*), infrahypostomal bridge (*ih b*), pharyngeal arch (*ph a*), pharyngeal sclerite (*ph s*), dorsal cornu (*d c*), ventral cornu (*v c*), and pharynx (*ph*); *C*, oral hook, showing oral teeth (*o t*); *D*, anterior spiracle, showing papillae (*pap*); *E*, posterior spiracles of third-instar larva (*sp 3-in lar*) on the integument of the third-instar larva (*int 3-in lar*), and uncast spiracles of the second-instar larva (*sp 2-in lar*) and the integument of the second-instar larva (*int 2-in lar*), also the peritreme (*per*), spiracular chamber (*sp ch*), and region of the button (*b*) of the third-instar spiracle; *F*, cuticular armature; *G*, anterior sensory papilla (*a s p*) and posterior sensory papilla (*p s p*); *H*, oral guard (*o g*) and oral papilla (*o p*); *I*, transverse channel (*tr c*).

18, *C, sp*) lie parallel and the third is approximately at 35 degrees to the other two. The lips of the openings are fringed with slender prongs of various lengths. One side of each stigmatic plate protrudes as a sharp linelike structure (fig. 17, *E*). A pear-shaped spiracular chamber (*sp ch*) extends from the spiracular slits to the trachea.

A new cuticula is found within the puparium, and hence a fourth instar must occur, hidden within the puparium.

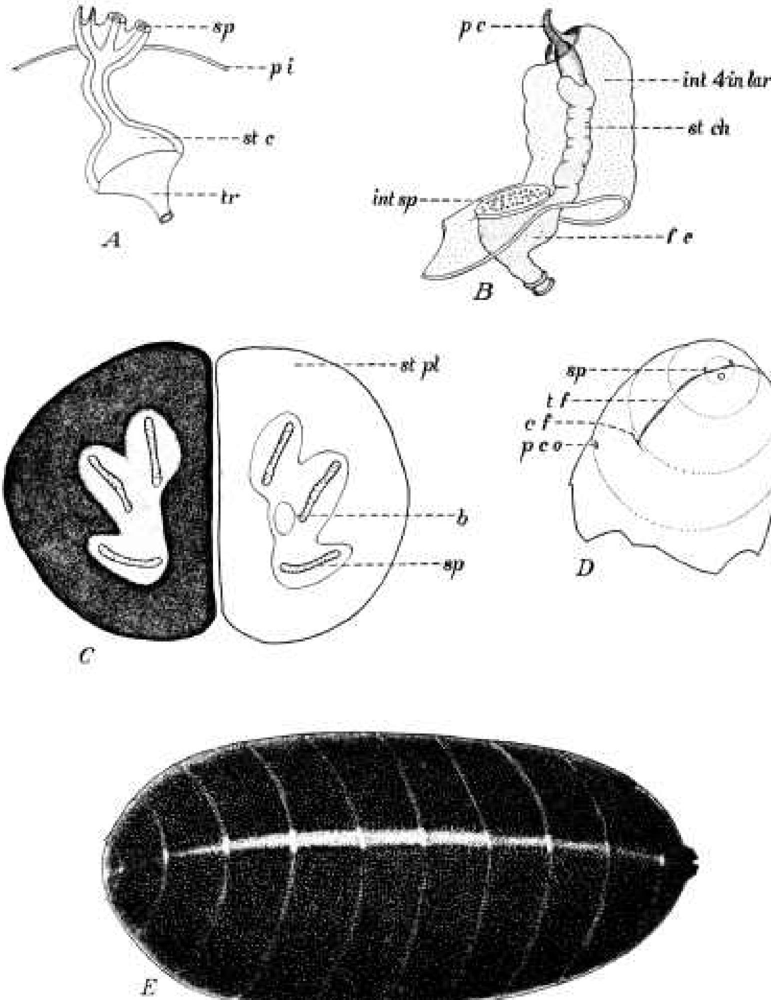

FIGURE 18.—*Paradexodes epilachnae*, pupal structures: *A*, Anterior spiracle of third-instar larva persisting in puparium, showing spiracle (*sp*), puparial integument (*p i*), stigmatic chamber (*st c*), and trachea (*tr*); *B*, accessory thoracic spiracle, showing pupal cornicle (*p c*), integument of fourth-instar larva (*int 4-in lar*), stigmatic chamber (*st ch*), internal spiracle (*int sp*), and felted chamber (*f c*); *C*, posterior spiracular plates, showing stigmatic plate (*st pl*), button (*b*), and spiracle (*sp*); *D*, anterior end of puparium, showing anterior spiracle (*sp*), transverse fracture (*t f*), circular fracture (*c f*), and pupal cornicle opening (*p c o*); *E*, lateral view of puparium.

THE PUPARIUM

The puparium (fig. 18, *E*) is approximately 5.6 mm. in length. It is ovate, slightly flat on one side, and the greatest width occurs one-third of the distance from the anterior end. The anterior end is broadly rounded and the posterior end is subconical. Puparia change in color from straw to brick red, and later to dark red with purple

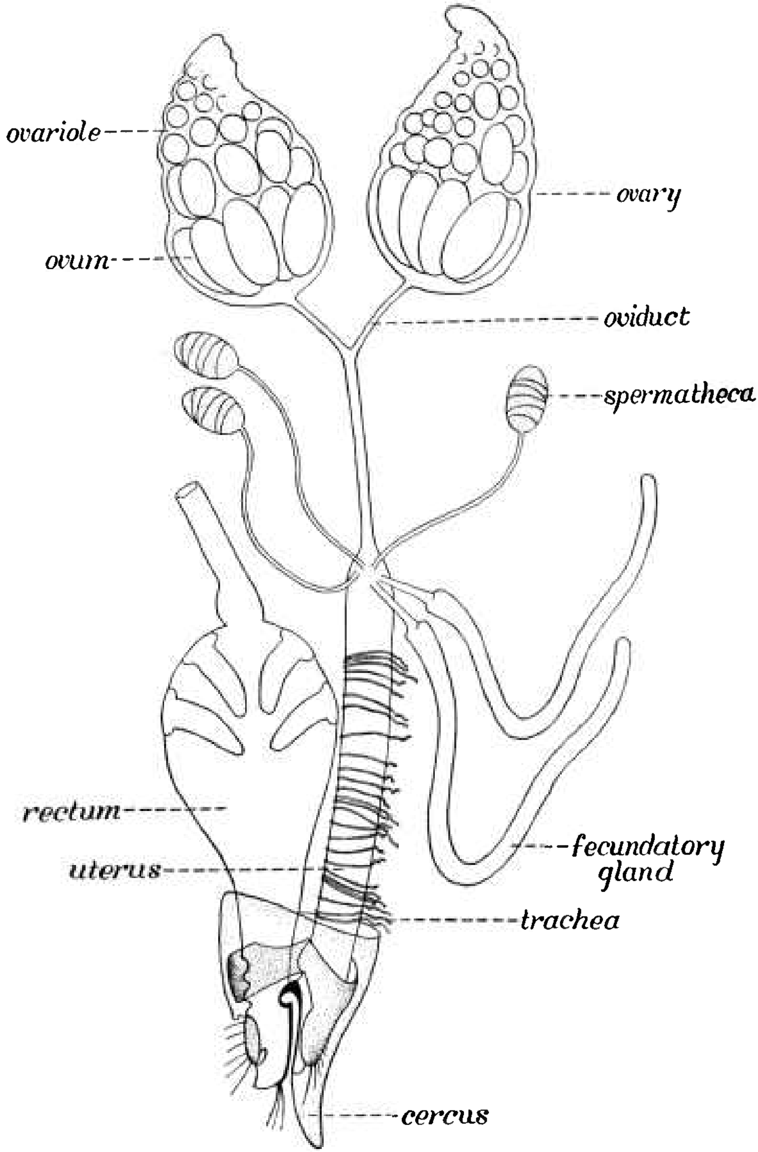

FIGURE 19.—Reproductive system of female *Paradexodes epilachnae.*

iridescence. The puparium is smooth, except for the remains of the cuticular armature and segmentation of the third-instar larva and the posterior spiracles.

Two separate lines of fracture occur on the anterior end of the puparium (fig. 18, *D*). A transverse line of fracture (*t f*) extends horizontally from the posterior limits of puparial segment 3 across the end of the puparium. This fracture appears simultaneously with the formation of the puparium. Indications of a circular line of fracture (*c f*) between segments 3 and 4 appear early in puparial development but are not complete until the adult parasite emerges.

After the first day the puparium is propneustic. The anterior spiracles of the third-instar larva persist dorsad of the transverse line of fracture (fig. 18, *A*). The posterior spiracular system ceases to be connected with the developing individual. The first appendages to be completely formed on the phanerocephalic individual are the accessory prothoracic spiracles (*B*), or special pupal spiracles. One of these temporary organs appears on each side of the pupa, and when completely formed the sclerotized pupal cornicle (*p c*) punctures the puparium on the posterolateral side of segment 4 (*D, p c o*), thus providing a source of air independent of the existing apertures. The accessory spiracles are sloughed prior to the emergence of the adult parasite. Near the base of the stigmatic chamber (*B, st ch*) is a second or internal spiracle (*int sp*) in the integument of the fourth-instar larva (*int 4-in lar*). Air passes through this spiracle from the puparial cavity into the felted chamber (*f c*).

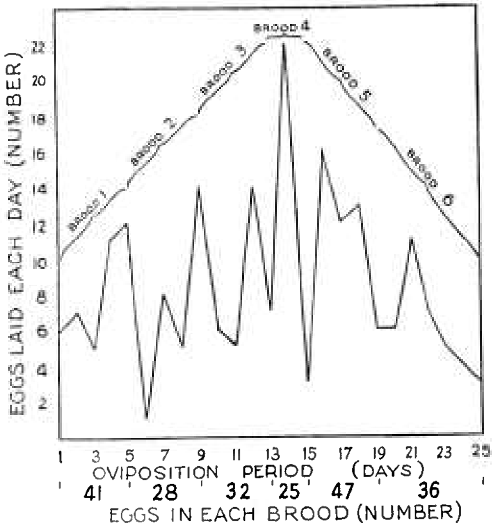

FIGURE 20.—The day-to-day variation of egg deposition in relation to the rhythmic development of the six broods of eggs in a female of *Paradexodes epilachnae*.

Reproductive Systems

In newly emerged females the narrow ovaries taper distally (fig. 19). Each ovary contains from 8 to 27 ovarioles. The number of ovarioles is not constant in the same or different females. Occasionally the ovarioles atrophy and no ova are produced, or the basal ova absorb the younger distal ones and the ovaries become disk-shaped.

Normally there are 6 ova in each ovariole, the largest being nearest the oviduct. Each ovum has 1 brood relative in each of the ovarioles. Periodically all the ova of 1 brood pass into the incubating uterus, where they are retained until the larval structures are complete. The uterus is capable of considerable extension. When there are 25 eggs present, the uterus is a single coil in the body cavity. One female examined had a 3-coiled uterus containing 78 eggs, of which 59

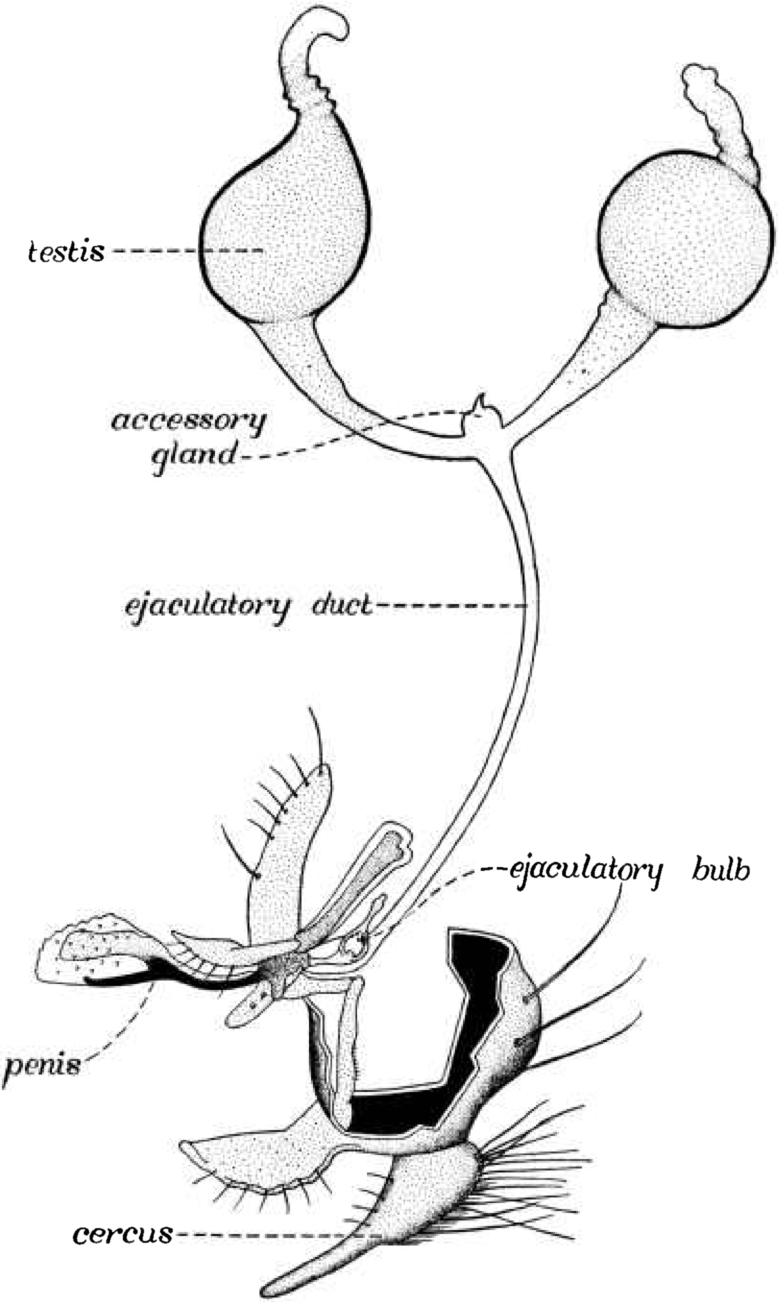

FIGURE 21.—Reproductive system of male *Paradexodes epilachnae*.

showed fully developed larval characters. The uterus may be distended at the base so that 3 eggs lie within the same diameter of the tube.

The eggs of each brood in the uterus may be distinguished from eggs of other broods by the condition of their development. A definite periodicity of egg deposition occurs, corresponding to the development of the six ovarian broods (fig. 20). If hosts are not available, the eggs are ejected after a few days.

In newly emerged males the two testes (fig. 21) are white and are covered with fatty tissue. The walls of the testes gradually sclerotize and become yellow. Between the insertions of the vasa efferentia on the ejaculatory duct are two small, partly fused, bulblike vehicular glands. At the posterior end of the vas deferens is a transparent organ, the ejaculatory bulb. Extending through this bulb is a rodlike apodeme, to the free end of which a set of valvular muscles are attached. The penis consists of a curved, heavily sclerotized ventral portion and a thinner, irregularly shaped dorsal portion which is covered for part of its length with blunt, recurved spines.

BIONOMICS

The Adult

The adults are most active in the field during the morning hours when the temperature range is between 50° and 70° F. During the warmer part of the day they are active in dense shade or remain motionless on foliage exposed to the sun. Much greater parasitization of host larvae was found on heavily shaded plants than on unshaded or sparsely growing plants. On August 31, 1933, the parasitization of larvae collected from plants in the shade was 51 and in the sun 20 percent.

In the insectary there was less restlessness among adults when a diffuse light entered the cage from all sides. The use of electric lights during the mornings and evenings lengthened the period of daily activity, but a rest period occurred at night even though the cages were lighted. Gravid females were less disturbed by bright or direct light than were males and young females.

Adults were not attracted to flowers or honeydew in the field. Adults in cages fed on sugar and raisins and lived longer in dirty cages than in clean ones, indicating that yeast and materials obtained from frass probably are beneficial.

The adults are usually easily handled under cage conditions. When adults are liberated in the field some must be removed forcibly from the cages and often they return after a short flight and alight on the shirt or arms of the operator.

Adult parasites emerge from puparia between 10 a. m. and noon. This rhythm or periodicity of emergence occurs in sets of puparia held either at constant or uncontrolled temperature. Occasionally adults emerge at the usual time even when the temperature is falling. Nightly temperature as low as 27° F. does not kill the puparia, and emergence may occur when the temperature is above 47°. Mechanical agitation or the application of contact moisture to the puparia under certain conditions may cause adults to emerge a day before those in untreated puparia.

The emergence of adult parasites from 14,591 puparia bred during July, August, and September 1933, was 84 percent. Newly emerged adults crawl about rapidly for a short time and then rest on some vertical support until the sclerotized parts have hardened. Occasionally normal-appearing adults emerged from small or otherwise abnormal puparia.

In a randomized sample of adults of *Paradexodes epilachnae* the numbers of males and females are likely to be nearly equal. However, slightly more males than females are produced at a developmental temperature of 72° F., and slightly fewer males than females are produced at 82°.

The larval and puparial stages of the male parasites are shorter than those of the female (table 3). At room temperature the average length of the puparial stage of 131 males was 11.3 days and the average length of the puparial stage of 96 females was 12.0 days. There is a tendency for adult males to emerge from puparia earlier in the day than females.

TABLE 3.—*Number of males and females of Paradexodes epilachnae emerging from puparia formed on 3 consecutive days from host larvae parasitized within a 24-hour period*

Day	Puparia	Adults emerging	Males	Females
	Number	*Number*	*Percent*	*Percent*
First	580	359	53.5	46.5
Second	687	525	50.3	49.7
Third	300	230	42.6	57.4

Males attempt to mate with females of the same age shortly after emergence, but fertilization does not occur until the males are 3 days old and the females are more than 1 day old. The average time in coitu for several pairs was 5 minutes. Seven females 5 days old were confined with several males of the same age, and all females had been fertilized inside of 1 hour. Of several females which mated only once, all produced viable eggs throughout their lives, one ovipositing over a period of 39 days. Four virgin females mated successfully when 6, 8, 21, and 26 days old, respectively, and produced viable eggs after 6 or more days had elapsed.

Under cage conditions the minimum length of time between female emergence and deposition of viable eggs was 6.3 days in June, 5.8 in July, and 8.5 in August. The period between fertilization and deposition of viable eggs for seven individual females ranged from 5 to 13 days.

The female deposits eggs nearly every day from the end of the preoviposition period until death. One female desposited eggs over a period of 39 days. In many cases the females dying in cages were found to contain many undeposited eggs. Experimentally, a few live first-instar larvae were removed from the uteri of dead females and placed on larvae of *Epilachna varivestis*, which they entered and in which they developed successfully. It is difficult to determine the number of eggs laid each day during the life of a female, but it is certain that on some days 10 or more are deposited.

Gravid females run in zigzag fashion over foliage on which host larvae are feeding. When a larva is encountered, the female stops abruptly and waits for the potential host to make some movement. Following this, the female moves about the host, tapping it with the first pair of legs. During this inspection the abdomen of the female gradually is brought up forward between the legs and in contact with the host. The period of contact during which the egg is deposited is only 1 or 2 seconds. Eggs may be deposited on any part of the body of the host.

The parasite develops successfully when oviposition occurs on any of the four larval stages (including the quiescent prepupal phase) and newly formed pupae of *Epilachna varivestis*. In a collection of several hundred larvae 4.55 percent of the second-instar, 18.5 of the third-, and 64.9 of the fourth-instar larvae were found to be parasitized. The stage or size of the host on which oviposition occurs in the field does not appear to affect the length of the larval period of the parasite.

Considerable superparasitism occurs in hosts parasitized in the field and in cages. Oviposition was observed 175 times on 22 hosts. On dissection only 83 parasite larvae were found in these hosts.

As many as 34 first-instar parasite larvae were dissected from one host. It is estimated that under cage conditions 75 percent of the parasite eggs are lost through superparasitism and the premature death of female parasites.

Under cage conditions the daily average number of progeny (puparia) produced by each female during her lifetime was 2.04 puparia, the maximum was 5.83, and the minimum was 0.20. The average total number of progeny produced by several females was 42 puparia per female. At 82° F. and 70-percent relative humidity several females in individual cages produced an average of 46.6 puparia, and the maximum number of puparia produced by any one female was 206.

Records of the mortality of adult parasites in breeding cages show that nearly 20 percent of the parasites died during the first 3 days. More females than males died during this period. The maximum length of life for parasites held in five cages was 49, 51, 54, 73, and 74 days, respectively. In one cage started in midsummer half of the females lived 22 days, one-fourth lived 34 days, and the last female died at the age of 54 days. The last male was 33 days old at death. The 28 females in the cage produced a total of 1,158 puparia or an average of 41.7 puparia for each female.

In October 322 adult parasites were divided among 2 cages. Host larvae were placed in 1 cage each day, but no larvae were ever placed in the other cage. It was found that females lived 8 days longer in the cage not provided with hosts.

The parasite in its several stages can withstand a temperature as low as 25° F., if of short duration. It can also withstand a temperature of 100° for a short period, except when the humidity is high. Excessive humidity causes the females to become restless and oviposition is then below normal. When the humidity is low many parasite eggs desiccate before the parasite larvae are able to leave the eggs and enter the hosts. The larval and puparial stages develop within the 50°–85° range of temperature. However, parasite larvae within hosts are not able to withstand high temperatures (98° to 103°) as successfully as the hosts. During hot periods in summer the parasite larvae succumb within their hosts, which are not so susceptible to high temperatures. The death of the parasite soon causes the death of the host, whereas unparasitized larvae are not seriously affected.

The average developmental period for parasite larvae bred in the insectary during each month from June to October 1932, inclusive, ranged from 9.4 to 12.8 days; and the average developmental period for puparia during the same months ranged from 9.2 to 13.7 days (table 4).

TABLE 4.—*Average developmental period of parasite larvae and puparia for each month from June to October 1932, inclusive, at Columbus, Ohio*

Month	Parasite larvae produced	Average time for development	Parasite puparia produced	Average time for development
	Number	*Days*	*Number*	*Days*
June	4,730	10.1	2,408	9.7
July	13,948	9.4	6,079	9.2
August	16,630	10.0	5,681	10.3
September	7,941	12.8	3,609	12.7
October	1,080	11.0	49	13.7

HABITS OF THE FIRST-INSTAR LARVA

The completely incubated parasite larva leaves the egg at the time of deposition and enters the host within 15 to 30 minutes. The shock associated with the entry of the parasite causes the host to stiffen its legs and become rigid. The collapsed chorion and a small amount of dried host blood is sloughed at the molt of the host next following deposition of the parasite egg, and there is no discoloration marking the point of entrance into the host.

The small first-instar larvae migrate throughout the body cavity of the host, even entering the head capsule and the coxae of the legs. Some larvae remaining close to the host integument may be observed moving about with the aid of the spined fusiform areas on the ventral surfaces.

Competing parasite larvae are killed by a single dominating larva, and the unsclerotized body parts are absorbed along with similar parts of the host.

HABITS OF THE SECOND-INSTAR LARVA

The mature first-instar larva becomes stationary, with the anal stigmata near or in a spiracular trunk of the host, and, after molting, perfects a connection with the spiracular trunk which persists until the second molt. A membranous funnel enclosing the posterior half of the larva is formed in which the cast cuticula and mouth parts of the first-instar larva are enclosed. Occasionally the entire second instar and the first phase of the third instar are spent in this location, and the cast cuticula and mouth hooks of the second instar are also enclosed in the reconditioned and somewhat larger funnel.

The host larva containing a second-instar parasite larva shows no outward signs of parasitization. During this stage the parasite feeds on fat reserves and pushes the vital organs of the host to one side.

Habits of the Third-Instar Larva

Usually the parasite larva molting into the third instar leaves the old spiracular funnel and attaches at a new place on a spiracular trunk of the host, where a new funnel is formed. The funnel partly enclosing the third-instar larva is sclerotized basally and membranous distally.

Growth is rapid after the second molt, and when mature the parasite larva extends the full length of the host, often causing the abdominal segments of the host to be extended beyond their normal position.

At first the third-instar larva is stationary within the spiracular funnel (fig. 22), but later it leaves this source of air supply and either penetrates the alimentary canal of the host near the oral or anal orifices or punctures the exoskeleton of the host on its dorsal surface.

To puncture the exoskeleton of the host the two kidney-shaped stigmatal plates of the parasite larva are flexed against the integument until the inner surface is cleansed of cellular tissue. Then the plates are placed flush with the surface of the integument and a vacuum is produced within the spiracular system of the parasite. This causes the integument of the host to press tightly about the serrate edges of the stigmatal plates, after which a series of movements of the plates causes the integument to tear. Although the tear in the integument may be large, the body fluid in which the parasite floats is extremely viscous and seals over the aperture flush with the stigmatal plates of the parasite. If the parasite larva is disturbed it tears away from the temporary attachment and retreats within the host, returning later to perfect a new attachment.

Effects of the Parasite on the Host

Host larvae containing first- or second-instar parasite larvae twitch or rock from side to side but feed as normal larvae. The host shows no signs of being parasitized until the parasite larva is in the third instar. At this time a small red area appears on each side of the body of the host in the region of the first to third abdominal segments. Two days before the mature larva emerges, the host becomes a glassy straw color because of the breaking down of the host tissues into a liquid state.

A parasite larva entering a host either produces a normal mature parasite larva or the host and parasite are killed because of the premature death of either individual.

The mature third-instar parasite larva usually cuts a narrow slit dorsally along the line of suture separating the thorax from the first abdominal segment of the host, and through this it emerges. Occasionally the larva emerges from the oral or anal aperture of the host. If the fluid remains of the host escape prematurely, the parasite pupates within the host skin.

It was found that more puparia were formed within exoskeletons of *Epilachna mexicana* than in other hosts. These puparia had the anal stigmata bearing the spiracular plates extended to a considerable length, indicating that the third-instar parasite larvae had utilized the oral or anal apertures of the host as a source of air supply.

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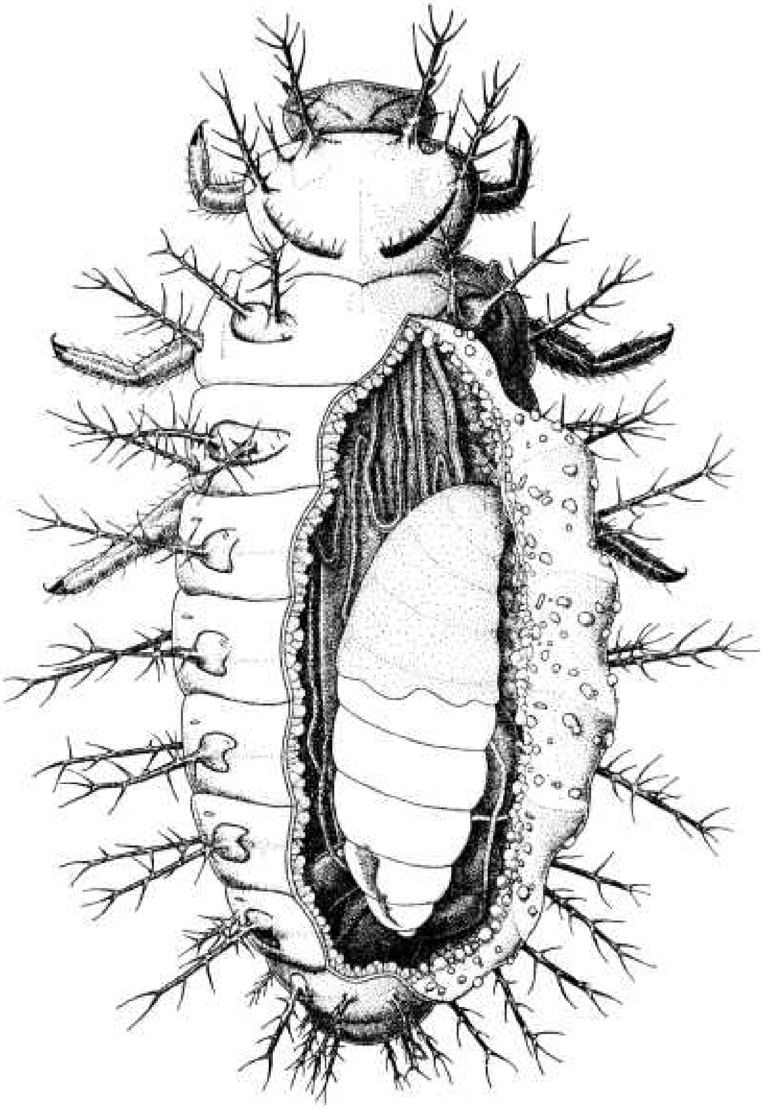

FIGURE 22.—Gross dissection of fourth-instar larva of *Epilachna varivestis*, showing a third-instar larva of *Paradexodes epilachnae* attached to a spiracular trunk.

Mature parasite larvae on leaving the hosts drop to the ground and crawl beneath debris or into loose soil and pupate there. Crevices produced at soil level by the swaying of plants in the wind are frequently entered by the larvae.

The depth at which pupation takes place depends on the texture of the soil and other conditions. In a group of 48 larvae placed on moist loose soil 75 percent pupated within 1 inch of the surface.

One individual was found at a depth of 4 inches. In these puparia 46 percent of the larvae had reversed their axes and pupated with the cephalic end up, 29 percent pupated with the caudal end up, and 25 percent pupated in a horizontal position.

Parasites in the puparial stage were more sensitive to low temperature when either less than 3 days old or approximately 5 days old than they were during the remainder of the puparial period.

PREDACIOUS COCCINELLIDS AS HOSTS

Several species of predacious Coccinellidae collected in the larval stage in Mexico were found not parasitized by *Paradexodes epilachnae*. Further tests were conducted at Columbus to determine whether predacious coccinellids were parasitized under cage conditions. In 1931 a total of 1,703 coccinellid larvae, representing 7 species, were collected in the field and exposed to parasites for periods of from 1 to 3 days. The parasites showed little interest in larvae of *Hippodamia convergens* Guer., *H. parenthesis* (Say), *H. tredecimpunctata* (L.), *Coccinella novemnotata* Hbst., *Cycloneda sanguinea* (L.), *Adalia bipunctata* (L.), and *Ceratomegilla fuscilabris* (Muls.), and no reproduction of the parasite occurred.

EXTENT OF BREEDING AND LIBERATION

From September 1930 to September 1935, 781,000 larvae of *Epilachna varivestis* were exposed to parasitization at Columbus. During the same period 145,500 adult parasites were bred and 82,000 were liberated in the field.

From 1931 to 1935, inclusive, colonies of *Paradexodes epilachnae* were released in 85 localities in 19 States. Parasites were released first during August 1931 and 10,369 individuals were liberated in 7 States before the season closed (table 5). From May 31 to October 18, 1932, 19,035 parasites were released in 14 States. From June 1 to October 16, 1933, 44,020 parasites were released in 17 States. From June 12 to October 13, 1934, 8,285 parasites were released in 3 States. In July 1935, 291 parasites were released at Columbus, Ohio.

TABLE 5.—*Numbers of Paradexodes epilachnae liberated in different States from 1931 to 1935, inclusive*

State	Parasites liberated in—					Total
	1931	1932	1933	1934	1935	
	Number	*Number*	*Number*	*Number*	*Number*	*Number*
Alabama	2,965	4,147	7,089	2,122	------	16,323
Connecticut	------	262	------	------	------	262
Delaware	------	507	550	------	------	1,057
Georgia	450	------	480	------	------	930
Indiana	------	491	420	------	------	911
Kentucky	1,391	1,009	2,117	------	------	4,517
Maryland	------	960	1,677	------	------	2,637
Mississippi	------	------	1,158	------	------	1,158
New Jersey	959	1,617	5,027	------	------	7,603
New Mexico	722	------	5,092	------	------	5,814
New York	------	------	715	------	------	715
North Carolina	------	1,586	1,305	------	------	2,891
Ohio	2,546	4,112	4,891	5,813	291	17,653
Pennsylvania	------	195	3,551	------	------	3,746
South Carolina	------	------	855	------	------	855
Tennessee	------	1,443	3,601	------	------	5,044
Texas	------	996	------	------	------	996
Virginia	1,336	1,267	4,844	350	------	7,797
West Virginia	------	443	648	------	------	1,091
Total	10,369	19,035	44,020	8,285	291	82,000

COLONIZATION

Parasites in the adult and puparial stages were shipped to various localities for colonization by air mail or, more efficiently, by train or automobile and handled by personal messenger.

Adult parasites shipped by air mail were contained in cardboard mailing tubes fitted with crossed muslin supports, water bottles, and pieces of loaf sugar. The receiving agents cared for shipments of parasite puparia until the adults emerged and could be liberated in the field. Adult parasites shipped with personal messenger were in ordinary breeding cages each containing 500 parasites. One messenger easily cared for 2 packages consisting of 3 cages each.

The number of adult parasites released in separate colonies ranged between 100 and 4,000 individuals. Some of the colonies were strengthened by additional liberations during the same season, and often the same sites were chosen for liberation in 2 to 5 consecutive years. In most cases a colony of between 100 and 200 parasites increased sufficiently after 2 generations (60 days) in the field to cause a high percentage of the larvae of *Epilachna varivestis* to be parasitized within a radius of several miles of the point of liberation (table 6).

TABLE 6.—*Percentage of parasitization of larvae of Epilachna varivestis by Paradexodes epilachnae in various localities and the length of time that the parasite had been present in the field*

Locality	Date of liberation	Parasites released	Survey		Host larvae collected	Rate of parasitization
			Date	Time after liberation		
		Number		*Days*	*Number*	*Percent*
Athens, Ala	May 31, 1932	174	Sept. 24, 1932	116	100	31
Athens, Ohio	July 21, 1932	436	Oct. 13, 1932	84	500	48
Birmingham, Ala	Sept. 30, 1933	4,029	Oct. 27, 1933	27	166	31
Burlington, Ohio	Aug. 22, 1933	200	Oct. 11, 1933	50	132	67
Chattanooga, Tenn	June 13, 1932	594	Sept. 15, 1932	94	400	67
Columbus, Ohio	Aug. 3, 1933	1,533	Sept. 29, 1933	57	500	90
Cullman, Ala	May 31, 1932	158	Sept. 24, 1932	116	100	49
El Paso, Tex	Aug. 4, 1932	539	Sept. 13, 1932	40	500	26
Elizabeth City, N. C	July 18, 1932	594	Nov. 3, 1932	116	67	73
Glasgow Junction, Ky	Aug. 15, 1933	200	Oct. 4, 1933	50	68	21

SPREAD FROM POINTS OF COLONIZATION

Parasites were released in bean fields infested with bean beetle larvae in the morning or late in the afternoon. The parasite is a strong flier, and it is believed that a great number of the individuals released in a certain locality traveled some distance before seeking hosts. This belief is supported by the fact that collections of bean beetle larvae made at the site of liberation a few days after parasites were released showed but little parasitization. In most instances 30 or more days was necessary before appreciable signs of parasitization began to appear at points of parasite liberation. At Columbus, Ohio, in 1932 the parasite was found as far as 11 miles from the point of liberation. In New Jersey parasites were recovered approximately 18 miles from the point of liberation. At Glasgow Junction, Ky., the parasitization was 20.6 percent in larvae collected 1 mile from the point where parasites had been liberated 50 days earlier.

The tendency of the parasites to spread may depend somewhat on the situation in which they are released. In the field the adult parasites are found most frequently on bean plants shaded by trees or weeds or along the sides of the fields resting on large-leaved plants. Likewise the percentage of parasitization was much greater among bean beetle larvae collected from weedy plots of beans or where shaded by trees. At Columbus, for example, the parasitization among 700 bean beetle larvae collected from beans growing in the sun was 20.4 percent on August 31, but among 680 larvae from beans grown to weeds the parasitization was 56.6 percent on August 31 and September 1.

The increase in amount of field parasitization is indicated best in the data obtained for Columbus during the summer of 1933. In figure 23 it will be observed that the rate of parasitization increased until the end of the season.

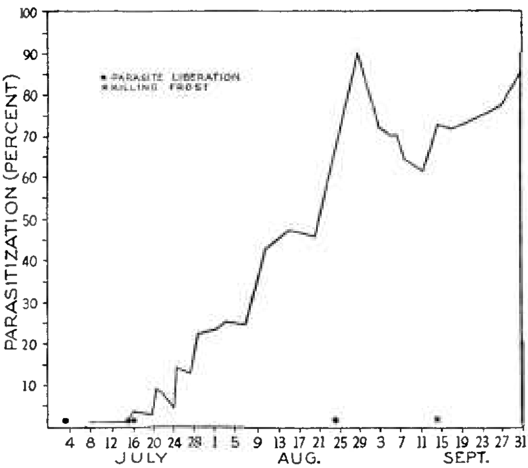

FIGURE 23.—Percentage of parasitization of larvae of *Epilachna varivestis* by *Paradexodes epilachnae* in the field at Columbus, Ohio, in 1933, from the time of first liberation of parasites until the end of the season.

STATUS OF THE PARASITE AT THE END OF THE SEASON

The indications are that the parasite breeds continuously in one or more hosts throughout the year in Mexico and is not adapted for meeting long periods of low temperature or moisture deficiency. In Mexico a parasitized bean beetle larva was found in the field December 3 and an adult parasite was seen there December 5. The parasite was also found breeding in *Epilachna virgata* near Cuernavaca, Morelos, in December. Collections of puparia obtained in February from sandy soil near Mexico City, where parasitized bean beetle larvae had been abundant during the summer months, contained no living parasites. In the United States adult parasites were collected from bean foliage at Henderson, Ky., November 19. Bean beetle larvae collected on November 10 at Suffolk, Va., were 15.5 percent parasitized. On October 10, 96 puparia were taken from soil at Columbus and held in the outdoor insectary. On December 7 the puparia were examined and 60 flies were found to have emerged. The unbroken puparia were dissected and were found to contain dead specimens in all instances. Cold-storage experiments with puparia, reported elsewhere in this bulletin, also show the inability of the parasite to withstand prolonged periods of low temperature.

The parasite has not been recovered in any locality in the United States the year following liberations in the field.

SUMMARY

Paradexodes epilachnae, a tachinid parasite of beetles of the coccinellid genus *Epilachna*, was described by Aldrich in 1923 from specimens reared by E. G. Smyth from *Epilachna varivestis* Muls. collected at Coapa, Federal District, Mexico, in 1922.

Studies conducted in Mexico at intervals from 1922 to 1930 showed *Paradexodes epilachnae* to attack *Epilachna varivestis* Muls., *E. mexicana* Muls., *E. obscurella* Muls., and *E. virgata* Muls. *E. borealis* (F.) proved to be a suitable host at Columbus, Ohio. The parasite was found in *Epilachna* larvae in Mexico from June 7 to December 3. Although it is not known how the parasite passes through the dry winter in Mexico, it seems imperative that host larvae be present in some numbers during this period.

Paradexodes epilachnae was found abundantly at Mexico City and in varying numbers within the area from Jalapa, Vera Cruz, west to Guadalajara, Jalisco, and south to Oaxaca, Oaxaca. The percentage of parasitization of *Epilachna* larvae at the beginning of the rainy season is very low, and the increase is gradual until the host populations have reached their greatest increase in August and September. In 1929 and 1930 the most severe infestation of *Epilachna varivestis* was found near Chalco, Federal District, 33 miles southeast of Mexico City. Here the parasitization averaged nearly 45 percent for a period of 15 days during the latter part of September. The maximum observed parasitization of larvae of *E. varivestis* in Mexico was 81.4 percent, this occurring on November 4, 1929.

Brachymeria carinatifrons Gahan was an abundant hyperparasite issuing from puparia in collections made at Coapa, Federal District, Mexico, in 1922, and at Cuernavaca, Morelos, in 1930. It was also collected at Cordova, Vera Cruz, and Oaxaca, Oaxaca, in 1930. *Phygadeuon subfuscus* Cress. and an undescribed species of *Myrmecopia* were reared in small numbers from puparia collected from soil at Columbus.

Small numbers of puparia were shipped to Birmingham, Ala., in 1922 and 1923, and approximately 60,000 additional puparia were received at Columbus between July 20, 1929, and October 12, 1930. Tests made at Mexico City and Columbus during 1929 and 1930 showed that the large predacious coccinellids common to both areas were parasitized neither in the field nor in cages. Serious attempts to colonize the parasite in areas of the United States infested with the Mexican bean beetle (*Epilachna varivestis*) were begun, therefore, in 1931.

Attempts to store larvae, adults, and puparia of *Paradexodes epilachnae* through the winter months at Columbus were unsuccessful, and the stock was maintained by continuous breeding from August 1930 to September 1935, approximately one generation occurring each month. During 8 months of the year that host larvae were not present in the field, larvae of *Epilachna varivestis* were reared also in the laboratory, chiefly from adults removed from hibernation.

Of the 145,500 adult parasites bred at Columbus, 82,000 were released in 19 States. The numbers of adults released in separate colonies ranged between 100 and 4,000 individuals. Many of the colonies were restocked for several consecutive years, and in most cases the parasites were found to have become established during the current season. However, in no instance has *Paradexodes epilachnae* definitely been collected from colonies released the previous season.

Paradexodes epilachnae may be bred in large numbers under usual laboratory conditions. The adults are not restless in confinement, and no serious bacterial or fungus disease attacks the various stages.

The females are capable of mating when from 1 to 26 or more days old, and one mating is sufficient. Females lived in cages as long as 74 days and males slightly less. The preoviposition period is approximately 5 days, and viable eggs may be deposited nearly every day for as many as 39 or more consecutive days.

Each ovary contains from 8 to 27 ovarioles consisting of 6 distinguishable ova. Periodically the large ova from each ovariole pass into the distensible incubating uterus, where they are retained until the larval structures are complete. A rather definite periodicity of egg deposition occurs if hosts are available, but if these are lacking the eggs are ejected after a few days.

The chorion is ruptured usually as the egg is laid on the host integument, and the larva burrows into the host immediately. The first-instar larvae are migratory and may penetrate even the head capsule and coxae of the host's legs. Although as many as 34 first-instar larvae were dissected from a host, only 1 larva reaches maturity in a host. The average length of the larval period in August is 10 days. Usually the full-fed larva leaves the host remnants and pupates in soil near the surface. The average length of the puparial period in August is 10.3 days.

The first- and third-instar larvae bear series of small fusiform areas ventrally, each containing two rows of heavily sclerotized ambulatory spines. The cephalopharyngeal mechanism is completely fused in the first instar; it consists of two articulated parts in the second instar and three parts in the third instar. A minute hatching spine opposes the minutely notched edge of the single oral hook in the first-instar larva. Three widely separated anal hooks appear to aid in the maintenance of a more or less temporary connection of the posterior spiracles with the respiratory system of the host.

The second- and third-instar larvae are amphipneustic. The large anterior spiracles in the first-instar larvae appear to be nonfunctional, but the three or four respiratory papillae on each anterior spiracle in the second- and third-instar larvae are functional. In the third-instar larva the posterior spiracles open on short, thick, semicircular anal stigmata, the two flattened sides of which are opposed. The heavily sclerotized ridges of the stigmata are instrumental in tearing through the host integument late in the development of the third-instar larva, after which a direct respiratory connection is made to the host exterior.

The individual within the puparium is propneustic after the first day of puparial formation. With the formation of the two accessory prothoracic spiracles the puparium is punctured slightly posterior to the circular line of fracture, and the posterior spiracles appear to be no longer functional.

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