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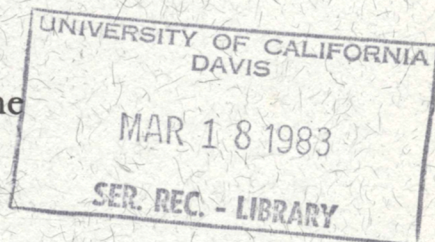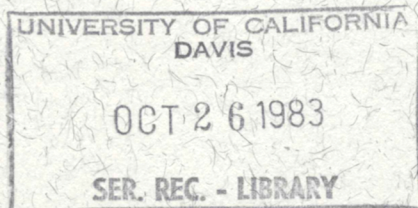
Laboratory Studies on the Biology of *Orgilus jenniae* (Hymenoptera: Braconidae), a Parasitoid of the Potato Tuberworm, *Phthorimaea operculella* (Lepidoptera: Gelechiidae)
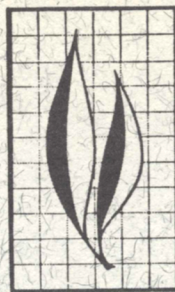
Robert V. Flanders and Earl R. Oatman

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Studies were conducted on behavior, host relationships, immature morphology and population growth potential of *Orgilus jenniae* Marsh, an exotic parasitoid of the potato tuberworm (PTW), *Phthorimae operculella* (Zeller). Results were compared with similar studies on the exotic species, *O. lepidus* Muesebeck and *O. parcus* Turner, previously colonized but not established in southern California.

Stalked eggs of *O. jenniae* are deposited in the abdominal hemocoel of host larvae. A solitary parasitoid larva develops internally, emerges before host pupation, and constructs a translucent-white cocoon within that of its host. The first of three larval instars is initially caudate- and and finally vesiculate-mandibulate; the last two are hymenopteriform. Immature dimensions and descriptions are presented. Parasitoids preferentially oviposit in first or second instar PTW in potato foliage, but there is an interaction between host age and density in tubers arising from actual parasitoid preference and characteristics of host mines. Developmental time from oviposition to adult parasitoid emergence depends on the host's age at the time of oviposition, as the first parasitoid molt is synchronized to occurrence of the fourth host instar. Parasitism significantly reduces host larval growth. If *O. jenniae* has a preoviposition period, it is less than 3-hrs, but female progeny are not produced during the first 6-hrs after adult emergence or mating. A diurnal oviposition rhythm does occur, with progeny production peaking during the last half of the photophase. Courtship, mating, searching and oviposition behaviors are described. The mean fecundity was 375.2 and 436.8 eggs/female, the mean sex ratio, 23.6% and 28.4% females, and the mean adult female longevity, 25.5 and 16.9 days, when hosts were in potato tubers and foliage, respectively, at $25 \pm 1\,°C$, $45 \pm 5\%$ RH and 12-hr photoperiod.

Parasitoid life tables and statistics for hosts in potato tubers and

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Laboratory Studies on the Biology of
Orgilus jenniae (Hymenoptera: Braconidae),
a Parasitoid of the Potato Tuberworm,
Phthorimaea operculella
(Lepidoptera: Gelechiidae)[1]

INTRODUCTION

ORIGILUS JENNIAE MARSH WAS reared from larvae of the potato tuberworm (PTW), *Phthorimaea operculella* (Zeller), received in quarantine at the Division of Biological Control, University of California, Riverside, in April, 1973. The host material was collected from potatoes near Cartago, Costa Rica. This new parasitoid was described by Marsh (1979). It is not known to occur in North America.

Orgilus jenniae was introduced as part of a continuing effort to import more effective biological control agents of the PTW into California. Several other parasitoids, including *O. lepidus* Muesebeck from Argentina and *O. parcus* Turner from South Africa, have been imported, but failed to become established (Oatman and Platner, 1974a). Oatman and Platner reported that *O. lepidus* was established in southern California, but it has not been recovered from the field since their report and is now also considered an establishment failure. The biologies of *O. lepidus* and *O. parcus* have been reported by Oatman, Platner, and Greany (1969) and Broodryk (1969), respectively.

Orgilus jenniae was annually released from 1973 to 1978 against PTW on potato, tomato, and eggplant in southern California, but despite initial, local establishments, it eventually disappeared. The inability to establish exotic PTW parasitoids in California, particularly the *Orgilus* species, and the possession of *O. jenniae* in culture enabled an investigation of the possible reasons for establishment failures. As a prerequisite to such an investigation, *O. jenniae* was studied to define its biological characteristics. The data obtained were compared to those derived from similar studies on previously imported *Orgilus* species and on PTW parasitoids indigenous to southern California.

PTW is a serious pest of potatoes throughout the world (Commonwealth Institute of Entomology, 1968; Lloyd, 1972). Its biology, temperature responses, economics, control and natural enemies have been reported by several investigators, including Bacon (1960), Broodryk (1971b), El Sherif (1961), Graf (1917), Hofmaster (1949), Lloyd (1972), Oatman and Platner (1974a), Picard (1913), Stanev and Kaitazov (1962), Traynier (1975) and Trouvelot (1924). PTW larvae mine both subterranean tubers and aerial parts of potato plants. Tuber infestations result in the most economically important damage, but PTW larvae in tubers are relatively immune from parasitoid attack and chemical control strategies. Biological, chemical, and cultural controls are based on the assumption that tuber infestations can be reduced by reducing aerial population densities (Graf, 1917; Bacon, 1960; Lloyd, 1972; Oatman and Platner, 1974a). Thus, while

most previous parasitoid studies involved relationships where the host was in tubers, the present study examined relationships with hosts both in tubers and foliage.

MATERIALS AND METHODS

Environmental conditions

All laboratory studies and culture activities occurred in insectary rooms at 25 ± 1 °C and 45 ± 5% RH. Eight 40-watt, cool-white, fluorscent tubes were utilized as light sources, and were regulated at a 12-hr light:dark cycle. A window air conditioner augmented the temperature control system of the insectary room and more evenly circulated air.

Culture of the host

The stock culture of PTW was reared as described by Platner and Oatman (1969), except that PTW pupae were directly transferred to glass battery jars for adult emergence and oviposition. 'Norgold' potato tubers were used as food. Egg-sheets were obtained daily from this culture, and the resulting larvae were used to maintain parasitoid cultures and initiate laboratory studies.

Culture of the parasitoid

The *O. jenniae* culture was maintained in the insectary of the Division of Biological Control, University of California, Riverside, since April, 1973. Cultural procedures were identical to those developed and described by Platner and Oatman (1972). 'White Rose' potato tubers punctured with a tack-studded device (Finney, Flanders, and Smith, 1947) were placed in a glass battery jar (15.2 cm dia., 20.3 cm high) which contained a PTW egg-sheet to infest the tubers for the parasitoid culture. Tubers with 1- to 4-day-old PTW larvae were added to a parasitoid oviposition-cage at weekly intervals. Clover honey was streaked on the inner surface of the glass cage-top to provide food for adult parasitoids.

Virgin male or female parasitoids were obtained from the culture by isolating cocoons in gelatin capsules (000) until adult emergence.

Holding and oviposition units

For potato tubers. 'White Rose' potatoes were used in all experiments where tubers served as the host substrate. The tubers were harvested from pesticide-free fields at the University of California's Moreno Field Station near Riverside. After harvest, tubers were stored at ca 10 °C for 1 to 6 months before use. Only uniform-shaped tubers which measured $7.5 \pm .5$ cm long were used.

Plywood sheets (1.3 cm thick) with protruding nails were used to hold the experimental units (Cardona and Oatman, 1975). The top of a plastic Petri dish (10 cm dia.),

with a centrally-bored hole was inverted onto each nail, resulting in a dish with a centrally protruding nail. Each dish was lined with a filter paper and fine, white sand was spread over the paper to facilitate host and parasitoid pupation. A punctured tuber was pressed length-wise onto each nail, leaving the tuber ca 1 cm from the sand surface.

Each tuber was infested with the appropriate number of PTW larvae by transferring recently hatched first instars with a camel-hair brush (0000). The tubers then were covered with inverted, clear, polystyrene containers (7.0-cm.-dia. bottom, 9.0-cm.-dia. top, 9.5 cm high) whose open end fit snugly within the Petri dish top. The top (closed-end) of each container had an organdy-covered, 6.0-cm-dia. ventilation hole. These assembled containers were used as holding units from tuber infestation to parasitoid exposure, and after exposure for parasitoid and host pupation. Following host emergence from the tuber and pupal-cell formation in the sand, the units were disassembled. The hole in the Petri dish top was taped and a dish bottom was placed over the sand to form an adult emergence unit.

For parasitoid oviposition, the ventilated holding container was replaced with a larger, clear polystyrene container (11.4-cm-dia. bottom, 12.1-cm-dia. top, 12.1 cm high) with organdy-covered, 5.1-cm-dia. ventilation holes on opposite sides. A 3.8-cm-dia. hole was cut on the bottom (closed-end) of the container. This hole was covered with 100-mesh brass screen through which honey could be forced. A 1.3-cm-dia. hole was also present on the bottom into which a water-filled, 2-dram glass vial with a cotton stopper was inserted. The container was inverted over the impaled tuber and surrounded the sand-covered Petri dish. The assembled oviposition unit remained over the tuber during parasitoid exposure.

For potato plants. 'Norgold' potatoes were used where aerial parts of the potato plant served as the host substrate. Plants were obtained by planting whole tubers in 3.8-liter plastic pots containing a planting mix. A 10:10:2 fertilizer was applied when stems were ca 5 cm high. The plants were grown in a greenhouse until ca 30 cm high, and then were transferred to the insectary for PTW infestation and subsequent parasitization studies.

In the insectary, the number of stems per pot was reduced to 3 by cutting extra stems at the soil surface. A self-adhesive weather-stripping material (9 × 6 mm) was placed around the outside circumference of each pot's upper rim. A clear acetate cylinder (16-cm-dia. top, 17.5-cm-dia. bottom, 51 cm high), which fit snugly around the pot's weather stripping, then was placed over each unit. An organdy-covered air vent (10 cm dia.) was located at mid-height on each side of the cylinder. The top half of a polystyrene container, whose bottom had been removed, fit snugly within the top rim of the acetate cylinder. The container's snap-lid possessed an organdy-covered, 10-cm-dia. vent and a 1.3-cm-dia. hole for the insertion of a water vial.

The assembled plant unit was utilized both as a holding unit and a parasitoid oviposition unit. Foliage was infested with the appropriate number of PTW larvae by transferring recently hatched first instars by means of a camel-hair brush. Larvae were distributed over all plant parts. Parasitoid females were introduced into the container through the water-vial hole in the lid. Honey was streaked on the inner surface of the lid prior to parasitoid introduction.

The plant unit was disassembled 8 days after initial PTW infestation. Plants in each pot were cut at the soil surface and placed in individual pupation units. A pupation unit consisted of a lid-less paper carton (12.5 cm dia., 15.2 cm high) whose closed-end possessed an organdy-covered, 10-cm-dia. vent. The carton's open-end was pressed into a 12.5-cm-dia. hole, cut in a 15-cm-dia. plastic Petri dish top. All the foliage from a

single pot was placed within the carton. The Petri dish top, attached to the carton, was then placed over a dish bottom which had been lined with filter paper and covered with sand. A square of hardware cloth (2.5 × 1.3 cm-mesh) with corners bent downward was used to keep the foliage above the sand. PTW larvae exiting the foliage dropped to the sand to pupate.

When host and parasitoid pupation in the sand was complete, the unit was disassembled, and an unaltered, Petri dish top was placed over the sand-covered, Petri dish bottom. These containers then were held until emergence of adults.

Determination of optimum host age and density for parasitization

For hosts in tubers. Cardona and Oatman (1975), Leong and Oatman (1968), Oatman, Platner, and Greany (1969), Oatman and Platner (1974b), and Odebiyi and Oatman (1972, 1977) determined optimum host age and density for parasitization in the tuber as noninteracting factors for various PTW parasitoids. In the present study a factorial design was used to determine both independent and interacting effects of host age and density on the progeny production of *O. jenniae*. Eight host-larval ages (0 to 1, 1 to 2, 2 to 3, 3 to 4, 4 to 5, 5 to 6, 6 to 7, and 7 to 8 days) within six host-infestation-densities (25, 50, 75, 100, 125, and 150 larvae initially transferred per tuber) were replicated once in each of five blocks. Mated, 1-day-old *O. jenniae* females were each exposed for 24 hr to a tuber having the appropriate host age and density combination. Effects of host age, density, and their interaction upon moth plus parasitoid and total male and female parasitoid emergences were tested by analyses of variance, using a logarithmic transformation.

Design of the initial study did not allow *O. jenniae* females a behavioral choice between the host age and density combinations. An experiment consequently was designed so that females had a choice between these factors. Twenty *O. jenniae* females were individually exposed to four tubers simultaneously in "host preference units." These units consisted of clear polystyrene boxes (30.0 cm long, 15.8 cm wide, 9.5 cm high) with opaque lids. At each end of the unit was an organdy-covered, 6.7-cm-dia. vent. Honey was forced through a 4.4-cm-dia. hole covered with 100-mesh brass screen on the top of the unit, and a 1.5-cm-dia. hole was used for insertion of a water vial. Four 'White Rose' potato tubers were each impaled with three nails to support them above the floor of the unit. From the results of the initial study, each of the tubers were infested with a different host age and density combination (age 1 to 2 days, infestation densities 50 and 125; age 4 to 5 days, infestation densities 50 and 125). Each tuber was coded as to its host age and density by a colored map pin. These units allowed direct observation of the searching *O. jenniae* females who had full access to all four tubers. Females were allowed to oviposit for 24 hr, and then the tubers were placed in the previously described tuber holding and pupation units. Numbers of total, female and male parasitoid progeny produced at each host age and density combination were analyzed by log likelihood ratio tests (G-tests) (Sokal and Rohlf, 1969).

For hosts in foliage. In a separate study, it was found that second instar PTW, infesting potato foliage, were preferred by ovipositing *O. jenniae* females. A preliminary study on PTW instar durations in potato foliage indicated that second instars prodominated from day 3 through 4 after initial infestation. A factorial design was used to determine the optimum host age and density combination for parasitization by *O. jenniae* females in the foliage. Two host ages (3 to 4 and 4 to 5 days) within six host densities (75, 100,

125, 150, 175 and 200 larvae initially transferred per foliar unit) were replicated once in each of five blocks. Mated, 1-day-old *O. jenniae* females were individually allowed to oviposit for 24 hr in a foliar unit containing the appropriate host age and density combination. Effects of host age, density and their interaction upon moth plus parasitoid, parasitoids, and total male and female parasitoid emergences were tested by analyses of variance, using a logarithmic transformation.

Determination of immature parasitoid morphologies and host relationships

To follow the development of the parasitoid relative to the host, several tubers infested with 1- or 4-day-old PTW larvae were exposed to numerous ovipositing *O. jenniae* females for 6 hr. A group of control tubers was also infested but not exposed to female parasitoids. The tubers were then placed in holding units. At the end of the oviposition period and every 12 hr thereafter, the larvae in a few tubers of each host age were extracted by heat (Platner, Greany, and Oatman, 1969). The host larvae escaping from a tuber dropped into a Petri dish bottom filled with water. Then they were fixed in Bouin's solution for 6 to 12 hrs, washed in 70 percent ETOH, and stored in 90 percent ETOH until dissection.

When host larvae began to emerge from the tuber to pupate in the sand of the holding unit, host and parasitoid larvae and pupae were extracted from the sand using a sodium hypochlorite solution (Finney, Flanders, and Smith, 1947). Fixation and storage of larvae and pupae collected from the sand were the same as for host larvae extracted from the tubers.

Before each host larva was dissected, head capsule width and body length measurements were taken. Each host larva then was dissected in a glycerol-water solution and parasitization was recorded with the host measurements. If the host was parasitized, the parasitoid egg or larva was extracted and its stage recorded with the host data. These data were used to determine the effects of the parasitoid on the host as well as those of the host on the life stages of the parasitoid.

The immature parasitoid stages obtained from host larvae initially parasitized at 4 days of age were used in the morphology studies. Parasitoid eggs and first instars were stained for 5 to 10 minutes with acetocarmine, washed with distilled water, and slide-mounted in Hoyer's medium. Second and third instars were cleared in a cold, 10 percent KOH solution for 6 to 10-hr, then washed in distilled water, stained and mounted. Head capsules of last instar were excised, cleared in a 10 percent KOH solution for 2 to 4 hr, then washed and slide-mounted.

Determination of food and water effects on adult parasitoid longevity

Effects of honey and water as a carbohydrate and moisture source on adult longevity were studied to establish the optimal requirements of adult *O. jenniae*. Four treatments were used: (1) neither water nor honey; (2) water but no honey; (3) honey but no water; and (4) both water and honey. Males and females were observed separately by placing 10 newly emerged virgin males or females in a respective, sealed potato tuber oviposition unit (no hosts were supplied) with a given treatment combination. Each treatment was replicated five times for each sex. Counts of dead individuals were made every 24 hr.

Determination of preoviposition period and diurnal oviposition rhythm

To determine the occurrence and duration of a preoviposition period in *O. jenniae* females, 100 potato tubers were each infested with 50 newly hatched PTW larvae and placed in individual holding units. At the initiation of the photophase, 4 days after larval infestation, 20 emerging parasitoid females were selected for study. Ten mated and 10 virgin females were placed in individual oviposition units with one of the previously infested tubers. The tuber in each unit was replaced every 3 hr during the 12-hr photophase. The tuber placed in the oviposition unit at the initiation of the scotophase remained during the entire 12-hr period. After parasitoid exposure the tubers were placed in individual holding units until adult emergence.

To ascertain the presence of a diurnal oviposition rhythm, 20 1-day-old, mated *O. jenniae* females were allowed to oviposit in 125, 4- to 5-day-old host larvae in tubers during the same time intervals and under the same conditions as in the preoviposition study.

Observation of parasitoid behaviors

Observations on courtship and mating behaviors of *O. jenniae* were made in transparent gelatin capsules (000). Behaviors within the gelatin capsules were identical to those seen in larger units, but the time to initiation of courtship activities was considerably reduced. Prior to adult parasitoid emergence, cocoons were isolated in capsules. Virgin females were exposed to virgin males within 6 hr of adult emergence.

Searching and oviposition behaviors of *O. jenniae* females were observed on potato tubers infested with host larvae of various ages.

Determination of parasitoid fecundity and construction of life tables

Life tables were developed for *O. jenniae* reared under insectary conditions ($25 \pm 1 °C$, $45 \pm 5 \%$ RH and a 12-hr photoperiod) on host larvae in 'White Rose' tubers and 'Norgold' foliage. Data on immature parasitoid development were obtained from the morphology and life cycle studies.

To obtain progeny production data, numerous parasitoid cocoons were isolated in gelatin capsules, and 30 females were selected at emergence. Twenty females were then mated and 10 of these were placed in individual tuber oviposition units in which the tubers had been infested with the previously determined optimal host density and age. The other 10 mated females were placed in individual plant units possessing the optimal host age and density combination. The remaining 10 virgin females were placed in individual tuber oviposition units also possessing the optimal host age and density. Every 24 hr, each parasitoid was transferred to an identical oviposition unit infested with the optimal number and age of hosts for the particular host substrate. Tuber and foliar units were held after parasitoid exposure until progeny emergence was complete and counts taken. These operations were repeated daily until all female parasitoids died. The data obtained were used to calculate daily progeny production, progeny sex ratio, and adult female longevity for each cohort.

In the construction of life tables for mated females, immature parasitoid survivorships were determined by counting female ovipositions in hosts either in the tuber or

foliage and then using the number of progeny emerging to calculate total immature mortality for the respective host substrate. Results from life cycle studies for hosts in the tuber were used to determine prepupal and pupal mortality. These data then were used to separate immature survivorship into two periods; (1) from oviposition to emergence from the host larva, and (2) from emergence from the host larva to adult emergence. Immature mortality due to superparasitization was assumed to be negligible, as high host densities used in the fecundity studies made superparasitization unlikely.

Data on development, survivorship, fecundity and progeny sex ratio of *O. jenniae* were used in the construction of life tables, as discussed by Krebs (1978). The life table statistics were calculated from formulae given by Krebs (1978) and as performed by Cardona and Oatman (1975) and Odebiyi and Oatman (1977).

RESULTS AND DISCUSSION

Optimum host age and density for parasitization

For hosts in tubers. Total moth plus parasitoid emergences indicated significant differences (P ≤ .05) only among host infestation densities. As host density per tuber increased, total emergence per tuber also increased. Densities of 125 and 150 larvae per tuber resulted in the highest mean total emergences (Table 1).

Table 1. INDEPENDENT EFFECTS OF HOST DENSITIY AND AGE ON PROGENY PRODUCTION BY MATED *Orgilus jenniae* WITH HOSTS IN POTATO TUBERS

Host infestation density	Mean Number Emerging[*],[†]			
	Total moths + parasitoids	Total parasitoids	Male parasitoids	Female parasitoids
25	13.0 e	9.2 d	6.2 d	3.0 c
50	25.8 d	15.6 c	10.7 c	4.9 b
75	37.0 c	19.3 bc	13.1 bc	6.2ab
100	47.6 b	21.1ab	14.3ab	6.8ab
125	55.9a	24.6a	17.2a	7.3a
150	64.4a	23.3ab	15.5ab	7.8a
Host age (days) at exposure				
0–1	42.2a	16.6 bc	11.1 bc	5.5a
1–2	41.2a	24.0a	17.2a	6.7a
2–3	40.7a	20.2ab	14.4ab	5.8a
3–4	43.1a	21.0ab	14.8ab	6.1a
4–5	40.2a	21.4ab	14.5ab	6.9a
5–6	43.6a	22.1a	15.5a	6.5a
6–7	36.3a	14.5 c	9.0 c	5.5a
7–8	37.6a	11.0 d	6.2 d	4.7a

[*]Each mean for host densities was based on five replications for each of eight host ages (40 reps/mean). Each mean for host ages was based on five replications for each of six host densities (30 reps/mean).
[†]Means followed by the same letter in a given column for host density or age were not significantly different at the 5 % probability level (Duncan's New Multiple-Range Test). Analyses were performed using a logarthmic transformation.

Total parasitoid emergence indicated that host density, age, and their interaction were all significant ($P \leq .05$). As with moth plus parasitoid emergences, total parasitoid production increased with host density. Host densities of 100, 125, and 150 larvae per tuber resulted in parasitoid emergence means that were not significantly different ($P \geq .05$), but the progeny production at 125 host-larvae per tuber was the only mean that singularly belonged to the highest homogenous subgroup (Table 1).

The total parasitoid production response to host age indicated that *O. jenniae* females produced higher numbers of progeny at host ages of 1 to 6 days (Table 1). However, within this homogenous subgroup, only the host ages 1 to 2 and 5 to 6 days singularly belonged to this highest subgroup.

Analysis of the significant host age and density interaction on total parasitoid production indicated that at host densities of 25 and 50 larvae per tuber, progeny production means were not significantly different ($P > .05$) with respect to host ages, but as infestation densities increased to 125 and 150 larvae per tuber, the means segregated into homogenous subgroups similar to the independent response to host age. Additionally, parasitoid-progeny productions were slightly higher at lower host densities on younger larvae, which changed to higher relative progeny productions at higher host densities on older larvae. The highest progeny production mean observed was 31.4 parasitoids per tuber and occurred at a host age of 4 to 5 days and an infestation density of 125.

Analysis of parasitoid female-progeny production revealed that only the independent effect of host density was significant ($P \leq .05$). Host densities of 125 and 150 larvae per tuber resulted in the highest female emergences (Table 1). The independent effect of host age resulted in statistically nonsignificant differences ($P > .05$) in female production, but the highest mean occurred at a host age of 4 to 5 days (Table 1).

Analysis of male parasitoid emergences showed that host density, age, and their interaction were all significant ($P \leq .05$). Male emergence means segregated into homogenous subgroups identical to those for total parasitoids (Table 1).

Results indicated that total parasitoid production relative to host age and age/density interaction were primarily responses in male-progeny productions. Host density directly affected both male- and female-progeny productions. A host infestation density of 125 larvae per tuber appeared optimal for *O. jenniae* progeny production, but host ages of 1 to 2 and 4 to 5 days appeared equally optimal at this density.

To differentiate between the two-age optima and their interactions with host density, experiments were performed using the host preference units wherein the parasitoid females had a behavioral choice, between the host age and density combinations. The mean numbers of female, male and total parasitoids produced are shown in Figure 1. G-tests for each of these dependent variables indicated that host age and density acted independently ($P > .05$) in influencing parasitoid production. However, the progeny production responses were nearly the same for either host density within a host age. *Orgilus jenniae* production nearly doubled in tubers containing 4- to 5-day-old host larvae, regardless of host density.

Broodryk (1969), Cardona and Oatman (1975), Finney, Flanders, and Smith (1947), Odebiyi and Oatman (1972, 1975), and Platner and Oatman (1972) suggested that the optimum host age for a PTW parasitoid may be a function of the depth of the larval mine in the tuber relative to ovipositor length, implying that the ovipositing parasitoid responds not only to host age but also to host availability. *Orgilus jenniae* females locate PTW larvae in tubers only by inserting the ovipositor into the holes where the hosts push frass from their mines. Thus, the significant interaction between host age and
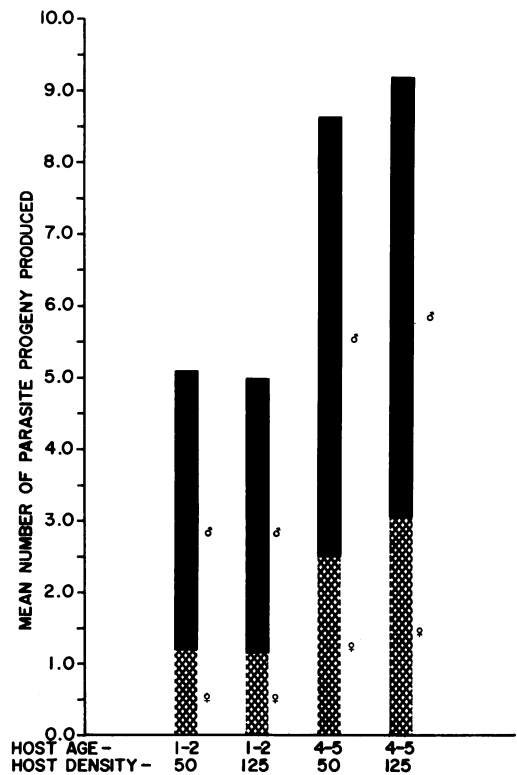
Fig. 1. Mean progeny production responses of mated
Orgilus jenniae females at 4 host age and density
combinations in potato tubers.

Table 2. POTATO TUBERWORM MINE LENGTHS IN POTATO TUBERS RELATIVE TO
DAY AFTER INFESTATION AND INITIAL LARVAL DENSITY PER TUBER

Initial density	Day 1		Day 2		Day 3		Day 4		Day 5	
	n	$\bar{x}$ (mm)*	n	$\bar{x}$ (mm)*	n	$\bar{x}$ (mm)*	n	$\bar{x}$ (mm)*	n	$\bar{x}$ (mm)*
25	11	1.916 a	11	2.016 c	11	2.488 c	15	3.850 b	12	4.788 a
50	9	2.301 a	22	2.222 bc	25	2.772 bc	21	3.541 b	20	5.398 a
75	22	2.016 a	22	2.092 bc	39	2.762 bc	37	3.572 b	28	5.160 a
100	26	1.940 a	19	2.130 bc	41	3.019 ab	43	3.870 b	33	4.700 a
125	32	1.930 a	45	2.584 a	41	3.090 ab	52	4.474 a	36	5.678 a
150	34	1.828 a	51	2.447 ab	51	3.339 a	52	4.549 a	38	5.597 a

*Means followed by the same letter in a given column are not significantly different at the 5% probability
level (Duncan's New Multiple-Range Test). Analyses were performed using a logarithmic transformation.

density found in the initial study appeared to result from the combined effect of host
availability and preferred host age for oviposition. To test this hypothesis, the change in
PTW larval mine-lengths over time was investigated. Five series of tubers were each
infested with 25, 50, 75, 100, 125, or 150 larvae. Beginning 1 day after tuber infesta-
tion, the larval mines in 1 tuber at each density were dissected and the lengths measured.
Measurements continued for 5 consecutive days. Analysis of variance of the logarith-

mically transformed lengths indicated that age, density, and their interaction were all significant (P ≤ .05). The independent effect of density on mine lengths for each age are shown in Table 2. One day following infestation, the mean mine lengths were not significantly different (P ≥ .05). On days 2, 3 and 4, the mine lengths in tubers containing higher larval densities were significantly longer than those in tubers with lower densities. The mean mine lengths were again not significantly different on day 5. The results suggested that changes in PTW mine length over time were a function of larval response to increasing density. Observations during mine dissections suggested that this response was due to aggression among PTW larvae. Larvae were observed to normally occupy separate mines, but to be cannibalistic if mines converged. Apparently the larvae detected other larvae mining in their vicinity and reduced inter-larval contact by more rapidly extending mine length. Assuming that the average number of larvae initiating mines per opening in the tuber's epidermis increased with increasing larval density per tuber, then the greater the number of larvae entering an opening, the more rapidly they extended their mines. The nonsignificant differences in mine lengths on the fifth day indicated that once the larvae in tubers possessing higher densities had extended their mines to a distance where inter-larval contact was sufficiently reduced, the stimulation to increase mine length also was reduced. Mine lengths in tubers with lower larval densities subsequently approached the length of mines in tubers with higher densities.

Orgilus jenniae possesses an ovipositor of 2.681 ± .0751 mm (P = .05, n = 35) in length, suggesting that from 3 days after tuber infestation the females were physically unable to reach most of the PTW larvae in the tubers. This apparent anomaly between parasitoid ovipositor length, host mine length, and parasitoid ovipositional preference for 4- to 5-day-old host larvae is explained by observations on the nature of the PTW mine. As the larva extends its mine, it blocks the original mine entrance with frass. When the larva extends its mine a sufficient length, a second exit hole to the tuber surface is produced. The frequency of occurrence of these secondary exit holes relative to initial host density was analyzed for counts taken on day 5 of the mine length study. A G-test indicated that there was a highly significant dependence (P < .001) between density and occurrence of secondary exit holes. The proportion of mines with exit holes was higher than expected at densities of 150 and 125 larvae per tuber, where 39.5 and 22.2 percent possessed secondary exit holes, respectively. The frequency of occurrence was lower than expected at densities of 100, 75, 50, and 25 larvae per tuber, where 9.1, 10.7, 5.0, and 8.3 percent of the mines possessed secondary holes, respectively. The secondary exit holes caused PTW larvae to again become available to ovipositing parasitoid females. Thus, the ability of *O. jenniae* to oviposit in 3-day or older host larvae in tubers appears to be a function of the occurrence of secondary exit holes, which was dependent on larval density per tuber. The interaction found in the initial study on optimum host age and density for parasitization then was a result of changes in host availability, which was dependent on mine length and secondary exit hole formation as affected by time after tuber infestation and larval density. The occurrence of secondary exit holes in host mines increases the host age availability for parasitoids, but a balance between preference and availability apparently occurs, depending upon the age of host actually preferred and ovipositor length.

Results indicated that when tubers are used as the host substrate, a host age of 4 to 5 days at a density of 125 larvae per tuber is optimal for *O. jenniae* progeny production. These conditions were used in all further studies involving tubers and where an optimal host age and density were required.

For hosts in foliage. The independent effects of host density and age on moth plus parasitoid, total parasitoids, and male and female parasitoid emergences are shown in Table 3. Analysis of the total number of moths and parasitoids emerging indicated that there were significant differences (P $\leq$ .05) in emergence only among host infestation densities. As host densities increased, emergence of moths and parasitoids also increased. Host densities of 175 and 200 larvae per foliar unit resulted in significantly higher mean total emergences.

Analysis of total *O. jenniae* progeny production indicated that only host age was significant (P $\leq$ .05). Separate analyses of male and female productions indicated non-significant (P > .10) responses to host density, and age/density interaction. However, parasitoid male and female production means increased with host density to peak at 175 hosts per foliar unit (Table 3). Although not statistically significant, an infestation density of 175 larvae per foliar unit appeared optimal for *O. jenniae* progeny production. A host age of 3 to 4 days was significantly optimal (P $\leq$ .05) for parasitoid production, but was primarily due to increased male production (Table 3).

The results indicated that when potato foliage is used as the host substrate, a host age of 3 to 4 days and an infestation density of 175 larvae per foliar unit are optimal for *O. jenniae* progeny production. These conditions were used in all studies involving potato foliage and where an optimal host age and density were required.

Immature parasitoid morphologies and behaviors

Egg. The female parasitoid deposits the egg in the hemocoel of the PTW larva. Eggs are usually found in the posterior of the abdomen but occasionally in the thorax. Initally, the egg floats freely in the hemolymph but eventually becomes attached to internal host organs. it frequently adheres to the malpighian tubules near the junction of the mid- and hind-gut, but also to fat bodies, salivary glands, or outer gut wall. The

Table 3. INDEPENDENT EFFECTS OF HOST DENSITIY AND AGE ON PROGENY PRODUCTION BY MATED *Orgilus jenniae* WITH HOSTS IN POTATO FOLIAGE

Host infestation density	Mean Number Emerging[*],[†]			
	Total moths + parasitoids	Total parasitoids	Male parasitoids	Female parasitoids
75	62.4 d	31.0a	18.2a	12.8a
100	80.3 c	41.7a	26.5a	15.2a
125	93.2 bc	44.5a	31.0a	13.5a
150	104.6 b	45.8a	30.4a	15.4a
175	124.9a	49.6a	32.6a	17.0a
200	128.6a	42.2a	26.7a	15.5a
Host age (days) at exposure				
3–4	99.5a	48.3a	33.1a	15.2a
4–5	98.5a	36.6 b	22.0 b	14.6a

[*]Each mean for host densities was based on five replications for each of two host ages (10 reps/mean). Each mean for host ages was based on five replications for each of six host densities (30 reps/mean).
[†]Means followed by the same letter in a given column for host density or age were not significantly different at the 5% probability level (Duncan's New Multiple-Range Test). Analyses were performed using a logarithmic transformation.

egg is usually attached by its stalk. Similarly, Broodryk (1969) found that the egg chorion of *Orgilus parcus* Turner possesses an adhesive substance by which it adheres to internal tissues of PTW larvae.

The egg of *O. jenniae* (Fig. 2a,b) is of a stalked type (Clausen, 1940). The ovarian egg is more slender than the newly deposited egg, otherwise being identical in size and
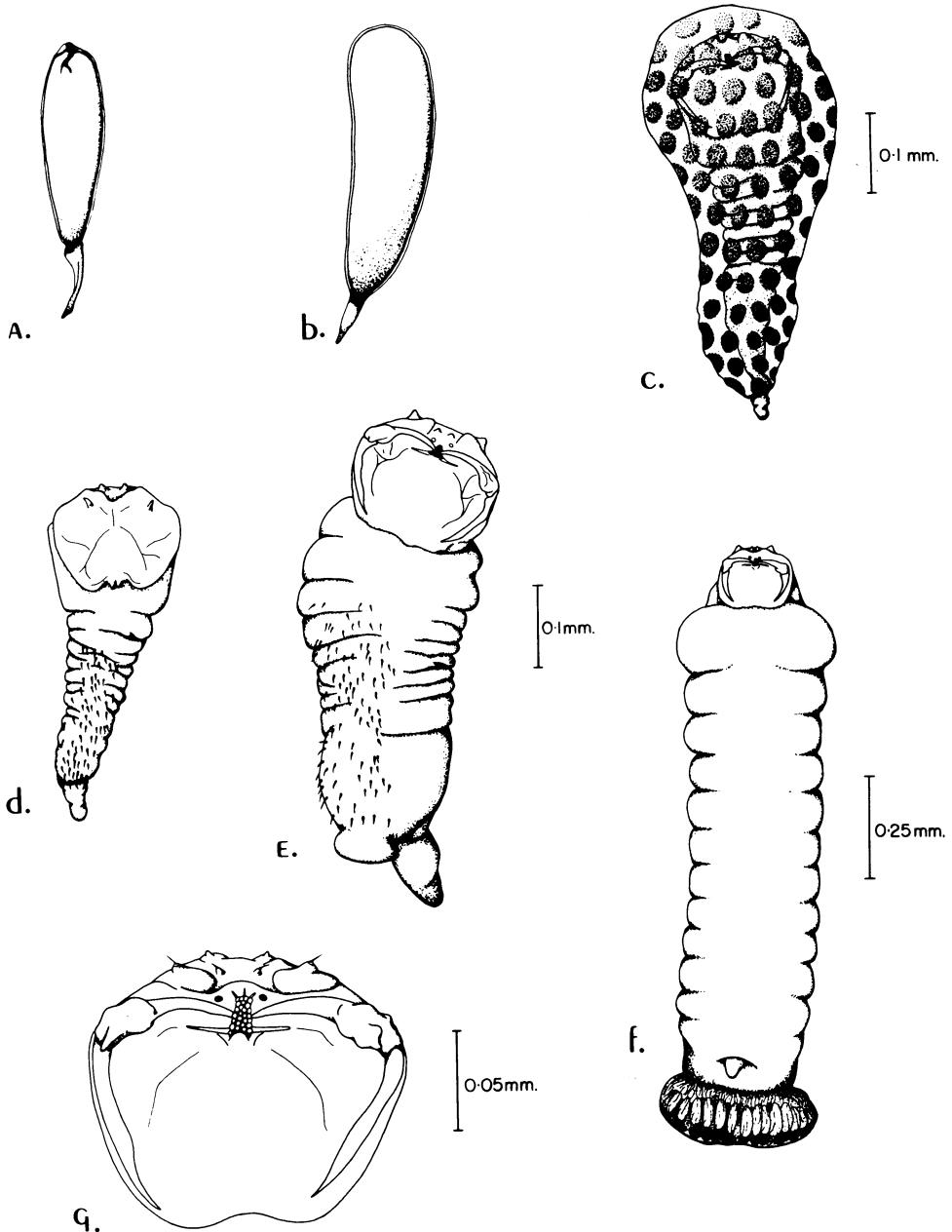

Fig. 2. Egg and first instar of *Orgilus jenniae:* a. egg, 0–6 hours; b. egg, 24–30 hours; c. egg with embryonic first instar, 48–54 hours; d. dorsal view of the caudate first instar; e. caudate-vesiculate first instar; f. ventral view of the mature vesiculate first instar; g. ventral view of the first instar head capsule.

structure. The ovarian egg is positioned within the maternal oviduct so that its stalked-end is directed caudad relative to the body of the female. Except for a faint (exaggerated in Fig. 2a) "Y"-shaped suture at the cephalic-end, the newly laid egg is translucent white with a smooth chorion. The "Y"-shaped suture presumably is associated with the micropylar opening and disappears with further egg development. Similarly, Juillet (1960) reported "V"-shaped sutures at the anterior of *Orgilus obscurator* (Nees) eggs.

The egg possesses two membraneous coverings. The outer chorionic membrane encloses the egg and forms the stalk. The inner membrane encloses a clear, granular fluid. The inner membrane and its enclosed fluid are not visible in the stalk.

The total length of the egg (including the stalk) increased from $0.282 \pm .0082$mm ($P = .05$, $n = 21$) at 0 to 6 hr after oviposition to $0.402 \pm .0154$mm ($P = .05$, $n = 32$) at 30 to 36 hr. Its maximum width increased from $0.051 \pm .0032$mm ($P = .05$, $n = 21$) at 0 to 6 hr to $0.174 \pm .0084$mm ($P = .05$, $n = 32$) at 30 to 36 hr. The increase in length and width was partially at the expense of the egg stalk which decreased in length from $0.085 \pm .0054$mm ($P = .05$, $n = 21$) at 0 to 6 hr to $0.065 \pm .0023$mm ($P = .05$, $n = 50$) at 24 to 30 hr. The stalk was reduced to a shriveled vestige 30 to 36 hr after oviposition.

The developing parasitoid embryo was discernible within the egg at ca 30 hr after oviposition. At 60 to 66 hr, the embryonic larva (Fig. 2c) was still surrounded by the transparent egg chorion, but large cellular structures were now visible in the membrane. Eclosion from the egg occurred ca 66 to 72 hr after oviposition. The first instar parasitoid emerged through a rupture of the chorion at the cephalic-end of the egg.

First instar

The embryonic first instar of *O. jenniae* in the 42- to 48-hr egg is of the caudate-mandibulate type (Clausen, 1940). The embryonic larva possesses 10 body segments (not including the head capsule), and a stout caudal horn which does not protrude into the stalk of the egg. The head capsule possesses a pair of sclerotized, sickle-like mandibles without teeth (Fig. 3a).

Following eclosion, the first instar is similar to the mature embryonic larva (Fig. 2d). Its caudate-mandibulate morphology is retained, but there are 11 body segments. At ca 94 to 98 hr after oviposition (28 to 34 hr after eclosion), an anal vesicle appears at the
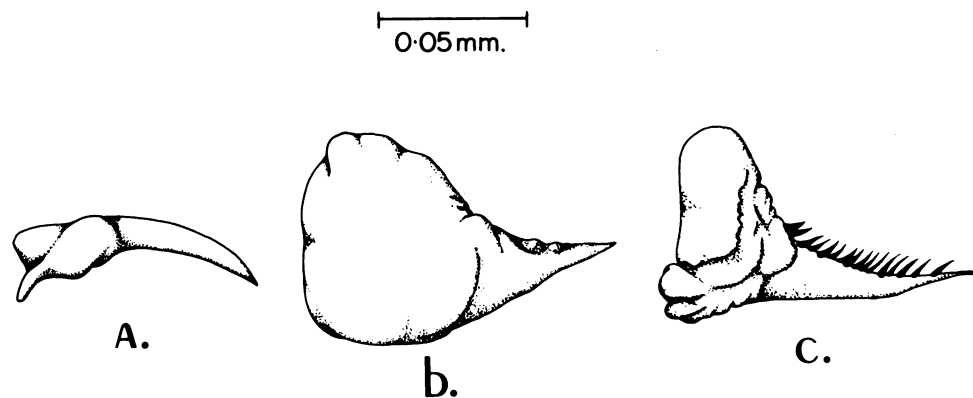

Fig. 3. Mandibles of *Orgilus jenniae* larvae: a. first instar; b. second instar; c. third instar.

caudal-end of the larva. The vesicle increases in size with time, while the caudal horn shrinks to a vestige on the venter of the posterior abdominal segment (Fig. 2e,f). The transformation from caudate- to vesiculate-mandibulate occurs gradually. Head capsule lengths and widths, and mandible lengths do not indicate a larval molt during this transformation. Broodryk (1969) and Oatman, Platner, and Greany (1969) reported similar transformations for *O. parcus* and *O. lepidus,* respectively. The number of body segments of *O. jenniae* increases to 12 after transformation. Just before the first molt, the mature, vesiculate, first instar possesses a full complement of 13 body segments (not including the vesicle) (Fig. 2f). Neither spiracles nor a tracheal system were discernible.

The first instar is always oriented within the host so that its cephalic-end is directed towards that of the host. It is always found in the posterior abdominal hemocoel near the junction of the host's mid- and hind-gut. The first instar possesses numerous small, stout, sclerotized spines on the dorsal surfaces of the abdominal segments (Fig. 2d,e). Although the positions of the spines vary, their distal tips are directed caudally and appear to maintain the position of the parasitoid larva within the host's hemocoel.

The head capsule width of the first parasitoid instar gradually increased from $0.154 \pm .0028$mm (P = .05, n = 59) in the caudate form to $0.167 \pm .0039$mm (P = .05, n = 8) in the mature vesiculate form. The head capsule length increased from $0.118 \pm .0023$mm (P = .05, n = 57) to $0.131 \pm .0069$mm (P = .05, n = 8). The body length (excluding head capsule and caudal horn/vesicle) increased from $0.259 \pm .0122$mm (P = .05, n = 52) in
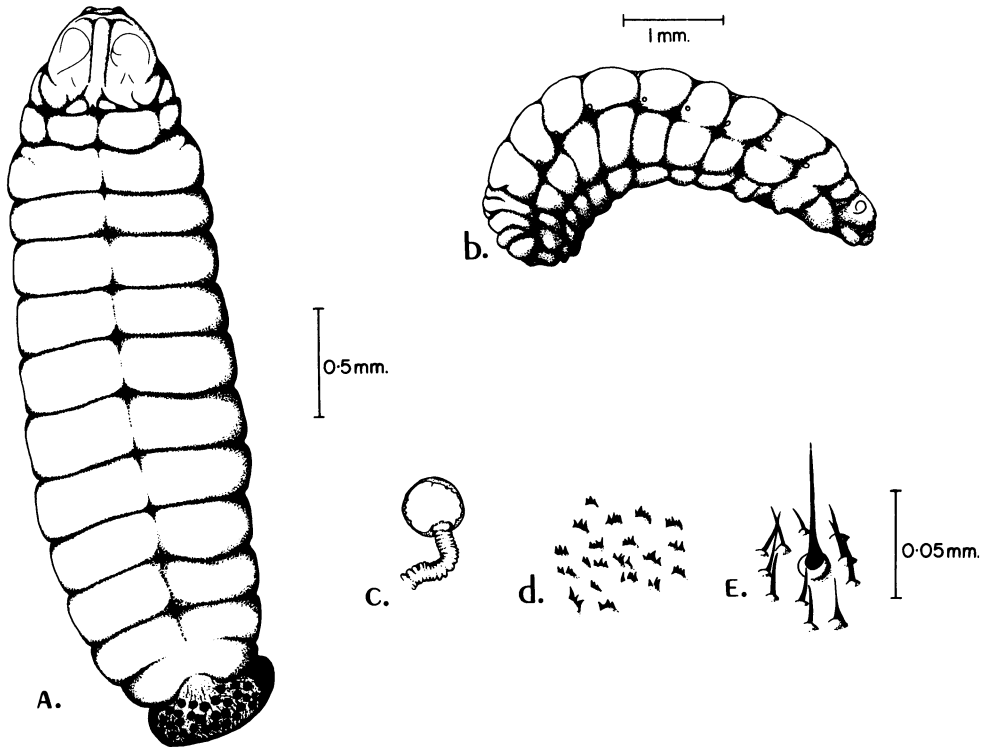

Fig. 4. Second and third instars of *Orgilus jenniae:* a. dorsal view of second instar; b. side view of third instar; c. spiracle of third instar; d. ventral spines of third instar's thoracic appendages; e. integumental setae of third instar.

the embryonic first instar to 0.961 ± .1807mm (P = .05, n = 9) in the mature vesiculate first instar. The length of the caudal horn was 0.079 ± .0088mm (P = .05, n = 14). The length of the mandible increased from 0.0716 ± .00103mm (P = .05, n = 118) to 0.0773 ± .00222mm (P = .05, n = 16). These gradual increases were not associated with a larval molt.

The head (Fig. 2g) is lightly sclerotized and dorso-ventrally flattened. The stout bases of the sickle-like mandibles articulate with sclerotized hypostomal rods (Fig. 3a). The head capsule bears various protuberances, structures and setae (Fig. 2g).

Second instar. The first molt occurs ca 140 hr after egg deposition (70 to 80 hr after eclosion from the egg). The second instar appears in the hemocoel of the host when the fourth instar host leaves the tuber to form a pupal cell in the soil.

The second instar is hymenopteriform and possesses a large caudal vesicle (Fig. 4a). The body possesses three thoracic and 10 abdominal segments, and the anal vesicle. The prothoracic segment is nondifferentiated and largely contiguous with the weakly sclerotized head capsule. The larval integument lacks spines or setae. Spiracles are not present, but lateral tracheal trunks with dorsal and ventral branches are visible on each side of the body. The mid-gut is expanded but not attached to the slender hind-gut. The internal salivary glands are visible as slender filaments radiating from the thorax to the ventral abdominal hemocoel.

The head capsule of the second instar had a width of 0.392 ± 0.0385mm and a length of 0.247 ± .0192mm (P = .05, n = 31). The body length was 2.167 ± .2050mm (P = .05, n = 31) (excluding head capsule and anal vesicle). The orientation and position of the second instar parasitoid within the host is similar to that of the first instar, except that it occupies most of the host's abdominal hemocoel.

The head capsule is similar to that of the third instar (Fig. 5), except that there is no silk press and no labial or maxillary palpi. The capsule and its associated structures are only weakly sclerotized. The maxillae and labium appear as nondifferentiated pro-tuberances devoid of spines or setae. The triangular mandibles possess relatively large, quadrate bases with blades that dorsally exhibit slight, nonserrate concavities (Fig. 3b). The bases of the mandibles articulate laterally with weakly sclerotized hypostomal rods. The length of the mandible was 0.905 ± .00585mm (P = .05, n = 20).

Third instar. The second larval molt occurs ca 190 hr after egg deposition (120 hr after eclosion from the egg or 48 hr after the first molt). The third instar parasitoid appears in the hemocoel of the fourth instar host after the host completed its pupal cocoon.

The third instar is hymenopteriform (Fig. 4b). The caudal vesicle is reduced to a vestige, and the entire body is more eruciform than the second instar. The body possesses 13 distinct segments. The integument bears numerous short and long setae, giving the integumental surface a rugose appearance (Fig.4e). No setal pattern is discernible. Pairs of stout, fleshy appendages are present on the ventral surfaces of the meso- and meta-thoracic segments. These appendages bear numerous sclerotized, toothed structures (Fig. 4d) whose tips are directed caudad. A pair of functional spiracles (Fig. 4c) occur on the meso- and metathoracic segments and the first 8 abdominal segments. The in-ternal tracheal system is the same as that in the second instar, except that the tracheal trunks and their branches are larger and more profuse. The salivary glands are larger than in the second instar. The hemocoel is filled with a yellowish fat body, embedded with numerous white deposits.

The head capsule width and body length (including head capsule) of the third instar were 0.494 ± .0578mm (P = .05, n = 55) and 4.359 ± .1467mm (P = .05, n = 30), respec-

tively. A frontal view of the head capsule is shown in Fig. 5a. The terminology of Short (1952) was used in identifying the structures and areas of the capsule. The head capsule is sclerotized and shows distinct antennal socket areas. The mouth parts protrude from a relatively nonsclerotized concavity below the frons and genae. The clypeus and labrum appear fused and relatively nondifferentiated (the suspensorial sclerite was not discernible) and recede into the head capsule from the frons. The bases of the mandibles are each enclosed externally by a fleshy covering which bears a small dorsal and a larger ventral seta. The sclerotized mandible possesses the typical quadrate base and a long, pointed, slight curved blade (Fig. 3c). The dorsal edge of the blade is slightly concave, bearing 15 to 16 teeth within this concavity. The mandible was $0.212 \pm .0032$mm

antennal socket
frons
clypeus
labrum
mandible
galea
lacinia
stipes
maxillary palp
hypopharynx
prelabium
labial palp
postlabium

A.

0·1 mm.

epistoma
mandible
pleurostoma
spur of hypostoma
hypostoma
stipital sclerite
salivary opening
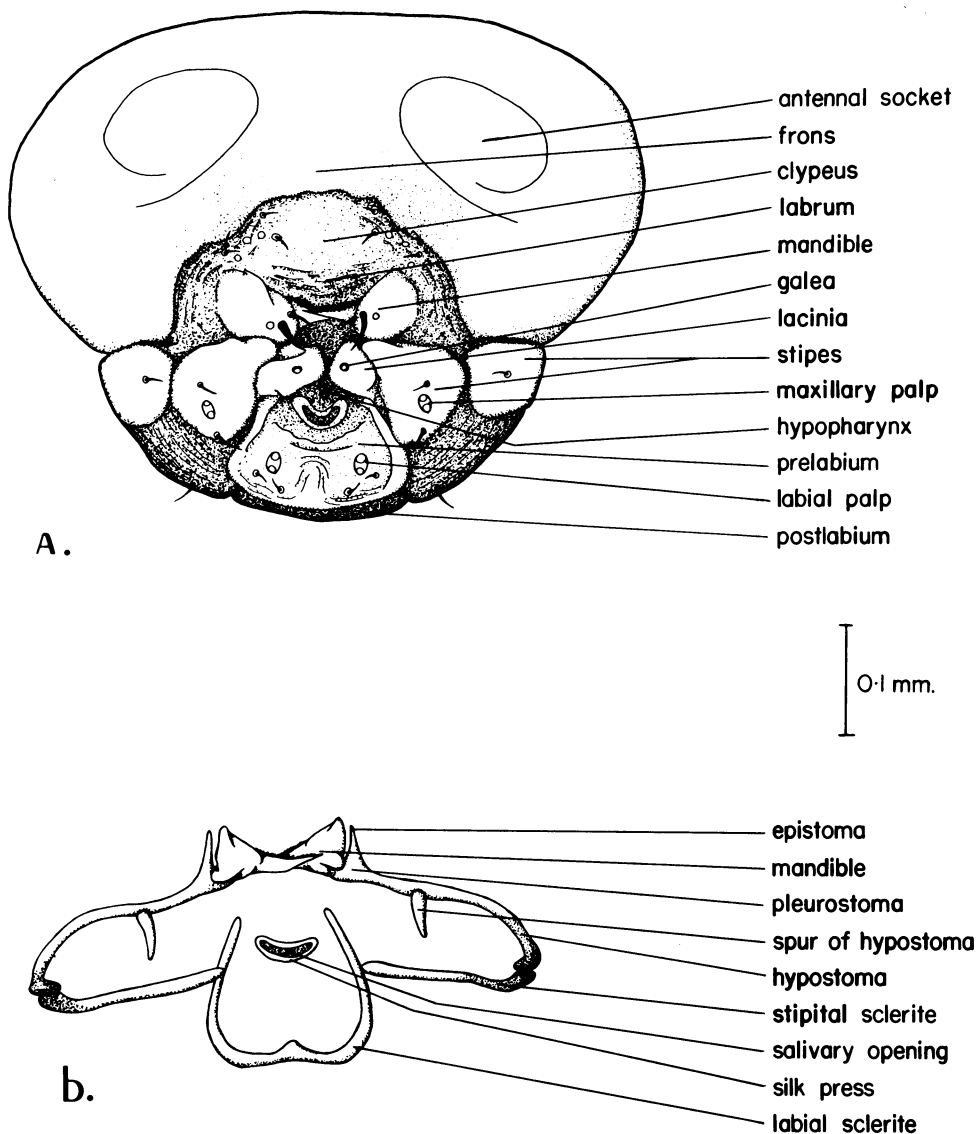silk press
labial sclerite

b.

Fig. 5. Third instar *Orgilus jenniae* head capsule morphology: a. frontal view of external features; b. frontal view of internal sclerotic structures.

(P = .05, n = 62) in length. The maxillae arise below the mandibles. The cardo is non-differentiated, and the stipes appear as two segments. The first stipital segment occurs just ventral to the lateral gena and possesses a single median seta. The second, larger segment of the stipes lies medially to the first and bears the maxillary palp and 2 setae (one seta dorsal and one ventral to the palp). An additional pair of protuberances, by their position and relative autonomy, apparently represent the maxillary laciniae. A circular area, apparently representing the galea, lies upon each lacinia. Short (1952) stated that the galea and lacinia are lacking in this genus, but the position and distinctness of these segments in O. *jenniae* tend to dispute his assertion. The labium is ventral to the maxillae. The prelabium appears as a quadrate area differentiated from the post-labium by the surrounding labial sclerite (Fig. 5b). The prelabium possesses a pair of labial palpi and 2 pairs of labial setae. The salivary opening with its surrounding silk press is located at the medio-dorsal edge of the prelabium. The fleshy hypopharynx is located just dorsal to the silk press. The postlabium, bearing numerous fine lines, is ventral and posterior to the prelabium and bears a pair of lateral setae.

The internal sclerotic bars of the head capsule are shown in Fig. 5b. The epistoma is incomplete (i.e., it does not form a complete arch). The spurs of the hypostoma do not reach the stipital sclerites.

Approximately 24 hr after the second larval molt, the third instar parasitoid began to emerge from the host larva. The parasitized host was a light-reddish color, as opposed to its normal green coloration. The parasitoid larva occupies nearly the entire abdominal volume of the host and its head protrudes into the host's thoracic cavity. The parasitoid larva lacerates a small hole with its mandibles near the left or right lateral line, between the second and third thoracic segments of the host, then emerges head first by alternate contractions and expansions of its body. The setae on the integument and the toothed structures on the thoracic appendages aid its emergence. As the larva emerges, it directs its head toward the caudal end of the host. Emergence is completed within 30 to 40 minutes. Following emergence, the parasitoid larva lies with its ventral side along the lateral line of the host, and with its head at the host's caudal end. The parasitoid larva then feeds on the remains of the host by lacerating the integument with its mandibles. The host is consumed progressively from posterior to anterior in 3 to 4 hr. As feeding continues, the body of the parasitoid rotates about the head of the capsule of the host, so that after feeding, the body of the larva is oriented with its head towards the cephalic end of the host's cocoon. All but the head capsule and sclerotized portions of the host's thorax are consumed. The fully engorged parasitoid larva acquires the previous reddish coloration of the host.

After feeding, the parasitoid larva constructs its pupal cocoon within that of its host. Cocoon construction requires 18 to 24 hr. The completed cocoon is "cigar"-shaped, translucent-white, and has a densely-woven inner and a more loosely-woven outer surface of silk. Its length was 4.999 ± .1304mm (P = .05, n = 15); its width, 1.672 ± .0803mm (P = .05, n = 15).

Prepupa and pupa

Upon completion of the cocoon, the inactive third instar parasitoid shortens and broadens. The mid- and hind-guts join and a rusty-brown meconial pellet is deposited at the caudal-end of the cocoon. The last larval skin remains wrapped around the transforming pupa and continues to enclose it as a loose membrane.

The parasitoid pupa is exarate. The wing pads are clearly discernible during the early stages of pupal development. Initially, the pupa is pale yellowish-red, but as development proceeds, darker, reddish-brown eyespots appear. Approximately 2 days after initiation of pupation, the thorax acquires a black coloration; 12 to 24 hr later, the dorsal abdominal sclerites also darken. Once the abdominal sclerites are completely pigmented, the parasitoid adult is fully formed, but does not emerge from the cocoon for at least 12 hr, and not until the beginning of the next photophase.

The female pupa possesses a long ovipositor, curved dorsally and anteriorly over the abdomen. The mean length of male pupae was $3.952 \pm .2288$mm ($P = .05$, $n = 12$); the length of female pupae, $4.065 \pm .1965$mm ($P = .05$, $n = 12$).

The parasitoid adult emerges from its cocoon and that of its host by chewing small circular holes at the cephalic-ends of both. Adult emergence begins only at the initiation of the photophase and continues for as long as 2 hr. Only 1 adult *O. jenniae* emerges per host cocoon, indicating that it is solitary. However, more than one egg was commonly found per host, but no more than one late first instar.

Parasitoid life cycle and host synchronization

The durations of the parasitoid and host stages are shown in Fig. 6. The wider bars on the horizontal duration lines indicate the period of maximum occurrence ($\geq 70\%$)
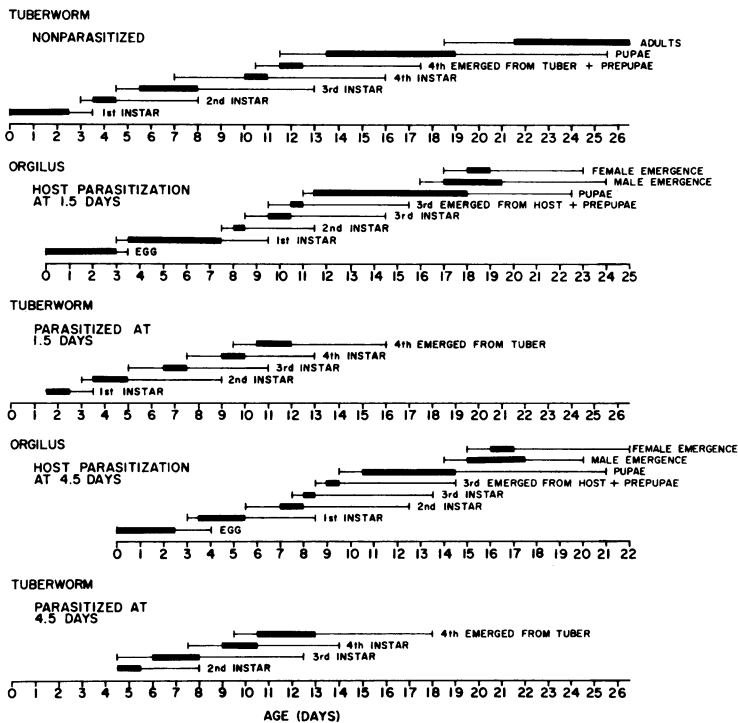

Fig. 6. Ranges in daily occurrences of developmental stages of *Orgilus jenniae* and potato tuberworm (heavy bars indicate maximal occurrence).

for a stage. The durations of occurrence of nonparasitized PTW instars are shown at the top of Fig. 6.

Results indicated that when *O. jenniae* oviposited in 1.5-day-old host larvae, the hosts were first instars, but when 4.5-day-old larvae were attacked, they were primarily second instars. When comparing the durations of the various parasitoid stages between the two periods of oviposition, major differences in the duration of the first parasitoid instar were noted. When oviposition occurred in 4.5-day-old hosts, the first instar required 2.5 to 3.0 days to complete development, but required 4.5 to 6.0 days when oviposition occurred in 1.5-day-old host larvae. The parasitoid egg and second instar had similar durations under both circumstances. The third instar had a slightly longer range in development time when oviposition occurred in younger hosts.

Finney, Flanders, and Smith (1947) found that the ability of the parasitoid, *Macrocentrus ancylivorus*, to synchronize to PTW development depended on the first molt occurring only in the fourth host instar. Similarly, the first *O. jenniae* molt occurred only in fourth instar hosts, regardless of host age at oviposition (Fig. 6). The second parasitoid molt rapidly followed and occurred only in fourth instar hosts that had exited tubers to spin cocoons. Thus, the duration of the first parasitoid instar, and of the total endoparasitic cycle, appeared dependent on the stage of the host at the time of parasitoid oviposition. This relationship enables the parasitoid's development to synchronize with that of its host. Although this may lead to synchronization of the parasitoid's generations to those of its host, the main benefit may be to allow the host to continue the provisioning of food to ensure an adequate amount of host tissues for the final development of the immature parasitoid.

These data indirectly suggest that the timing of the first *O. jenniae* molt is dependent on the hormonal activities occurring within the host larva (as discussed by Askew, 1971; Doutt, 1959; and Fisher, 1971). In studying the PTW parasitoid, *Diadegma stellenboschense* (Cameron), Broodryk (1971a) tested the effect of the host's hormone system on the development of the immature parasitoid by ligaturing fourth PTW instars at the mesothorax and then exposing them to ovipositing parasitoid females. Since the parasitoid larvae did complete development in the abdomens of the hosts, he concluded that *D. stellenboschense* developed independently of the host's hormone system. However, if decreased concentration of juvenile hormone in the abdominal hemolymph of the last instar, as would normally occur or by ligaturing the host at the mesothorax (Wigglesworth, 1972), was the stimulus for the parasitoid to molt, then Broodryk's conclusion was unjustified. This study on *O. jenniae* and previous studies on other internal PTW parasitoids (Broodryk, 1969, 1971a; Cardona and Oatman, 1975; Finney, Flanders, and Smith, 1947; Leong and Oatman, 1968; Oatman, Platner, and Greany, 1969; Oatman and Platner, 1974b; and Odebiyi and Oatman, 1972, 1977) indicate that the first parasitoid molt is critical for developmental synchronization. The stimulus for this molt may be the reduction in the juvenile hormone concentration in the fourth instar host's hemolymph. If the immature parasitoid is dependent on the hormonal system of the host for synchronization, then environmental conditions (i.e. temperature) may only indirectly affect the internal parasitoid's development rate.

Once *O. jenniae* larvae reached the third instar, they remained within the host larvae for ca 1 day and then emerged to feed externally on the host's remains. Emergence from the host to initiation of the pupal stage required 12 to 24 hr. Male and female life cycles were the same before pupation, but male pupae required 12 to 24 hr less time to complete development than females. The complete parasitoid life cycle from egg deposition to adult emergence required $16.2 \pm .28$ days (P = .05, n = 59) for males and $16.8 \pm .51$

days (P = .05, n = 34) for females when oviposition occurred in 4.5-day-old host larvae. When oviposition occurred in 1.5-day-old larvae, 18.0 ± .29 days (P = .05, n = 81) were required for male development and 18.9 ± .37 days (P = .05, n = 51) for females. The life cycle of the parasitoid was reduced by ca 1.5 days when the host was 1.5 vs. 4.5-days-old at parasitoid oviposition. The life cycle of the PTW from eclosion to adult emergence required 19.9 ± .40 days (P = .05, n = 87). Adult parasitoid emergence occurred at approximately the same time as adult PTW emergence, regardless of when parasitoid oviposition occurred. The parasitoid did not affect the host's duration of development (Fig. 6).

Effect of parasitoid on growth of host

In reviewing the biology of the Braconidae, Matthews (1974) noted that many studies mentioned suppression of host growth rates following parasitization. For example, Fuhrer and Keja (1976) found that *Apanteles glomeratus* (L.), an internal parasitoid of *Pieris brassicae* L., physiologically blocked the growth of the parasitized host. In studying the effect of *O. obscurator* on the European pine shoot moth, Syme and Green (1972) found that parasitized larvae were smaller than nonparasitized larvae. Consequently, the effects of *O. jenniae* on the growth of PTW larvae were investigated. The results for the two host ages at parasitoid oviposition are shown in Table 4.

Parasitization by *O. jenniae* significantly affected the growth of PTW larvae. Regardless of the host stage at the time of oviposition, reduction in PTW head capsule width

Table 4. EFFECT OF *Orgilus jenniae* on POTATO TUBERWORM GROWTH

Host age at parasitization	Host instar	Parasitized x̄ (mm) n		Nonparasitized x̄ (mm) n		Significantly different at 5% level*	Mean difference ± 95% confidence limits if sig. different (mm)
		Head capsule widths					
1.5 days	1st	0.2028	73	0.2010	20	no	
	2nd	0.3247	91	0.3373	19	yes	0.0126 ± 0.01150
	3rd	0.5084	72	0.5281	18	no	
	4th	0.7428	69	0.8555	17	yes	0.1127 ± 0.03350
	4th emerged	0.7524	135	0.9066	28	yes	0.1524 ± 0.01958
4.5 days	2nd	0.3227	55	0.3282	13	no	
	3rd	0.5187	71	0.5502	29	yes	0.0315 ± 0.02268
	4th	0.8045	70	0.8850	44	yes	0.0805 ± 0.02711
	4th emerged	0.8339	117	0.9181	64	yes	0.0842 ± 0.01923
		Body lengths					
1.5 days	1st	1.700	73	1.629	20	no	
	2nd	2.315	91	2.272	19	no	
	3rd	4.055	70	3.772	18	no	
	4th	6.197	67	7.812	16	yes	1.615 ± 0.7877
	4th emerged	5.707	134	7.818	28	yes	2.111 ± 0.3627
4.5 days	2nd	2.489	12	2.553	130	no	
	3rd	3.682	59	3.884	19	no	
	4th	5.271	55	6.086	43	yes	0.815 ± 0.7090
	4th emerged	4.429	117	5.646	64	yes	1.215 ± 0.2389

*Tested by 2-sampled t-tests, using pooled variances.

was apparent after the first molt following parasitoid oviposition. Reduction of body length was not significant until the fourth instar.

A comparison of body lengths and head capsule widths of larvae attacked at 1.5 days with those attacked at 4.5 days, indicated that growth was most severely affected in the former. The longer the parasitoid was internally present, the greater the reduction in host size.

Upon dissecting parasitized and nonparasitized host larvae, the only apparent internal difference was that parasitized larvae possessed smaller fat bodies, particularly fourth instars. In all cases, direct internal physical damage to the host was never apparent before parasitoid emergence.

Effect of food and water on adult parasitoid longevity

Studies to determine the effects of food and water on adult parasitoid longevity indicated that both males and females require carbohydrates and free water to achieve maximum longevity. Mean longevity was significantly increased when both honey and water were available, as compared to all other treatment combinations. The availability of water alone increased mean longevity only slightly above that for nothing. The availability of honey alone increased longevity significantly above that for either water alone or nothing. As mean longevity increased in both sexes, longevity ranges and variances also increased.

Mean longevity for males was less than that for females for each treatment combination. In the presence of both water and honey, females had a mean longevity of 26.3 days (range:8.5 to 43.5 days); males, 20.3 days (range:4.5 to 32.5 days).

Both honey and water were supplied in all studies reported herein.

Preoviposition period and diurnal oviposition rhythm

Results of the study to determine the presence of a preoviposition period in *O. jenniae* are shown in Table 5. Analyses of variance, using a logarithmic transformation, showed no significant differences among time interval means for either total or male parasitoids

TAble 5. PROGENY PRODUCED BY MATED AND UNMATED *Orgilus jenniae* FEMALES DURING THE FIRST 24 HOURS OF ADULT LIFE

	Mated Females			Unmated females*		
Hours after emergence†	Total parasitoids $\bar{x}$	Male parasitoids $\bar{x}$	Female parasitoids $\bar{x}$	Total parasitoids $\bar{x}$	Male parasitoids $\bar{x}$	Female parasitoids $\bar{x}$
0–3	5.4 a	5.4 a	0.0	4.4 a	4.4 a	0.0
3–6	4.7 a	4.7 a	0.0	3.5 a	3.5 a	0.0
6–9	7.3 a	7.2 a	0.1 c	5.9 a	5.9 a	0.0
9–12	7.4 a	6.1 a	1.3 b	5.6 a	5.6 a	0.0
12–24	12.7 a	8.3 a	4.4 a	7.8 a	7.8 a	0.0

*Each mean was based upon 10 replications. Means followed by the same letter in a given column were not significantly different at the 5% probability level (Duncan's New Multiple-Range Test). Analyses were performed using a logarithmic transformation.

†For each time interval, each female was exposed to one tuber containing 50, 4- to 5-day-old potato tuberworm larvae.

produced. However, the mean number of female progeny produced showed significant differences (P ≥ .05) between oviposition periods. No female progeny were produced during the first 6 hr after mating by any of the 10 females. During the 6- to 9-hr interval, only one female was produced. The highest number of female progeny was produced during the 12 hr scotophase, but on a per-hour basis was the same as during the last 3 hr of the photophase.

The results indicated that there was no preoviposition period or if there was one it was less than 3 hr. In mated females there was a 6- to 9-hr period after emergence or mating when eggs were not fertilized. This period may have resulted from an inability to activate sperm, closure or blockage of the sperm duct after mating, or a diurnal rhythm in either sperm activity or female response to the passage of eggs down the oviduct.

Results of the study to determine the presence of a diurnal rhythm in either progeny production or sex ratio are shown in Figure 7 as means of parasitoid progeny produced per hour. Analyses of the data indicated significant differences (P ≤ .05) between means for total, male, and female progeny produced. During the first 3 hr after the initiation of the photophase, there was a general but nonsignificant (P > .05) increase in total progeny production over that during the second 3-hr period. The reduced total progeny production during the second 3-hr period was a result of reduced male progeny production, but the differences were not significant (P > .05). The highest total, male, and female progeny productions occurred during the last 6 hr of the photophase. Hourly progeny production means were not significantly different (P > .05) from each other for
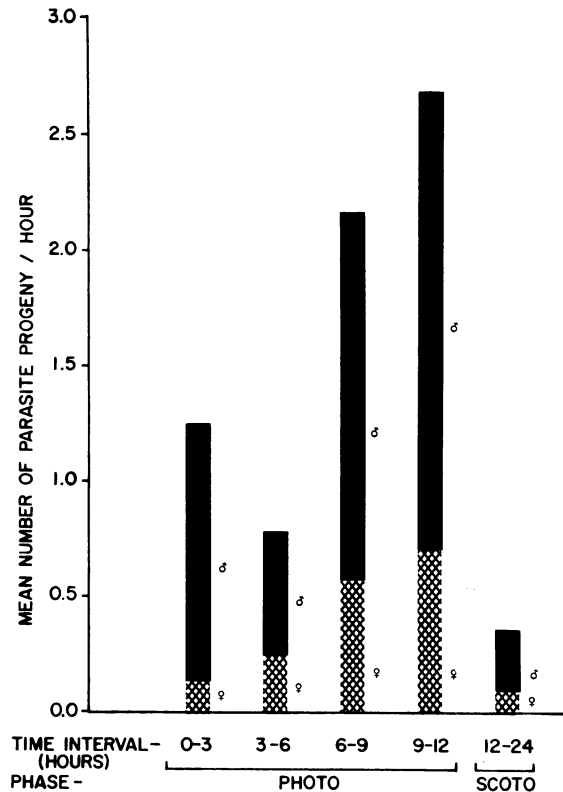

Fig. 7. Diurnal rhythym in progeny production for
1 to 2-day-old mated, *Orgilus jenniae.*

the last two time intervals of the photophase, but were significantly higher than during the first two time intervals for total, male, and female progeny productions. Male and female progeny productions during the scotophase were the lowest observed, but hourly were not significantly different from those during the first 6 hr of the photophase. The progeny sex ratios between time periods were not significantly different (P > .05) with a total mean of 24 percent female.

Results indicated that *O. jenniae* exhibits a diurnal oviposition rhythym, but that does not affect progeny sex ratio. The inability to produce female progeny during the first 6 hr after mating, as found in the preoviposition studies, apparently is due to the female's inability to fertilize eggs—not to the diurnal oviposition rhythym.

Courtship and mating behaviors

Upon placing a male *O. jenniae* in a gelatin capsule with a female, recognition of the female was evidenced by the initiation of wing-fanning by the male. Wing-fanning consisted of 3- to 10-second periods of rapid wing vibration with the wings extended perpendicular to and slightly above the body. During wing-fanning, the male either remained motionless or ran towards the female. After each wing-fanning period, the wings were returned to their normal resting position over the dorsum of the body. This behavior was observed only in the presence of virgin females and probably was in response to the recognition of a female sex pheromone (Cole, 1970; Van den Assem, 1970; Vinson, 1972; Obara and Kitano, 1974; Kitano, 1975; and Matthews, 1975). Orientation apparently also was involved, as the male always directed its head towards the female before or during wing-fanning.

Once the initial wing-fanning was completed, the male moved toward the female. Male-female contact was apparently made by random or visual means, as wing-fanning was not repeated unless the male did not contact the female. If male-female contact was not made, the male reoriented to the female by wing-fanning. This behavior was repeated until contact was made.

Once contact occurred, the male rapidly attempted to mount the female's dorsum. Initially, the female always attempted to escape from such advances by kicking with her metathoracic legs. During the attempt to mount, the male rapidly stroked the antennae of the female with his antennae. Male antennal stroking consisted of placing each antenna along the inside edge of the corresponding female antenna. The male circled the female's antennae with the tips of his and then alternately pulled each of her antennae laterally and dorsally back. With each stroke, the male slid his encircling antenna up the corresponding antenna of the female until they became disengaged. The antennae were reengaged for each new stroke.

While stroking her antennae, the male moved backward over the abdominal dorsum of the female and curved his abdomen down and forward under hers. The female continually tried to escape until a stimulation threshold apparently was surpassed, causing the female to cease resisting and assume a stationary copulation posture. The female only attained this posture if the male successfully mounted from behind. Attempts to mount the female anteriorly or laterally always resulted in her refusal to attain the stationary posture.

The female's copulatory posture consisted of a semi-rigid stance with the tip of the abdomen slightly raised, the genital opening on the abdominal venter fully exposed, and the antennae extended anteriorly and parallel to the substrate surface. Once this

posture was attained, the female remained stationary throughout copulation.

Once the female attained the copulatory posture, the male stopped the antennal stroking and immediately made genital contact. The male then became quiescent and maintained his dorsal position on the female. His antennae were positioned over and parallel to the female's antennae, and his wings were held vertically above the body.

Copulation required from 23 to 52 seconds ($\bar{x} = 31.5$). During copulation, the male and female remained motionless except for slight abdominal contractions. The male broke genital contact by walking forward, off the dorsum of the female. The male then typically exhibited grooming behavior. However, except for slight abdominal contractions, the female remained stationary for 15 to 90 seconds after genital contact was broken. Following this post-copulatory phase, the female also exhibited grooming behavior.

Once mated, females always attempted to escape from other stimulated males. Females were never observed to mate more than once. This apparently was due to their inability to reattain the copulatory posture, as discussed by Matthews (1975) and Van den Assem (1969). If a virgin female attained the copulatory posture, but successful mating did not ensue, the female remained virginal despite subsequent advances by males. Van den Assem (1969) termed such females "pesudo-virgins."

Males were observed to mate at least five times, and responded to virgin females almost immediately after a previous mating.

Searching and oviposition behaviors

In searching for host larvae on potato tubers, the female characteristically ran across the surface while tapping with her antennae. The primary source of attraction was PTW frass exuding from larval mines. Upon encountering frass with her antennae, the female stopped and investigated with antennal palpations. This primary response to frass was verified by identical female response to PTW frass removed from the tuber's surface and placed in a sterile, Petri dish.

After investigating the frass with her antennae, the female moved slightly forward of the frass pile, raised her abdomen and brought the ovipositor tip forward to contact the frass. She then tapped the frass pile with the ovipositor tip, apparently to locate the host's mine entrance. The female could only insert the ovipositor into the mine through the entrance. Females frequently had difficulty in locating mine entrances and repeatedly lowered their abdomens to relocate the frass piles with their antennae. Once the entrance was found, she rapidly inserted the length of her ovipositor into the mine. Her movements then became rapid and she frequently rotated herself about the axis of the inserted ovipositor while rapidly palpating the tuber's surface with her antennae. Contact with and insertion of the ovipositor tip into the host larva was indicated by a cessation of body movements. The antennae ceased their rapid palpations and were held parallel to the tuber's surface. Oviposition required only 1 to 2 seconds once the host larva was located.

After oviposition, the female removed the ovipositor and ran a short distance from the mine. She then characteristically attained a stationary posture on the tuber with her antennae held motionless and parallel to the surface. In this posture, she slightly raised the tip of her abdomen, lowered her head and throax, and flexed the tip of her ovipositor down to the tuber surface. The ovipositor then was vibrated slightly and slowly flexed upward so that its tip eventually was held above the abdomen. This ovipositor

flexion only occurred after egg deposition. Its purpose presumably was to reposition a new egg in the oviduct for the next oviposition. Initially, females flexed their ovipositors only once to resume searching and oviposition, but females that had deposited numerous eggs in a short period flexed their ovipositors with increasing frequency after each oviposition. Eventually, the female apparently was unable to position new eggs even after repeated flexions. She then became agitated, often left the tuber surface, and typically did not resume searching for 10 to 40 minutes. When she again exhibited interest in host mines, she flexed the ovipositor before reinitiation of searching.

Parasitoid fecundity and life table studies

Results of the fecundity studies for mated and unmated *O. jenniae* females ovipositing in hosts in tubers, and mated females ovipositing in hosts in foliage are shown in Fig. 8. The results are depicted as daily, total (male plus female) progeny production means. Daily progeny production always peaked during the first 3 days of adult life and progressively decreased thereafter. The daily progeny production means for females ovipositing in hosts in potato foliage usually was higher than in hosts in tubers. The daily means of mated and unmated females ovipositing in hosts in tubers were essentially the same. Total progeny production for females ovipositing in hosts in tubers was 375.2 ± 41.54 (P = .05, n = 10) for mated females and 383.7 ± 65.12 (P = .05, n = 10) for unmated females, while 436.8 ± 59.26 progeny (P = .05, n = 10) were produced by mated females ovipositing in hosts in foliage. Of the total progeny produced by mated females on tubers, 23.6 percent were female, while 28.4 percent were female when ovipositing in hosts in foliage. The highest proportion of the progeny were female during the first
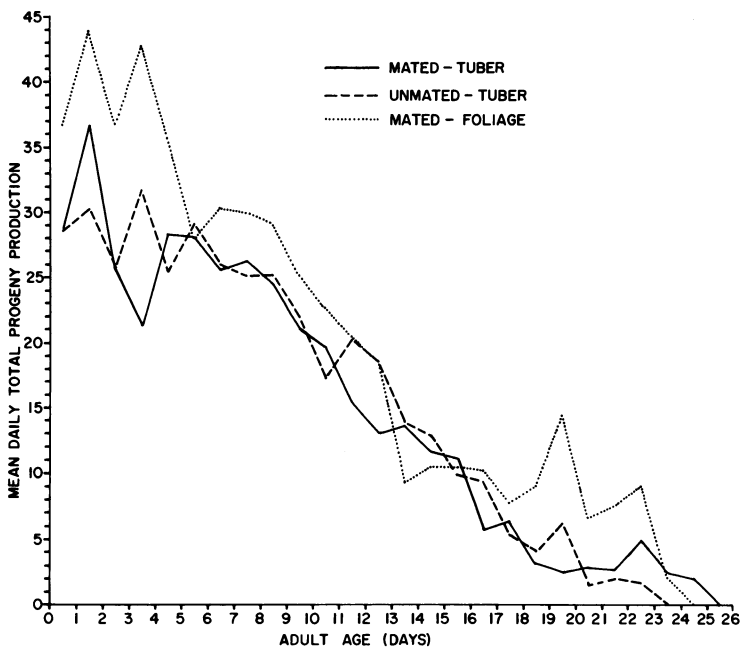

Fig. 8. Mean daily total fecundities for mated and unmated *Orgilus jenniae* females ovipositing in hosts in potato tubers, and mated females ovipositing in hosts in foliage.

5 days of oviposition, regardless of whether mated females oviposited in hosts in potato foliage or tubers. After this initial peak, the daily proportion of female progeny gradually decreased. The highest proportion of females produced per day was 37.8 percent in tubers and 39.3 percent in foliage. Unmated females produced no female progeny, confirming that *O. jenniae* is an arrhenotokous species. Longevity of adult females on tubers was 25.5 ± 4.24 days (P = .05, n = 10) when mated and 20.8 ± 3.18 days (P = .05, n = 10) when unmated, while on foliage it was 16.9 ± 3.18 days (P = .05, n = 10). Results indicated that, despite the shorter longevity, females ovipositing in hosts in foliage produced slightly more total and female progeny than females on tubers and, consequently, that potato foliage was more suitable for oviposition than tubers.

In the construction of laboratory life tables for other PTW parasitoids, immature mortalities were considered negligible at temperatures where innate capacities for increase were maximal (Cardona and Oatman, 1975; Odebiyi and Oatman, 1977). Immature mortalities at other temperatures were computed by comparing the parasitoid emergences with that at the optimum temperature standard. In the present study, *O. jenniae* immature mortality was determined by comparing observed numbers of ovipositions to actual numbers of progeny emerging. These studies were conducted under the same age and density conditions as in the fecundity studies.

Sixteen females were observed for a total of 191 ovipositions in hosts in tubers. Only 108 adult parasitoid progeny emerged for a 43.5 percent total (egg to pupa) immature mortality. When percent immature mortality was linearly regressed on percent total emergence of moths plus parasitoids, no significant correlation was found ($r^2 = .0057$, P > .10) and the slope of the regression line was not significantly different from 0 (P > .05). Prepupal and pupal parasitoid mortality was 10.5 percent in the life cycle studies. Therefore, for the construction of parasitoid life tables, 33 percent immature parasitoid mortality was assumed to occur from the egg to initiation of the prepupal stage, and 10.5 percent from the prepupal stage to adult emergence when parasitizing hosts in potato tubers. Additionally, life tables were constructed assuming 0 percent immature parasitoid mortality to compare *O. jenniae* with other PTW parasitoid studies where this level of mortality was assumed.

Fifteen parasitoid females were observed for a total of 76 ovipositions in hosts mining in potato foliage. Only 33 adults emerged for a total immature mortality of 43.4 percent. However, when percent immature mortality was linearly regressed on percent total emergence of moths plus parasitoids, a highly significant, negative correlation was found ($r^2 = .7073$, P ≤ .01), and the slope of the regression line was significantly different from 0 (P ≤ .05). The regression equation and the data indicated that immature mortality was negligible above 67 percent total emergence. The primary period of host mortality occurred when hosts were manually transferred to the foliage. Host mortality and consequent parasitoid mortality were usually negligible after parasitoid oviposition. However, when the foliage deteriorated or otherwise became unsuitable after parasitoid oviposition, immature host and parasitoid mortalities resulted. Foliar deterioration occurred in all but four of the foliar units used to determine immature parasitoid mortality. The correlation between immature parasitoid mortality and total emergence consequently was a result of the direct dependence of parasitoid mortality on host mortality. In the foliar fecundity studies, foliage deterioration was minimized and total percent emergence was 70.6 percent. Therefore, parasitoid life tables were constructed for hosts in the foliage assuming 0 percent immature mortality.

In the construction of the life tables, the mean expectations of life (e_x) (the mean expectation of life for those individuals surviving to the beginning of the specific age

interval) were calculated (Krebs, 1978). At the initial pivotal age of 0.5 days, e_x for *O. jenniae* parasitizing hosts in tubers and assuming 43.5 percent immature mortality was lower (27.1 days) than when parasitizing hosts in foliage (33.9 days). This was due to the difference in immature mortalities, as e_x was 42.5 days when assuming 0 percent
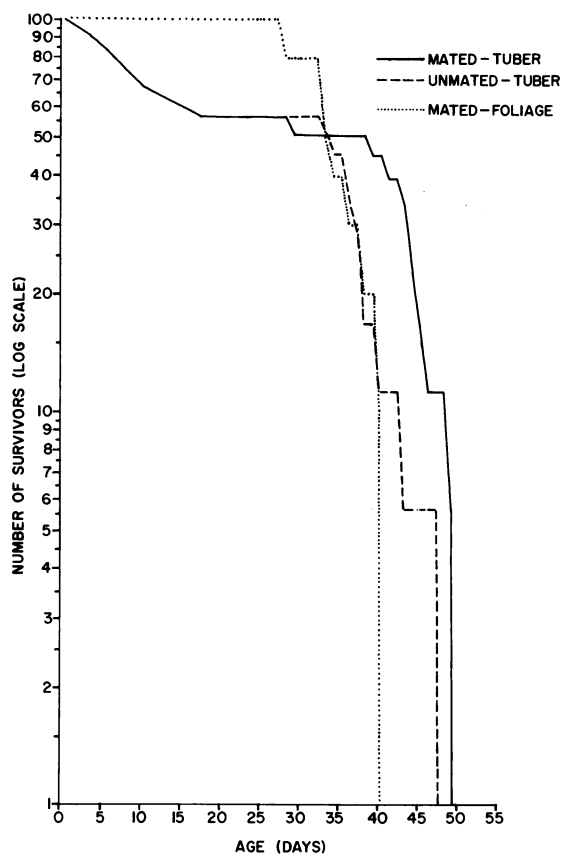

Fig. 9. Laboratory survivorship curves for mated and unmated *Orgilus jenniae* females parasitizing hosts in potato tubers and for mated females parasitizing hosts in potato foliage.

Table 6. LABORATORY LIFE TABLE STATISTICS FOR *Orgilus jenniae* PARASITIZING HOSTS IN POTATO TUBERS AND FOLIAGE AT 25 °C, 45 ± 5% RH AND 12-HR PHOTOPERIOD

Life table statistic	Host in tuber		Host in foliage
	43.5% immature parasitoid mortality	0.0% immature parasitoid mortality	0.0% immature parasitoid mortality
R_o	49.972	87.445	123.146
r_m	1.177	0.204	0.225
λ	1.194	1.227	1.252
t	22.06	21.84	21.38

immature mortality in tubers. At adult emergence (17.5 days), e_x for adult females in foliage was less than that for females on tubers (16.9 and 25.5 days, respectively). These results also are seen in the survivorship curves for mated and unmated females in tubers (using 43.5 percent immature mortality) and mated females in foliage (Fig. 9).

The net reproductive rate (R_o), innate capacity for increase (r_m), finite rate of increase (λ), and generation time (t) were calculated for each life table (Table 6). When parasitizing hosts in tubers and assuming 43.5 percent immature mortality, R_o (the average number of female progeny produced per female) was nearly half that obtained when 0 percent immature mortality was assumed. When parasitizing hosts in potato foliage, R_o was ca 2.5 and 1.5 times greater than in tubers, assuming 43.5 and 0 percent immature mortality, respectively. When parasitizing hosts in potato foliage, r_m (the actual rate of increase of the population under constant environmental conditions in which space and food are unlimited, and when a stable age distribution has been achieved) was greater than that seen at either of the two levels of parasitoid mortality when parasitizing hosts in tubers. Being inversely proportional to r_m, t was shorter when parasitizing hosts in potato foliage. This was due to the production of higher numbers of female progeny earlier in adult life than occurred when *O. jenniae* parasitized hosts in tubers. Since the natural log of λ equals r_m, it exhibited the same trends as r_m in comparing parasitization of hosts between tubers and foliage, and indicated the number of times the population would multiply itself per unit of time. These statistics indicated that, under the given experimental conditions, parasitization of PTW larvae in potato foliage resulted in greater and more rapid population increases of *O. jenniae* than parasitization of hosts in tubers.

Cardona and Oatman (1975) determined R_o, t, and r_m for PTW infesting tubers at various constant temperatures, 50 percent R.H., and a 12-hr photoperiod. A comparison of the population growth potential of *O. jenniae* relative to that of the PTW at 25 °C, as found by Cardona and Oatman, is dependent on the assumed immature parasitoid mortality. If 43.5 percent immature parasitoid mortality is assumed, then R_o for *O. jenniae* is lower, t is shorter, and the consequent r_m is about the same as that of the PTW in potato tubers. If 0 percent immature parasitoid mortality is assumed, then R_o is higher, t is still shorter, and the consequent r_m of *O. jenniae* is higher than that of the PTW. Assuming that the life tables obtained by Cardona and Oatman for the PTW in potato tubers are approximately the same as would be obtained in foliage, then the population growth potential of *O. jenniae* is much greater than that of its host. However, the immature host mortalities obtained by Cardona and Oatman were much lower than those observed in the present studies. The comparisons are consequently tentative, but the population growth potential of *O. jenniae* apparently is at least equal to that of the PTW in tubers and is much higher in foliage.

Parasitoid comparisons

In comparing the basic biological characteristics of *O. jenniae* with those reported for *O. lepidus* and *O. parcus* by Oatman, Platner, and Greany (1969) and Broodryk (1969), respectively, the only differences found were those concerning fecundity, adult longevity, and sex ratio. Immature morphologies, behaviors, and host relationships appeared similar for all three species.

Oatman, Platner, and Greany (1969) reported an average fecundity, adult female longevity, and progeny sex ratio of 632.2 progeny/female, 17.6 days, and 40 percent

females, respectively, for *O. lepidus* ovipositing in 3- to 4-day-old PTW larvae in tubers at 26.7 °C. *Orgilus lepidus* apparently has a higher fecundity and female sex ratio than does *O. jenniae*, but a nearly equal adult longevity. The population growth potential of *O. lepidus* consequently is greater than that of *O. jenniae* when parasitizing hosts in potato tubers.

Broodryk (1969) reported an average fecundity, adult female longevity, and progeny sex ratio of 64.8 eggs/female, 31.6 days, and 50 percent females, respectively, for *O. parcus* ovipositing in first instar PTW larvae mining in potato foliage at 26.5 °C. No data were reported for oviposition in PTW larvae mining in potato tubers. These data suggest that the population growth potential of *O. jenniae* is greater than that of *O. parcus* when parasitizing hosts in potato foliage.

Huffaker, Robb, and Logan (1977) criticized attempts to compare the potentials of natural enemies entirely on the basis of fecundities or intrinsic rates of increase. Such statistics have little relevance to the host population regulation potential of a parasitoid species. Additionally, the establishment potentials of parasitoid species cannot be predicted or compared based entirely on such sets of measurements. Thus, although the potentials for increase among *O. jenniae, O. lepidus,* and *O. parcus* are different, these data cannot entirely explain past or future establishment failures or successes.

With the relatively large number of indigenous parasitoid species attacking the PTW in southern California, the competitive interactions between indigenous and introduced species apparently has been and will continue to be the primary obstacle to the successful establishment of exotic PTW parasitoids (Cardona and Oatman, 1975; Debach, 1966; Oatman and Platner, 1974a; Odebiyi and Oatman, 1977). If true, then the differences of potentials for increase among the three introduced *Orgilus* species would only indirectly affect their potentials for establishment. The most important considerations probably are the nature of the competitive interactions existing among the indigenous PTW parasitoids and the relative competitive abilities of the parasitoid being colonized. Since all three of the species of *Orgilus* exhibit very similar biological characteristics, other than those relating to the power of increase, the factors that adversely affected establishment of *O. lepidus* and *O. parcus* in southern California probably are the same, and these factors probably also adversely affected attempts to colonize *O. jenniae*. Thus, a subsequent study of the competitive interactions of *O. jenniae* with certain indigenous, ecologically similar PTW parasitoids also should provide information on reasons for failures to establish *O. lepidus* and *O. parcus* in southern California.

SUMMARY AND CONCLUSIONS

The biology, host relationships and population growth potential of *Orgilus jenniae* were studied at 25 ± 1 °C, 45 ± 5 percent R.H. and 12-hr photoperiod. The studies were conducted with host larvae of the potato tuberworm infesting either 'White Rose' potato tubers or 'Norgold' potato foliage. The results were compared to those previously reported for *O. lepidus* and *O. parcus* as a preface to subsequent studies attempting to determine the factors inhibiting establishment of *Orgilus* species on potato tuberworm (PTW) in southern California.

In determining the optimum host age and density of PTW larvae mining in potato tubers for *O. jenniae* progeny production, a significant interaction was found to occur between these two factors. The interaction resulted from an interrelationship between

parasitoid ovipositor length, PTW larval mine length, occurrence of secondary exit holes in PTW mines, and preferred host stage for parasitoid oviposition. Results indicated that when tubers were used as the host substrate, a host age of 4 to 5 days (2nd instar) at a density of 125 larvae per tuber were optimal for *O. jenniae* progeny production.

PTW larvae, 3- to 4-days-old (1st and 2nd instars), mining in potato foliage were preferred for oviposition by *O. jenniae*. The optimal host density for progeny production by a single, mated female was 175 larvae per foliar unit.

The stalked egg of *O. jenniae* is deposited in the abdominal hemocoel of the PTW larva. There are three larval instars, the first being initially caudate-mandibulate and finally vesiculate-mandibulate; the other two, hymenopteriform. Descriptions and dimensions of the immature stages were given. Superparasitism occurred under the experimental conditions, but despite frequently finding two or more parasitoid eggs, no more than one late first instar was ever found in a host larva. The parasitoid larva developed in the hemocoel of the still-living host. At maturity, the parasitoid larva emerged by lacerating a hole in the lateral line of the host larva and continued feeding externally until only the head capsule and other sclerotized parts of the host remained. The parasitoid larva then formed a translucent-white pupal cocoon within that of its host. Adult emergence occurred only at the initiation of the photophase. The results indicated that *O. jenniae* is a primary, solitary, larval endoparasitoid of the PTW.

Duration of the parasitoid life cycle was studied at host ages of 1.5 days (1st instar) and 4.5 days (2nd instar). When oviposition occurred in 4.5-day-old PTW larvae, the first parasitoid instar required 2.5 to 3.0 days to complete its development, but required 4.5 to 6.0 days when oviposition occurred in 1.5-day-old host larvae. All other parasitoid stages had similar durations under both circumstances. Difference in duration of the first instar was due to the first parasitoid molt occurring only in the fourth host instar, regardless of the age of the host larva at oviposition. The parasitoid life cycle from oviposition to adult emergence averaged 16.8 and 18.9 days for females when oviposition occurred in 1.5- and 4.5-day-old host larvae in tubers, respectively. Adult parasitoid emergence occurred at approximately the same time as adult PTW emergence.

Although the internal presence of *O. jenniae* larvae did not affect the duration of development of PTW larvae, it did affect the growth of the host. Regardless of the host stage at parasitoid oviposition, the host's head capsule width was reduced after the first molt following oviposition. Reduction of the host's body length was not significant until the fourth host instar.

If *O. jenniae* possessed a preoviposition period, it was less than 3 hr in duration. There was a 6- to 9-hr-period following emergence or mating when the female did not fertilize eggs and thus did not produce female progeny. *Orgilus jenniae* exhibited a diurnal oviposition rhythm in which progeny production gradually increased during the photophase to peak at the end of the phase. Oviposition also occurred during the scotophase but always was lower than that during the photophase.

The courtship and mating behavior of *O. jenniae* were described. The female apparently can only be stimulated to assume a copulatory posture once in her lifetime. If successful copulation did not follow the attainment of this posture, she did not accept subsequent advances by males, remaining functionally virginal for the rest of her life.

The searching and oviposition behaviors of *O. jenniae* females also were described. The females exhibited a characteristic flexion of the ovipositor after each successful oviposition. The purpose of the flexion presumably was to reposition a new egg in the oviduct for the next oviposition.

Studies on the fecundity of mated and unmated *O. jenniae* females ovipositing in

hosts in potato tubers and mated females ovipositing in hosts in foliage indicated that daily progeny production peaked during the first three days of adult life and decreased thereafter. Unmated females produced no female progeny, confirming that *O. jenniae* is an arrhenotokous species. Average total progeny production of mated females was 375.2 when parasitizing hosts in tubers and 436.8 in potato foliage. Progeny consisted of 23.6 and 28.4 percent females when oviposition occurred in hosts in tubers and foliage, respectively. The average adult longevity of mated, ovipositing females was 25.5 days on tubers and 16.9 days in potato foliage.

Life tables were constructed for parasitization of hosts in tubers using 43.5 and 0.0 percent immature parasitoid mortality, and in foliage using 0.0 percent immature mortality. The net reproductive rate, innate capacity for increase, finite rate of increase, and generation time were calculated for each life table to compare the population growth potential of *O. jenniae* under each set of conditions. The results indicated that, under the given environmental conditions, parasitization of PTW larvae in potato foliage resulted in greater and more rapid population increases of *O. jenniae* than parasitization of hosts in tubers. A comparison of the population growth potential of *O. jenniae* with that of the PTW, as reported in previous studies, indicated that the population growth potential of *O. jenniae* is at least equal to that of the PTW in potato tubers and is much higher in foliage.

In comparing the biological characteristics of *O. jenniae* with those previously reported for *O. lepidus* and *O. parcus*, the only differences found were those concerning fecundity, adult longevity, and sex ratio. The population growth potential of *O. jenniae* apparently is less than that of *O. lepidus* and greater than that of *O. parcus*. However, the differences in potentials for increase do not explain the previous establishment failures of *O. lepidus* and *O. parcus*, and provide no indication of the potential for establishment of *O. jenniae*. The biological similarities between the species suggest that a study of the competitive interactions of *O. jenniae* with certain PTW parasitoids indigenous to southern California may reveal factors which prevented the establishment of *O. lepidus* and *O. parcus*.

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