Morphology and Development of Immature Stages of *Galeopsomyia fausta* (Hymenoptera: Eulophidae: Tetrastichinae)

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ABSTRACT *Galeopsomyia fausta* LaSalle (Hymenoptera: Eulophidae) is a Neotropical eulophid solitary ectoparasitoid of the immature stages of *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae). In Central and South America, the activity of this wasp has resulted in good biological control of *P. citrella*. Characterization of the immature morphology of parasitoids is important for the identification to the species level before adult emergence and for the quantification of the impact of these natural enemies in biological control programs. This article reports our study of the immature stages of *G. fausta* from a laboratory colony maintained on *P. citrella* that were examined using scanning electron microscopy (SEM). The wasp has a typical hymenopteriform egg attached to the leaf chamber where *P. citrella* pupates. The parasitoid has three instars, very similar to each other, holopneustic, hymenopteriform, and 13-segmented. Its cuticle has multiple spines. The cranium is conspicuous and has a mandibulate suctorial mouth. On completion of its larval development an exarate pupa is produced. The distinctive attachment of the egg to the leaf and typical pupal morphology allow the identification of this parasitoid by using a binocular microscope, but identification of the larvae requires SEM.

KEY WORDS *Galeopsomyia fausta*, Eulophidae, larval development, larval morphology, biological control

Galeopsomyia fausta LaSalle (Hymenoptera: Eulophidae: Tetrastichinae) is a Neotropical species that has been recorded as a widespread parasitoid of the leafminer *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae) in Central and South America (LaSalle and Peña 1997, Schauff et al. 1998). Native hosts of *G. fausta* are not known; thus, it represents an example of an indigenous parasitoid recruited onto an invading pest species. In the Neotropics, the activity of *G. fausta* has resulted in satisfactory biological control of *P. citrella* (Cano et al. 1996, Castaño et al. 1996, Cave 1996, Cobo 1996, French and Legaspi 1996, Ruíz et al. 1996, Sá et al. 2000). For this reason, this species was imported to Spain in 1998 (Llácer et al. 1998) and further evaluated as a candidate for the biological control of *P. citrella*. *G. fausta* was released in Spain (Urbaneja et al. 2000), but it failed to establish.

Tetrastichinae are usually primary idiobiont endoparasitoids of the eggs, larvae, or pupae of Diptera, Hymenoptera, or Lepidoptera through a marked association with small gallicolous hosts. However, some species develop as ectoparasitoids or as facultative hyperparasitoids (Askew 1968, Askew and Shaw 1979, Gauld and Bolton 1988). The genus *Galeopsomyia* has been associated with gall-forming insects (LaSalle 1994), but *G. fausta* is the first case reported on a leafminer (LaSalle and Peña 1997). *G. fausta* is a parthenogenetic species, and its extremely male-biased sex ratio has been related to the activity of symbiotic microorganisms (Argov et al. 2000, Zchori-Fein et al. 2001). It is primarily a pupal parasitoid, although larvae and prepupae of *P. citrella* also are attacked (Cobo 1996). According to Cobo (1996), *G. fausta* paralyzes the host before depositing an egg nearby, a typical idiobiont ectoparasitic behavior (Godfray 1994). The egg of *G. fausta* (Cobo 1996) is elongate and oval, as is commonly observed in Eulophidae (Cameron 1939, Clancy 1946, Askew and Ruse 1974), but no further information about *G. fausta* immature stages is available. The Eulophidae usually have three to five instars. The first instar is hymenopteriform, 13-segmented, and occasionally has fleshy tubercles or rows of spines on its body, and the mature larva is generally not setose (Askew 1968). Cocoon formation is very unusual (Gauld and Bolton 1988).

The adult of *G. fausta* has been described previously (LaSalle and Peña 1997, Schauff et al. 1998), but until now, very little information about the morphology and biology of its immature stages was available because of both its recent discovery and its concealed life history.

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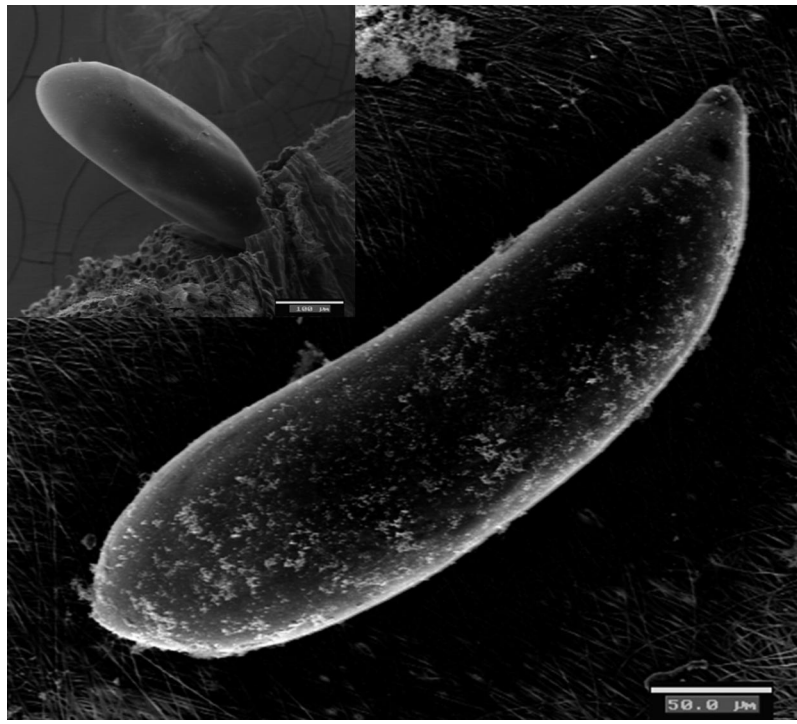

Fig. 1. One-day-old egg. One-day-old egg still attached to leaf (inset).

Larval morphology can be important for the identification to the species level before adult emergence and can simplify the quantification of the impact of natural enemies in biological control programs by means of life table construction and key factor analysis (Bellows and Van Driesche 1999) because immature instars can be easily collected in the field (Carignan et al. 1995, Bahena et al. 1999). Although characteristics of the larval body of chalcidoids are known (Roskam 1982, Henneicke et al. 1992), information on the larval morphology of eulophids is scarce. Therefore, the current study was aimed at providing basic information on the external morphology and development of immature stages of *G. fausta.*

Materials and Methods

G. fausta were obtained from a colony that was initiated from *G. fausta* imported from Nicaragua and Colombia (Llácer et al. 1998). The colony was maintained on *P. citrella* in a glasshouse at 25°C and 75% RH, following standardized protocols developed at Institut Valencià d'Investigacions Agràries (IVIA), Montcada, Spain, to rear both *P. citrella* and its parasitoids (Urbaneja et al. 1998). Voucher specimens were deposited at the IVIA reference insect collection.

To obtain enough immature stages of *G. fausta* for microscopic observation, pupae of *P. citrella* were exposed to *G. fausta* adult females under controlled conditions. Citrus leaves holding *P. citrella* pupal chambers <1 d old were randomly detached from the plants where the rearing of *P. citrella* took place. Detached leaves were deposited in groups of 15 on a layer of agar (2% weight) in petri dishes (140 mm in diameter), and one *G. fausta* adult female was released into each dish. Petri dishes were placed in a climatic cabinet at 25 ± 1°C and a photoperiod of 16:8 (L:D) h. One day later, females were extracted and released in

Table 1. Measurements (mean ± SE, in millimeters) of *G. fausta* larvae at specified intervals after parasitization

Days after parasitism	First instar				Second instar				Third instar			
	n	Body length	*n*	Head capsule width	*n*	Body length	*n*	Head capsule width	*n*	Body length	*n*	Head capsule width
2	5	0.23 ± 0.01	9	0.080 ± 0.006								
3	7	0.34 ± 0.02	6	0.080 ± 0.009	3	0.32 ± 0.02	1	0.15				
4					5	0.38 ± 0.02	5	0.150 ± 0.008				
5					5	0.58 ± 0.06	5	0.160 ± 0.006				
6					5	1.07 ± 0.07	5	0.160 ± 0.006				
7									5	1.20 ± 0.07	4	0.230 ± 0.003
8									5	1.30 ± 0.14	5	0.250 ± 0.007
9									5	1.81 ± 0.10	4	0.240 ± 0.007

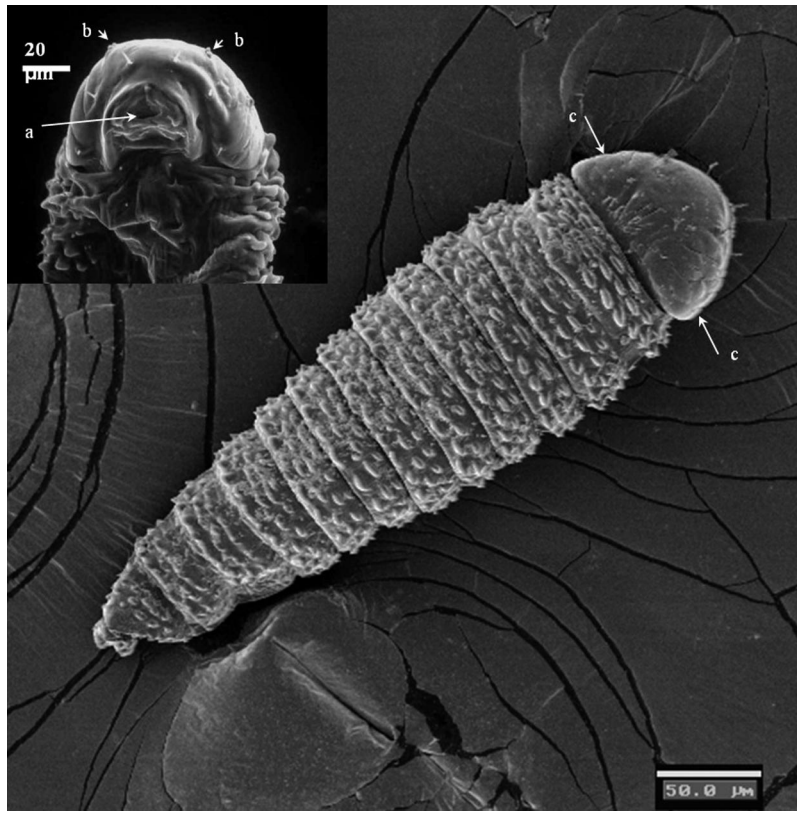

Fig. 2. Late first instar showing spines and ocular discs (c). Ventral side of cranium, showing the mandibulate suctorial mouth (a), antennae (b), and setae (inset).

a newly prepared petri dish. This procedure was repeated as often as necessary to obtain enough individuals for further processing.

Each day, after removing the adult parasitoids, a certain amount of *P. citrella* pupal chambers were opened and checked under a stereomicroscope (Leica MZ6, Leica, Wetzlar, Germany) with a cold light source (Leica CLS100). Nonparasitized hosts were rejected, and the inspection was finished once 15 parasitized pupal chambers had been selected. These were individually deposited on an agar layer (2% weight) in a petri dish (55 mm in diameter) and kept in a climatic cabinet under the same environmental conditions as described for rearing. These pupae were observed daily under a light microscope to check parasitoid development until adult emergence. The remaining pupal chambers were kept undisturbed (same climatic conditions), and five specimens were collected daily and prepared for observation by scanning electron microscopy (SEM).

Eggs and larvae of *G. fausta* were transferred for fixation to a 2.5% glutaraldehyde solution in a sodium cacodylate buffer (0.2 M, pH 7.4) for 4 h at 4°C (Hayat 1978). After several rinses in sodium cacodylate buffer, insects were dehydrated in 15-min changes in a graded acetone–water series (30–90%) and three 40-min changes in 100% acetone. After dehydration, specimens were critical point dried by using a Tousimis Autosamdri-814 critical point drier. Subsequently, insects were gold-coated in a Bio-Rad SC-500 sputter coater. Pupae of *G. fausta* were prepared following the method described by Rumph and Turner (1998). A minuten pin (0.2 mm in diameter) was used to create punctures restricted to the side of the pupa opposite that for viewing so that they were not visible when pupae were affixed to standard SEM stubs. Afterwards, pupae were progressively dehydrated in several 15-min alcohol series (80, 90, 95, and 100%). After dehydration, pupae were placed directly into 12-ml screw-cap vials containing 3 ml of undiluted hexamethyldisilazane (HMDS) and soaked for 45 min. The HMDS was decanted, 3 ml of fresh undiluted HMDS was added, and the pupae were allowed to soak for another 45 min. The specimens were then removed from the HMDS and allowed to air dry overnight. Afterwards, pupae were mounted on aluminum SEM stubs and gold-coated. Specimens were inspected under a Hitachi S-4100 scanning electron microscope, and images were taken using the EMIP 3.0 system.

Additionally, four neonate larvae and four 2-d-old larvae were inspected on a Philips XL 30 environmental scanning electron microscope, which allows the observation of fresh specimens without processing.

Measurements (maximum body length and width) of immature stages were taken. The number of instars

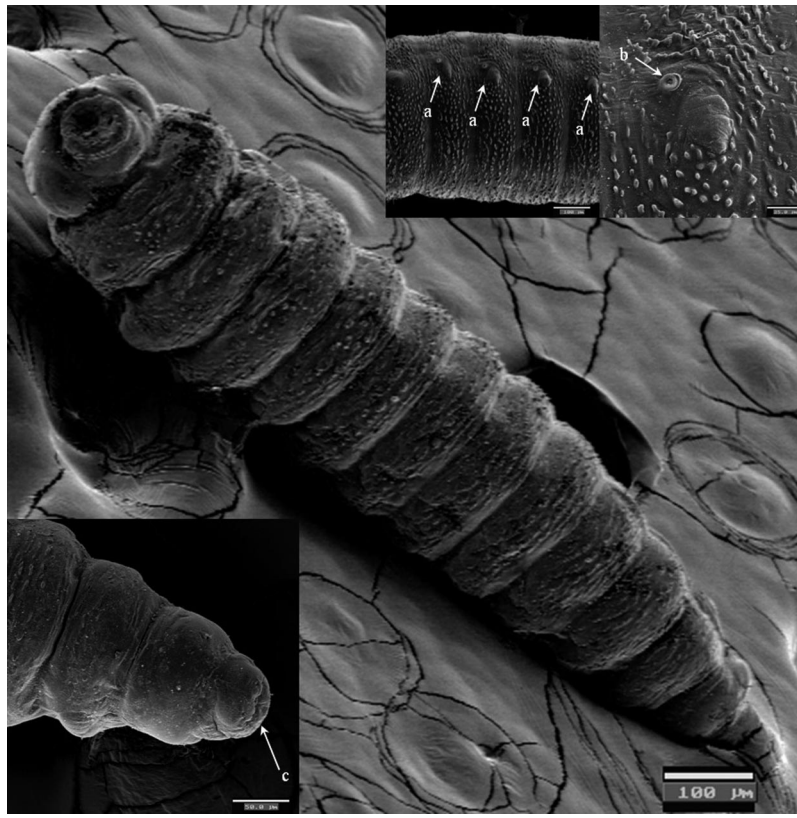

Fig. 3. Late second instar with suctorial mouth on the ventral side of the head. Abdomen of second instar larvae with pseudopoda (a) and spiracles (b) (top inset). Enlarged view of pygidium showing fissure (c) (bottom inset).

was determined using the width of the head capsule (Dyar 1890).

Results

Under laboratory conditions (25 ± 1°C and a photoperiod of 18:6 [L:D] h), *G. fausta* reared on its host *P. citrella* had a developmental time of 18–20 d from oviposition to adult emergence.

Eggs. Eggs observed by light microscopy were hymenopteriform (Fig. 1), approximately 3 times longer than wide, and round at one end and narrowed at the opposite end, which was attached to the leaf surface. The eggs, in groups of one to three, but usually solitary, were always found on the top of the pupal chamber, close to the hosts's head.

G. fausta eggs are almost transparent when newly deposited, but they become opaque whitish before hatching. Eggs averaged 447 ± 65 μm in length by 133 ± 23 μm in width at the widest point. The chorion was smooth, with no tubercules or spines, but some particles attached to its surface were observed. No micropyle and no aeropyles were observed (Fig. 1).

When the embryo completed its development, the neonate larva broke through the round end of the egg. Breakthrough occurred 2 d after oviposition. Although more than one egg per pupae could be observed, no more than one adult was observed to emerge in any case.

Larvae. The cranium has simple acute mandibles with heavily sclerotized blades. Head capsule measurements (Table 1) indicate three instars. Larvae were hymenopteriform and had 13 body segments (Figs. 2–4). All three instars bear many processes and spines, and the last abdominal segment has a fissure (Fig. 3).

First Instar. After emergence, the neonate larvae (223 ± 13 μm in length) move onto the host, which is ≈2 mm in length (Jacas and Garrido 1996). In spite of the enormous difference in size, *P. citrella* pupae die soon after the larval attack. Neonate larvae are whitish and almost transparent but became yellowish during development. The cranium (Fig. 2) is triangular and conspicuous; its basal part is as wide as the first thoracic segment. Dorsally, two ocular discs occupy most of the basal edges of the head. Ventrally, it has a prominent semicircular structure containing a mandibulate mouth (Fig. 2). This structure is surrounded by six setae, and two antennae are visible.

The integument of both the thoracic and the abdominal segments of the first instar are completely covered by spines. These spines occur on a series of three rings per segment except for the last segment.

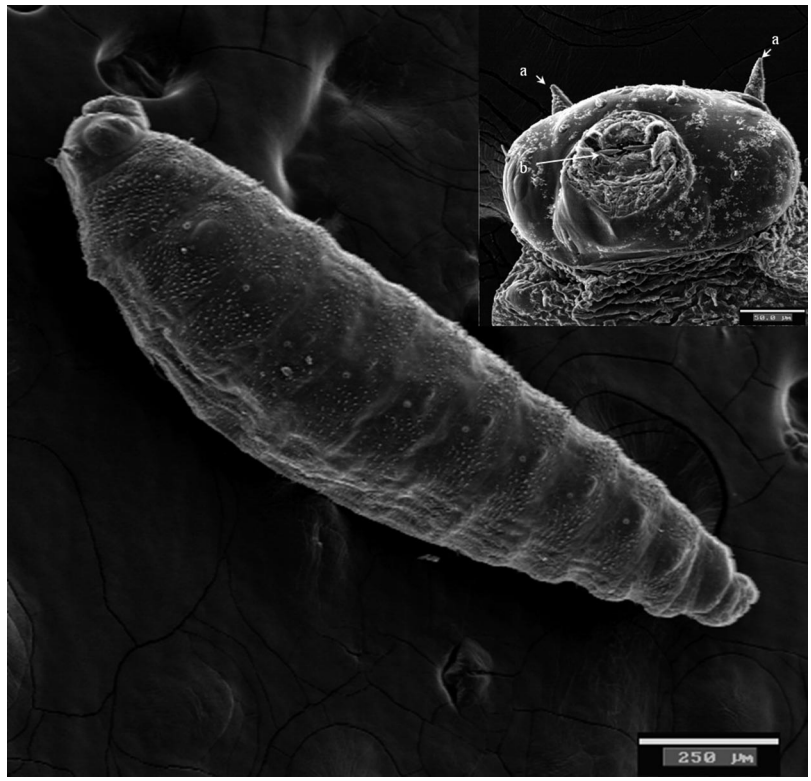

Fig. 4. Late third instar showing suctorial mouth and spiracles. Head showing antennae (a), and mandibulate suctorial mouth (b) with labrum, mandibulae, maxillae, and labium (inset).

This instar lasts for ≈2 d. At the end of this period, larvae averaged 338 ± 23 μm in length.

Second Instar. Early second instars measured 317 ± 19 μm in length (Fig. 3). The cranium is oval, and the ocular discs are more clearly defined. The suctorial structure is a typical mandibulate sucking tube, and the antennae are larger than in first instars.

During the second instar, the integument of the thorax and the abdomen still has spines and protuberances, but their distribution is not as regular as on the first instar. Pseudopoda are evident on both sides of the thoracic and abdominal segments, and these pseudopoda invariably have a spiracle at their base (Fig. 3). This instar lasted for ≈4 d. At full growth, these larvae were 1072 ± 65 μm in length.

Third Instar. This instar is very similar in appearance to the second instar (Fig. 4). It measured 1,195 ± 73 μm in length initially and 1,813 ± 97 μm at completion of its development 3 d later. Antennae were visible as were the mandibles within the suctorial mouth (Fig. 4).

When ready to pupate, the parasitoid larva had totally consumed the body contents of the host, leaving only the outer cast of the host's pupa. The meconium was expelled in one single pellet. Once the meconium had been ejected, the larva moved away from it and pupated.

Pupa. The pupa of *G. fausta*, as in all Hymenoptera, is exarate. It is not protected by any special cocoon. Initially, the pupa is yellowish. Later, it becomes darker with red eyes, and eventually it turns uniformly black.

Pupae averaged 1,550 ± 136 μm in length (Fig. 5). No morphological differences were observed between 1-d-old yellow pupae and 6-d-old black pupae. Some characteristics could be easily observed in the pupae such as the four-segmented tarsi or a petiole wider than longer. The head is heavily reticulate, and the length of the gastral segments decreased from first to fourth, with the fifth segment just a little bit longer than fourth but shorter than the first.

On completion of pupal development, which took ≈1 wk, the adult chews a hole in the leafminer pupal chamber.

Discussion

Although many of the characteristics observed in *G. fausta* immature instars are common among chalcidoids, this species displays a few distinctive features. Hymenopteriform eggs are typically attached to the leaf surface of the host's pupal chamber, a trait that until now we had not observed in any other *P. citrella* parasitoid. This trait allows distinction from eggs deposited by other leafminer parasitoids. In the Tryphoninae (Hymenoptera: Ichneumonidae), anchored eggs are an adaptation to prevent them from being removed by the host until the parasitoid's larva

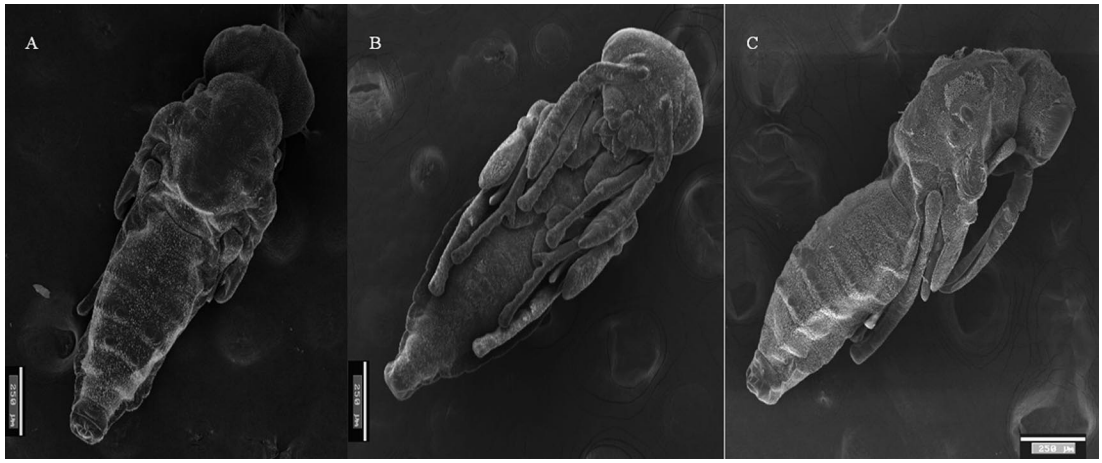

Fig. 5. Dorsal (A), ventral (B), and side (C) view of pupa.

hatches (Mason 1967). Egg position and attachment to the leaf within the pupal chamber could be a protective behavior of *G. fausta* against the abdominal movements of *P. citrella* pupa, because in contrast to Cobo (1996), we found that *G. fausta* females did not paralyze the host at oviposition, and *P. citrella* abdominal mobility was observed until *G. fausta* first instar eventually killed the host. *G. fausta* is therefore a koinobiont ectoparasitoid, a rare combination for a parasitoid (Quicke 1997). Koinobiont ectoparasitism is a risky strategy because the parasitoid egg can be dislodged by the active host (Godfray 1994).

The three instars observed, holopneustic, hymenopteriform, and 13-segmented, are typical for eulophid larvae (Clausen 1962, Askew 1968). As in most Chalcidoidea (Gauld and Bolton 1988), the cranium is triangular and conspicuous and has distinct mandibles (Gauld and Bolton 1988). As in other ectoparasitoids, the mouth is transformed into a suctorial tube (Cals-Usciati et al. 1985, Quicke 1997). This arrangement includes a preoral sucker, and feeding is achieved by pharyngeal pumping and continuous suction of host tissue fragments shred into tiny fragments by the mandibles (Cals-Usciati et al. 1985, Thompson 1986). Because these are typical eulophid larvae, no distinction from other ectoparasitoids of *P. citrella* could be achieved unless prepared for SEM.

The pupa of *G. fausta* was not protected by any cocoon but instead by the shelter provided by its host, and it has many of the features that characterize the imago (Schauff et al. 1998), allowing for its identification. On completion of pupal development, use of mandibles to chew the emergence hole has been observed to be an important pathway for pesticide intoxication from residual pesticides in this leafminer as well as other citrus leafminer parasitoids (unpublished data).

Our results show that *G. fausta* can be unambiguously identified by SEM. Moreover, the characterization presented demonstrates that routine identification for management purposes can be applied to eggs and pupae by using a binocular microscope.

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