POSTOVIPOSITIONAL WEB-SPINNING BEHAVIOR IN A HYPERPARASITE, SIGNIPHORA COQUILLETTI ASHMead (HYMENOPTERA: SIGNIPHORIDAE)

by

J. B. WOOLLEY¹ and L. E. M. VET²

(¹Department of Entomology, University of California, Riverside, California, U.S.A.; ²Department of Ecology, Zoological Laboratory, University of Leiden, Leiden, The Netherlands)

SUMMARY

After oviposition the uniparental hyperparasite Signiphora coquilletti Ashmead was observed to spin a web over her host, Trialeurodes vaporariorum (Westwood) previously parasitized by Encarsia formosa Gahan. Signiphora coquilletti was subsequently reared from webbed T. vaporariorum pupae and from webbed pupae of Tetraleurodes mori (Quaintance), T. stanfordi (Bemis), Aeleuroplatus coronatus (Quaintance), and A. gelatinosus (Cockerell). Oviposition and web-spinning behavior of S. coquilletti are described, and the ultrastructure of the webs is discussed. We believe that webs may function as a physical barrier to host searching females of competing Encarsia species, or that they may serve as an intraspecific host-marking device. Two additional hypotheses are that webs afford protection against predation of Signiphora immatures in host pupae, or that they reduce mortality of Signiphora by tying host pupae to leaf surfaces.

INTRODUCTION

Web-spinning behavior by adult parasitic Hymenoptera has rarely been reported. We describe the post-ovipositional web-spinning behavior of the uniparental hyperparasite Signiphora coquilletti Ashmead (Hymenoptera: Signiphoridae). This species is a member of the parasite complex of the greenhouse whitefly, Trialeurodes vaporariorum (Westwood) in southern California. Other parasites found on this host at Riverside, California are Encarsia formosa Gahan, E. pergandiella Howard, E. meritoria Gahan, and Eretmocerus californicus Howard. During laboratory studies of this complex, (VET & VAN LENTEREN, 1981) one of us (L.V.) discovered the interesting and unique ovipositional behavior of S. coquilletti. After ovipositing in a blackened whitefly pupa previously parasitized by E. formosa, a Signiphora female did not leave the host but began to walk back and forth over it dragging her abdomen. Silken threads were observed to issue from the apex of her abdomen.
METHODS

Following this discovery we placed individual S. coquillettii females in petri dishes containing leaves of Nicotinia glauca Graham on which several parasitized and unparasitized T. vaporariorum pupae were present. The Signiphora females were of unknown age and were taken from various whitefly parasite collections. Under a dissecting microscope we observed many ovipositional sequences, 5 of which were complete, in that they began with host finding and ended in the construction of webs.

In addition, we prepared pieces of leaf tissue approximately 0.5 cm square with whitely pupae and webs attached for scanning electron microscopy (SEM) using two techniques. Method 1: fresh material was submerged in 70% ethanol in a watch glass and dehydrated by gradual replacement of the solution with absolute ethanol. When the dehydration was complete the material was critical-point dried in a Tousimis Samdri PVT-3 critical-point drying apparatus using CO₂ as the transitional fluid. The specimen was then mounted on an aluminum stub with conductive silver paste and coated with a Au-Pd alloy in a Hummer Sputter Coater. Method 2: leaves with host bodies and webs attached were allowed to dry in covered petri dishes on the lab bench. 0.5 cm square sections of leaf tissue were then mounted on aluminum stubs and coated with a Au-Pd alloy as described under Method 1.

WEB-SPINNING BEHAVIOR

A complete behavioral sequence can be described as follows. A Signiphora female approaches and mounts the host pupa, drumming with the apices of her antenna back and forth over the dorsal surface of the pupa, paying particular attention to the fringed margin. If she accepts the host, this drumming behavior continues for 2–3 minutes. If the host is rejected, the parasite leaves the pupa within 30–60 seconds. If the host is accepted, the parasite walks off the dorsum of the pupa, backs up to it, and inserts her ovipositor into the host pupa just under the waxy fringe at the dorso-lateral margin. This initial drilling activity lasts for 12–15 minutes. During this period the parasite may construct a feeding tube as the ovipositor is not withdrawn in one smooth motion, but is withdrawn slowly in a stepwise manner over a period of 1–3 minutes. After drilling, she removes her ovipositor, turns 180° to face the feeding tube, and feeds for 11–17 minutes. After feeding, she reinserts her ovipositor into the same area of the pupa and oviposits for 5–15 minutes. Following oviposition she cleans her ovipositor with her hind tibiae, and often grooms her wings, antennae, and mouthparts with her fore legs. At this point the parasite may either leave the host or begin her webbing activity.
Figure 1. Trialeurodes vaporariorum pupa (arrow) initially parasitized by Encarsia formosa and subsequently by Signiphora coquillettii and covered by a Signiphora web, magnification about 20 ×.

Figure 2. A webbed T. vaporariorum pupa from which a Signiphora adult has emerged. Emergence hole at lower right. SEM (Method 2), 100 ×
Figure 3. Portion of a *S. coquillettii* web on *Tetraleurodes mori*. SEM (Method 2), 4800 ×.

Figure 4. A single strand of a *S. coquillettii* web on *Trialeurodes vaporariorum*. SEM (Method 1), 49,100 ×, bar represents 200 nm.
If the parasite initiates the web-spinning activity, she then begins to walk back and forth over the host pupa in various directions, dragging the tip of her abdomen over the host or leaf surface. These dragging movements resemble the host marking behavior displayed by other hymenopterous parasites such as some Scelionidae (Wilson, 1969; Safavi, 1968), e.g. *Telenomus sphingis* (Ashmead) (Rabb & Bradley, 1970). A fine strand of webbing material issues from the apex of her abdomen during this activity. At the beginning and end of each pass over the host pupa the parasite presses the tip of her abdomen to the leaf surface in order to anchor the single strand of web. Adjacent whitely pupae and leaf veins are also used for this purpose. On several occasions the webbing behavior lasted for over 30 minutes, resulting in a closely knit web 2–3 mm in diameter which completely covered the now hyper-parasitized whitely pupa (Fig. 1). After completing a web the parasite leaves the host pupa. In every case in which this complete behavioral sequence was observed, a *Signiphora* adult was subsequently reared from the host. When emerging from a host pupa covered by a dense web, a *Signiphora* adult chews small, round holes first through the integument of the host pupa and then through the web (Fig. 2).

We examined more than 100 webs on field-collected whiteflies of various species during the course of these studies and found that the majority of the webs consisted of several hundred strands, but some webs were found to consist of only a few strands. In almost every case, when these pupae were isolated in gelatin capsules, *S. coquillettii* emerged or a dead *Signiphora* pupa was identified upon dissection. A list of the webbed host species from which *S. coquillettii* was reared is presented in Table 1.

<table>
<thead>
<tr>
<th>Whitefly</th>
<th>Hostplant</th>
<th><em>S. coquillettii</em></th>
<th>other parasites</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Trialeurodes vaporariorum</em></td>
<td><em>Nicotinia glauca</em></td>
<td>29</td>
<td>19</td>
</tr>
<tr>
<td><em>Tetraleurodes mori</em></td>
<td><em>Citrus spp.</em></td>
<td>52</td>
<td>17</td>
</tr>
<tr>
<td><em>Aleuroplatus coronatus</em></td>
<td><em>Quercus agrifolia</em></td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td><em>A. gelatinosus</em></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>T. stanfordii</em></td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>

1 Rearings were made by isolating individual webbed whitely pupae in gelatin capsules. 2 Webs with parasite emergence holes were found on *Trialeurodes tentaculatum* on *Quercus agrifolia*.

**Table 1**

*Signiphora coquillettii* reared from webbed whitely hosts.
ULTRASTRUCTURE OF THE WEB

Webs were initially examined under a dissecting microscope and then after preparation as previously described, with the SEM (JOEL 35C). Under low SEM magnification (100 ×) it was clearly seen that the webs are composed of individual strands which criss-cross in an apparently random manner, forming a dense net over the host (Fig. 2). At high SEM magnification (4800 ×) it can be seen that individual strands of webbing seem to be fused in certain areas (Fig. 3). This was a common observation, and in other SEM plates we noted that the ends of individual web strands flared out slightly where they were appressed to the leaf surface. These observations suggest that the web material is sticky when first produced, and that it may remain sticky for some time. Under high SEM magnification (50,000 ×) the strands were seen to be single fibers, circular or elliptical in cross section, with a smooth surface marked by closely spaced, transverse, annular ridges (Fig. 4) The ridges may be an artifact of the method used to prepare this particular specimen (Method 1).

DISCUSSION

The ovipositional behavior of Signiphora coquillettii is similar to that of other signiphorid species in some respects, but very different from that of the aplelinid parasites of whiteflies. In our observations, S. coquillettii required up to 3 minutes for drumming and host acceptance, up to 15 minutes for drilling, up to 17 minutes for host feeding, and up to 15 minutes for oviposition. Van Lenteren et al. (1980) found that Encarsia formosa required an average of only 16 seconds for drumming, and slightly less than one minute each for drilling and oviposition. Other signiphorids require lengthy periods for host feeding and oviposition (Agekyan, 1968; DeBach et al., 1958; Clausen, 1924), and this may be common in the family. Another unusual feature of S. coquillettii’s ovipositional behavior is the apparent requirement of host feeding before oviposition. In E. formosa host feeding is never followed by oviposition in the same host (Van Lenteren et al., 1980). Host feeding followed by oviposition in the same host has been observed in at least two other signiphorids: S. merceti Malenotti (Agekyan, 1968) and a Chartocerus sp. (Woolley, unpublished).

The most notable feature of S. coquillettii’s postovipositional behavior is the web-spinning activity. As noted below, analogous postovipositional web-spinning behavior has been reported in the parasitic Hymenoptera only in the Eupelmidae. We can only speculate at this point on the function or adaptive value of the webs to S. coquillettii, but we
have developed several hypotheses. Signiphorids in general are characterized by a rather low fecundity and ovipositional frequency. Quezada et al. (1973) studied the biology of S. borinquensis Quezada, DeBach, and Rosen, a species closely related to S. coquillettii, and found that S. borinquensis has monootene ovarioles in which only one mature egg is present per ovariole at any given time. They also found this species to have a relatively low fecundity and ovipositional frequency. Other workers have found low fecundities and low ovipositional frequencies in Signiphoridae (e.g. Clausen, 1924). We have no data on the fecundity or ovipositional frequency of S. coquillettii, but in several dissections of mature females we found two mature ovarian eggs present in every case. It is reasonable to assume that S. coquillettii has a fecundity and ovipositional frequency comparable to that of S. borinquensis and other signiphorids for which data are available. The webs are apparently a form of parental investment in a species with a relatively low fecundity and ovipositional frequency.

Rearrings made in the course of this study and by other workers have shown that S. coquillettii is a common hyperparasite of several whitefly species in southern California. Each of these whitely species can be expected to have one or several primary parasites, typically (but not exclusively) aphelinids of the genera Encarsia and Eretmocerus. The parasite complex of the greenhouse whitefly, of which S. coquillettii is a member, is perhaps the best known, and includes several Encarsia species which exhibit hyperparasitic male development (adelphoparasitism), for example E. pergandiella, E. meritoria, and E. formosa (Gerling, 1965, 1966a, 1966b). In particular, E. meritoria and E. pergandiella are known to attack and kill many female larvae of their own and related species by laying male eggs in previously parasitized hosts. Signiphora eggs or larvae may be at risk to females of these Encarsia species if male Encarsia have a more rapid developmental rate or are otherwise more competitive within the host. We do not know if Signiphora females will oviposit in whiteflies containing male Encarsia eggs or larvae. It is even possible that male Encarsia may feed directly on Signiphora larvae or pupae. The webs may serve as a physical barrier to host searching females of these Encarsia species. E. formosa searches at random and cannot locate its hosts except by direct antennal contact (van Lenteren et al., 1976, and such direct antennal contact is a prerequisite for host selection in E. formosa (van Lenteren et al., 1980). An Encarsia female walking over a dense web might not encounter a host underneath, or she may not be able to examine it sufficiently for host selection. Also, these webs seem to accumulate droplets of honeydew, and dust particles which parasites avoid, and which may afford additional barriers to host searching. The webs may thus prevent mul-
tiple hyperparasitism of whitefly pupae containing *Signiphora* immatures. The webs may also function as an intraspecific host-marking device, preventing superparasitism by *Signiphora* females. A third hypothesis for the function of the webs is that they offer some protection against predation of whitefly pupae containing *S. coquillettii* immatures. Finally, it is possible that webs reduce mortality of *S. coquillettii* immatures by tying the host pupae to leaf surfaces. We regard the latter two hypotheses as possible, but less likely than the former two hypotheses.

We have found few references in the literature to web spinning by adult hymenopterous parasites. *Delanoë & Arambourg* (1965) studied the biology of *Eupelmus urozonus* Dalman (Hymenoptera: Eupelmidae) in the laboratory using the host *Myopites stylata* F., a tephritid which forms galls in the pistils of *Inula viscosa* Aiton (Compositae). On this host, *E. urozonus* lays a single egg on the inner wall of the gall chamber near the host larva, and then covers the egg with a fine, white, silken web which is produced through the ovipositor by a series of back and forth motions lasting from 2½–5 minutes. Similar webbing activity has been reported for other eupelmids (*Packard, 1916; Phillips & Poos, 1921; Taylor, 1937*). None of these eupelmids sting their host directly before oviposition, thus venom is not injected, and in these cases the webs appear to partially immobilize the host larvae, to protect the parasite eggs, and to keep the parasite eggs in the vicinity of the host larvae.

In the case of *S. coquillettii* such functions are not applicable, as the eggs of this parasite are deposited externally on parasite pupae or prepupae which are within the whitefly pupal case. The webs are then spun over the immobile pupal case of the whitefly host. The senior author is currently conducting further research on the biology of *S. coquillettii* and on the morphological adaptations which make this interesting and unique behavior possible.

**ACKNOWLEDGEMENTS**

We would like to thank Max E. Badgely for doing part of the photography, and Dr. K. Bakker, Dr. G. Gordh, Joop C. van Lenteren, and Mike Rose for critical readings of several drafts of this paper and for many stimulating discussions concerning the biology of *S. coquillettii*. This study was partly supported by a Fulbright-Hays grant to Louise Vet.

**REFERENCES**


J. B. Woolley, Department of Entomology, University of California, Riverside, California 92521, U.S.A.

L. M. Vet, Department of Ecology, Zoological Laboratory, University of Leiden, Kaisersstr. 63, 2300 RA Leiden, The Netherlands.