

**LIFE HISTORY AND IMMATURE STAGES OF *STEFFANOLAMPUS SALICETUM*  
(HYMENOPTERA: CHALCIDOIDEA: PERILAMPIDAE)**

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**Abstract**

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The life history and immature stages of *Steffanolampus salicetum* (Hymenoptera: Chalcidoidea: Perilampidae) are described for the first time based on field studies in a mixed hardwood forest in southern Ontario. *Steffanolampus salicetum* females were collected on a windblown maple tree and subsequent examination of wood samples in the laboratory revealed that this wasp is a primary parasitoid of *Ptilinus ruficornis* (Coleoptera: Anobiidae). Both the oviposition behaviour and the morphology of the first-instar or planidial larva are unique in Perilampidae but the structure of the egg is virtually identical to *Perilampus*. The phylogenetic implications of these results are discussed. Rates of *Ptilinus* parasitism by *Steffanolampus* are low, which suggests that there is very little potential for the use of these parasitoids as agents of biological control.

**Introduction**

*Steffanolampus* is the only endemic genus of Perilampidae in the Nearctic region (Darling 1997). It did, however, take considerable time and effort to establish this most basic distributional fact. As documented in considerable detail by Peck (1974), the type and only included species (*Perilampus salicetum* Steffan) was originally described from material collected in Austria before 1877. This species has not been collected in Europe in the intervening 120 years and although the circumstances surrounding the introduction remain unclear, it is almost certain that the type specimens were the result of an infestation of wood imported from North America. Peck (1974) also provides a detailed treatment of the distribution and host associations of *Steffanolampus* and notes its association with maple trees (*Acer* spp.) infested with anobiid beetles. However, the exact nature of this host association, that is, whether the wasps are primary parasitoids of xylophagous beetles or hyperparasitoids associated with these beetles, has remained elusive. This is surprising because these chalcidoid wasps are rather large (females are up to 5 mm in body length) and have a distinctive appearance. The females have upturned ovipositors and raised processes on the pronotum, both of which facilitate easy identification (Darling 1997, p. 540, fig. 6).

In recent years considerable progress has been made in elucidating the phylogenetic affinities of the chalcidoid wasps with planidial first-instar larvae, Perilampidae (*sensu* Darling 1997) and Eucharitidae (*sensu* Heraty 1997). Much of this progress is a result of the discovery of the life history and immature stages. The egg and first-instar larva of both of these families are unique in Chalcidoidea. The eggs are laid in or on plant material some distance from the host (cf. in, on, or in very close proximity to the host), and the first-instar larvae are heavily sclerotized, active planidia, "minute wanderers" (*sensu* Smith 1912) that either find and attack the host directly or attach to an intermediate host (cf. relatively inactive hymenopteriform larvae that begin feeding on the host

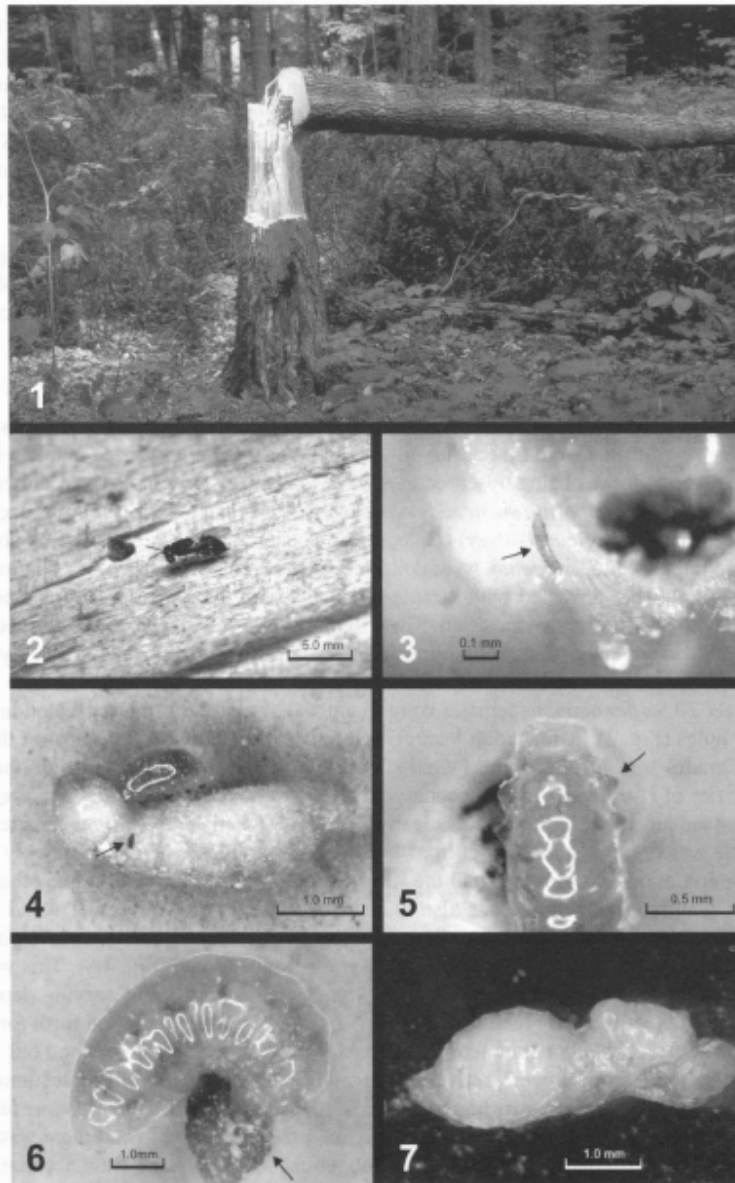
shortly after eclosion from the egg). There is good published information on the life history and immature stages for three of the five subfamilies of Eucharitidae (Darling 1992; Heraty 1994) and for the perilampid subfamily Chrysolampinae (Darling and Miller 1991). The greatest gaps in our knowledge concern the Perilampinae. Of the six described genera, published information is available for only *Perilampus* Latreille (Bergold and Ripper 1937; Clancy 1946; Principi 1947; Tripp 1962; Tanton and Epiala 1984; Heraty and Darling 1984) and for *Krombeinius* Bouček (Darling 1995). Three of the four genera for which there is no published information on life history and immature stages are associated with woodboring beetles (*Steffanolampus*, *Monacon* Waterston, and *Burksilampus* Bouček, cf. *Euperilampus* Walker which are generally considered to be hyperparasitoids of Lepidoptera through Ichneumonidae; see Darling 1997). Xylophagous beetles are particularly interesting hosts for parasitoid Hymenoptera because wood-boring beetles are the likely hosts in which parasitoidism originated (Quicke 1997). In addition, xylophagous beetles are the ancestral hosts of many clades of parasitoid wasps and of many enigmatic and relictual families of parasitoids (e.g., Orussidae, Vanhorniidae, Stephanidae, Megalyridae; Goulet and Huber 1993). Both the host association and morphological features of *Steffanolampus* suggest that information on the life history and immature stages of *Steffanolampus salicetum* could provide valuable information on the phylogeny of the Perilampinae and hence Perilampidae.

#### Methods

Field studies and collections were conducted at the Joker's Hill property of the University of Toronto (Canada, ON: York Region, NW of Newmarket and S of Hwy 9, 44° 03' N, 79° 29' W, 300m). This property is an ecologically significant area in the Oak Ridges Moraine and contains a mixture of habitat types including quality old growth forest (see <http://www.erin.utoronto.ca/~w3pkota/jh.html> for more detailed information and a map of the study area). The specific study site was located on the eastern half of the property (E of Dufferin Street), in an area of mixed hardwood forest (sugar maple, *Acer saccharum* Marsh; red maple, *Acer rubrum* L.; American beech, *Fagus grandifolia* Ehrh.; and yellow birch, *Betula allegheniensis* Britton). The field collections and observations were made in 1997 and 1998 and centered on a windblown maple tree (*Acer saccharum* Marsh). The tree fell in a windstorm in the spring of 1997 (Bill Fox, pers. comm.) and shattered in a way which exposed a considerable area of heartwood (Fig. 1). Weekly observations were also made at woodpiles of beech and maple at the study site from 25 June to 23 August 1997, both before and after *Steffanolampus* was first encountered, allowing for rather precise data on the flight time of the adults of both host and parasitoid. A detailed photographic record of the observations was made by the author and form the basis for drawings provided herein. The identifications of the parasitoid as *Steffanolampus salicetum* and the host as *Ptilinus ruficornis* Say were made by the author, and the latter was confirmed by Dr. Donald Bright, Research Branch, Agriculture and Agri-Food Canada, Ottawa.

Specimens and samples of the wood were brought back to the Royal Ontario Museum (ROM) for *ex situ* behavioural studies, rearing and dissection. Wood samples either were kept continuously at room temperature or overwintered outdoors and brought indoors in April 1998 and reared at room temperature. Wood samples from the field with beetle entrance tunnels were examined with a stereomicroscope for eggs and planidia, and the wood was subsequently split open along the length of the tunnel and monitored for activity. Immature stages were preserved in 80% ethanol or slide-mounted.

Beetle larvae were maintained in petri dishes of various sizes for observation. The observation dishes contained blocks of wood of varying sizes with either naturally occurring galleries or holes drilled to accommodate grubs. Observation dishes were maintained at room temperature although photoperiod and humidity were not controlled.



FIGURES 1-7. 1. Windblown sugar maple tree, showing exposed heartwood, the site of attack by *Ptilinus ruficornis*. 2. *Steffanolampus salicetum* female examining entrance holes of *P. ruficornis*; note: female beetle is partially emerged from the hole, and exhibiting guarding behaviour. 3-7. Immature stages of *S. salicetum*. 3. First-instar or planidium (arrow) attached to frons of late instar larva of *P. ruficornis*. 4. Second-instar feeding on host prepupa; note: exuvium of planidium (arrow). 5. Early third-instar; note: fleshy protuberances (arrow). 6. Late third-instar; note: shriveled remains of host (arrow). 7. Female pupa.

Eggs and first-instar larvae of *S. salicetum* were examined with a combination of compound microscopy (phase and interference contrast) and scanning electron microscopy (SEM). Slides were prepared using Hoyer's medium both with and without clearing of the immature stages for 4 hours in Nesbitt's solution (eggs, DCD Slide Nos. 1981, 1982, 2047, 2049; planidia, DCD Slide Nos. 1983–1996, 1998–2000). Planidia were critical point dried before examination by SEM (DCD SEM Nos. 474–478, 483–490). Descriptions of the egg and planidium are a composite of multiple specimens examined with both SEM and light microscopy. A photographic archive of the behaviours and the dissections is maintained at the ROM.

Terms for morphological structures of the first-instar larva follow Heraty and Darling (1984). Voucher specimens of adult *S. salicetum* and *P. ruficornis*, and slide-mounted and SEM-prepared eggs and first-instar larva of *S. salicetum* are deposited in the ROM entomology collection.

## Results

### Natural History Observations of *Steffanolampus salicetum* and *Ptilinus ruficornis*

**1997:** *Steffanolampus* were first observed and collected on a mixed beech/maple woodpile on 17 July. This woodpile was being observed every 3–5 days in order to collect specimens and life history information on *Vanhornia eucnemidarum* Crawford (Hymenoptera: Vahnornidae) and their recorded host *Isorhipis ruficornis* (Say) (Coleoptera: Eucnemidae), which were first collected on 25 June. Five females of *S. salicetum* were collected (no males were observed) and returned to the ROM, where they were provided with samples of wood from the woodpile and dampened filter paper in an attempt to induce oviposition. These females and substrates were observed daily for between seven and ten days; no eggs or oviposition behaviour was observed. On 20 July the wind-blown sugar maple was found. The exposed heartwood had many 2–3 mm entrance holes and approximately 20 *Steffanolampus* females were found walking on exposed heartwood in the vicinity of these holes (Fig. 2). A few adult beetles were present on the wood but most of the *Ptilinus ruficornis* females were in the wood. Females were usually visible 2–3 mm inside the entrance holes. No males of *P. ruficornis* were encountered on the wood. Females of *Steffanolampus* would approach and antennate the entrance holes leading to tunnels formed by *Ptilinus* females. If a live female beetle was present in the tunnel in a "head out" orientation, she would quickly thrust her head and pronotum out of the tunnel and the wasp would move off and investigate other entrance holes. This "guarding behaviour" was also elicited by putting small slivers of wood above the entrance hole. In the absence of a guarding response by the female beetle, the *Steffanolampus* female would turn around and slowly walk backwards into the tunnel (Fig. 4A). This was a slow, apparently deliberate behaviour and the female would stay in the hole at varying depths (up to about three-quarters of the body length), with its body slowly rocking back and forth for up to one minute. On 25 July, *Steffanolampus* females were still present on the maple wood but in smaller numbers; no *Ptilinus* females were actively excavating tunnels (frass was not accumulating beneath the holes) but a few were guarding in response to inspection by *Steffanolampus* females. On 10 August, *Steffanolampus* females were not present on the maple stump and there was no beetle activity. Dead *Ptilinus* females were present in the tunnels; there was no frass accumulation and guarding behaviour could not be elicited by artificial means. Samples of wood with holes and entrance tunnels were collected on 25 July and 10 and 23 August and returned to the ROM for inspection and dissection. This wood was split parallel to tunnels (as in Fig. 4) and both the exposed surface of the wood and the inner surfaces of the tunnels were examined for immature stages of the host and parasitoid. None were found on the 25 July samples after an extensive search of 6 tunnels using a stereomicroscope. These wood samples were subsequently examined every 2–3 days for activity. On 5–7 August, planidia were found crawling on the walls of one

tunnel and some planidia had their heads burrowed into the walls of the gallery; many dead planidia were also found. This wood was then split radially around the hole and small eggs were found imbedded in the wood (Fig. 4C). These eggs were located 0.7 to 1 mm from the wall of the tunnel. Also, very elongate beetle larvae (length, 1.5 mm; width approximately 0.08 mm) were found in the heartwood, approximately 2.25 mm from the wall of the tunnel at a depth of approximately 3.25 mm and oriented parallel to the grain of the wood (Fig. 4E). These larvae (DCD Slide Nos. 1997, 2001) are virtually identical to the first-instar larva of the European species *Ptilinus pectinicornis* (L.) illustrated by Cymorek (1971) and are regarded as the first-instar larvae of *P. ruficornis*. On 23 August, a sample of the wood with beetle holes was collected from the stump and dissected at the ROM. Beetle larvae were found in the wood; they were small (approximately 0.4 mm), C-shaped scarabaeiform grubs virtually identical to the second-instar larvae illustrated by Cymorek (1971). One of these larvae had a planidium attached to the venter of the thoracic region (as in Fig. 4G).

**1998:** The maple tree was visited regularly during the summer. An emergence trap was erected over the stump on 11 June and monitored weekly until the end of July; no *Ptilinus* nor any *Steffanolampus* were collected. In addition, neither beetle nor wasp activity was noted on the log on any of the 7, 11, 15, or 23 July visits.

Wood samples were dissected in the spring of 1998. On 5 April, the wood kept at room temperature was cut into approximately 3 cm sections across the grain. Many of these sections were riddled with galleries and frass and many large (4–5 mm) C-shaped grubs were collected. A few adult beetles and pupae were also found in the wood. These beetle larvae were examined for planidia. Planidia were found on only two larvae of approximately 30 larvae. One beetle larva had a single planidium on the venter and the second had two planidia, one ventrad and one attached to the gena (Fig. 3). The beetle larvae were still actively feeding and tunnelling in the wood and were maintained in observation dishes. These were observed every few days. One larva with planidium was preserved on 27 April and the second larva and its planidium were still alive on 8 September; however these were found dead in February 1999. Additional samples of wood were dissected in July and August 1998; large numbers of *Ptilinus* (P) were found (larvae, pupae and adults) but very few had *Steffanolampus* planidia (S): 18 July (32P, 1S), 5 August (42P, 4S), 18 August (34P, 1S), 19 August (27P, 0S), 20 August (23P, 0S; 11P, 0S). In addition, *Ptilinus* adults, but no adult *Steffanolampus*, emerged in the containers with the wood samples. These data indicate that the parasitism rate by *Steffanolampus* is less than 3.5%. In May 1999, *P. ruficornis* were still emerging from the wood samples collected in August 1997 and March 1998; 59 adult beetles of both sexes and five larvae emerged in the period between September 1998 and May 1999. No *Steffanolampus* were recovered which provides additional evidence of the low level of parasitism.

In June, 1999 a subsample of the lab-reared infested wood was again dissected. On 20 June, a prepupa of *P. ruficornis* was collected with an attached parasitoid larva (Fig. 4). The larva was about 1.2 mm in total length and the head was deeply imbedded into the body of the host. On the basis of size and the presence of the planidial exuvium, this is regarded as the second-instar larva of *S. salicetum*. On 22 June, the parasitoid was 3.25 mm in length and different in appearance, i.e., there were distinct lateral protuberances present on the thoracic segments (Fig. 5). Although no exuvium was recovered, this is regarded as the early third-instar. The larva was feeding completely externally and the host was still largely intact. By 27 June the parasitoid had increased to 5 mm in length and had almost completely consumed the host (Fig. 6); this is regarded as the late third-instar and the lateral protuberances are no longer visible. The mouthparts were disengaged from the host tissues and the nondescript hymenopteriform grub was quiescent on the host. On 28 June, the larva voided its meconium and shrunk in length to 4.5 mm. The prepupal stage lasted about 24 hours and on 29 June a white female pupa was present (Fig. 7). The pupal stage lasted 13

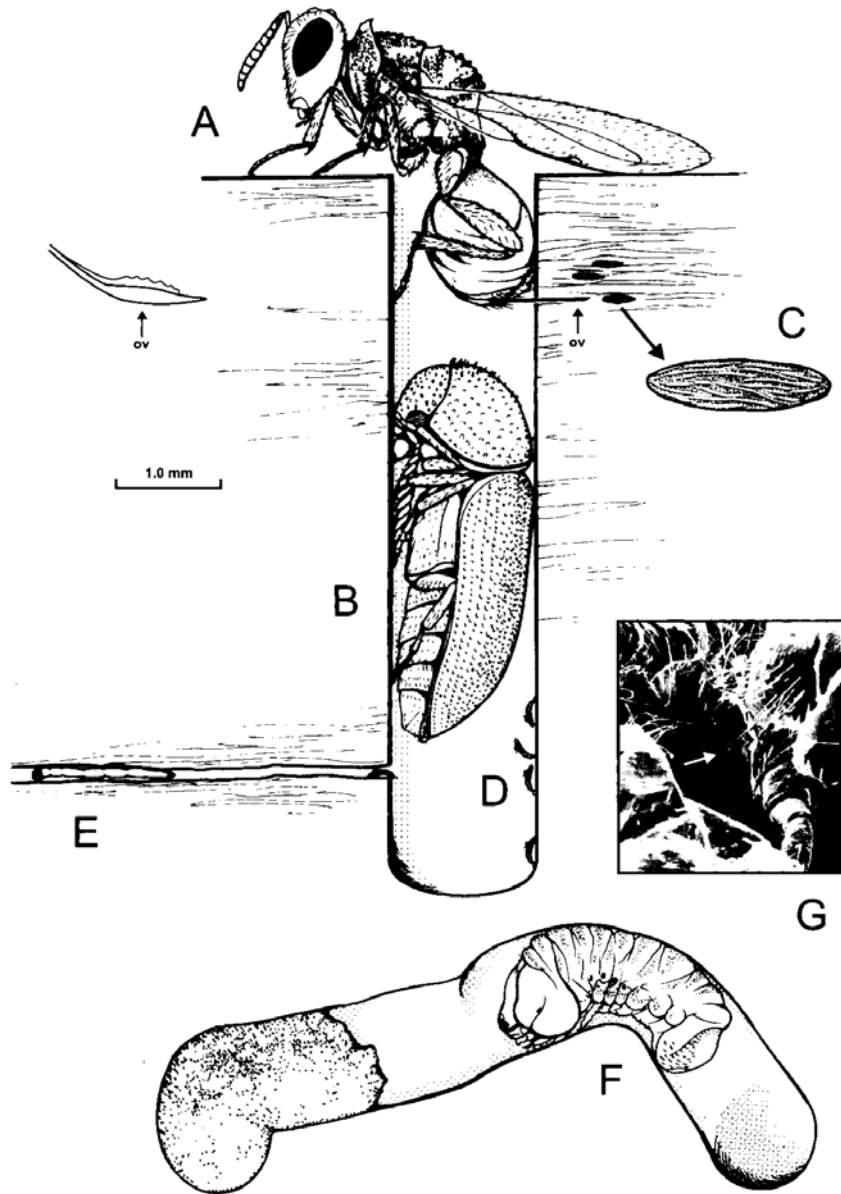


FIGURE 8. Diagrammatic representation of the interactions between *Steffanolampus salicetum* and its host, *Ptilinus ruficornis*. A. Female wasp in entrance hole, ovipositing into wood; ov, lateral view of apex of ovipositor. B. Dead female beetle passively blocking tunnel. C. Oviposition site and detail of *Steffanolampus* egg. Note: the weak ribbing of the chorion. D. Planidial first-instar larvae of *Steffanolampus* moving around in tunnel. E. First-instar beetle larva in wood. F. Final-instar beetle larva in gallery system with accumulated frass. G. SEM of planidium on venter of beetle larva. All illustrations except C and G to same scale.

days; the pupa was completely black on 8 July and the adult eclosed on 11 June. This rearing record provides incontrovertible documentation that *S. salicetum* is a primary parasitoid of *P. ruficornis*, and completes its development by feeding on the pupal stage of the host.

Figure 8 is a diagrammatic summary of various aspects of the life history of *S. salicetum* and its host *P. ruficornis*, based on field observations, laboratory dissections, and reasoned speculation based on published information on a European species of *Ptilinus* (Hickin 1963; Cymorek 1971). Primary attack is initiated when the mated female of *P. ruficornis* excavates an entrance tunnel across the grain of the wood. The females assume a "head out" orientation (B) and oviposit into the wood. The ovipositor length is approximately 2.4 mm ( $n = 4$ ), which corresponds with the position that the first-instar larvae were found in the wood (E). Females die in the tunnels inhibiting the entry of predators and parasitoids. The beetle larvae begin feeding on the wood, moving randomly through the heartwood, and frass accumulates in the gallery system (F). After 5 or 6 instars, the larvae pupate and complete development. Females of *Steffanolampus* arrive on the wood after the beetle has initiated the entrance tunnels and continue to arrive after the females have died. The wasps walk backwards into available tunnels (A) and oviposit about 1 mm from the wall of the tunnel (C). This distance corresponds with the length of the ovipositor, which has strong teeth on the upper valve (A, ov). The planidia emerge from the egg and crawl back into the entrance tunnel (D), and apparently locate oviposition sites of the beetle, thereby gaining access to their hosts. The planidia attach to the beetle larva and remain on the exterior of the host (G), apparently reattaching at each successive moult. Feeding and subsequent development of the *Steffanolampus* planidium begins with host pupation.

#### **Immature Stages of *Steffanolampus salicetum***

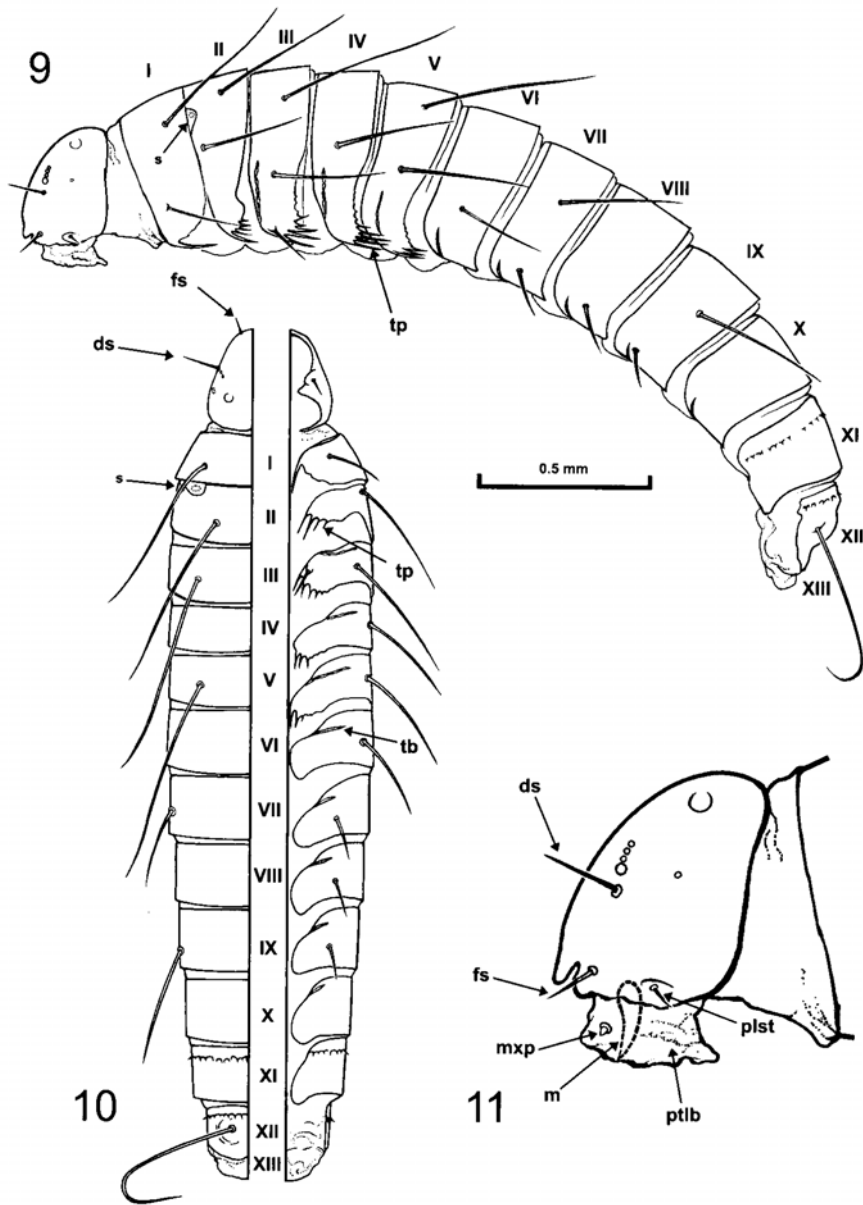
**Ovarian Egg.** Length approximately 0.42 mm, maximum width approximately 0.05 mm, fusiform and slightly curved, with chorion appearing lightly stippled ( $n = 10$ ; DCD Slide No. 1981).

**Deposited Egg (Fig. 8C).** Length approximately 0.4 mm, maximum width approximately 0.1 mm, fusiform or spindle-shaped. Chorion weakly ribbed, evenly sculptured throughout ( $n = 5$ ; DCD Slide Nos. 1982, 2047; DCD Photographs 1998-6, 10-19).

**First-Instar Larva (Figs. 3, 8G, 9-11).** Planidium, length approximately 0.2 mm, maximum width approximately 0.04 mm, cleared and slide-mounted specimens approximately 0.3 mm; fusiform, round in cross-section. Cranium and 13 body segments, I-XII sclerotized, yellow in color, XIII translucent, membranous, forming a caudal pad or "sucker".

**Cranium (Fig. 11)** heavily sclerotized, with distinct hook on anterior margin; antenna absent, with three pairs of distinct cranial setae: forward-directed dorsal seta (ds) inserted in weak, circular depressions, backward-directed pleurostomal seta (plst), and forward-directed frontal seta (fs). Mandibles (m) large, symmetrical and sharply curved, bases broad and rounded. Labrum not distinctly differentiated. Postlabium (ptlb) well-developed, membranous and extensible, with short, stout peg-like structures that may represent the maxillary palpi (mxp); with a bead-like row of 4 campaniform sensilla above the dorsal seta, the first clearly the largest, and a large circular depression dorsad.

**Tergites I-XII** heavily sclerotized, separated ventrad by membranous areas (i.e., tergites do not completely encircle body), all tergites without tergopleural line. Spiracle(s) present dorsolaterad between tergites I and II, located beneath raised flap on tergite I. Tergites I and II apparently fused at least above the spiracle and separate only ventrad, not capable of telescoping; tergites III-XII separate, not fused, capable of telescoping. Setae all very long, longer than the width of their respective tergites; dorsal and lateral setae of I-V at least twice the width of tergites. Tergites I, II, V, VII, and IX with two pairs of setae, dorsal and lateral; tergites IV, VI, VIII with a single pair of lateral setae; tergite III with three pairs of setae, dorsal, lateral and ventral, the ventral pair not



FIGURES 9–11. First-instar larva of *Steffanolampus salicetum*. 9. Lateral habitus drawing. 10. Schematic representation of dorsal (left) and ventral (right) aspects showing shape of tergites and the position and length of the setae. 11. Lateral view of cranium and mouthparts. Abbreviations: ds, dorsal seta; fs, frontal seta; m, mandible; mxp, maxillary palp; plst, pleurostomal seta; ptlb, postlabium; s, spiracle; tb, tubercles; tp, tergal projections.



much smaller than the other setae; tergites X and XI without setae. Caudal cerci long and flexible, arising dorsad on tergite XII. Lateral margins of tergites I–V extended caudad as long needle-like projections (tp). Tergites VI–XI rounded ventrad, margin smooth without spines or serrations, XII extending only to lateral margin, not ventrad; with a row of triangular tubercles (tb) present on the ventral anterior margin of III–X, serrations present in a similar position on XI but complete dorsal; serrations also present on XII.

### Discussion

These field and laboratory studies clearly document that *S. salicetum* is a primary parasitoid of *P. ruficornis*. The phenological observations reported for *Ptilinus* at Joker's Hill are in accordance with the extensive data on flight activity, spatial and temporal distribution of the sexes as presented in Acciavatti (1972). His study, conducted in a similar forest type in upstate New York (Tully), reported a flight period of *P. ruficornis* from 10 June to 25 July. He also noted that the sex ratio of beetles emerging from infested wood was about 1:1 (302♂, 324♀), that there was a high preponderance of females observed on uninfested wood (35♂, 234♀), and that only females were found boring into the wood (229♀). *Steffanolampus* was not encountered in that study but there was a low level of parasitism by *Pelecotoma flavipes* Melsheimer (Coleoptera: Rhipiphoridae). In a study of dead maple trees in Ithaca, New York (Darling, unpublished) both *Steffanolampus* and *Pelecotoma* were collected together suggesting the possibility that *Steffanolampus* was a hyperparasite attacking *Pelecotoma*. The direct observations reported herein and the absence of the rhipiphorid from the Joker's Hill site confirm that *Steffanolampus* is a primary parasitoid of *Ptilinus*.

The oviposition sites and behaviour of female *Steffanolampus* are unique for the family Perilampidae. Their more precise oviposition behaviour explains the unwillingness of female *Steffanolampus* to oviposit in the lab. It is relatively easy to induce species of *Perilampus* and *Monacon* to oviposit under artificial situations simply by providing them with either plant material or damp filter paper. Pheromones are used in both the courtship (Hickin 1963) and aggregation of boring females (Acciavatti 1972) and these olfactory stimuli could be used by female *Steffanolampus* as kairomones to locate infestations of *Ptilinus*.

One of the fundamental differences between perilampids and eucharitids involves oviposition sites; eucharitids oviposit directly into plant tissue (Heraty 1997) whereas perilampids lay their eggs on leaves, flowers or stems (Perilampinae), or in preformed cavities in plant tissue (Chrysolampinae) (Darling 1997). The insertion of eggs into the wood by *Steffanolampus* females is eucharitid-like. This behaviour cannot be explained simply as a way of attacking xylophagous beetles feeding in concealed situations; *Monacon* species attack ambrosia beetles (Curculionidae: Platypodinae) but deposit eggs on the bark surrounding the entrance hole and it is the planidia that enter the tunnels, avoid the guarding behaviour of the males, and attach to the host beetle larva (Darling and Roberts 1999).

The planidium *S. salicetum* is virtually identical to those previously described for *Perilampus* and are very different from the planidium of *Monacon robertsi*, which is also a primary parasitoid of xylophagous beetles infesting the heartwood of dead or dying trees (Darling and Roberts, in press). The most distinctive feature of *Steffanolampus* planidia are the extremely long setae on the post-cranial segments; however, the distribution of dorsal, lateral and ventral setae conforms to the characterization of Perilampidae presented in Heraty and Darling (1984). Longer setae are present in *Perilampus* planidia that remain on the exterior of the host throughout their development, for example, *P. chrysopae* Crawford (Clancy 1946), but the setae of *Steffanolampus*, particularly those on the segments I–V, are at least twice as long as those described in any species of *Perilampus*. Another significant feature of these planidia is the dorsal fusion of tergites I and II;

these tergites are not fused in species of *Perilampus* studied to date (Heraty and Darling 1984). The fusion of these tergites could be a synapomorphy of *Steffanolampus*, *Krombeinius* (Darling 1995), and *Monacon* (Darling and Roberts, in press). Planidia are needed for additional species of *Perilampus* to test the generality of free tergites in this speciose and ecologically diverse genus. Fusion of tergites I and II is currently regarded as a synapomorphy of Eucharitinae (Heraty 1994), and free tergites are the groundplan state in Eucharitidae and Perilampidae. Fusion of these tergites has apparently occurred convergently in Eucharitinae and Perilampinae.

The behaviour of the planidia of *S. salicetum* is also similar to that of the strictly ectoparasitic planidia of *Perilampus* and *Monacon*, e.g., *P. chrysopae* Crawford (see Clancy 1946) and *M. robertsi* (Darling and Roberts 1999). These planidia never enter the haemocoel of the host but remain external and apparently transfer from the shed exuvium to the next larval instar of the host at each successive moult. Most species of *Perilampus* studied are hyperparasitoids, attacking hymenopteran (Ichneumonidae and Braconidae) and dipteran (Tachinidae) parasitoids of Lepidoptera (see Laing and Heraty 1981 for a local example of this life history, *P. fulvicornis* Ashmead). These planidia enter the haemocoel of their ultimate host and emerge to begin feeding as an ectoparasite when the host pupates. Planidia that enter the haemocoel of the host have stouter recurved hooks on the head presumably to facilitate penetration of the host haemocoel (e.g., *P. tristis* Mayr, Bergold and Ripper 1937; *P. hyalinus* Say, Tripp 1962). These spines are probably homologous to the dorsal and cranial setae of strict ectoparasitoids like *S. salicetum*.

The subsequent larval instars of *S. salicetum*, although not studied in detail, are consistent with those reported for other perilampine genera. Of note is the feeding position of the second-instar, which is imbedded into the host as reported for the third-instar of *M. robertsi* Bouček (see fig. 2d in Darling and Roberts 1999). This feeding position may be a result of limited space in the gallery system for both the host and parasitoid. The lateral protuberances of the third-instar larva of *Steffanolampus* are similar to those reported and illustrated in *Perilampus* (e.g., *P. tristis*, Bergold and Ripper 1937; *P. chrysopae*, Clancy 1946; *P. hyalinus*, Tripp 1962).

There seems to be very little potential of *S. salicetum* as a biological control agent for *P. ruficornis* and other destructive anobiid beetles. Xylophagous anobiids not only attack dead and dying trees but are also serious pests of wood products (Craighead 1950), such as sawlogs and cordwood, flooring, woodwork, structural timbers and furniture (Acciavatti 1972). The low levels of parasitism found in even large aggregations of anobiid hosts suggests that other biological control agents would be more effective. Parasitoids are not overly effective in controlling infestations of most xylophagous beetles that feed in heartwood (cf. cambium feeders like bark beetles). A recent case in point is the newly introduced Asian longhorned beetle for which fungal pathogens are thought to offer the best biological control possibilities (Richard Hoebeke, pers. comm.). *Steffanolampus salicetum* does, however, exhibit interesting behaviours and a complex life cycle that is closely coordinated with that of its hosts and are therefore worthy of study in their own right.

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