



Full Length Article

Ultramorphology of the Ovipositor of *Venturia canescens* (Gravenhorst) and Possible Mechanisms for Oviposition

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ABSTRACT

Morphology, ultrastructure and possible mechanics of the ovipositor of *Venturia canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae) is described using scanning and transmission electron microscopy. The ovipositor of *V. canescens* consisted of three pairs of valvulae. First pair or dorsal valvulae and the second pair or ventral valvulae constituted the ovipositor shaft and the third pair formed the ovipositor sheaths. The ventral valvulae possessed five conical ridges or barbs at the distal end. The diameter of the ovipositor shaft decreased from proximal to distal end of the ovipositor shaft terminating in a very sharp tip. The dorsal valvulae possessed a blunt tip and a pre-apical notch on the dorsal surface. The dorsal and ventral valvulae collectively formed the egg canal with the help of two functional units called olistheters for the transport of eggs. A robust longitudinal ridge on ventral tip of dorsal valvulae that tapered on both ends is called sperone. The ovipositor sheaths covered the ovipositor shaft completely when at rest. Groups of ctenidia covered the internal surface of the sheaths throughout its length. The surfaces of all the valvulae were covered with sense organs. The knowledge of these structures helps understand their functions in host location, discrimination and oviposition behavior. © 2012 Friends Science Publishers

Key Words: *Venturia canescens*; Ovipositor mechanics; SEM; TEM; Oviposition; Olistheter

INTRODUCTION

The Hymenoptera use the ovipositor for laying eggs in their preferred places *e.g.* the soil (Pair, 1995; Carpenter & Bloem, 2003), plant tissues (Deyrup, 1975) or insect bodies (Sait *et al.*, 1995). The hymenopteran ovipositor basically comprised two pairs of valvifers, three pairs of valvulae originating from 8th and 9th segments (LeRalec & Wajnberg, 1990). The first valvifers (gonocoxites VIII) are continuous with the rami of the first valvulae (gonapophyses VIII) or ventral stylets. The second valvifers (gonocoxites IX) extend as the third valvulae (gonostyli) or ovipositor sheath and ventrally bear the fused second valvulae (gonapophyses IX) or dorsal stylets (Fig. 1). The egg canal is formed inside the shaft of the ovipositor which intern, is formed of interconnected 1st (ventral) and 2nd valvulae (dorsal stylets). The hymenopteran parasitoid ovipositor is used to probe and drill the host for selection or rejection by perceiving stimuli from the host hemolymph and to transfer eggs from the body of the parasitoid to that of the host (Van Lenteren, 1981; Quicke *et al.*, 1995). The parasitic hymenoptera attack a wide variety of hosts mostly belonging to the immature stages of orders with complete metamorphosis. The hymenopteran ovipositor has evolved different structural and physiological characteristics to cope with the diverse circumstances which it is subjected to in nature. The diversity in ovipositor structure is being utilized in

taxonomic and systematic works by many entomologists to establish phylogeny in various groups. (Field & Austin, 1994; Quicke & Fitton, 1995; Quicke *et al.*, 1995; LeRalec *et al.*, 1996; Austin & Field, 1997).

Venturia canescens is a solitary, koinobiont, thelytokous, endoparasitoid of lepidopterous larvae (Eliopoulos *et al.*, 2003; 2005; Eliopoulos & Stathas, 2005). The potential of *V. canescens* as insect control agent against stored grain pests *e.g.* *Ephestia kuehniella* Zeller (Elliot *et al.*, 1983; Harvey & Vet, 1997), *Cadra cautella* (Press *et al.*, 1977, 1982), *E. elutella* (Scholler, 2000), *Plodia interpunctella* (Harvey & Thompson, 1995; Harvey *et al.*, 2001; Heinlein *et al.*, 2002) and *Corcyra cephalonica* (Harvey & Thompson, 1995; Harvey *et al.*, 1996) is enormous. It is known that *V. canescens* is also capable of host discrimination (Rogers, 1972; Ganesalingam, 1974; Waage, 1979; Mudd & Corbet, 1982; Harrison *et al.*, 1985; Hubbard *et al.*, 1987).

The structure of the ovipositor of *V. canescens* has been discussed (Deither, 1947; Ganesalingam, 1972; Rogers, 1972; Fergusson, 1988; Gauld & Bolton, 1988) but none of these authors utilized SEM and TEM to find the finer details of the morphology and ultrastructure of the ovipositor. The present study was designed to describe the morphology and ultrastructure of the ovipositor and possible oviposition mechanics of a potential biological control agent, *V. canescens*.

MATERIALS AND METHODS

Parasitoid rearing: The parasitoid wasp, *V. canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae), was reared on the Indian meal moth, *Plodia interpunctella* Hubner (Lepidoptera: Pyralidae), in 4-L sterilized jars kept in a constant temperature room maintained at $26.8^{\circ}\text{C} \pm 2$, $65\% \pm 3$ relative humidity, and a 16:8 light–dark photoperiod. The wasps were fed with a 50% honey solution.

Scanning electron microscopy: Freshly enclosed parasitoids were anaesthetized with CO_2 after which the ovipositor stylets and sheaths were excised, dehydrated in a graded ethyl alcohol series, and mounted on aluminum stubs using double-sided sticky tape. The specimens were shadow-coated in a sputter coater (Polaron SEM Coating Unit E 5100 Series II'Cool' Sputter Coater) with a thin film of gold-palladium alloy for 5 min and viewed using a scanning electron microscope (JEOL JSM-35) at an accelerating voltage of 15 kV. Structures present on the specimens were photographed.

Transmission electron microscopy (TEM): Parasitoids were anaesthetized with CO_2 and placed in 2.5% glutaraldehyde in 0.1 M cacodylate buffer (pH = 7.2), following which the ovipositor stylets were cut while still under the solution and fixed in 25% glutaraldehyde and 10% acrolein in 0.1 M cacodylate buffer (pH = 7.2) overnight. Then the specimens were rinsed two times in the same buffer and postfixed in 1% OsO_4 in 0.1 M cacodylate buffer (pH = 7.2) for 90 min, embedded in 2% agar, dehydrated in ethanol, treated with propylene oxide, and infiltrated for 3 days with mixtures of variable composition (1:1, 3:1 & full) of Spurr's resin and propylene oxide. Specimens were then transferred to embedding molds with Spurr's resin and polymerized in an oven set at 60°C for 24 h. Ultra-thin sections were cut with a ultramicrotome (Reichert, OMU-3) using a diamond knife and mounted on 50-mesh pioloform-coated grids. Sections were stained with uranyl acetate and Reynolds lead citrate, examined and photographed using a transmission electron microscope (JEOL-1200 EX) at an accelerating voltage of 80 kV.

RESULTS

The ovipositor (Fig. 2) of *V. canescens* consisted of three pairs of valvulae or gonapophyses. Out of these three pairs of valvulae or gonapophyses, 1st pair or dorsal valvulae and 2nd pair or ventral valvulae constitute the ovipositor shaft (Fig. 3) and the third pair forms the ovipositor sheath (Fig. 4). The 1st and 2nd valvulae or gonapophyses are also called stylets. The average length of the ovipositor shaft (Fig. 2) was 3 mm long. It was a stiff structure that tappers towards the distal end. As a unit, the ovipositor shaft contained an egg canal through which egg was transported (Figs. 5 & 7). The 1st or ventral valvulae or gonapophyses

originated from first valvifer of the 8th segment and remained isolated from each other almost all of their length and are also called ventral stylets (Figs. 1 & 5). These valvulae or gonapophyses possessed five conical ridges or barbs at the distal end (Figs. 3 & 5). The diagonal length of these conical ridges or barbs from proximal to distal were 25.3 μm , 18.7 μm , 9.3 μm , 6 μm and 5.3 μm . These conical ridges or barbs became smaller and smaller towards the distal end; the first being largest and the fifth being smallest. The diameter of the ventral valvulae decreased from proximal to distal end of the ovipositor shaft terminating in a very sharp tip. The 2nd or dorsal valvulae or gonapophyses or stylets originated from the anterior end of the second valvifer located on the 9th segment and were joined together throughout their length (Figs. 1, 3 & 5). These possess a blunt tip, a pre-apical notch (Fig. 3) on the dorsal surface and their diameter gradually decreases towards distal end. The notch was approximately 153 μm from the distal tip, 24 μm wide from the widest point and about 17 μm deep from the deepest point. The increase in diameter from distal to proximal end was very sharp in case of ventral valvulae as compared to that of the dorsal valvulae where it was very gradual. The surface of the notch was smooth except at two circular sites at the opposite sides of the notch at the lowest point and a ridge in the center of the notch (Fig. 6). Sense organs were scattered on the surface of the notch especially in the two circular patches which possessed a large number of different kinds of sense organs. The dorsal and ventral valvulae or gonapophyses collectively form the egg canal with the help of two functional units called olisthetes and two thin longitudinal septa, one from each of the ventral valvulae or gonapophyses for the transport of eggs (Fig. 7). The olistheter consists of a tongue-like longitudinal structure called rachis on the ventral wall of the dorsal valvulae and is situated at right angle to its surface that fits into a longitudinal groove present on the dorsal wall of the ventral valvulae called aulax. This tongue (rachis) and groove (aulax) like arrangement extends throughout the length of the ovipositor shaft of *V. canescens*. The wall of the egg canal is formed by the dorsal valvulae on the dorsal side and by the ventral valvulae on the lateral and ventral side. A seal is formed on the mid-ventral wall of the egg canal by cuticular longitudinal septa, one from each of the ventral valvulae. A robust longitudinal ridge is present at the mid-ventral surface of the dorsal stylets near its tip which is called sperone (Fig. 3 & 7). The sperone starts just behind the apex of the dorsal stylets, very prominent and tapering on both sides in area of five barbs or serrations and terminate behind the pre-apical notch inside the egg canal. The dorsal stylets, the ventral stylets and the sperone were found to possess their own lumens (Fig. 7). The lumens of the dorsal and ventral stylets contained different types of tissues which could not be seen in the lumen of the sperone. The ovipositor sheaths or third pair of valvulae consisted of one segment and were thick, strong and divided into bands or annulations on the outer surface up to half of the length of

Fig. 1: Schematic diagram of the ovipositor of *Venturia canescens* [After, Imms *et al.* (1977)]

P = pygostyle, VF1 and VF2 = Valvifers 1 and 2 respectively, 1VV, 2VV and 3VV = Valvulae 1, 2 and 3 respectively, T9 and T10 = Terga 9 and 10 respectively

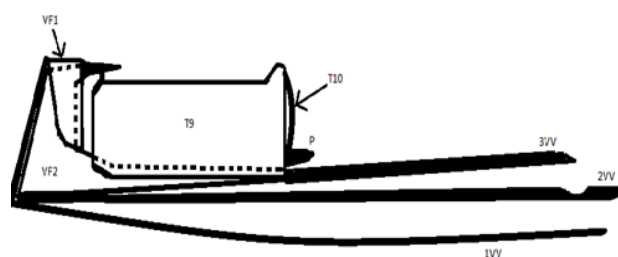


Fig. 2: SEM micrograph of the ovipositor of *Venturia canescens*

Scale bar = 1 mm

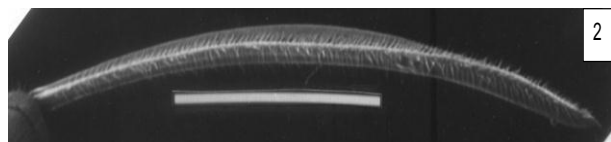


Fig. 3: SEM micrograph of the tip of the ovipositor shaft of *Venturia canescens*.

B = barb, D = Dorsal/2nd valvula or stylet, N = Notch, S = sperone, V = Ventral/1st valvula or stylet. Scale bar = 10 µm

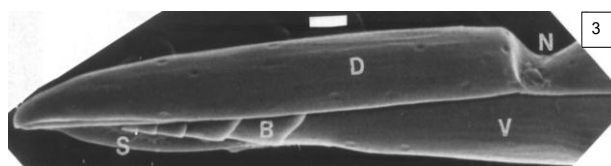
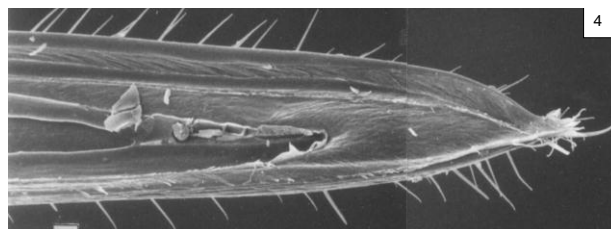


Fig. 4: SEM micrograph of the tip of the ovipositor sheath of *Venturia canescens*

Scale bar = 10 µm



the ovipositor (Figs. 8 & 9). The annulations were very strong at the proximal end (Fig. 8) of the ovipositor and less pronounced in the middle portion and absent at the tip (Fig. 10) of the third valvulae. The sheaths originated from the posterior end of the second valvifer located on the 9th segment (Fig. 1). The two longitudinal parts of the sheath were free throughout their length except at the very tip where they were fused (Fig. 4). These sheaths covers the ovipositor shaft (dorsal & ventral valvulae) completely when at rest (Fig. 2). Groups of ctenidia cover the internal

Fig. 5: SEM micrograph of the dorsal and ventral stylet unit forming the egg canal in *Venturia canescens*

B = barb, D = dorsal stylet, EC = egg canal, R = rachis and V = ventral stylet. Scale bar = 100 µm

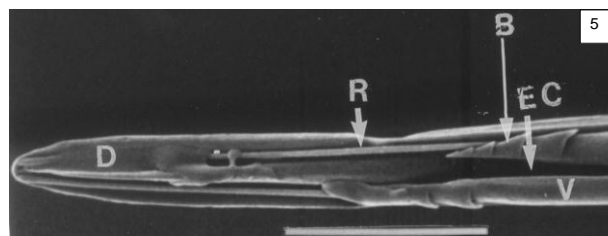
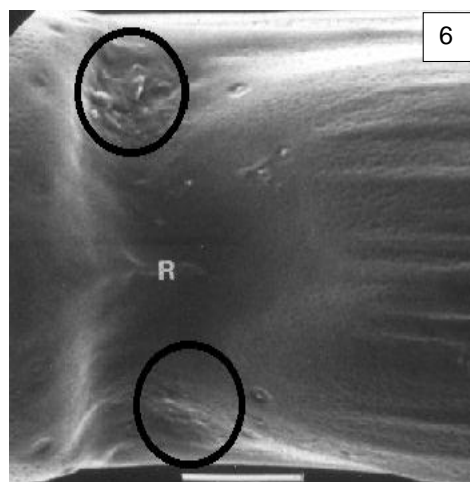


Fig. 6: SEM micrograph showing sense organs in the two circular areas and ridge (R) in the notch of dorsal stylets

Scale bar = 10 µm



surface of the sheaths throughout its length (Figs. 8 & 9). The density of groups of 2-9 ctenidia increases from proximal to distal end of the ovipositor sheaths. Tufts of cuticular microtrichia or spines cover the entire internal surface of the sheaths near the apex (Fig. 10). The outer surface of the sheaths was covered with sense organs throughout its length (Fig. 2). The number and kinds of these sense organs increases from proximal to distal end of the ovipositor sheaths. A tuft of different sense organs was present at the very tip of the ovipositor sheaths (Fig. 4).

DISCUSSION

The cocking behavior is displayed by *V. canescens* before and after egg-laying in which the ovipositor is moved above the abdomen in a specific way and then return to its horizontal resting position (Mudd & Corbet, 1982; Harrison *et al.*, 1985). An egg is passed into a spindle shaped cavity present at the tip of the long ovipositor of *V. canescens* by a cocking or flexing movement of the abdomen after oviposition (Rogers, 1972). During the process of stabbing the ovipositor is unsheathed (Ozkan & Gurkan, 2001) and

Fig. 7: TEM micrograph of the ovipositor shaft showing ventral and dorsal stylets forming olistheter arrangement and egg canal

A = aulax, EC = egg canal, LD = lumen of the dorsal stylet, LV = lumen of the ventral stylet, R = rachis, S = sperone, and SP = septum. Scale bar = 2 μ m

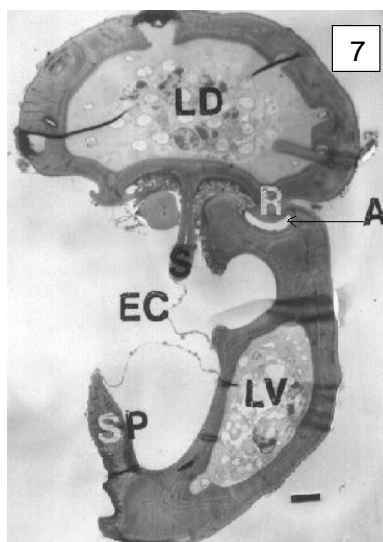
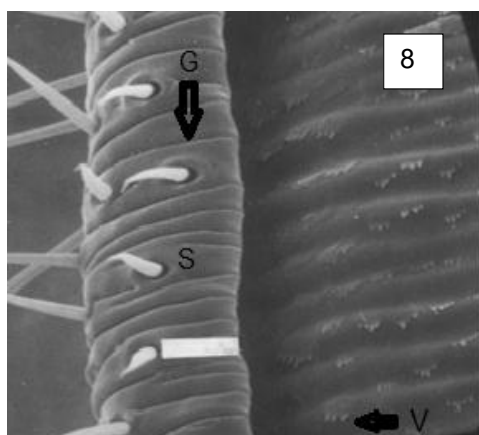


Fig. 8: SEM micrograph of a portion of the sheath from the proximal end showing well pronounced stripes or bands on the outer surface and groups of villi or ctenidia on the inner surface

G = groove, S = stripes and V = villi. Scale bar = 10 μ m



both the ventral and dorsal stylets or valvulae come in contact with the body wall of the host at the same time to avoid any chance of fracturing the independently contacting stylets (Boring, 2010). At this point, a single egg is present in elongated cavity close to the tip of the ovipositor (Rogers, 1972; Boring, 2010).

Five barbs or serrations are present on the tips of ventral stylets of the ovipositor of *V. canescens*. Much variation was observed in the number, position of occurrence and function of these barbs in hymenopteran groups (Van Achterberg & Quicke, 1991). *Orgilus lepedus*

Fig. 9: SEM micrograph of a portion of the sheath from the middle showing well pronounced bands on the outer surface and groups of ctenidia on the inner surface

G = groove, S = stripes and V = villi. Scale bar = 10 μ m

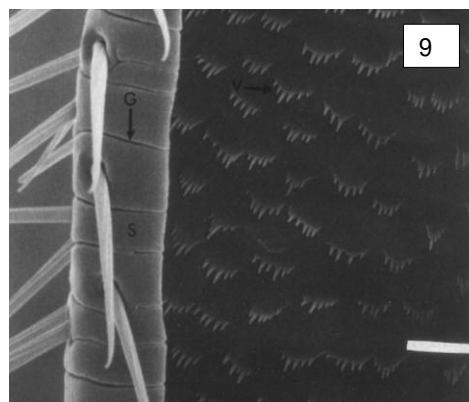
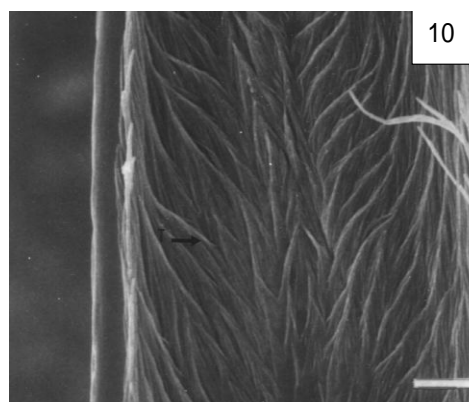


Fig. 10: SEM micrograph of a portion of the sheath from the distal end showing well pronounced microtrichia on the inner surface and groups of microtrichia

T = microtrichia Scale bar = 10 μ m



(Hawke *et al.*, 1973), *Biosteres (Opus) longicaudatus* (Greany *et al.*, 1977), *Trybliographa rapae* (Brown & Anderson, 1998), *Trichogramma galloi* and *T. pretiosum* (Consoli *et al.*, 1999) and *Homolobus truncator*, (Boring, 2010) use them for piercing the host integument and supporting the ovipositor during oviposition. Then, the barbed ventral stylets pierce the host integument by alternating insertions making a hole which is wide enough for the penetration of blunt dorsal stylet (Skinner & Thompson, 1960). After that the ventral stylets move backwards until the barbs become attached to the host integument and then the thick dorsal stylets find the space to move into the host body up to the point of dorsal notch (Boring, 2010). Then the ventral stylets move forward again as the dorsal stylets do not occupy much of the space of the wound made by the ventral stylets. At this point the ventral and dorsal stylets make a tight contact with the host

integument and the ovipositor is locked temporarily into the host body for egg laying. Pre-apical notch not only provides for momentary locking mechanism (Belshaw *et al.*, 2003; Boring, 2010) but also determine the depth of penetration of the ovipositor into the host (Van Veen, 1982). The surface of the pre-apical notch was smooth other than a longitudinal ridge in the center and two circular rough areas (due to the presence of sense organs) at the sides of the pre-apical notch at the deepest point. It is suggested that these two areas and the longitudinal ridge helped in the tightening of the locking mechanism for oviposition by providing an abrasive surface. The sense organs, most probably the campaniform sense organs present at the surface of the pre-apical notch including the two circular rough areas helped the parasitoid wasp in sensing the position of dorsal and ventral stylets or valvulae during the process of locking mechanism.

Apically directed finger-like projections or ctenidia present on the surface of the dorsal stylets helped to hold the egg in position (Rogers, 1972) as well as to stop the backward movement of the egg during oviposition process (Boring, 2010). Ctenidia also provides lubrication for the moving stylets by sustaining required amount of liquid and thus reduced friction between stylets of the ovipositor during oviposition (Bender, 1943; Robertson, 1968; Shah, 2012). After the ovipositor is inserted in the tissues of the host, the egg is moved forward by alternating rhythmic movements of the ventral stylets or valvulae (Rogers, 1972; Austin & Browning, 1981; Cole, 1981; Dweck *et al.*, 2008; Boring, 2010).

The ctenidia in combination with ventral stylets or valvulae, assist in moving the egg in the basal section of the ovipositor shaft while the valvilli help in moving the egg in the terminal part of it using hydrostatic pressure for a speedy delivery of the egg into the host. A speedy delivery of the egg is required to avoid any reaction from the host e.g. escape of the host or injury to the parasitoid (Boring, 2010). This is in agreement with Rogers (1972) that *V. canescens* takes fraction of a second to lay an egg. In aculeate Hymenoptera, the venom is transferred into the host with the help of valvilli (Quicke *et al.*, 1992; Marle & Piek, 1986). In case of *V. canescens* the valvilli help in keeping the egg near the tip of the ovipositor (Rogers, 1972). Boring (2010) reached to the same conclusion in case of *Homolobus truncator* Say (Hymenoptera: Braconidae). However, in case of *Itopectus maculator*, Cole (1981) suggested that the egg travels along the entire length of the ovipositor after its insertion into the host integument.

It is suggested that the sperone present on the mid-ventral surface of the dorsal stylets leads the egg out of the egg canal. It originated just before the pre-apical notch in the egg canal and kept on increasing its height towards the distal end of the ovipositor shaft, reached maximum height in the area of barbs of the ventral stylets and ends near the apices of the dorsal stylets where its height is decreased to zero. When the ovipositor is locked into the host, the ventral stylets move forward and backward in unison and egg is

moved forwards. The surface of the egg is continuously raised as it moves over the sperone. At last when both of the lateral stylets move backward and the egg reached the maximum height of the sperone, it comes out of the egg canal and into the host tissues very quickly under the force of hydrostatic pressure of the valvilli of the ventral stylets (Boring, 2010). The egg is greatly deformed in the egg canal and becomes very elongated because the diameter of the ovipositor shaft is very small. The pressure faced by the egg in the lumen of the egg canal also forces the egg to be squeezed out of the egg canal. The ejection of egg from the lumen of the egg canal creates a vacuum which draws the 2nd egg in the longitudinal cavity near the tip of the ovipositor shaft by a cocking movement by the wasp. The sperone had also been described by other entomologists in other Hymenoptera (Rahman *et al.*, 1998; Boring, 2010). After successful oviposition, the ventral valves are withdrawn to the level of pre-apical notch and the locking mechanism is released and the ovipositor can be withdrawn very easily (Boring, 2010).

The ovipositor shaft is kept covered all the times during rest by a third pair of valvulae or ovipositor sheaths. Annulations were observed on the sheaths which increase the elasticity of the ovipositor sheaths during cocking and stay away from the passageway of the penetrating portion of the ovipositor shaft (Dweck *et al.*, 2008). Annulations were more pronounced in proximal portion of the sheath and reduce in intensity towards the distal end of the ovipositor as the proximal portion needs more elasticity for the bending ovipositor (Dweck *et al.*, 2008). The annulations were also observed in other hymenopteran parasitoids (Dweck *et al.*, 2008). As the ovipositor shaft begins to penetrate the host integument, the third valvulae slide basally along the former, forming gradually expanding loops where they are separated from the ovipositor shaft. The microtrichia are concentrated on the inner surface of the ovipositor sheaths near their tips. These microtrichia are probably used to clean the sense organs present on the ovipositor stylets between insertions of the ovipositor into the host. These sense organs must be kept uncontaminated for proper functioning of the ovipositor in selection and discrimination of the host for oviposition. The presence of sense organs on the tip of the ovipositor stylets corresponds to the high density of microtrichia on the inner surface of the sheaths at the tip. Similar type of microtrichia supposed to perform the same function, were found on the 3rd valvulae of the ovipositor of other parasitoids (LeRalec *et al.*, 1996; Nenon *et al.*, 1997).

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