Morphology and distribution of antennal multiporous gustatory sensilla related to host recognition in some *Trichogramma* spp.

Sara Ruschioni¹, Roberto Romani², Paola Riolo¹, Nunzio Isidoro¹

¹Dipartimento di Scienze Agrarie, Alimentari ed Ambientali, Università Politecnica delle Marche, Ancona, Italy

Abstract

Trichogramma spp. (Hymenoptera Trichogrammatidae) are endoparasitic wasps that attack the eggs of mainly Lepidoptera species. The morphology of the antennal multiporous gustatory sensilla of five Trichogramma species is studied and compared: Trichogramma cacoeciae Marchal, Trichogramma chilonis Ishii, Trichogramma dendrolimi Matsumura, Trichogramma turkestanica Meyer, and Trichogramma sibericum Sorokina. Scanning electron microscopy of the female antennae shows the presence of numerous peculiar sensilla on the ventral apical side of the club, for which a gustatory function is hypothesized. These appear as multiporous sensilla, although the pores are not distributed all over the surface of the hair, as they are only on the ventral margin. Also, these sensilla are located exclusively on antennal areas that come into contact with the substrate. Variations in the numbers and distributions of the multiporous gustatory sensilla were found between the species examined, as well as within individuals belonging to the same species. Functional aspects and variations in the distributions of these sensilla are discussed.

Key words: multiporous gustatory sensilla, ultrastructure, Trichogramma, Hymenoptera, egg parasitoid.

Introduction

Trichogramma spp. (Hymenoptera Calcidoidea Trichogrammatidae) are minute endophagous egg parasitoids that are used worldwide for the control of several lepidopteran pest species (Nagarkatti and Nagaraja, 1977; Stinner, 1977; Hassan, 1993; Pinto and Stouthamer, 1994). Evidence has accumulated that they have considerable interspecific and intraspecific variations in host preference (Kot and Plewka, 1974; Stchepetinlnikova, 1974; van Dijken et al., 1986; Pak, 1988; Hassan, 1989). Endoparasitoids of the genus Trichogramma are one of the most important natural enemies used for biological control around the world (Hoffman and Frodsham, 1993), as they are used more than any other entomophagous species for the biological control of insect pests (Stinner, 1977; King et al., 1985; van Lenteren, 2000).

The process of parasitisation by these parasitic wasps comprises a series of interconnected stages: host habitat location, host location, host recognition, and host acceptance (Vinson, 1976; 1984; 1985). Host recognition and acceptance are mainly driven by physical and chemical cues, which are mostly detected by the sensilla on the antennae and the ovipositor; these assess the suitability of a host by examining the surface and internal contents of the host (Schmidt, 1994). After contact with the host egg, the females of Trichogramma show intensive antennation of the host surface, followed by drilling of the chorion before its acceptance (Salt, 1935; Klomp and Teerink, 1962). Antennation is also important for measuring the curvature of the host, which is used by the parasitoid as an estimate of the host size. Trichogramma will use this information to decide on the clutch size and the sex ratio to be allocated to a particular host (Schmidt and Smith, 1985; 1987). The females examine the host by drumming the host surface with the apicoventral part of the club, which bears sickle-like antennal sensilla (Amornsak *et al.*, 1998).

Many different terms exist for these sensilla and synonymy among the terms can cause confusion (Isidoro et al., 1996). Some authors refer to them as "falcate" sensilla, on the basis of their external appearance when observed under scanning electron microscope (SEM) (Zacharuk, 1985; Amornsak et al., 1998; Consoli et al., 1999). Voegelé et al. (1975) used the term "sole chercheuse" to identify the functional area where these sensilla are grouped, and Olson and Andow (1993) called them "multiporous pitted sensilla trichoid C". They have also been named as "multiporous gustatory sensilla" on the basis of their morpho-functional features (Isidoro et al., 1996). Furthermore, Isidoro et al. (1996) describe the ventral surface of the antennae as the "touch and taste area", where the multiporous gustatory sensilla (MGS) are located. In the present study, we use this last terminology, as the MGS and the touch and taste area (TTA). These appear to be the most appropriate terms, as they are based both on morphological (SEM) and functional features.

Due to the lack of detailed data on the ultrastructure of these peculiar sensilla, the aim of this study was to carry out a detailed morphological investigation using both SEM and transmission electron microscopy (TEM). We compared five different *Trichogramma* species: *T. cacoeciae* Marchal, *T. chilonis* Ishii, *T. dendrolimi* Matsumura, *T. turkestanica* Meyer, and *T. sibericum* Sorokina. The aim was to assess:

- differences in the numbers and distributions of the MGS on the ventral area of the antennae;
- external modifications of the MGS;
- differences in the internal organization of the sensilla (i.e. number of sensory neurons).

²Dipartimento di Scienze Agrarie e Ambientali, Università di Perugia, Perugia, Italy

Materials and methods

The five *Trichogramma* species, *T. cacoeciae*, *T. chilonis*, *T. dendrolimi*, *T. turkestanica* and *T. sibericum*, were provided by Horticulture Research and Development Centre of Agriculture and Agri-Food Canada. Laboratory cultures were reared on eggs of *Ephestia kuehniella* Zeller (Lepidoptera Pyralidae), which have a volume of 0.28 mm³ (Bai *et al.*, 1992), and in which usually only one parasitoid will develop. The rearing was carried out in a climatic cabinet, at 23 ± 2 °C, 50% relative humidity (range, 30-60%), and a light:dark cycle of 16:8 h.

For SEM observations, 20 females of each of the five *Trichogramma* spp. were immersed in 60% ethanol solution, in water. After dehydration through a graded ethanol series, the heads with the antennae were dried, gold coated in a Balzer Union SCD 040 unit, and examined under SEM (Philips XL 30).

For TEM observations, 10 females of each of the five Trichogramma spp. were anesthetized with CO₂ and immersed in 2.5% glutaraldehyde, in 0.1 M cacodylate buffer, 5% sucrose, pH 7.2-7.3. Then the antennomeres were detached, to aid the fixative penetration, and left at 4 °C for 2 h. After rinsing overnight in cacodylate buffer, the specimens were post-fixed in 1% osmium tetroxide at 4 °C for 1 h, and then rinsed in the same buffer. Dehydration through a graded ethanol series was followed by embedding in Epon-Araldite, with propylene oxide as bridging solvent. Thin sections were taken with a diamond knife on an L.K.B. Nova ultramicrotome, and mounted on collodium-coated 50-mesh grids. Finally, the sections were examined under TEM (Philips EM 400T) after staining with uranyl acetate (20 min, room temperature) and lead citrate (5 min, room temperature).

Results

Trichogramma female antennae are geniculate at the scape-pedicel joint (figure 1a). The scape is the longest antennomere, at usually ca. 100 µm long, and followed by the pedicel (figure 1a). The flagellum is divided into the funicle, which is composed of several short antennomeres known as anelli, and a terminal large antennomere (ca. 75 μm long) known as the club (figure 1a). All of the segments have several sensory organs of different types, and the club is the antennomere that has the most sensilla (figures 1a, 1b). When observed laterally, the club appears triangular, with the largest side on the dorsal part, and the two smaller sides on the ventral part (figure 1a). It is possible to distinguish various sensilla with different morphologies and functions. On the distal part of the ventral side of the club, there is a peculiar arrangement of sensilla trichoidea that appear to be lined up regularly, to the tip of the club itself (figure 1b).

SEM observations show curved sensilla trichoidea laterally flattened, about 15 μ m long, starting from a socket showing a basal round depression of the cuticle (figure 2a). The sensillum appears slightly narrow at its base (figure 2a). On the lateral sides of the shaft, there are some grooves that run first longitudinally, then obliquely, through the peg shaft up to the tip (figure 2b).

The grooves merge along the outermost margin of the peg; i.e. the part that comes into contact with the substrate. At the point where the grooves merge, they form a crest that has several pores (figure 2b).

The average number of sensilla (\pm standard error) found on the TTA of each species varied (figures 2c, 2d, 2e, 2f, 2g), as follows: *T. cacoeciae* (n = 25), 23.96 \pm 0.15; *T. chilonis* (n = 14), 26.71 \pm 0.40; *T. dendrolimi* (n = 27), 19.33 \pm 0.46; *T. sibericum* (n = 26) 22.23 \pm 0.86; and *T. turkestanica* (n = 18) 24.50 \pm 1.02.

TEM investigation showed no differences in the organization of the internal cellular components among the different species investigated. Each sensillum is innervated by 10 sensory neurons (figures 3a, 3b, 3c). The bundle of 10 dendrites is surrounded by a common dendritic sheath. The outer dendritic segments are surrounded by accessory cells (figures 3b, 3c), which contain 9 microtubules each (figure 3c), and are arranged in a ring around the periphery of the dendrites. After entering the peg lumen, the outer dendritic segments branch at the level of the multiporous area (figure 3d). A sheath cell completely envelops all of the sensory cell bodies.

Discussion and conclusions

The overall antennal structure described in this study is essentially similar to that previously described for other *Trichogramma* species (Amornsak *et al.*, 1998; Olson and Andow, 1993; Voegelé *et al.*, 1975; Isidoro *et al.*, 1996; Consoli *et al.*, 1999).

The MGS are positioned in the areas that normally come into contact with the substrate to be tasted (Weseloh, 1972; Northon and Vinson, 1974; Bin *et al.*, 1988; Vinson *et al.*, 1988). These sensilla have to touch the actual surface to taste any active chemical compound(s). The presence of non-volatile contact chemicals that have roles in host recognition has been described for several parasitoid species (Vinson, 1985; 1991; Bin *et al.*, 1993).

The large number of sensilla on the antennal club of *T*. cacoeciae, T. chilonis, T. dendrolimi, T. turkestanica and T. sibericum increases the spatial density of the chemical reception, and might be useful for the detection of chemical markers on a host that has already been parasitized (Olson and Andow, 1993). We also looked for correlation between the area involved in touching the substrate (TTA) in each species and the number of sensilla (MGS) present in this area. For the number of MGS, the highest and the lowest values were found for T. chilonis and T. dendrolimi, respectively. Considering the size of the TTA involved in host antennation, the species that uses the whole TTA is T. chilonis, while T. cacoeciae antennates the host with just the tip. Therefore, it appears that there is no correlation between TTA size and MGS number.

Voegelé *et al.* (1975) suggested that the variation in the number of chemosensory hairs is both size and species specific, and might help to explain differences in the ability of different *Trichogramma* species in the handling of hosts that are highly clustered. Voegelé *et al.* (1975) also even suggested the possibility of using

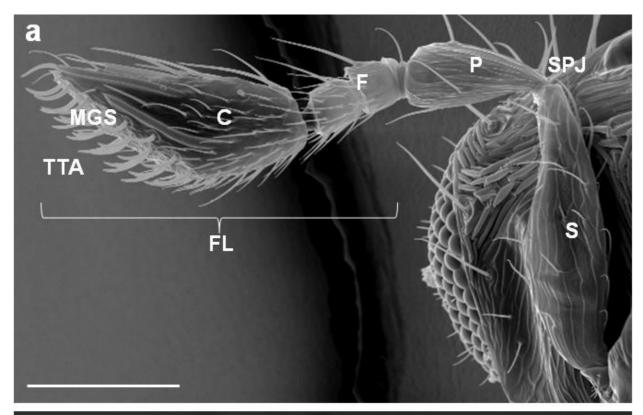




Figure 1. SEM micrographs showing the general structure of the female *T. cacoeciae* antennae. (a) Whole antenna. (b) Ventral view of the antennae. S, scape; P, pedicel, SPJ, scape-pedicel joint; F, funicle; FL, flagellum; C, clava; TTA, touch and taste area; MGS, multiporous gustatory sensilla. Scale bars: (a) 50 μm; (b) 20 μm.

the number of MGS to distinguish between *Trichogramma* species using females instead of males. As in the present study, the literature includes reports of different numbers of these sensilla among *Trichogramma* species. Voegelé *et al.* (1975) reported averages of 21.71, 27.77 and 20.23 sensilla in *Trichogramma brasiliensi* (Ashrnead), *Trichogramma evanescens* Westwood and *Trichogramma maltbyi* Nagaraja et Nagarkatti respectively. About 20 sensilla have been reported in *Trichogramma brassicae* Bezdenko (Isidoro *et al.*, 1996).

Armonsak et al. (1998) reported 35.5 sensilla in *Trichogramma australicum* Girault. However, even if the numbers of MGS in each of these studies appear to be statistically different, the Voegelé et al. (1975) statement is in contrast with the results here. Indeed, in some cases, we observed large differences in MGS numbers within the same species. This is the case for *T. sibericum*, where the MGS numbers ranged from 11 to 26, thus showing a variation of up to 15 sensilla, followed by *T. turkestanica*, with a variation of 14 sensilla. On this basis, the

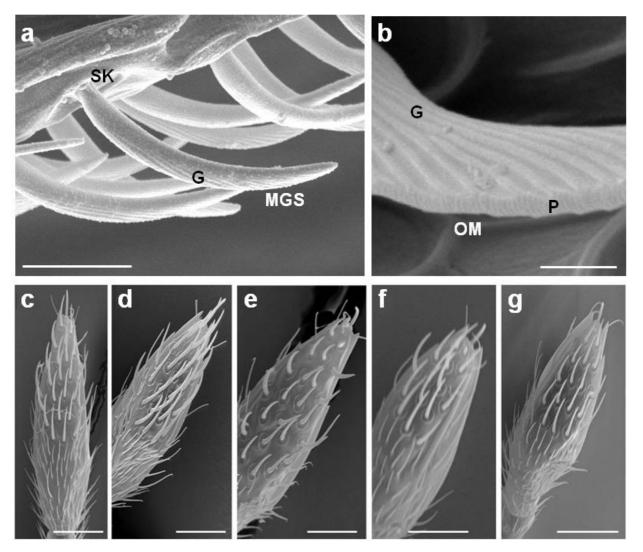


Figure 2. SEM micrographs showing the MGS of *Trichogramma* spp. (a) In *Trichogramma* spp., showing the socket (SK) in a round depression, and grooves (G) that run through the body of the peg, to the tip. (b) Detail showing the grooves (G) merging along the outer margin (OM) of the peg, where there are the pores (P). (c-g) Ventral sides of the clubs across the different *Trichogramma* species, showing the differences in the MGS numbers. (c) *T. cacoeciae*. (d) *T. chilonis*. (e) *T. sibericum*. (f) *T. dendrolimi*. (g) *T. turkestanica*. Scale bars: (a) 5 μm; (b) 1 μm; (c, d, e, f, g,) 20 μm.

use of the number of MGS as a taxonomic tool is not reliable enough to distinguish between species.

Isidoro *et al.* (2001) formulated the hypothesis of an inverse correlation between the number of neurons innervating a single MGS and the total number of the MGS of the same type on the surface of the antenna. Isidoro *et al.* (2001) compared platygastroids with other groups of parasitoids, and illustrated how the pattern seen for platygastroids, as few MGS with many neurons, is reversed in all of the other superfamilies of parasitoids. For example, the ventral side of the female apical antennomere in a trichogrammatid can have 20 MGS innervated by 10 neurons each, while in a diapriid, each of the last 6 antennomeres have ca. 60 to 80 MGS with 5 neurons each.

A hypothesis that was supported with data for the different superfamilies and for different species belonging to the same family was investigated. Thus, a detailed study of the structural organization of the MGS in the TTA was carried out. All of the TEM investigations showed 10 sensory neurons for each sensillum in all of these the *Trichogramma* species; therefore, there are no differences in the ultrastructural organization between these species that are inversely correlated with the external structures, such as the number of MGS. Therefore, our data do not support the hypothesis formulated by Isidoro *et al.* (2001) at the family level.

Antennal sensilla have been classified as aporous, uniporous and multiporous, depending on the presence, number and distribution of pores on the cuticular part of the sensilla (Altner and Prillinger, 1980; Zacharuck, 1985). Uniporous and multiporous antennal sensilla are involved in chemoreception. The putative functions of the sensilla can be deduced from the number of pores (Keil, 1999). Aporous sensilla are usually mechanoreceptors (Keil, 1999). Uniporous sensilla usually have a

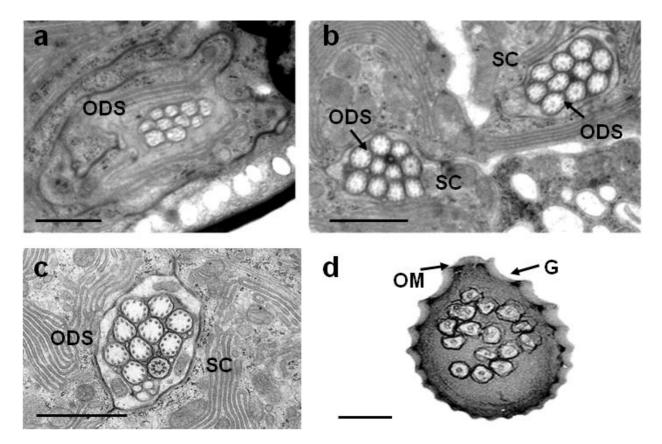


Figure 3. Ultrastructure of the MGS on the ventral and apical sides of the club in *T. dendrolimi*. (a, b, c) Crosssections of the dendrites innervating a single MGS at the level of the outer dendritic segment. (d) Cross-section of an MGS taken through its medial section. Dendritic branches can be seen within the lumen of the shaft. OM, outer margin; G, groove; ODS, outer dendritic segment; SC, sheath cell. Scale bars: 1 μm.

gustatory function (Barbarossa *et al.*, 1998), and multiporous sensilla most likely have an olfactory function (Keil, 1999; Steinbrecht, 1997). The MGS described in the present study appear as multiporous sensilla, although the pores are not distributed all over the surface of the hair, as they occur only on the ventral margin. Also, these sensilla are located exclusively on antennal areas that come into contact with the substrate. Therefore, Isidoro *et al.* (1996) considered these sensilla as having a gustatory function.

The literature indicates that gustatory sensilla are often both mechanoreceptors and contact chemoreceptors. McIver (1975) supported this hypothesis by suggesting increasing flexibility, due to the constriction at the base of the sensilla that might help in the sensitivity of the mechanoreceptor neurons. In *Trichogramma*, ultrastructural investigations have never shown the presence of a tubular body, a key feature of mechanoreceptors. This means that the MGS do not function as mechanoreceptors, but are only taste receptors.

Acknowledgements

We thank the three anonymous reviewers who helped us to greatly improve our manuscript. The SEM and TEM data were obtained at the University Electron Microscopy Centre (CUME, Perugia University, Italy).

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Authors' addresses: Sara RUSCHIONI (corresponding author, e-mail: sara.ruschioni@hotmail.it), Paola RIOLO, Nunzio ISIDORO, Dipartimento di Scienze Agrarie, Alimentari ed Ambientali, Facoltà di Agraria, Università Politecnica delle Marche, via Brecce Bianche, 60131 Ancona, Italy; Roberto ROMANI, Dipartimento di Scienze Agrarie e Ambientali, Facoltà di Agraria, Università di Perugia, Borgo XX Giugno 74, 06121 Perugia, Italy.

Received December 13, 2011. Accepted May 31, 2012.