Morphology and Distribution of Antennal Sensilla of Gryon gallardoi (Brèthes) (Hymenoptera: Scelionidae) Females

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RESUMO - Usando a microscopia eletrônica de varredura, foram descritas e ilustradas a morfologia externa e a distribuição das sensilas antenais da fêmea de Gryon gallardoi (Bréthes), um importante parasitóide de ovos de coreídeos. As antenas são genículo-clavadas, dotadas de 12 antenômeros. Ao longo do flagelo, foram registradas glândulas dorsais e sete tipos de sensilas: papilárias, caúnicas, de dois tamanhos - uma mais alongada e outra mais curta, estilocônicas, cavilhas, falciformes e tricóides, com variação numérica e espacial entre os flagelômeros. Aspectos referentes à função das sensilas, em associação ao comportamento de tamborilamento antenal de G. gallardoi são discutidos. Assim, a descrição e a determinação do padrão de distribuição das sensilas antenais de G. gallardoi, no presente estudo, é um avanço no sentido de elucidar os mecanismos envolvidos nos comportamento de seleção de hospedeiros dessa espécie.

PALAVRAS-CHAVE: Ultraestrutura, seleção de hospedeiros, parasitóide de ovos

ABSTRACT - With the aid of scanning electron microscopy, the external morphology and distribution of the antennal sensilla were described for females of Gryon gallardoi (Bréthes), an egg-parasitoid of coreids. The geniculated and clavated antennae are composed of 12 antennomeres. Along the flagellum we registered dorsal glands and seven types of sensilla: papillary, chaetica of two sizes – long and short types, styloconic grooved-peg, sickle-shaped and trichodea with numerical and spatial variation among the flagellomereres. Functional aspects of the sensilla are discussed in the context of G. gallardoi antennal drumming behavior. Thus, the determination and the description pattern of antennal sensilla in G. gallardoi, in the present study, is an advance regarding the elucidation of the mechanisms involved in the host selection behavior of this species.

KEY WORDS: Ultrastructure, host selection, egg parasitoid

Gryon gallardoi (Brèthes) is solitary egg parasitoid, associated to the tobacco-grayish-bug, Spaltocera dentiventris (Berg) (Hemiptera: Coreidae) in Rio Grande do Sul State (Santos et al. 2001) and to Leptoglossus zotanus (Dallas) (Hemiptera: Coreidae) in São Paulo State, Brazil (Souza & Amaral-Filho 1999, Solis et al. 2001). During oviposition, G. gallardoi females continuously touch the surface of the host egg with their antenna, a behavior known as drumming. Such behavior seems to be determinant in the choice processes for this parasitoid, being also registered for other species of Scelionidae (Weber et al. 1996, Field & Keller 1999, Dasilao & Arakawa 2004). In many species of egg parasitoids, the mechanisms involved in the drumming behavior are not yet clear. Nevertheless, some important features can be inferred by means of descriptive studies of the antennal sensilla. These structures can exhibit different sensorial roles as touch (mechanosensilla), smell and taste (chemosensilla) (Schneider 1964, Zacharuck 1985), either isolated or grouped. Because the antennal sensilla bear specialized receptors, they perceive stimuli and can determine female behavior, mainly in the processes involving host selection such as habitat location, recognition, discrimination, and acceptance (Isidoro et al. 1996, Vinson 1998, Isidoro et al. 2001).

Especially in Hymenoptera, the antennal sensilla present conspicuous morphological differences, besides showing diverse patterns of distribution. Thus, they might be utilized in taxonomic studies at the species level (Norton & Vinson 1974, Villa & Mineo 1990a), and even to establish phylogenetic relationships among species (Basibuyuk & Quicke 1998).

Based upon such morphological variations, the sensilla can be classified in general as multiporous, uniporous and
aporous (Zacharuck 1985). Those bearing pores are usually associated to chemoreception (smell and taste). In this case, the pores could be numerous and distributed all over their wall (multiporous sensilla) or restricted to their tip (uniporous sensilla) (Zacharuck 1985). In some cases, especially in Scelionidae, the porous sensilla can be associated to exocrine glands, known as accessory glands (Isidoro et al. 1996, Isidoro et al. 2001). The aporous sensilla are associated to mechanoreception roles as touch, thermo, and hygroreception (McIver 1985).

Considering the paucity of information about the antennal sensilla of grionineous as a whole, the present study aimed to describe the external morphology and the distribution of those structures in *G. gallardoi* females, with the aid of scanning electron microscopy. This knowledge provides the morphological basis for the understanding of the process of recognition, discrimination and host acceptance involved in the drumming behavior, already investigated for this species in laboratory conditions (Rocha 2005).

**Material and Methods**

_Gryon gallardoi_ females were obtained from a mass rearing on _S. dentiventris_ eggs kept under controlled abiotic conditions (25 ± 1°C, and 12h photophase) at the Laboratório de Biologia, Ecologia e Controle Biológico de Insetos of the Faculdade de Agronomia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil. Only newly emerged individuals were used; they were fixed and preserved in Dietrich solution (600 ml of alcohol 96°, 300 ml of distilled water, 100 ml of formaldehyde 40% and 20 ml of acetic acid). For scanning electron microscopy (SEM), whole specimens were critical point dried (BALZERS®, model CPD030), mounted with double-side tape on aluminum stubs, sputter-coated with gold particles (BALZERS®, model SCD050), observed and photographed in a scanning electron microscope (JEOL®, model JSM 58000), at the Centro de Microscopia Eletrônica of UFRGS. The employed terminology was adapted from Villa & Mineo (1990a, b).

**Results**

The antenna of *G. gallardoi* females is geniculated, bearing 12 antennomeres (A): scape (A1), pedicel (A2) and (Fig. 1A-D; Table 1). The papillary sensilla were found only on the distal antennomeres or club (A8-A12), along the median region of the ventral surface, being one in A12 and two from A11 to A10. The other sensilla: papillary (pl), chaetica of two sizes-long (ch1) and short (ch2), styloconic (st), grooved pegs (gp), sickle-shapped (sk) and trichoids (tr). They showed numerical and spatial variation among the antennomeres (Fig. 1A-D; Table 1). The papillary sensilla were found only on the distal antennomeres or club (A8-A12), along the median region of the ventral surface, being one in A12 and two from A11 to A10.
Table 1. Sensilla numerical variation per antenommere in the dorsal and ventral surfaces of the antennae of G. gallardoi (Hym.: Scelionidae) females. pl = papillary; ch1 = chaetica 1; ch2 = chaetica 2; sk = sickle-shaped; gp = grooved pegs; st = styloconic. The letter “a” followed by arabic algarisms represent the antennomeres. Trichoid sensilla were ommited.

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<tr>
<th>Antennal side/ antenommere (n = 10)</th>
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A8 (Table 1; Figs. 1A, B and 2A). They have a protruding and flattened surface, bearing transversal grooves. The lateral margins are folded in, with an expanded base, forming a nearly ellipsoid pit (Figs. 2B and C). The exposed region of the sensillum is 5.4 μm in length by 1.4 μm in width, being shorter in A12 (approximately 2.1 μm in length) (Fig. 2B).

Two types of chaetica sensilla (ch1 and ch2) are equally distributed on the left and right antennae (Figs. 1A and B). Both are setiform and bear longitudinal grooves and a pore at the apex as well (Figs. 2D and E). The ch1 sensilla, longer and stiffer, measure about 16 μm in length (Fig. 2D). The ch2 type, shorter and lightly bent towards the antenmneplex, measure approximately 7.7 μm in length (Fig. 2E). The localization of the chaetica sensilla is the same on the left and right antennae (Table 1). The cal type ones are present laterally between the dorsal and the ventral antennal surfaces, from A3 to A12, and near the middle surface of the dorsal surface, from A5 to A12 (Figs. 1A and D). The ch2 sensilla were found only on the ventral portion, from A5 to A12, two at each side of the middle portion, near to the antennomere apex (Fig. 1B).

Each antenna has only one styloconic sensillum, located on the anterior ventral surface, near the A3 base (Table 1; Figs. 1A and B). Its surface is apparently smooth and there is no evidence of the existence of pores neither grooves. They have a rounded apex, broader than the base, are fitted to the cavity and measure about 2.7 μm in length (Fig. 3A).

The grooved-peg sensilla were found either on the ventral and dorsal surface. At the ventral surface, they show a different distribution pattern between the left and right antennae (Table 1; Figs. 1A and B). At the right antenna, they are positioned in A3 and A4 and at the left in A3 and A5. In both, they are positioned near the apex of each antennomere,
The sickle-shaped sensilla were found on both surfaces of the antennomeres (Table 1). They are curved towards the antennal apex and lightly compressed laterally (Fig. 3C). Tiny pores cover its surface. These sensilla are more numerous at the dorsal portion (Table 1), being distributed near the apical and basal margins of A3 to A12 (Fig. 1C). Those located near the apical margin extend distally, surpassing the membranous area existing between the antennomeres. At the ventral portion, they are less numerous and distributed in a different manner at the left and right antenna (Table 1). At the right antenna, they occur in pairs on flagellomeres A3 to A6, one at each lateral side, near to the apical margin (Fig.1B).

The trichodea sensilla were recorded on all flagellomeres, showing considerable diversity in size and curvature. The great majority show a longitudinally grooved surface and are insert at an enlarged cavity. In the proximal antennomeres, these sensilla are more scattered and less abundant (Fig.3D). From the antennomere A7 they become gradually more abundant towards the distal region. At the ventral portion, they are shorter and decumbent, curved to the antennomere middle portion (Fig. 3E). At the club, they are found facing the papillary sensilla.

The dorsal glands (dg) are represented by a shallow and striated groove, located along the median-dorsal region of the flagellomeres A5 to A12 (Fig. 3F).
Concerning the number of antennomeres, the antennae of _G. gallardoi_ females agree with the descriptions for other grionines (Masner 1979, Villa & Mineo 1990a,b). In Telenominae, including the genera _Trissolcus_ Ashmed and _Telenomus_ Haliday, the antennae have from 10 to 11 antennomeres (Bin 1981).

By showing various pores, the papillary sensilla belong to the multiporous category, as proposed by Zacharuck (1985). But different terminologies are employed to them. They were described for Scelionidae by Bin (1981) as plates. The terms multiporous plate (Barlin & Vinson 1981, Basibuyuk & Quicke 1998), multiporous grooved plate (Zacharuck 1985) and basiconic sensillum (Cave & Gaylor 1987) also were used to designate these structures.

According to Bin (1981), the distal antennomeres, being broader and endowed with papillary sensilla, delimitate a region in the Scelionididae female antenna named clava. The distribution of these sensilla in the antennomeres varies among species. For this reason, this author suggests the expression ‘claval sensilla formula’ to designate the ordinate array of papillary sensilla in each antennomere of a given club and the utilization of this criterium as a tool for taxonomic identification of genera, group-species, or species. In this way, the claval sensilla formula of the papillary sensilla found in _G. gallardoi_ female antennae was 1-2-2-2-2 (respectively, from A12 to A8), corroborating what has been recorded for others scelionids as _Trissolcus_ spp. (Bin 1981), and the grionines _G. boseli_ (Villa & Mineo 1990a) and _G. pennsylvanicum_ (Villa & Mineo 1990b).

The shape described for the *G. gallardoi* papillary sensilla agrees with those found by Bin (1981) for a great number of Telonominae, and by Cave & Gaylor (1987) for *Telenomus reynoldsi* Gordh & Coker. Nonetheless, in a small group of *Trissolcus* species, Bin (1981) verified that the papillary sensilla had a more elongated surface, with the apex little elevated, being more flattened transversely and inserted in a shallow pit.

Regarding their role, the papillary sensilla seem to be associated to tasting, being also named multiporous gustatory sensilla in Platygastridae and Scelionidae (Isidoro et al. 1996). However, their gustatory role definition has solely been based upon morphological and behavioral studies, since there is a lack of electrophysiological work concerning such sensilla.

The morphological evidences for the gustatory role rely on the location of their pores inside grooves, lobes or spherical protuberances (Isidoro et al. 2001), and on the presence of a great number of sensorial neurons associated to the pores (Zacharuck 1985, Isidoro et al. 1996). Considering this, Isidoro et al. (2001) suggest that during the drumming behavior, chemical compounds of the egg might be moved through the grooves or lobes towards the pores, allowing the recognition and host discrimination by tasting. In *G. gallardoi*, the employed SEM technique did not allow to verify the presence of pores. According to Isidoro et al. (1996), pore visualization is only possible when the specimens are previously treated with protease to remove secretions that cover the sensilla surface. These secretions, produced by exocrine glands associated to the papillary sensilla, seem to be related to the dissolution and/or degradation of substances left on the host eggs, mediating their recognition by parasitoids (Isidoro et al. 2001).

The behavioral evidences that suggest the gustatory role of the papillary sensilla are related to the way females examine their hosts (Bin 1981, Isidoro et al. 1996). Behavioral studies carried out with *G. gallardoi* demonstrated that females evaluate and choose their hosts by drumming (Solís et al. 2001, Wiedenmann et al. 2003), partially rejecting eggs either already parasitized or old (Rocha 2005). These studies demonstrated that during drumming, the antennal portion that stays in touch with the host is the club, strongly suggesting that it is related to the perception of chemical stimuli by contacting the egg, as recorded for other Scelionidae species (Bin 1981, Isidoro et al. 1996, Isidoro et al. 2001). In studies in which the antennal club of parasitoid females was removed, they became unable to discriminate their egg hosts (Vinson 1998).

The grooved-peg sensilla are also named multiporous grooved sensilla (Zacharuck 1985, Cave & Gaylor 1987). Due to their insertion in an enlarged pit, they are also referred as coeloconica (Schneider 1964, Ochieng et al. 2000). According to Slifer (1970), these sensilla are associated to an olfactory role, perceiving long distance stimuli. Their functional specificity seems to depend on the thickness of their wall (Zacharuck 1985). They might also play a mechanoreception role, considering their association to a basal dendrite (Zacharuck 1985), involving both thermal and hygroreception (Altmir & Lofts 1985).

The grooved-peg sensilla found in *G. gallardoi* females occur in the same antennomeres registered for *G. boxelt* (Villa & Mineo 1990a) and *G. pennsylvaniaicum* (Villa & Mineo 1990b). However, these authors registered a different distribution for them on the dorsal surface of the antennomeres. In such cases, they were distributed in pairs from A8 to A12 in the left antenna, in a number of two in A12, and of one from A11 to A7 in the right antenna. In *T. reynoldsi*, Cave & Gaylor (1987) registered the peg type only in the dorsal surface, near the apical external margin of the antennomeres A6, A4, and A11, and referred them as multiporous grooved sensilla.

Cave & Gaylor (1987) suggest that the peg type sensilla do not engage in host recognition and discrimination in the egg parasitoid Scelionidae, because they are not present in the antennal club of these insects.

The sickle-shaped sensilla are also referred as multiporous punctured sensilla (Zacharuck 1985), Cave & Gaylor (1987) described them as horn-like sensilla, ascribing also the term “trichoid curlvata” to them in *T. reynoldsi*. In other egg parasitoid families, as for example Trichogrammatidae, they correspond to the multiporous trichoida sensilla (Olson & Andow 1993).

In Scelionidae, the sickle-shaped sensilla are encountered in all flagellary antennomeres, especially on the dorsal surface; nevertheless, its distribution may show variations among species (Cave & Gaylor 1987, Basibuyuk & Quicke 1998). In *G. gallardoi*, the distribution pattern of these sensilla is different between the ventral regions of the right and left antennae. In the same way, but in both surfaces, Villa & Mineo (1990b) pointed out to the existence of differences in the distribution of sensilla between the left and right antennae of *G. pennsylvaniaicum*. In most works, the authors did not compare the sensilla distribution between the right and left antennae. Thus, erroneous conclusions could be attained in such cases, especially when the number and distribution of sensilla are used with taxonomical purpose.

The role of the sickle-shaped sensilla seems to be related to sense of smell, due to their thin wall and the presence of many tubular pores (Zacharuck 1985). They may exhibit considerable variation within Hymenoptera, regarding cell number, pore distribution, insertion cavity shape, among others. In *Trichogramma nubilale* (Erthe & Davis) (Hymenoptera: Trichogrammatidae), Olson & Andow (1993) verified that these sensilla show a basal constriction and are inserted in an enlarged cavity, thus presenting mechanoreception characteristics. Because their location on the ventral portion in this case, the authors suggest that besides having a chemoreceptive function, they might be associated to the perception of changes in physical characteristics of the egg chorion of their lepidopteran hosts, whose architecture is greatly variable. In *G. gallardoi*, as in other Scelionidae, the sickle-shaped sensilla do not present basal constrictions; they are inserted in a narrow cavity and characterized as chemoreceptive sensilla, being more abundant in the dorsal surface (Cave & Gaylor 1987; Villa & Mineo 1990a,b; Isidoro et al. 1996). Their pronounced curvature towards the antennal surface associated to the fact that long bristles surround them, make their direct contact with the host difficult. These evidences suggest that these sensilla do not detect signals directly from the host, but perceive chemical stimuli from long distance (Isidoro et al. 2001), regarding host location and/or sexual recognition (Cave & Gaylor 1987).
They are also named grooved basiconic (Norton & Vinson 1974, Ochieng et al. 2000) or uniporous gustatory sensilla (Zacharuck 1985). In G. boseli, Villa & Mineo (1990a) registered them only on the ventro-lateral surface, where they occur in a number of two per antennomere, at the apical portion, from A7 to A11, and of eight on A12. Based upon the description of these authors, such sensilla correspond to the ch1, described in the present work for G. gallardoi. In the same way, sensilla corresponding to this type were found in G. pennsylvanicum on the dorsal surface from A8 to A12 in the left antenna, and from A9 to A12, in the right antenna, being two in A12 and one in the other antennomeres. The ch1 sensilla were also similar to those encountered in T. reynoldsi por Cave & Gaylor (1987). The ch2 sensilla of G. gallardoi seem to match those registered for G. pennsylvanicum in the ventral surface, from A5 to A12. In this case, they show the same distribution pattern, except for A12, where six of them were registered.

The chaetica sensilla function as both mechano and chemoreceptors (Zacharuck 1985). Such a double function is ascribed to the existence of a dendrite not attached to the pore (McIver 1985, Isidoro et al. 1996). The chemoreceptive function of the chaetica sensilla seems to be associated to the perception of contacted liquid stimuli, being thus gustative (Zacharuck 1985). Their gustative function has been evidenced through behavioral studies. Bin (1981) inferred that these sensilla, by being stiffer than the others, tend to touch the substrate first, and so might detect information directly from the host. Ultrastructural studies associated to behavioral ones, carried out by Isidoro et al. (1996) in several parasitoid families, including scelionid wasps such as T. basalis, corroborated that. Due to the occurrence in great abundance on antennal areas that touch either the substrate, the host, or the opposite sex during mating, they were called gustative sensilla by these authors. In T. nubilale, the chaetica sensilla are localized in the antennal apex, a local that touch the substrate first. They are also associated to host recognition (Olson & Andow 1993).

The styloconic sensilla, classified as aporous, are associated to thermal and hygroeceptive function in many insects (Zacharuck 1985, Altner & Loftus 1985) ascribed such functions to the absence of pores on them, to their narrow cavity, and to the presence of dendritic segments externally at their base. Studies regarding their sensitivity to changes in temperature and humidity should be carried out to confirm such functions for them in G. gallardoi.

Location of the styloconic sensilla is variable among species of Scelionidae. In T. reynoldsi, Cave & Gaylor (1987) registered them on the dorsal surface of the antennomeres A4 and A10. Villa & Mineo (1990b) mentioned a styloconic sensillum in G. pennsylvanicum on the ventral surface of the antennae, but in a different number and distribution per antennomere. In these species, the authors found one in A5 of the right antenna, two and one respectively for the A5 and A6 of the left antenna.

The trichoid sensilla, which were considered aporous by Zacharuck (1985), are also referred as setiform (Zacharuck 1985, Cave & Gaylor 1987). According to Villa & Mineo (1990a,b), these sensilla correspond to short structures, spine shaped, which occur on the pedicel base and on the ventral surface of the scape. According McIver (1985), these sensilla have mechanoreceptive function, considering the presence of a single sensorial neuron. Therefore, these sensilla would be associated to a tactile function, being able to perceive differences in substrate texture, movement and wind direction (Isidoro et al. 1996).

According to Isidoro et al. (1996), the trichodea sensilla that occur in the antennal club and are associated to the papillary and to the chaetica type, in conjunction form a functional portion of the antenna defined as “touch and taste area”. This area would be responsible for host recognition and acceptance, detecting chemical substances and diverse textures present either on the host surface or substrate during the drumming behavior. In behavioral studies carried out with G. gallardoi females, the drumming behavior lasted longer when either eight or twelve day-old eggs were utilized (Rocha 2005). This fact could be related to a supposed chemical or physical change at the egg surface, which would hinder its recognition by the club sensilla. Nevertheless, electrophysiological studies as well as chemical and morphological analysis of the S. dentiventris egg surface are required to validate this hypothesis.

The dorsal glands are distributed in the same manner as in G. pennsylvanicum (Ashmead) (Villa & Mineo 1990b), but different from G. boseli Mineo et Szabo, where they were registered from A12 to A7 (Villa & Mineo 1990a). In Trissolcus basalis (Wollaston), Isidoro et al. (1996) registered these structures from A7 to A12. According to these authors, the internal wall of this dorsal depression bears numerous pores, which correspond to the opening of the glands. The corresponding function is not clear, and in most studies, it is not even mentioned. Nevertheless, Isidoro et al. (1996), while observing the mating behavior of T. basalis, related them to sexual recognition.

The description and determination of the distribution pattern of antennal sensilla in G. gallardoi females accomplished on the present work is an advance regarding the elucidation of the mechanisms involved in the host selection behavior of this species. In view of the kind of sensilla found in the antennal club, one can infer that chemical compounds present in the host, besides its texture, have an important role in the host recognition and acceptance. Therefore, additional studies, at the ultrastructural level, using transmission electron microscopy should be carried out, in association with electrophysiological ones, in order to elucidate the real function of these structures in relation to the egg parasitoids.

Acknowledgments

To Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for financial support (Process number 47057/2001-2) and for fellowships conceded to the authors.
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Received 29/XII/06. Accepted 04/VI/07.