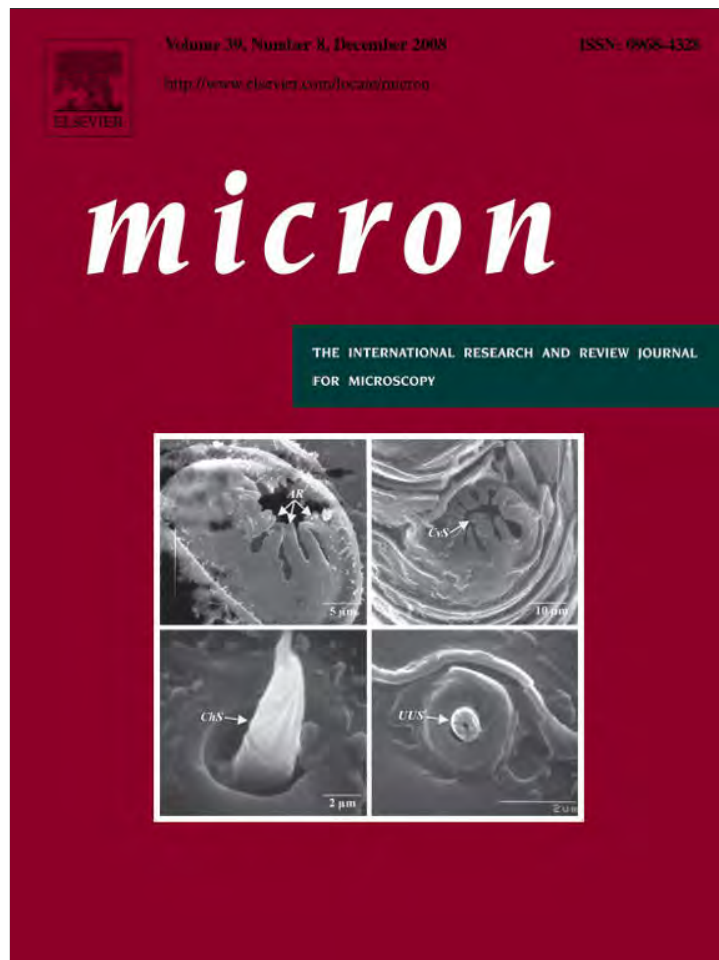


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Morphological characterization of the antennal sensilla of the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), with reference to their probable functions

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ABSTRACT

The Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), is one of the most significant economic pests of citrus worldwide. This insect vectors three phloem-restricted bacteria in the genus *Candidatus Liberibacter* that cause huanglongbing (citrus greening), the most severe disease limiting citrus production worldwide. We examined the external morphology of the antennal sensilla of male and female *D. citri* using scanning electron microscopy (SEM) and determined the putative functions of the identified sensilla using transmission electron microscopic (TEM) techniques. The filiform antennae of *D. citri* were of the conventional type comprised of a basal scape, pedicel and a long, thread-like flagellum, which is composed of eight flagellomeres. Eleven morphologically unique sensillar types were found and described on the antennae of male and female *D. citri*. Of those identified, the two apical setae, multiporous types I and II sensilla trichoidea, and the antennal rhinaria were porous and may be involved in perception of host- and mate-related volatile chemicals. However, the aporous types I, II and III sensilla trichoidea may have mechanosensory functions and the chaetica sensilla, cavity sensilla and unidentified uniporous sensilla may be involved in proprioception, thermo-hygroreception and cold detection, respectively. The shape, external morphology and array of sensilla on the antennae of male and female *D. citri* were similar. The only major difference observed was in the morphology of the short apical setae, whose tips were recessed inward in females but not so in males. The results are discussed in relation to plausible roles of the identified sensilla in mate and host location by this species.

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1. Introduction

The Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), is an economic citrus pest of worldwide importance (Radke et al., 1981; Halbert and Manjunath, 2004; Wenninger and Hall, 2007). *D. citri* was first detected in Florida in 1998 and has spread rapidly throughout the state (Tsai et al., 2000; Halbert et al., 2003). It is known to vector the bacterium, *Candidatus Liberibacter*, responsible for huanglongbing (greening disease) in citrus groves (Lee, 1996; Halbert and Manjunath, 2004; Bové, 2006). Greening invades the tree phloem, causing fruit drop, misshapen, bitter and unmarketable fruit and sometimes results in tree death (Halbert and Manjunath, 2004; Michaud, 2004; Bové, 2006). Several aspects of the developmental biology (Liu and Tsai, 2000; Tsai and Liu, 2000; Michaud, 2004; Nava et al., 2007) and

behavioral ecology (Wenninger and Hall, 2007) of *D. citri* have been studied; however, information on host and mate finding mechanisms of the species is almost completely lacking (Wenninger et al., in press).

Insect antennae play important roles in host location and host discrimination (Moran and Brown, 1973; Ullman, 1985; Nehlin et al., 1994). Antennae of insects contain sensory sensilla, which function in detection of various stimuli involved in host habitat and mate location (Godfray, 1994; Chapman, 1998). Numerous studies have characterized antennal sensilla of various insects (e.g., Ochieng et al., 2000; Soroker et al., 2004; Onagbola and Fadamiro, 2008); however, very few of such studies have focused on Psylloidea (e.g., Moran and Brown, 1973; Singleton-Smith et al., 1978; Ossiannilsson, 1992; Soroker et al., 2004; Kristoffersen et al., 2006). To date, we are unaware of any published information on the antennal sensilla of *D. citri*, despite its worldwide economic importance.

Abundant information is available on mate finding behavior by acoustic means in several psyllid species (Campbell, 1964; Yang

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et al., 1986; Tishechkin, 1989, 2005). Some information is also available on the role of chemicals in mate and host finding by psyllids (Soroker et al., 2004; Kristoffersen et al., 2006; Wenninger et al., in press). The majority of these studies are behavioral (Yang et al., 1986; Tishechkin, 1989, 2005; Lapis and Borden, 1993; Wenninger et al., in press), electrophysiological (Soroker et al., 2004), and morphological (Singleton-Smith et al., 1978; Kristoffersen et al., 2006) investigations of either the adult psyllids or the adult psyllid antennae. Of the few studies that were conducted on antennal sensilla of psyllids, only Kristoffersen et al. (2006) conducted a more detailed morphological investigation, including transmission electron microscopy (TEM), revealing presence of various mechanosensory (non-porous) and olfactory (porous) sensilla on the antennae of *Trioza apicalis* Förster (Hemiptera: Triozidae). However, the probable functions of the identified sensilla were not discussed.

As part of our ongoing research on mate and host location mechanisms of *D. citri*, it became necessary to characterize and determine the abundance and distribution of the antennal sensilla of *D. citri* using standard scanning electron microscopy (SEM) techniques. The putative functions of the identified sensilla were also determined based on features revealed by TEM and inference from published information on antennal sensilla of psyllids and other sternorrhynchal insects. The goal of this investigation was to characterize the antennal sensilla of *D. citri* to facilitate a better understanding of their function in relation to how semiochemicals may mediate mate and host location in *D. citri*.

2. Materials and methods

2.1. Scanning electron microscopy

Adult male and female *D. citri* were obtained from a continuously reared greenhouse culture established in 2000 from field populations in Polk Co., FL, USA. This culture is maintained on sour orange (*Citrus aurantium* L.) and 'Hamlin' orange (*C. sinensis* (L.)) seedlings at 27 ± 1 °C, $63 \pm 2\%$ RH, and 14:10 h L:D photoperiod. The antennae of adult psyllids were excised under $40\times$ magnification (Leica, Wild MC3 stereomicroscope, Heerbrugg, Switzerland) and kept in 70% ethanol for ~ 24 h before dehydration in a graded series of 75, 80, 85, 90, and 99.9% ethanol:water (van Baaren et al., 1996; Onagbola and Fadamiro, 2008); antennae were maintained for 1 h at each gradation. Thereafter, antennae were mounted on aluminum stubs with double-sided copper sticky tape and kept in a drying chamber (25 ± 1 °C, $10 \pm 1\%$ RH) for ~ 5 days. The antennae were sputter coated with gold/palladium (40:60) in a LADD SC-502 (Vermont, USA) high resolution sputter coater and subsequently examined with a KeveX[®] S-530 (Hitachi, Tokyo, Japan) SEM operated at 10, 15 or 20 kV.

2.2. Transmission electron microscopy

Adult male and female *D. citri* were first anesthetized in a freezer (-20 °C) for ~ 5 min and decapitated with a fine knife under stereomicroscopy. Similar to the TEM techniques described by Childers and Achor (1991) and Achor and Childers (1995), the isolated heads were fixed in 3% glutaraldehyde and 0.1 M cacodylate buffer at 6 °C for ~ 24 h. The specimens were first rinsed in the buffer followed by post-fixation in 1% osmium tetroxide for ~ 2 h. Specimens were later infiltrated in 50, 75 and 100% Spurr's resin for ~ 24 , 12 and 12 h, respectively, and embedded in pure Spurr's plastic and polymerized at 60 °C for ~ 72 h thereafter. Ultrathin sections of psyllid antennae were cut with a diamond knife on a LKB-Huxley ultra-microtome #8365 (Cambridge, UK) and stained with 2% uranyl acetate (~ 15 min)

followed by lead citrate (~ 5 min). Sections were then rinsed with 2% sodium hydroxide solution and excess distilled water prior to examination under a Morgagni #268 (Eindhoven, Netherlands) transmission electron microscope (TEM) at 60 kV.

3. Results

3.1. General description of *D. citri* antennae

Adult male psyllids (2.36 ± 0.02 (mean \pm S.E.); range = 2.13–2.51 mm, $N = 15$) were slightly smaller than females (2.44 ± 0.03 ; range = 2.21–2.63 mm, $N = 15$) with antennal lengths of ~ 0.44 mm (440 μ m) and 0.45 mm (450 μ m), respectively. The filiform antennae of both sexes were of the conventional type comprised of a basal scape, pedicel and a long flagellum, which was composed of eight flagellomeres. The scape, pedicel and flagellum constituted ~ 27.5 , 28.5 and 44.0% of the entire antennal length, respectively. The entire antennal surface was covered with annular scales (Fig. 1).

3.2. Terminology

Antennal sensilla have been differently named by various authors despite similarity in their external morphology and positions on the antennae (Moran and Brown, 1973; Singleton-Smith et al., 1978; Ossiannilsson, 1992; van Baaren et al., 1996; Soroker et al., 2004; Kristoffersen et al., 2006; Onagbola and Fadamiro, 2008). To avoid this inconsistency in terminology, we classified and named the various sensilla observed on antennae of *D. citri* based on their morphological details as revealed by SEM and TEM and followed the nomenclature of Ossiannilsson (1992), Chapman (1998), Park and Hardie (2003), Kristoffersen et al. (2006) and Onagbola and Fadamiro (2008).

3.3. Types of sensilla

3.3.1. Porous sensilla

Table 1 shows the abundance and the distribution of the various types of sensilla observed on the antennae of *D. citri*. Four morphologically different types of hair-like olfactory sensilla were identified on the antennae of *D. citri* (Fig. 2A1–D1, SEM; A2–D2, TEM). These included the long (Fig. 2A1; length, $l = 33.7$ μ m, basal diameter, b.d. = 3.1 μ m) and short (Fig. 2B1; $l = 10.7$ μ m, b.d. = 4.8 μ m) apical setae (Kristoffersen

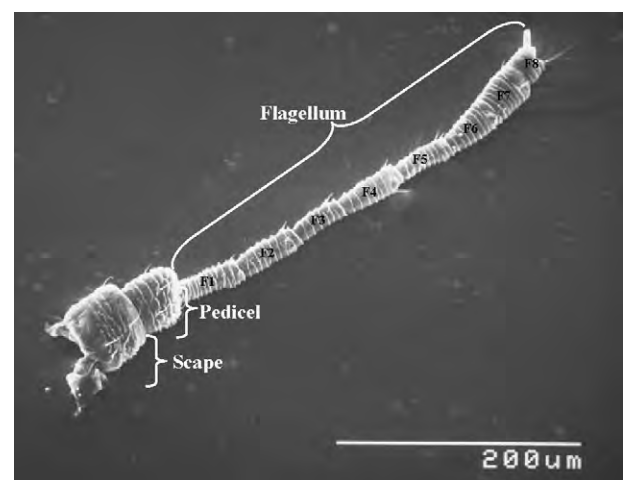


Fig. 1. Scanning electron micrograph (SEM) of an excised antenna of a female *D. citri* showing the scape, pedicel and flagellum. The male antenna is similar in shape and morphology, but slightly smaller.

Table 1
Abundance and distribution of sensilla on the antennae of male *D. citri*

Sensilla	Antennal segment									
	Scape	Pedicel	Flagellum							
			F1	F2	F3	F4	F5	F6	F7	F8
MST-1	–	–	–	1	–	1	–	1	2	–
MST-2	1	–	–	–	–	–	–	–	–	–
LAS	–	–	–	–	–	–	–	–	–	1
SAS	–	–	–	–	–	–	–	–	–	1
AST-1	14	16	–	–	–	–	–	–	–	–
AST-2	–	–	2	1	2	1	1	2	2	1
AST-3	2	2	1	–	–	–	–	–	–	–
ChS	1	–	–	–	–	–	–	–	–	–
CvS	–	–	–	1	–	1	–	1	1	–
AR	–	–	–	1	–	1	–	1	1	–
UUS	–	1	–	–	–	–	–	–	–	2
Total	18	19	3	3	2	3	1	4	6	5

Number and location of the various sensilla observed on the antennae of male *D. citri*. An identical number was recorded for females. F1–F8, antennal flagellomeres 1–8; MST-1 and MST-2 are multiporous sensilla trichoidea types I and II, respectively; LAS, long apical setae; SAS, short apical setae; AST-1, AST-2 and AST-3 are aporous types I, II and III sensilla trichoidea, respectively; ChS, chaetica sensilla; CvS, cavity sensilla (present in the AR); AR, antennal rhinaria; UUS, unidentified uniporous sensilla.

et al., 2006) and the multiporous sensilla trichoidea (MST) type I (MST-1; Fig. 2C1; $l = 7.3 \mu\text{m}$, b.d. = $1.2 \mu\text{m}$) and type II (MST-2; Fig. 2D1; $l = 6.3 \mu\text{m}$, b.d. = $0.9 \mu\text{m}$). The surfaces of the two apical setae and the MST-1 sensilla were longitudinally grooved (Fig. 2A1–C1), whereas the surface of the MST-2 sensilla appeared smooth (Fig. 2D1). The shafts of the long apical setae were slightly curved and those of the short setae and the MST-1 sensilla were straight (Fig. 2). The tips of the apical setae are morphologically different between male and female antennae with female's being recessed inward (Fig. 3). The MST-1 sensilla protruded from the antennal cuticle underneath layers of annular scales and near antennal rhinaria (AR) (Fig. 4A–C) but appear to have arisen from cuticular pits when viewed from underneath sheets of antennal scales (Fig. 4A and C). The MST-1 sensilla occurred on flagellomeres 1, 2, 4 and 7 in this species. The MST-2 sensilla had a strongly bent shaft (Fig. 2D1) and occurred only on the antennal scape. The TEM photomicrographs (Fig. 2A2–D2) of these porous sensilla revealed wall pores suggesting a plausible role in perception of olfactory stimuli.

3.3.2. Aporous sensilla

Trichoid sensilla were the dominant type on the antennae of *D. citri* constituting ~84% of the total number of the antennal sensilla with ~28 and 31% on scape and pedicel, respectively (Table 1). Three types of aporous sensilla trichoidea (AST) occurred on the antennae of both sexes of *D. citri* (Fig. 5A1–C1, SEM; A2–C2, TEM). The AST-1 sensilla (Fig. 5A1; $l = 11.1 \mu\text{m}$, b.d. = $1.1 \mu\text{m}$) had slightly bent shafts with bent tips and occurred on the antennal scape and pedicel. The shafts of AST-2 (Fig. 5B1; $l = 8.9 \mu\text{m}$, b.d. = $1.1 \mu\text{m}$) and AST-3 (Fig. 5C1; $l = 5.6 \mu\text{m}$, b.d. = $0.8 \mu\text{m}$) were straight. The AST-2 and AST-3 sensilla appeared similar in external morphology but were different in size with AST-2 being longer than the AST-3. The AST-2 sensilla occurred on the lateral portions of each antennal flagellomere, whereas the AST-3 occurred on the medial portions of the scape, pedicel and flagellomeres 1, 2, 4 and 5. These three trichoid sensilla had basal insertions into conical sockets and were characterized by fluted surfaces (Fig. 5A1–C1). Transmission electron micrographs of their cross-sections (Fig. 5A2–C2) revealed aporous walls suggesting a non-olfactory function for these sensilla.

3.3.3. Other types of sensilla

One plate-like antennal rhinarium (Fig. 6A, AR) was located on the ventral (mid ventral or ventro-lateral, position varied) surface of flagellomeres 2, 4, 6 and 7 on the antennae of both sexes. Each AR formed a covering surrounding a deep pit from which a cavity sensillum (Fig. 6B, CvS) protrudes. One chaetica sensilla (ChS) was identified on the dorsal surface of the antennal scape. The ChS was peg-like with a grooved surface and was recessed within a pit (Fig. 6C, ChS). An unidentified (maybe campaniform) uniporous sensilla (Fig. 6D, UUS) occurred in cuticular depressions underneath annular scales around the bases of the apical setae and on the antennal pedicel.

4. Discussion

The various types of sensilla and their distribution on the antennae of male and female *D. citri* as revealed in this study were consistent with those reported for other psyllid (Ossiannilsson, 1992; Soroker et al., 2004; Kristoffersen et al., 2006), sternorhynchal (Park and Hardie, 2003) and hymenopteran insect species (van Baaren et al., 1996; Ochieng et al., 2000; Onagbola and Fadamiro, 2008). However, some of these sensilla have been differently characterized by the various authors cited above. Eleven sensillar types were observed on the antennae of male and female *D. citri* with no difference in their abundance and distribution between the sexes. Among these sensilla, greater attention was focused on the identified mechano- and olfactory sensilla owing to their probable importance in mate and host finding by *D. citri*. A major sexual dimorphism was identified only in the external morphology of the short mechanosensory setae, whose blunt tip was recessed inward in females but not in males.

The long and short apical setae protrude at an angle (~75°) on the same plane (~180°) of the apico-lateral tip of the antennae. They appear to emerge from deep cuticular pits and connect to the surface of the ridged circular basal sockets through a membranous cuticle. The presence of these setae has been observed on the antennae of other psyllid species including *Psylla pyricola* Förster (Singleton-Smith et al., 1978) and several members of the Diaphorinae group (Ossiannilsson, 1992). As is the case with other types of sensilla, the apical setae have been differently named by various authors. For example, Singleton-Smith et al. (1978) and Soroker et al. (2004) characterized them as “chaetica sensilla” while Ossiannilsson (1992) and Kristoffersen et al. (2006) identified them as “apical setae”. To avoid future confusion, we propose to characterize these sensilla as apical setae in the present study. The location of the two apical setae (van Baaren et al., 1996; Soroker et al., 2004; Onagbola and Fadamiro, 2008) and presence of membranous connections between the sensillar shaft and the antennal cuticular surfaces (Chapman, 1998) suggests a mechanosensory function for these setae.

Typically, porous sensillar walls suggest olfactory functions (Steinbrecht, 1984; Hallberg et al., 2003; Kristoffersen et al., 2006; Onagbola and Fadamiro, 2008). Odorant substances including sex pheromones and host plant volatiles diffuse through the wall pores of antennal sensilla into the sensillar lymph and are transferred to olfactory receptors on the dendrites of olfactory neurons by odorant binding proteins (Leal, 2005). The photomicrographs of the cross-sections of the apical setae did reveal porous walls suggesting an olfactory function. Sensilla with a similar morphological conformation were also reported on the antennae of the psyllid *T. apicalis* (Kristoffersen et al., 2006). Furthermore, van Baaren et al. (1996) described sensilla with a similar external morphology and positioned in a similar location, as “chaetica sensilla” with dual chemo- and mechanoreception functions on the antennae of two mymarid wasp

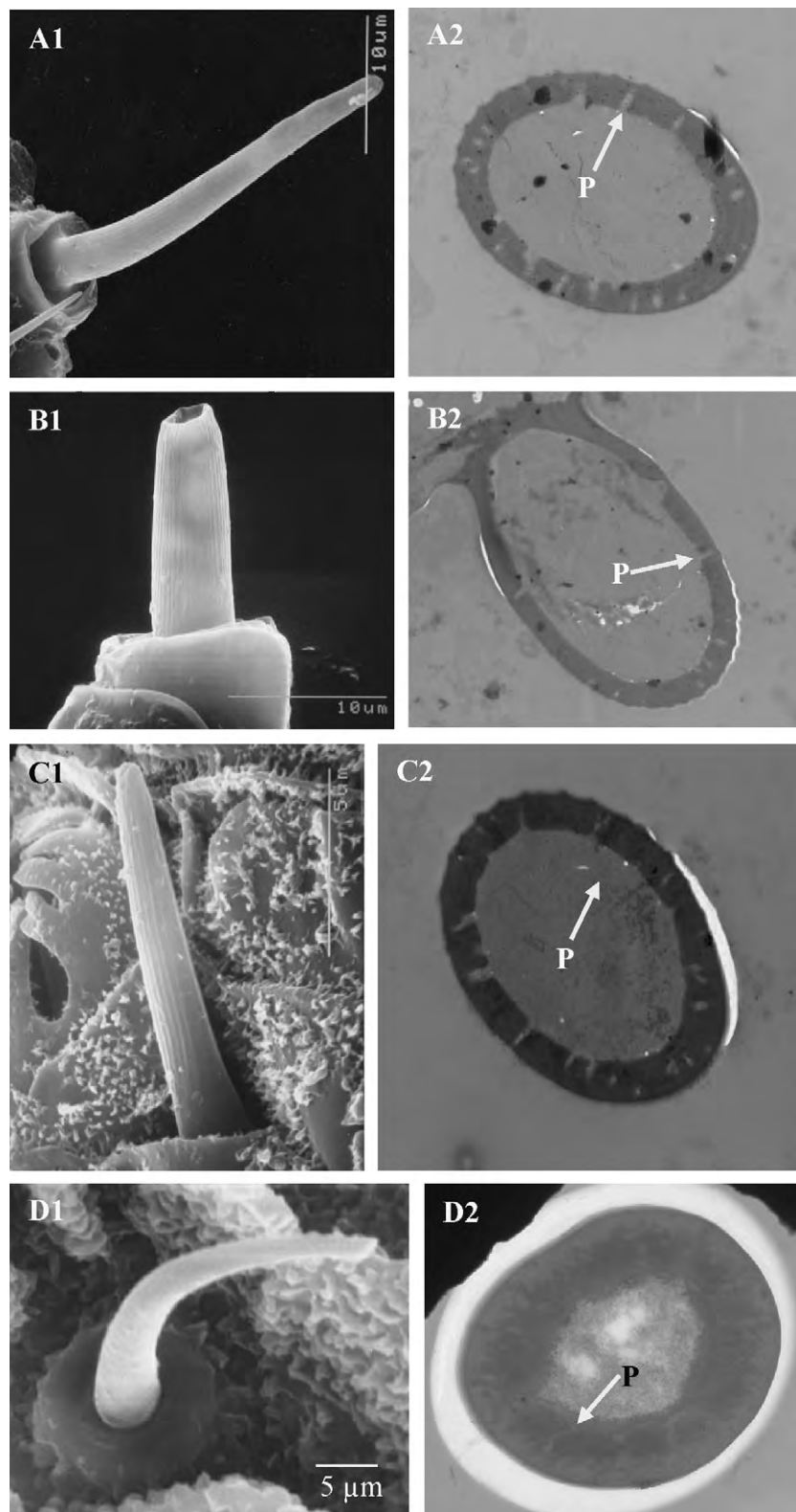


Fig. 2. Micrographs of the olfactory sensilla on the antennae of *D. citri*: SEM micrographs of the long (A1) and short (B1) apical setae, types I (C1) and II (D2) multiporous sensilla trichoidea and the TEM micrographs of their respective cross-sections A2–D2. P, pore in the sensillar walls.

species, *Anaphes victus* Huber and *Anaphes listronoti* Huber. Thus, the apical setae identified on antennae of *D. citri* may be analogous to chaetica sensilla and may have both chemo- and mechanosensory functions.

Careful observation of the MST-1 sensilla revealed that it protruded from the antennal cuticle underneath layers of annular scales and near antennal rhinaria. However, other authors (e.g., Kristoffersen et al., 2006) have reported the MST-1 sensilla as

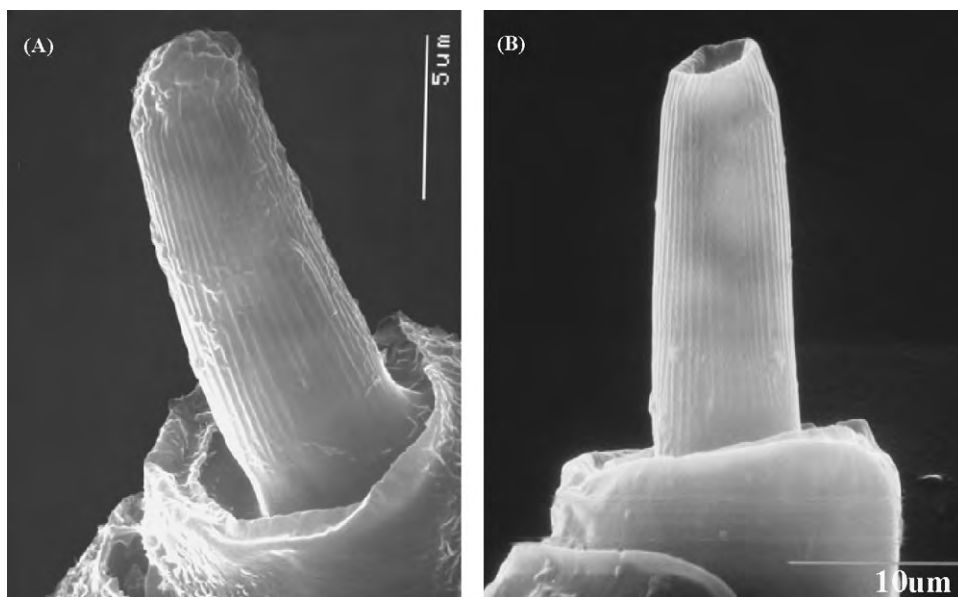


Fig. 3. Photomicrographs of the short apical setae on antennae of *D. citri*: sexual dimorphism in male and female based on blunt, un-recessed tip of male setae (A) and recessed tip of female setae (B).

having originated from cuticular pits probably because it was observed from the antennal surface, where its view may have been obscured by the annular scale covering. Although these sensilla vary in size, depending on their location on the antennal flagellum, they appear to be morphologically similar otherwise. Our TEM study revealed wall pores on the MST-1 sensilla suggesting an olfactory function. Sensilla with a similar external morphology to the MST-1 characterized in the present study were described by Kristoffersen et al. (2006) as types I and II hair-shaped sensilla for *T. apicalis*. It is plausible that the MST-1 sensilla are analogous to the sensilla trichoidea, which Moran and Brown (1973) and Soroker et al. (2004) characterized on antennae of the African citrus psyllid, *Trioza erythrae* (del Guercio) (Hemiptera: Psyllidae) and *Cacopsylla bidens* (Sulc) (Hemiptera: Psyllidae), respectively, given that their studies did not distinguish between the chemo- and mechanosensory sensilla. Only one or at most two multiporous type II sensilla trichoidea (MST-2) occur on the proximal portion of the dorsal surface of the antennal scape. The MST-2 sensillar shaft surface was smooth and wall pores were not apparent when viewed under the SEM; however, the photomicrographs of its cross-sections revealed the presence of wall pores suggesting an olfaction function for these sensilla. Both the MST-1 and the MST-2

sensilla occur on the antennae of both sexes of *D. citri* and are likely olfactory in function, perhaps involved in perception of host-related stimuli.

Three aporous trichoid sensilla with fluted-surface shafts and basal insertions into conical sockets were found on the antennae of both male and female *D. citri*. The presence of aporous trichoid sensilla has also been reported on antennae of other psyllid species including *Trioza* spp. (e.g., Ossiannilsson, 1992; Kristoffersen et al., 2006). The external morphology of the aporous types I, II and III sensilla trichoidea on the antennae of *D. citri* resembles that of the types I (ST1-AP) and II (ST2-AP) aporous trichoid sensilla reported on the antennae of *Anaphes* species (van Baaren et al., 1996) and *Pteromalus cerealellae* (Ashmead) (Hymenoptera: Pteromalidae) (Onagbola and Fadamiro, 2008). Because the shafts of these sensilla are connected to conical basal sockets by cuticular membranes, Chapman (1998) suggested they might have mechanosensory functions. Similar mechanosensory sensilla were also characterized by Kristoffersen et al. (2006) on the antennae of the psyllid, *T. apicalis*.

Presence of antennal rhinaria (AR) has long been recognized on antennae of psyllids and other sternorrhynchal insects (Onillon, 1969; Moran and Brown, 1973); however, they have been

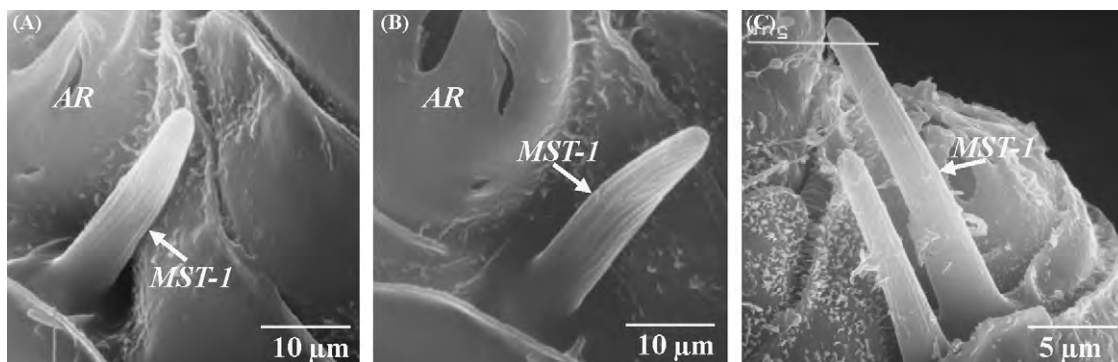


Fig. 4. Type I multiporous sensilla trichoidea (MST-1): different views (A–C) of the MST-1 sensilla revealing its origin from antennal cuticle and not from a cuticular pit. AR, antennal rhinaria.

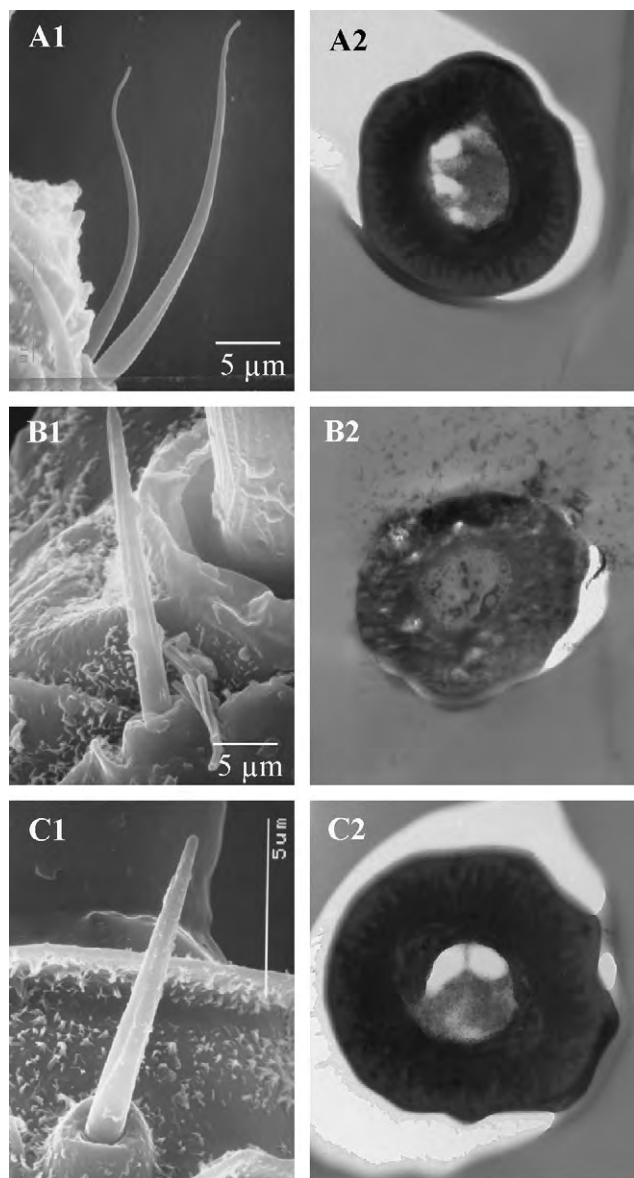


Fig. 5. Micrographs of the aporous sensilla trichoidea types on the antennae of *D. citri*: SEM micrographs of sensilla trichoidea types I (AST-1, A1), II (AST-2, B1) and III (AST-3, C1) and the TEM micrographs of their respective cross-sections A2–C2.

characterized by different names. For example, Moran and Brown (1973) characterized them as “sensoria”, which are similar to aphid plate organs or to coeloconic sensilla, on flagellomeres 2, 4, 6, 7 and 8 of the antennae of *T. erythrae*; Singleton-Smith et al. (1978) described them as “partitioned sensory organs” (PSOs) on the antennae of *P. pyricola*; Ossiannilsson (1992) differentiated members of the Psyllinae, Diaphorinae and Aphalarinae groups based on the number and position of the “olfactory organ”, rhinaria; and Heie (1995), Bernays et al. (2000) and Park and Hardie (2003) described primary and secondary antennal rhinaria on the antennae of aphids. As described for other Diaphorinae species (Ossiannilsson, 1992), the AR of *D. citri* occur on flagellomeres 2, 4, 6 and 7. The AR of *D. citri* appear to be structurally similar to the primary rhinaria found on the antennae of the black bean aphids, *Aphis fabae* Scopoli (Hemiptera: Aphididae) (Park and Hardie, 2003).

Generally, the AR are known to play a major role in the chemical ecology of sternorrhynchal insects (Campbell et al., 1990; Hardie

et al., 1994; Visser and Piron, 1997). They are reported to be involved in perception of pheromones as well as host odors (Anderson and Bromley, 1987; Hardie et al., 1994, 1995). Hardie et al. (1994, 1995) and Park and Hardie (1998, 2003) reported involvement of the primary AR in perception of host-related volatiles. Based on the available published data (Ossiannilsson, 1992) including photomicrographs of sternorrhynchal antennae (Park and Hardie, 2003), secondary AR have been characterized as sex pheromone receptors (Bromley et al., 1979; Bromley and Anderson, 1982; Park and Hardie, 2003). However, no secondary AR were observed on the antennae of both sexes of *D. citri* in the current investigation. This suggests that the AR on the antennae of *D. citri* are primary AR and may play a significant role in host plant location. The AR on the antennae of this species may function in perception of volatile stimuli emanating from young citrus flush given that this is the exclusive site for egg-laying in this species (Mead, 1977; Halbert and Manjunath, 2004). Furthermore, the shape, location and number of the AR have been used to discriminate related sternorrhynchal species (Heie, 1995; Ossiannilsson, 1992; Bernays et al., 2000) and sexes (Bernays et al., 2000). There was no sexual dimorphism between the number and location of the AR on the antennae of *D. citri*. This further supports the hypothesis that the AR of this species are involved in perception of host plant-related substances given that such a function is required by both sexes. A recent report suggests that male *D. citri* may be attracted to a female-produced chemical (Wenninger et al., in press). However, the results of the present study indicate minimal sexual dimorphism between the antennae of male and female *D. citri*. It is still unclear which sensilla on the antennae of male *D. citri* may be involved in perception of sex pheromones given that there was no evidence of secondary AR, which are known to be involved in sex pheromone perception in other species (Bromley and Anderson, 1982; Park and Hardie, 2003).

The cavity sensilla (CvS) were housed within the AR and were not exposed to the antennal surface. The description of the type II cavity sensilla reported on the antennae of *T. apicalis* (Kristoffersen et al., 2006) suggested that it may be similar to the CvS on the antennae of *D. citri*. Sensilla that are recessed within deep pits similar to the CvS have been differently termed on the antennae of various insect species by different authors as “pit organs” (Wcislo, 1995) or “coeloconic sensilla” (Bleeker et al., 2004; Onagbola and Fadamiro, 2008). We could not obtain a good cross-section photomicrograph of the CvS in this investigation. However, cross-section photomicrographs obtained for the CvS on the antennae of another psyllid species revealed the sensilla to be non-olfactory (Kristoffersen et al., 2006). Furthermore, it has been suggested that sensilla that are recessed from the antennal surface and located within cavities, may be involved in perception of humidity and temperature (Steinbrecht, 1984; Stange and Stowe, 1999; Onagbola and Fadamiro, 2008) and may play a role in preventing desiccation (Kristoffersen et al., 2006).

Sharply pointed setae were found among the aporous sensilla trichoidea on the proximal section of the dorsal surface of the scape. These sensilla are similar in shape to the sensilla trichoidea (ST) but are much shorter and recessed within cuticular depressions. Our TEM revealed these sensilla to be devoid of wall pores, suggesting a non-olfactory role. Sensilla with a similar morphology and location have been described on the antennae of other insect species and termed chaetica sensilla (ChS) with suggested mechanosensory or proprioceptive functions based on their characteristic morphology and location on the proximal region of the scape (Ochieng et al., 2000).

The unidentified (maybe campaniform) uniporous sensilla (UUS) occurred on the antennal pedicel and around the bases of

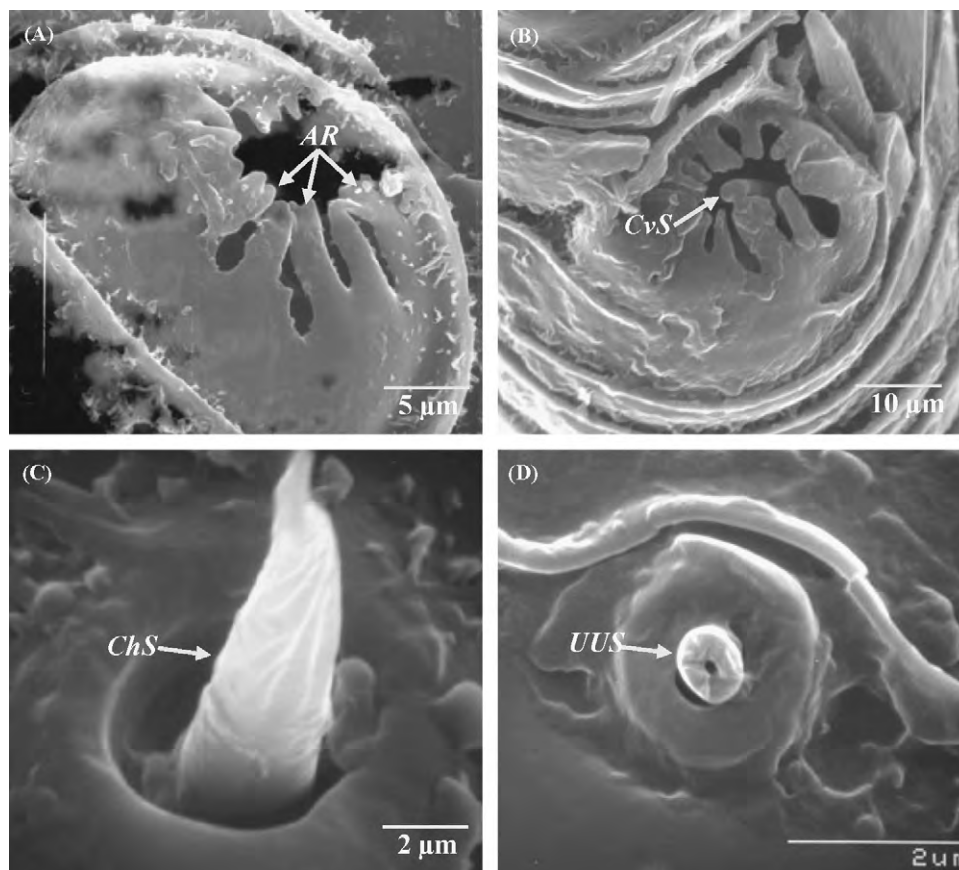


Fig. 6. Other types of sensilla observed on the antennae of male and female *D. citri*: the plate-like antennal rhinaria (AR) (A); cavity sensillum (CvS) (B); the chaetica sensillum (ChS) (C); the unidentified uniporous sensilla (UUS) (D).

the two apical setae of *D. citri*. Each of the UUS sensilla found on the antennae of male and female *D. citri* has a single pore on its flattened tip. Occurrence of the UUS sensilla around the bases of the apical setae and presence of tip pores suggests that these sensilla may be analogous to the sensory cavity sensilla (type I), which are innervated by a single sensory cell on antennae of *T. apicalis* (Kristoffersen et al., 2006). However, sensilla with tip pores are most often finger- or hair-like and are always located on the apical regions of antennae (Slifer, 1969; Isidoro et al., 1996; Onagbola and Fadamiro, 2008) where they function in gustation or contact chemoreception (Altner and Prillinger, 1980; Olson and Andow, 1993; Onagbola and Fadamiro, 2008). The external morphology and location (in cuticular depressions of the antennal cuticle and underneath the antennal annular scales) of the UUS sensilla observed on the antennae of *D. citri* do not support the hypothesis of a contact chemoreception function. We suggest that the UUS sensilla described in this study may be campaniform sensilla because other authors including Ossiannilsson (1992) and Kristoffersen et al. (2006) have also reported the presence of campaniform sensilla on the antennal pedicel of other psyllid species. The structure and position of the UUS sensilla appear analogous to that reported on the antennae of carabid beetles, which were identified as campaniform sensilla and suggested to function as cold receptors (Merivee et al., 2003; Ploomi et al., 2003). However, considering the description by Schneider (1964) that campaniform sensilla have neither pores nor openings and given that micrographs of similar sensillar types on antennae of other psyllid species are not available for comparison, we propose to retain the “unidentified uniporous sensilla” term to describe this sensillar type until further studies with other related species have been conducted.

As observed with other psyllid species (e.g., Soroker et al., 2004; Kristoffersen et al., 2006), there was very little distinct sexual dimorphism in the antennal morphology of *D. citri*. The lone observed difference was the tip of the short apical setae, which recessed inward on the antennae of females but was rounded on the antennae of males. This lone structural difference remained consistent among several male and female *D. citri* antennae ($N \geq 5$ per sex) compared. However, our TEM sections revealed no morphological difference in the wall structure of the short apical setae between male and female *D. citri*.

To our knowledge, this study is the first to describe the detailed morphology of the antennal sensilla of *D. citri*. Five olfactory and at least three mechanosensory sensilla were characterized supporting plausible use of olfactory (Wenninger et al., in press) and vibratory (Yang et al., 1986; Tishechkin, 1989, 2005) cues for host and/or mate finding in this species. The results obtained provide direct morphological evidence that the antennae of *D. citri* possess structures that can play a role in both chemo- and mechanosensory modalities for mate finding and host plant location. These results substantiate the possibility that synthetic repellents and/or attractants may be developed for practical pest control applications, which should exploit chemically mediated host plant finding mechanisms in this species.

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