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Tephritid Olfaction: Morphology of the Antennae of Four Tropical Species of Economic Importance (Diptera: Tephritidae)¹

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ABSTRACT Four types of sensilla are present on the antennal surface of four tropical tephritid species of economic importance—the Mexican fruit fly, *Anastrepha ludens* (Loew); the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann); the melon fly, *Dacus cucurbitae* Coquillett; and the oriental fruit fly, *D. dorsalis* Hendel. Three types of porous sensilla occur only on the funiculus. Two types of multiporous pitted sensilla (MPS)—thick-walled and thin-walled—house dendritic branches, and both are probably chemoreceptors. Electrophysiological recordings from cells associated with a thick-walled MPS in *C. capitata* showed that it responds to trimedlure, a known attractant. Multiporous grooved sensilla also occurring on the funiculus were, however, too small for recordings. No-pore sensilla are found only on the scape and pedicel, and electrophysiological recordings show them to be mechanoreceptors.

KEY WORDS Insecta, fruit flies, chemoreceptors, mechanoreceptors

THE IMPORTANCE of olfaction in the behavior of tephritids is well known (Prokopy et al. 1984, Sivinski & Calkins 1986). Pheromones or other compounds have a major role in releasing various behaviors in several tephritid species. Previous research on olfactory responses of tephritid flies has concerned whole-organism, attractant responses to various compounds (Beroza & Green 1963, Keiser et al. 1975). Only relatively recently has the behavior of certain fruit flies and its specific chemical (Fletcher 1977, Schoonhoven 1982) and visual cues, or both, been described (Prokopy & Owens 1983). However, before a true understanding is gained of the mechanisms involved in tephritid behavior, basic knowledge of the structure and function of the receptors must be obtained.

Although the antennal sensilla of several species of Diptera have been investigated (Dethier et al. 1963, Slifer & Sekhon 1964, Lewis 1971, Bay & Pitts 1976, White & Bay 1980, Hood Henderson & Wellington 1982, Honda et al. 1983), information on olfactory receptors in tephritid flies is only recently available. Hallberg et al. (1984) described the structure of sensilla on the surface and within the single olfactory pit of the funiculus of the olive fly, *Dacus oleae* (Gmelin). Giannakakis & Fletcher (1985) characterized the distribution and surface

structure of antennal sensilla on male and female Queensland fruit flies, *D. tryoni* (Froggatt).

Here we describe the antennae and associated sensilla of four tropical tephritid pests—the Mexican fruit fly, *Anastrepha ludens* (Loew); the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann); the melon fly, *Dacus cucurbitae* (Coquillett); and the oriental fruit fly, *D. dorsalis* (Hendel). We also demonstrate the function of several sensillar types by electrophysiological recordings from cells associated with them.

Materials and Methods

Insects. *Anastrepha ludens* emerged from pupae obtained from the USDA-APHIS rearing facility in Monterrey, Mexico. Because of quarantine regulations, adult *Ceratitis capitata*, *Dacus cucurbitae*, and *Dacus dorsalis* used for morphological studies performed in the continental U.S. were obtained in a fixative (Chauthani & Callahan 1966) from the ARS-USDA Tropical Fruit and Vegetable Research Laboratory in Honolulu, Hawaii. For electrophysiological studies performed in Hilo, Haw., adult *C. capitata* were used from pupae at the Tropical Fruit and Vegetable Research Laboratory in Hilo.

Microscopy. Whole mounts used for light microscopy were prepared from antennae fixed for at least 24 h in a solution described by Chauthani & Callahan (1966). Dehydration was in a graded series of ethanol and xylene. Mounting was in Canada balsam or Permount. Sections of antennae used for light microscopy were prepared as for transmission electron microscopy (TEM). Sections 2 μ m

¹ This article reports the results of research only. Mention of a proprietary product does not constitute an endorsement or a recommendation for its use by USDA.

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Table 1. Measurements (μm) made from light micrographs of antennae of male and female *A. ludens*, *C. capitata*, *D. cucurbitae*, and *D. dorsalis* ($\bar{x} \pm \text{SE}$; $n = 5$)

Segment	Species	Length (μm) δ : φ		Width (μm) δ : φ	
Scape	<i>A. ludens</i>	148 $\pm$ 16 :	111 $\pm$ 12	Base	123 $\pm$ 13 : 115 $\pm$ 20
				Distal	174 $\pm$ 16 : 177 $\pm$ 13
	<i>C. capitata</i>	132 $\pm$ 22 :	125 $\pm$ 22	Base	110 $\pm$ 12 : 100 $\pm$ 0
				Distal	147 $\pm$ 12 : 160 $\pm$ 12
	<i>D. cucurbitae</i>	180 $\pm$ 14 :	196 $\pm$ 5	Base	104 $\pm$ 5 : 105 $\pm$ 5
				Distal	150 $\pm$ 6 : 157 $\pm$ 9
	<i>D. dorsalis</i>	192 $\pm$ 21 :	234 $\pm$ 19	Base	112 $\pm$ 8 : 98 $\pm$ 7
				Distal	160 $\pm$ 10 : 158 $\pm$ 9
Pedicel	<i>A. ludens</i>	175 $\pm$ 18 :	171 $\pm$ 36	Base	125 $\pm$ 16 : 140 $\pm$ 12
				Distal	198 $\pm$ 16 : 203 $\pm$ 21
	<i>C. capitata</i>	133 $\pm$ 19 :	130 $\pm$ 25	Base	113 $\pm$ 17 : 120 $\pm$ 17
				Distal	161 $\pm$ 18 : 185 $\pm$ 12
	<i>D. cucurbitae</i>	229 $\pm$ 19 :	235 $\pm$ 12	Base	107 $\pm$ 10 : 110 $\pm$ 20
				Distal	198 $\pm$ 4 : 202 $\pm$ 18
	<i>D. dorsalis</i>	210 $\pm$ 12 :	240 $\pm$ 12	Base	105 $\pm$ 12 : 104 $\pm$ 5
				Distal	184 $\pm$ 7 : 170 $\pm$ 21
Funiculus	<i>A. ludens</i>	420 $\pm$ 19 :	447 $\pm$ 25		176 $\pm$ 18 : 185 $\pm$ 10
	<i>C. capitata</i>	312 $\pm$ 19 :	327 $\pm$ 13		193 $\pm$ 10 : 195 $\pm$ 12
	<i>D. cucurbitae</i>	605 $\pm$ 6 :	667 $\pm$ 35		180 $\pm$ 14 : 184 $\pm$ 13
	<i>D. dorsalis</i>	632 $\pm$ 41 :	681 $\pm$ 17		193 $\pm$ 10 : 177 $\pm$ 17
Arista	<i>A. ludens</i>	1,190 $\pm$ 68 :	1,163 $\pm$ 22		39 $\pm$ 2 : 46 $\pm$ 5
	<i>C. capitata</i>	1,065 $\pm$ 37 :	1,030 $\pm$ 51		41 $\pm$ 5 : 44 $\pm$ 5
	<i>D. cucurbitae</i>	1,120 $\pm$ 25 :	1,195 $\pm$ 25		46 $\pm$ 5 : 44 $\pm$ 5
	<i>D. dorsalis</i>	1,110 $\pm$ 49 :	1,050 $\pm$ 32		42 $\pm$ 4 : 38 $\pm$ 2
Total length of scape + pedicel + funiculus					
	<i>A. ludens</i>	743 $\pm$ 10 :	729 $\pm$ 56		
	<i>C. capitata</i>	577 $\pm$ 20 :	582 $\pm$ 37		
	<i>D. cucurbitae</i>	1,014 $\pm$ 19 :	1,098 $\pm$ 40		
	<i>D. dorsalis</i>	1,034 $\pm$ 35 :	1,155 $\pm$ 39		

thick were stained with an aqueous 1% methylene blue/1% sodium borate solution. Both whole mounts and sections were examined using a Leitz Ortholux phase contrast microscope.

For scanning electron microscopy (SEM), either excised antennae or whole heads with antennae still attached were fixed several days in either a 5% formalin solution or Chauthani & Callahan's (1966) fixative prior to dehydration in a graded series of ethanol (Dickens & Payne 1978). Specimens were then air-dried or critical point-dried and attached to aluminum stubs by conductive silver paint. Preparations coated with ca. 200 Å of a 60:40 gold/palladium mixture using a Hummer I were viewed on a JSM-35 scanning electron microscope at accelerating voltages of 20 to 30 kV.

For TEM studies, whole antennae or funiculi severed from adult *A. ludens* were immersed 2–8 h in a cold 3% glutaraldehyde fixative (pH 7.4) buffered with sodium cacodylate (Norton & Vinson 1974). A slight vacuum was applied to remove air bubbles adhering to specimens during fixation. Following several cacodylate buffer washes, postfixation was in 2% OsO₄ for 2 h. Dehydration was through a graded series of ethanol and propylene oxide. Embedding was in Spurr's (1969) medium. An LKB ultramicrotome and diamond knife were used to cut thin sections ca. 800 Å thick, which were picked up on copper grids and stained with

lead citrate (Sato 1967) and uranyl acetate. Sections on grids were viewed with either an Hitachi HU-11E or HS-8-2 TEM at an accelerating voltage of 50 kV. For orientation purposes, adjacent 1–2- μm -thick sections were cut and examined by light microscopy.

Electrophysiology. Details of techniques are described elsewhere (Boeckh 1962, Dickens 1979, Dickens et al. 1984). In general, single-ended recordings were made using tungsten wire 0.125 mm in diameter electrolytically sharpened to a tip of approximately 1–2 μm . The recording electrode was positioned under optical control (150 $\times$ –200 $\times$) until contact was made with the funicular surface near the base of an apparent olfactory hair. Although one could discern individual cuticular structures on the funiculus at this magnification, it was not always possible to determine from which hair or even from which type of hair the recordings were made. However, this magnification was suitable for identification of individual sensilla on the scape and pedicel. The indifferent electrode, also a tungsten needle, was inserted into either the scape or head capsule. Recorded signals were amplified and conditioned by a Grass P-15 AC microelectrode preamplifier prior to display on a Tektronix 5113 analog storage oscilloscope. Records of electrical activity were made on polaroid film using a Tektronix C-5A oscilloscope camera.

Fig. 1. SEM of antenna of *C. capitata* female showing shape and segments. a, arista; an, exposed antennal nerve; f, funiculus; pd, pedicel; s, scape; sp, sensory pit.

Fig. 2. SEM of NPS on pedicel of an *A. ludens* female. np, no-pore sensillum.

Trimedlure, a known attractant of the medfly, was used at $0.1 \mu\text{g}/\mu\text{l}$ as the olfactory stimulus. The stimulus compound diluted in hexane was delivered as a $10\text{-}\mu\text{l}$ sample placed on filter paper. Stimulation methodology is discussed elsewhere (Dickens et al. 1984).

Statistical Methodology. Morphometric differences between the sexes of a species were tested for significance ($P < 0.05$) using a *t* test for two means (Ostle 1963).

Voucher specimens have been deposited in the insect collection of the Department of Entomology, Mississippi State University, Mississippi State.

Results

Shape and Segments of the Antennae. Both sexes of all four species have the same shape and number

of antennal segments (Table 1). However, in both *Dacus* species, the combined scape, pedicel, and funiculus is longer in females than males ($P < 0.05$).

The scape articulates with the antennal socket between the large compound eyes (Fig. 1). The pedicel is distally enlarged and dorsally evaginated and joins the greatly enlarged funiculus. From the dorsoproximal region of the funiculus arises an elongated trichoid arista, and a single sensory pit occurs on the medial side of the funiculus in each sex of all four species examined.

Distribution and Structure of Surface Antennal Sensilla. Antennal sensilla were grouped according to location, length, surface structure, and cross-sectional morphology (Altner 1977, Zacharuk 1980). Except for the longitudinally ridged trichoid mechanosensory hairs along the distal margins of both

Table 2. Measurements (μm) of sensilla on the antennae of *A. ludens*, *C. capitata*, *D. cucurbitae*, and *D. dorsalis*. Range derived from at least five measurements of each sensillar type for each sex and species

	<i>A. ludens</i> ♂:♀	<i>C. capitata</i> ♂:♀	<i>D. cucurbitae</i> ♂:♀	<i>D. dorsalis</i> ♂:♀
No-pore				
Length	23-115.0 : 24-181	13-95.0 : 20.0-115	38-80.0 : 28.0-115	43-132.0 : 31.0-117
Diameter base	5.9-7.3 : 4.0-6.3	3.3-6.0 : 3.0-7.5	4.2-5.6 : 3.8-4.7	2.5-7.5 : 3.0-7.0
Diameter mid-height	3.6-4.6 : 1.5-3.1	1.7-4.5 : 2.0-5.0	2.8-4.2 : 1.6-3.9	2.0-5.0 : 2.0-5.0
Thick-walled multiporous pitted sensilla				
Length	12.5-13.8 : 15.7-17.1	12.0-23.0 : 17.3-23.3	16.0-24.0 : 18.0-22.0	16.2-23.5 : 17.7-22.3
Diameter base	1.6-2.3 : 2.0-2.5	2.0-2.3 : 2.0-2.3	2.1-2.3 : 2.0	2.1-2.3 : 2.0
Diameter mid-height	1.6-2.3 : 1.2	0.8-1.27 : 1.0-1.2	1.4-1.5 : 1.3	1.35-1.54 : 1.3
Thin-walled multiporous pitted sensilla				
Length	4.0-7.0 : 8.0-14.0	6.0-11.0 : 6.0-11.0	8.0-14.0 : 8.0-13.0	7.0-11.0 : 9.0-12.0
Diameter base	1.3-1.6 : 1.0-2.5	1.3-1.5 : 1.3-2.0	1.4-1.7 : 1.0-1.7	1.3-2.0 : 1.7-2.3
Diameter mid-height	0.9-1.3 : 0.8-1.3	1.0-1.2 : 0.7-1.3	1.0-1.5 : 1.0-1.2	1.0-1.5 : 1.2-1.7
Multiporous grooved sensilla				
Length	1.7-2.1 : 1.7-3.0	1.4-2.5 : 1.7-2.2	2.3-3.1 : 2.8-3.7	2.3-3.3 : 1.5-2.0
Diameter base	0.8-1.2 : 0.8-1.0	0.7-0.8 : 0.7-0.8	0.8-1.0 : 0.8-1.0	0.8-1.0 : 1.0
Diameter mid-height	0.8-1.0 : 0.7	0.7-0.8 : 0.7	0.6 : 0.6-0.7	0.7 : 0.6-0.8

Fig. 3. SEM of proximal (A), medial (B), and distal (C) regions of funiculus of a *D. dorsalis* female. k, thick-walled MPS; mt, microtrichia; n, thin-walled MPS.

Fig. 4. (A) SEM of thick-walled MPS on the antenna of an *A. ludens* female showing pitted surface. (B) TEM of cross-section of thick-walled MPS of male *A. ludens* near base. (C) TEM of cross-section of thick-walled MPS of female *A. ludens*. cu, cuticle; d, dendrite; db, dendritic branch; k, thick-walled MPS; nt, neurotubule; p, pore; sl, sensillum liquor.

the scape and the pedicel, each type of hair is distributed over the entire funicular surface. The surface of the antennae is also forested with non-innervated setae or microtrichia. These structures are curved, longitudinally ridged (for example, Fig.

Fig. 5. (A) SEM of thin-walled MPS on the antenna of a *D. dorsalis* female showing pitted surface. (B) Higher magnification of surface of thin-walled MPS of a *D. dorsalis* female to magnify pore density. (C) TEM of cross-section of thin-walled MPS of an *A. ludens* male showing porous wall and dendritic branches within sensillum. db, dendritic branch; n, thin-walled MPS; nt, neurotubule; p, pore; sl, sensillum liquor.

Fig. 6. (A) SEM of MPGS on the funiculus of a *C. capitata* female showing no apparent material associated with clefts. (B) Same, with substance apparently exuding from clefts. (C) TEM of a cross-section of a MPGS on the funiculus of an *A. ludens* female showing pores and digitiform nature of cuticular wall. g, mpgs; p, pore.

3A and 5A), and cross-sections show an electron-dense center.

No-Pore Sensilla (NPS). The NPS, located distally on the scape and pedicel, are generally longer along the ventral margin of each of these segments (Fig. 2). These sensilla are distally pointed and longitudinally ridged, with socketed bases. They range in length from 13 μm to >180 μm in the species examined and are the largest sensilla on the antenna (Table 2).

Thick-Walled Multiporous Pitted Sensilla (MPS). Thick-walled MPS are located over much of the funiculus but are more numerous on its distal and lateral portions (Fig. 3 A–C). These, the largest funicular sensilla, range from 12 to 24 μm in length. These distally pointed sensilla have a nonsocketed base and a pitted surface (Fig. 4A). Proximally, the cuticular wall is nonporous and approximately 0.3 μm in diameter. Dendrites of two or three neurons and their associated neurotubules are present in the sensillum liquor within each sensillum (Fig.

Fig. 7. Single-cell response of an NPS on the pedicel of a *C. capitata* male to mechanical stimulation. Arrow indicates onset of stimulus.

Fig. 8. Single cell response of two olfactory cells associated with a thick-walled MPS on the funiculus of a *C. capitata* male to volatiles emanating from hexane solvent and 1 μg of trimedlure. Arrow indicates onset of stimulus.

4B). In the distal region of the sensillum, dendritic branching occurs, and the cuticular wall is somewhat thinner (approximately 0.23 μm) and porous (Fig. 4C). Each dendritic branch has at least one neurotubule. Pores are 186–240 $\text{\AA}$ in diameter and lack pore kettles. In a *C. capitata* male, this sensillar type had a pore density of about 28 pores/ μm^2 .

Thin-Walled Multiporous Pitted Sensilla (MPS). Thin-walled MPS occur over the entire surface of the funiculus; however, they are most numerous in the proximal and ventral regions (Fig. 3 A–C). These sensilla are shorter than the thick-walled MPS and range in length from 4 to 14 μm (Table 2). They have a nonsocketed base and are often curved proximally (Fig. 5A). Numerous pits on the surface (Fig. 5A and 5B) are shown in cross-section to be pores (Fig. 5C). The walls of this sensillar type were approximately 0.1 μm thick and pore openings ranged from 503 to 670 $\text{\AA}$ in an *A. ludens* male. In a *D. dorsalis* female, these sensilla had a pore density of 54–67 pores per μm^2 .

Multiporous Grooved Sensilla (MPGS). MPGS, the smallest sensilla on the funiculus, are 1.4–3.7 μm long (Table 2). These sensilla have a longitudinally grooved surface (Fig. 6 A and B) which, in cross-section, can be seen to be composed of 11 digitiform processes (Fig. 6C). Although the digitiform processes of this sensillar type often appear “closed” (Fig. 6A), occasionally they appear open with a viscous substance associated with them (Fig. 6B). No definitive cell membranes could be identified in cross-sections of these sensilla (Fig. 6C).

Electrophysiology. Single-cell recordings were obtained from NPS on the scape and pedicel, and from thick-walled MPS on the funiculus of the medfly. Short volleys of spikes in response to mechanical stimulation of NPS indicated a mechanoreceptive function (Fig. 7A). Recordings made from cells associated with a thick-walled MPS on the funiculus of a medfly showed cells responsive to

Table 3. Comparison of multiporous pitted sensilla on the funiculus of several tephritid species

Species	Sensillar type	Length	Wall thickness (μm)	Pores/ μm^2
<i>D. oleae</i> ^a	Long single-walled	15	0.3	10
	Short single-walled	10	0.2	15
<i>A. ludens</i>	Thick-walled, multiporous pitted	12–24	0.23–0.3 ^b	28
<i>C. capitata</i>				
<i>D. cucurbitae</i>				
<i>D. dorsalis</i>				
	Thin-walled, multiporous pitted	4–14	0.1 ^b	54–67

^a Data from Hallberg et al. (1984).

^b Measurements made only from transmission electron micrographs of *A. ludens*.

the volatile, trimedlure, a known attractant (Fig. 8 A and B).

Discussion

Each of the tephritid species investigated had similar antennal morphology with regard to the number of segments, types of sensilla, and the presence of a single sensory pit. Although the size of the various sensillar types varied from species to species, their surface structure was consistent. The only significant conspecific morphometric difference was in the total length of the antennae of male and female *Dacus* species (Table 1). The density of cuticular structures on the funiculus made it impossible to count the number of funicular sensilla in scanning electron micrographs. However, the greater length of the female antenna might suggest females have more sensilla than males, as is true of the Queensland fruit fly, *D. tryoni* (Giannakakis & Fletcher 1985).

The NPS described here are similar to mechanoreceptive sensilla described for other insect species (Altner 1977, Dickens & Payne 1978, Zacharuk 1980). Both their socketed base and longitudinally ridged surface structure are characteristic of mechanoreceptive sensilla. Their location along the distal margins of the scape and pedicel, and the phasic nature of the response given by associated neuron(s), indicate their function in the orientation of the antenna.

Both thick- and thin-walled MPS have nonsocketed bases, multiporous pitted walls, and housed dendritic processes. Sensilla with similar structure function as olfactory receptors in several other insect species (Altner 1977, Zacharuk 1980). Hallberg et al. (1984) also described two types (based on surface structure and cross-sectional morphology) of MPS on the funiculus of the olive fly, *D. oleae*. However, a somewhat different situation was presented for the Queensland fruit fly, *D. tryoni*, by Giannakakis & Fletcher (1985), who classified funicular hairs with multiple surface pits in four categories based on pit density and hair shape as discerned from scanning electron micrographs. The multiporous pitted sensilla of the species examined in the current study more closely resemble those of the olive fly (Table 3). Thick- and thin-walled MPS correspond both in length and wall thickness to the long and short single-walled sensilla in the

olive fly. However, pore densities of the two sensillar types in the species we examined are greater than densities observed in the olive fly and more closely resemble those of the sensilla trichodia and sensilla basiconica II in the face fly, *Musca autumnalis* DeGeer (Bay & Pitts 1976).

MPS are similar to those in other insect species (Altner 1977, Zacharuk 1980), including *D. oleae* (Hallberg et al. 1984) and *D. tryoni* (Giannakakis & Fletcher 1985). Sensilla with a similar grooved morphology in locusts (Boeckh 1967, Steinbrecht 1969, Waldow 1970) and a cockroach (Altner et al. 1977) house thermosensory, hygroscopic, or olfactory receptors.

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