

## ANTENNAL SENSILLA OF PARTHENOGENETIC AND BISEXUAL *LISSORHOPTRUS ORYZOPHILUS* (COLEOPTERA: CURCULIONIDAE)

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### ABSTRACT

Antennal sensilla were compared in parthenogenetic females and bisexual adults of rice water weevil, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), using scanning electron micrographs. The antenna of parthenogenetic females and of both sexes of bisexual reproductive weevils consisted of the scape, pedicel, and 6 flagellar segments. Females, regardless of mode of reproduction, had longer antennal segments than males. The 3 adult forms/genders can be correctly classified into their respective groups with a set of discriminant mathematical functions based on 4 morphological measurements of length or maximum width of segments of the antennae. For both sexes, 6 morphological sensilla types were found on the antennae, including hydrofuge scales I (hsI), trichoid sensilla (ts), 2 types of squamiform sensilla (ssI, ssII), tuft hairs (th), and Böhm bristles (Bb). No remarkable sexual differences in the types or distribution of sensilla were found on the antennae among parthenogenetic and both sexes of bisexual reproductive weevils, except for hsI. Both the length and basal diameter of hsI of females were significantly greater than those of the males. The hsI of the parthenogenetic females were significantly longer than those of the bisexual females. The numbers of branches of hsI on the sixth flagellum of the parthenogenetic females were significantly more than on both sexes of bisexual adults. The numbers of branches of hsI of the females were significantly more than those of the males. From the information gained from this scanning electronic microscope study of antennae, we can separate rice water weevils by gender and reproductive mode.

Key Words: antennae, scanning electron micrograph, *Lissorhoptrus oryzophilus*, weevil, parthenogenetic, bisexual

### RESUMEN

Se compararon las sensilas de las antenas de hembras adultas partenogenéticas y bisexuales del gorgojo del arroz de agua, *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), utilizando micrográficas de un microscopio electrónico de barrido. Las antenas de hembras partenogenéticas y de ambos sexos de los gorgojos bisexuales reproductivos consisten de un escapo, un pedicelo y 6 segmentos flagelares. Las hembras independientemente del modo de reproducción, tenían segmentos antenales más largos que los machos. Las tres clases de adultos (el macho y las dos formas reproductivas de hembras) pueden ser clasificados correctamente en sus grupos respectivos con un conjunto de funciones matemáticas discriminantes basado en 4 medidas morfológicas de la longitud o la anchura máxima de los segmentos de las antenas. Para ambos sexos, se encontraron 6 tipos morfológicos de sensilas en las antenas, incluyendo las escamas hidrófugas I (hsI), sensilas tricoideas (ts), dos tipos de sensilas escuamiformes (ssI, ssII), pelos pilosos (th) y setas Böhm (Bb). No se encontraron diferencias sexuales notables en la clase y distribución de sensilas en las antenas entre los gorgojos partenogenéticos y en ambos sexos de los gorgojos bisexuales reproductivos, con la excepción de hsI. Tanto la longitud y el diámetro basal de hsI de las hembras eran significativamente mayores que las de los machos. Las hsI de las hembras partenogenéticas fueron significativamente más largas que las de las hembras bisexuales. El número de apéndices de hsI en el segmento sexto del flagelo de las hembras partenogenéticas fueron significativamente mayores que en ambos sexos de los adultos bisexuales. El número de apéndices de hsI de las hembras eran significativamente mayores que en los machos. De la información obtenida en este estudio sobre las antenas utilizando el microscopio electrónico de barrido, podemos separar los gorgojos acuáticos del arroz por el sexo y por el modo de reproducción.

The “rice water weevil” (RWW), *Lissorhoptrus oryzophilus* Kuschel (Coleoptera: Curculionidae), is one of the most important insect pests of rice in its native region of the southeastern United States and in its introduced regions of Japan, Korea, China (Chen et al. 2005; Saito et al. 2005; Zhu et al. 2005) and Italy (Caldara et al. 2004). Reproduction of the weevil is sexual in its native region and parthenogenetic in California and other areas where introduced (Takenouchi 1978, Zhu et al. 2005; Yang et al. 2009).

Adult antennae of many insect species possess various types of sensilla with different functions that play important roles in various behaviors during adult life (Gao et al. 2007). Antennal sensilla, which function in detecting various stimuli, are implicated in the recognition of food, hosts, or partners (Schneider 1964; Onagbola et al. 2008). The complexity and abundance of insect antennal sensilla are inextricably linked with the diversity of insect behavioral ecology (Fauchaux et al. 2006).

Numerous studies have characterized the antennal sensilla of various species of beetles including weevils by using electron microscope techniques (Mustaparta 1973; Breidbach 1990; Okada et al. 1992; Kim & Yamasaki 1996; Merivee et al. 1997; Sen & Mitchell 2001; Merivee et al. 2002; Said et al. 2003; Romero-Lopez et al. 2004; Tanaka et al. 2006; Crook et al. 2008; Yan et al. 2011). For RWW, there is only 1 report concerning the location, distribution, and type of antennal sensory structures of bisexual weevils (Hix et al. 2003). The differences between bisexual and parthenogenetic RWW in terms of the morphology of antennae have not been determined.

Additionally, since the RWW is an international target of quarantine efforts (Zhu et al. 2005) and has 2 forms of reproduction when intercepted via quarantine or discovered in a new geographical region, specimens need to be classified as to gender and reproductive mode. Currently, there is no rapid and reliable method to identify these 2 forms morphologically or biologically. So, we believe it is necessary to establish a simple and reliable method to distinguish the reproductive forms based on a few measurements of antennae, which are physically durable and useful for reliable identification. In this paper we compare the morphology of the antennae and sensory structures of parthenogenetic and bisexual adult RWW and establish a set of discriminant functions to separate adult specimens into reproductive forms and genders.

## MATERIALS AND METHODS

### Insects

Parthenogenetic RWWs were collected from a rice field in Xiangshan County, Zhejiang Prov-

ince, along the Southeastern coast of China, and killed in a 75% ethanol solution on site and stored at -20 °C until used. Bisexual RWWs were collected in the USA from Beaumont in southeastern Texas, placed in a 75% ethanol solution for 1 wk after which the ethanol solution was removed before shipment to China, where RWWs were stored at -20 °C until used.

### Preparation for scanning electron microscopy (SEM)

For scanning electron microscopy (SEM), the antennae of the parthenogenetic and bisexual RWWs were immersed in glutaraldehyde (2.5%) at 4 °C for more than 8 h (overnight). After washing 3 times with 0.1 M phosphate buffered saline (PBS) (pH 7.4), the samples were fixed in osmic acid for 2 h and then passed through a series of ethanol concentrations (50, 70, 80, 90, 95, and 100%) for 15 min each. The samples were mounted on holders after critical point drying and examined using a SEM of XL30-ESEM (Philips Research, Eindhoven, The Netherlands) after gold coating with K500X sputter coater (Emitech Ltd., Ashford, Kent, United Kingdom).

### Statistical Analysis

In classifying sensilla, the terminology of Schneider (1964), Hix et al. (2003), and Hu et al. (2009) was applied. For measurement of the length of branches of hsI, all branches of an hsI were measured and the average was calculated. The total length of hsI is the length from the top to the base end. Measurements of antennal segments and of each type of sensillum were compared between sexes by the least significant difference (LSD) in a widely-used statistical program (DPS Software, Tang 2010) at  $P < 0.01$  after analysis of variance. Stepwise discriminant analysis was made among the 3 forms/genders of the RWW, using a module in the DPS software (Tang 2010).

## RESULTS

### General morphology of the antennae

The antennae of *L. oryzophilus* adults were made up of a scape, pedicel, and 6 flagellomeres (Fig. 1). The diam of the flagellum increased toward the distal end. Antennal segments of parthenogenetic and bisexual weevils had the same general organization and pattern of sensory structures. Total length of the antenna and the length and maximum width of each antennal segment are shown in Table 1. Total length of the antenna and the length of the scape of parthenogenetic and bisexual females were significantly longer than those of the males. The other segments of the antennae

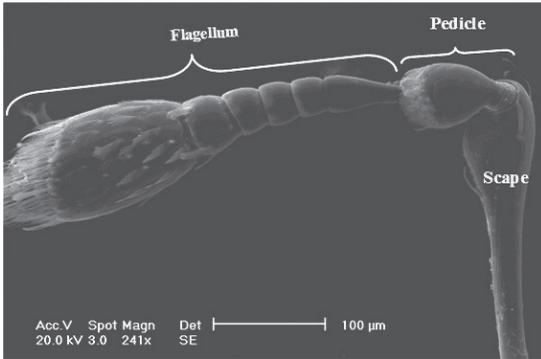


Fig. 1. Scanning electron micrograph of antenna of parthenogenetic *Lissorhoptrus oryzophilus*, showing scape, pedicel and flagellum segments.

of females tended to be longer than those of males, but there was no significant difference (LSD,  $P > 0.01$ ), except for the fifth flagellomere. When the antennae of the 2 types of females were compared with each other, there were no significant differences in lengths of the antennal segments between females of parthenogenetic and bisexual weevils, but the maximum widths of the second to sixth flagellomeres of parthenogenetic females were wider than those of bisexual females and males.

#### Morphological Types of Sensilla

For parthenogenetic females and both sexes of bisexual adults, we observed 6 types of sen-

silla, including hydrofuge scales, trichoid sensilla, 2 types of squamiform sensilla, tuft hairs and Böhm bristles. The location of these sensilla (excluding Böhm bristles) was the same as Hix (2003) observed. Trichoid sensilla (ts) were the most abundant structures on RWW antennae and were concentrated at the apex of the sixth flagellar segment. Hydrofuge scales I (hsI) covered the proximal  $\frac{1}{2}$  of the sixth flagellomere. (Fig. 2A). Ten to 14 squamiform sensilla I (ssI) were found covering the distal  $\frac{1}{3}$  of the surface of the sixth flagellomere (Fig. 2A). These ssI were arrayed along the border separating the ts and the hsI. Between 2 to 6 and about 3 ssI were observed on the fifth flagellomere (Fig. 2A) and scape (Fig. 2C), respectively.

Tuft hairs (th), the second most abundant structures on the antennae, occurred on the proximal end of the pedicel (Fig. 2B), where 5 to 10 squamiform sensilla II (ssII) were surrounded by tuft hairs (Fig. 2B). Besides the 5 types of sensilla mentioned above, which were the same as described by Hix (2003), we also found Böhm bristles (Bb), which are short straight pegs with a blunt tip in a wide articulating socket. These new sensilla were found on the base of the pedicel at the scape/pedicel junction (Fig. 2D, 2E).

Although ssI on the scape were significantly longer in females than in males (Table 2), there was no significant difference between parthenogenetic and bisexual females. The differences in length of a ssI on the fifth flagellomere among the 3 forms/genders were not significant, but the ssI on the sixth flagellomere of parthenogenetic

TABLE 1. THE LENGTH AND WIDTH OF ANTEMMOMERES IN THE PARTHENOGENETIC AND BISEXUAL ADULTS OF *LISSORHOPTRUS ORYZOPHILUS*.

Antennomere	Parthenogenetic Females	Bisexual Males	Bisexual Females
	Length ( $\mu\text{m}$ )		
Scape	300.7 $\pm$ 18.0 A	325.7 $\pm$ 14.8 A	237.4 $\pm$ 10.0 B
Pedicel	79.3 $\pm$ 4.1 A	71.5 $\pm$ 5.2 A	63.7 $\pm$ 1.6 A
1 <sup>st</sup> Flagellomere	64.0 $\pm$ 2.3 A	66.9 $\pm$ 4.4 A	55.6 $\pm$ 1.2 A
2 <sup>nd</sup> Flagellomere	24.2 $\pm$ 0.9 A	27.4 $\pm$ 1.1 A	25.2 $\pm$ 1.0 A
3 <sup>rd</sup> Flagellomere	25.4 $\pm$ 1.0 A	29.1 $\pm$ 0.6 A	26.1 $\pm$ 1.1 A
4 <sup>th</sup> Flagellomere	27.7 $\pm$ 0.9 A	26.2 $\pm$ 1.1 A	24.2 $\pm$ 1.1 A
5 <sup>th</sup> Flagellomere	35.3 $\pm$ 0.6 A	33.7 $\pm$ 0.9 AB	29.9 $\pm$ 1.3 B
6 <sup>th</sup> Flagellomere	193.7 $\pm$ 3.4 A	191.4 $\pm$ 3.0 A	175.1 $\pm$ 10.5 A
Total length of antenna	750.3 $\pm$ 20.3 A	772.0 $\pm$ 22.2 A	637.1 $\pm$ 14.0 B
	Maximum width ( $\mu\text{m}$ )		
Scape	69.1 $\pm$ 4.2 A	68.7 $\pm$ 1.6 A	63.1 $\pm$ 1.0 A
Pedicel	66.6 $\pm$ 1.8 A	60.2 $\pm$ 2.2 AB	55.5 $\pm$ 2.4 B
1 <sup>st</sup> Flagellomere	39.0 $\pm$ 2.0 A	33.4 $\pm$ 1.6 AB	30.5 $\pm$ 1.5 B
2 <sup>nd</sup> Flagellomere	41.0 $\pm$ 1.2 A	33.0 $\pm$ 2.0 B	31.3 $\pm$ 1.5 B
3 <sup>rd</sup> Flagellomere	45.2 $\pm$ 1.5 A	34.0 $\pm$ 1.3 B	32.5 $\pm$ 1.5 B
4 <sup>th</sup> Flagellomere	49.0 $\pm$ 1.8 A	36.5 $\pm$ 1.4 B	36.4 $\pm$ 0.2 B
5 <sup>th</sup> Flagellomere	60.5 $\pm$ 2.4 A	46.7 $\pm$ 1.4 B	45.2 $\pm$ 0.9 B
6 <sup>th</sup> Flagellomere	104.6 $\pm$ 1.5 A	91.4 $\pm$ 1.6 B	93.1 $\pm$ 0.5 B

Values are mean  $\pm$  standard error ( $n = 6$ , i.e., 6 adults of each gender/reproductive mode). The values for each parameter among gender/reproductive modes in a row followed by same letters are not significantly different ( $P > 0.01$ , LSD).

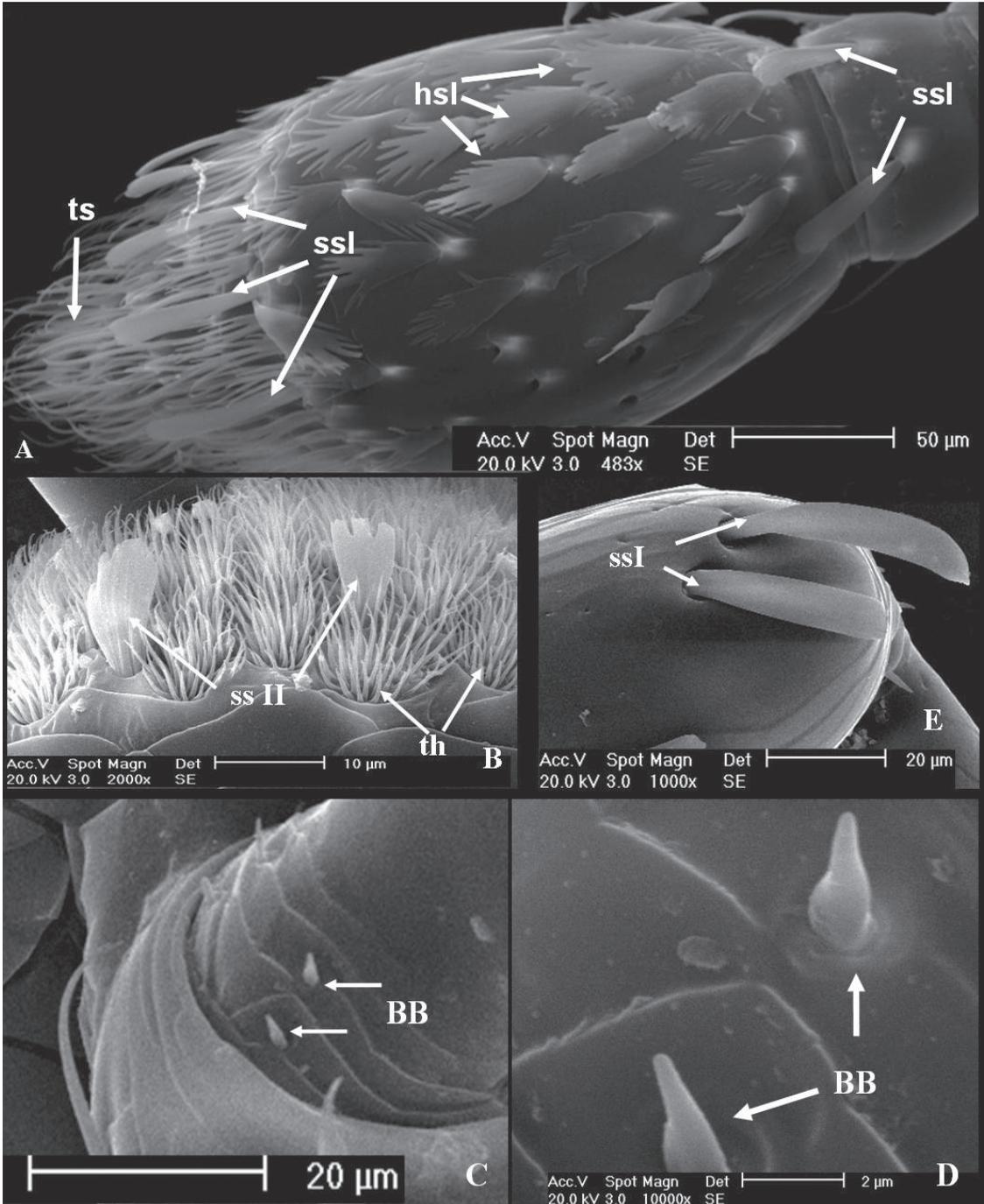


Fig. 2. Scanning electron micrograph showing antennal sensilla of parthenogenetic *Lissorhoptrus oryzophilus*. Hydrofuge scales I (hsl) and trichoid sensilla (ts) in plate A, squamiform sensilla I (ssI) in plate A and C, squamiform sensilla II (ssII) and tuft hairs (th) in plate B, and Böhm bristles (Bb) in plates D and E.

females was significantly longer than that of both sexes of bisexual adults (Table 2). The hsl type was the most variable (in length, basal diam and no. of branches) sensillum between parthenogenetic and bisexual weevils. Both length

and basal diameter of the hsl in females (Fig. 3) were significantly greater than in males; furthermore, the length of the hsl in parthenogenetic females was significantly greater than in bisexual females (Table 2). On the sixth flagel-

TABLE 2. SIZES OF ANTENNAL SENSILLA OF PARTHENOGENETIC AND BISEXUAL ADULTS OF *LISSORHOPTRUS ORYZOPHILUS*.

Sensillum	Location	Form/Gender	Length ( $\mu\text{m}$ )	Width ( $\mu\text{m}$ )
Squamiform sensilla I (ssI) ( $n^* = 10$ )	Scape	Parthenogenetic Females	37.33 $\pm$ 1.60 A	7.93 $\pm$ 10.44 A
		Bisexual Females	35.62 $\pm$ 1.53 A	8.71 $\pm$ 10.73 A
		Bisexual Males	27.18 $\pm$ 11.93 B	7.96 $\pm$ 10.30 A
$n = 10$	5th Flagellomere	Parthenogenetic Females	27.19 $\pm$ 11.36 A	7.39 $\pm$ 10.39 A
		Bisexual Females	22.56 $\pm$ 11.23 A	7.90 $\pm$ 10.53 A
		Bisexual Males	24.06 $\pm$ 10.96 A	5.23 $\pm$ 10.28 B
$n = 20$	6th Flagellomere	Parthenogenetic Females	34.65 $\pm$ 10.49 A	6.00 $\pm$ 10.26 AB
		Bisexual Females	27.95 $\pm$ 10.76 B	6.38 $\pm$ 10.26 A
		Bisexual Males	26.57 $\pm$ 10.79 B	5.30 $\pm$ 10.18 B
Squamiform sensilla II (ssII) ( $n = 10$ )	Pedicle	Parthenogenetic Females	14.37 $\pm$ 10.68 A	6.89 $\pm$ 10.50 A
		Bisexual Females	12.33 $\pm$ 10.43 A	
		Bisexual Males	12.06 $\pm$ 10.66 A	
Hydrofuge scale I (hsI) ( $n = 50$ )	6 <sup>th</sup> Flagellomere	Parthenogenetic Females	26.65 $\pm$ 10.24 A	9.71 $\pm$ 10.17 A
		Bisexual Females	25.03 $\pm$ 10.41 B	9.15 $\pm$ 10.20 A
		Bisexual Males	17.85 $\pm$ 10.32 C	4.89 $\pm$ 10.15 B
Trichoid sensilla (ts) ( $n = 20$ )	6 <sup>th</sup> Flagellomere	Parthenogenetic Females	17.77 $\pm$ 10.94 A	0.93 $\pm$ 10.04 B
		Bisexual Females	20.49 $\pm$ 185 A	1.55 $\pm$ 10.09 A
		Bisexual Males	19.22 $\pm$ 10.75 A	1.12 $\pm$ 10.07 B
Tuft hairs (th) ( $n = 20$ )	Pedicle	Parthenogenetic Females	4.54 $\pm$ 10.30 A	0.47 $\pm$ 10.02 A
		Bisexual Females	3.22 $\pm$ 10.13 B	0.36 $\pm$ 10.02 B
		Bisexual Males	4.17 $\pm$ 10.23 A	0.52 $\pm$ 10.03 A
Böhm bristles (Bb) ( $n = 10$ )	Pedicle	Parthenogenetic Females	3.57 $\pm$ 10.24 A	0.98 $\pm$ 10.07 AB
		Bisexual Females	3.14 $\pm$ 10.24 A	0.88 $\pm$ 10.04 B
		Bisexual Males	2.83 $\pm$ 10.15 A	1.08 $\pm$ 10.04 A

\* $n$ , number of sensilla observed. Values are mean  $\pm$  standard error. The values for each sensillum within a parameter by sexual gender followed by same letters are not significantly different ( $P > 0.01$ , LSD).

lomere of parthenogenetic females the number of hsI branches (Table 3) was larger and the branches were longer than in bisexual adult females and males. Also the ratio of the length of an hsI branch to total hsI length of parthenogenetic females was greater than of bisexual adult females and males. In bisexual adults, females had more branches than males (Table 3). The lengths of other sensilla in females were longer than in males, but most of the differences were not significant (Table 2).

#### Discrimination of Parthenogenetic and Bisexual Forms Based on Antennal Morphological Measurements

Multivariate stepwise discriminant analysis using all 16 morphological variables listed in Table 1, except the total length and sum of the maximum width of every flagellomere, for 5 individu-

als of each reproductive form/gender, resulted in the following 3 discriminant functions:

$$Y1 = -878.4104 + 1.6378X1 + 38.1472 X2 - 23.7646 X5 + 16.0877 X14 \text{ for parthenogenetic females;}$$

$$Y2 = -569.1130 + 1.3665 X1 + 29.5358 X2 - 16.7619 X5 + 11.8034 X14 \text{ for bisexual females;}$$

$$Y3 = -459.1374 + 1.1616 X1 + 26.5655 X2 - 15.1317 X5 + 11.1317 X14 \text{ for bisexual males.}$$

Four variables were selected in the functions ( $\chi^2 = 49.413$ ,  $P < 0.0001$ ) in which  $X1$  = length of scape;  $X2$  = length of pedicel;  $X5$  = length of third flagellomere;  $X14$  = maximum width of fourth flagellomere. If  $Yg(x)$  = maximum [ $Yg(x)$ ], then individual  $x$  belongs to group  $g$ , where  $g = 1, 2, 3$ , corresponding for parthenogenetic females, bisexual females and bisexual males, respectively. When a weevil is required to be identified as to its mode of reproduction or sexual gender,  $X1$ ,  $X2$ ,  $X5$  and  $X14$  should be measured and the all 3

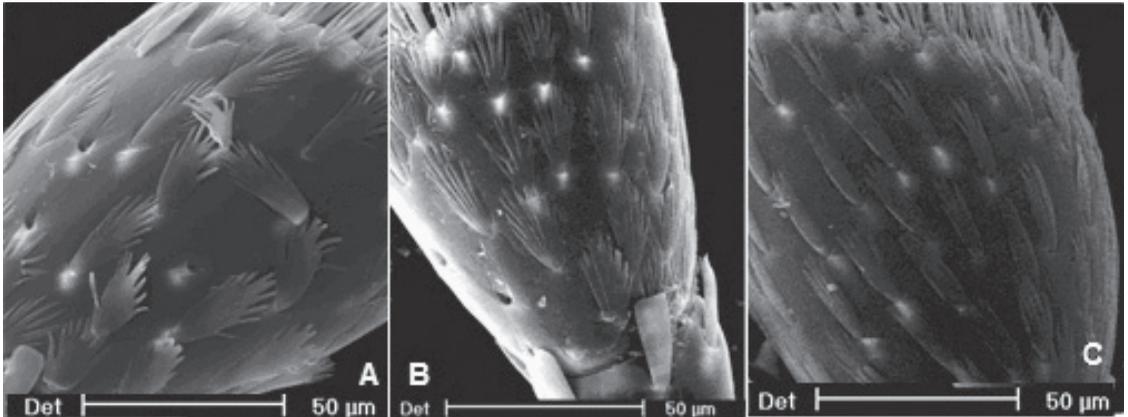


Fig. 3. Scanning electron micrograph showing hydrofuge scales I (hsI) of parthenogenetic and bisexual *Lissorhoptus oryzaophilus*. A) parthenogenetic female weevil; B) bisexual adult female weevil; C) male of bisexual adult weevil.

discriminant values  $Y1$ ,  $Y2$  and  $Y3$  calculated by the above functions. The maximum value among the 3 functions, i.e.,  $\max[Yg(x)]$ , indicates the specimen belongs to group  $g$ . According to the functions, 100% of 15 individuals (5 individuals of each reproductive form/gender) were correctly classified as to each one's mode of reproduction and gender. Thus 3 independent individual samples, 1 sample of each mode/gender that was not used to establish the discriminate functions, without exception were correctly classified. Therefore, the discriminant functions were reliable for identifying the genders and reproductive modes of all specimens.

#### DISCUSSION

The descriptions in this study of the external morphology, and the types and distributions of sensilla on the antennae of bisexual and parthenogenetic adults of *L. oryzaophilus* are largely in conformity with those reported for bisexual adults by Hix et al. (2003). Based upon the measurements of the antennomeres, a set of mathematical discriminant equations was generated, which can be applied to reliably classify RWW adults into corresponding reproductive modes and sexual genders.

There is no obvious sexual dimorphism with respect to sensilla type or distribution. The only

visible difference between the sexes is the morphology of the hsI, whose length, basal diameter, and number of branches in parthenogenetic females is significantly greater than those of bisexual females. In bisexual adults, the length, basal diameter, and number of branches of the hsI sensillum of females were significantly greater than of males. The Bb type described here is similar to the sensilla on the antennae of other coleopteran species (Jourdan et al. 1995; Merivee et al. 1998; Merivee et al. 1999; Merivee et al. 2000; Merivee et al. 2001; Merivee et al. 2002; Crook et al. 2008; Hu et al. 2009). The Bb type is also referred to 'small trichoid sensilla type 3' in *Aleochara bilineata* and *A. bipustulata* (Skilbeck & Anderson 1996), and 'sensilla chaetica' in *Habrobracon hebetor* (Dwerk & Gadallah 2008). Location of Bb at the scape/pedicel junction in many insects, suggests these sensilla are classical mechanoreceptors which perceive antennal position and movement (Jourdan et al. 1995; Skilbeck & Anderson 1996; Merivee et al. 1998; Castrejón-Gómez et al. 1999; Merivee et al. 1999; Merivee et al. 2001; Merivee et al. 2002; Faucheux 2006; Crook et al. 2008; Dwerk & Gadallah 2008; Hu et al. 2009). Reasonably, we can assume that Bbs found on RWW antennae have similar mechano-sensing functions.

Trichoid sensilla (ts) are normally the most common and numerous structures on insects'

TABLE 3. MORPHOLOGY OF HYDROFUGE SCALE I (HSI) ON THE 6TH FLAGELLOMERE.

Gender	Number of branches of hsI	Percentage of branch length to total hsI length
Parthenogenetic Females	$8.6 \pm 0.2$ A	$21.4 \pm 0.76$ A
Bisexual Females	$7.2 \pm 0.2$ B	$16.2 \pm 0.47$ B
Bisexual Males	$4.1 \pm 0.2$ C	$15.5 \pm 0.67$ B

$n = 50$ , total number of hydrofuge scale I (hsI) observed. Values are mean  $\pm$  standard error. Percentage of branch depth to total length of hsI was calculated as: depth of branch depth to total length of hsI. The values in each column followed by same letter are not significantly different ( $P > 0.01$ , LSD).

antennae. These sensilla sometimes are known as 'sensilla trichodea' or 'sensilla trichodea type 2' (Merivee et al. 2002; Chen & Fadamiro 2008; Hu et al. 2009). In moths, they have been demonstrated to be sex pheromone-recognizing sensilla (Mochizuki et al. 1992; Lung et al. 1999; Faucheux et al. 2006). Sensilla of this type are found on the antennae of many beetles and are thought to be olfactory receptors (Jourdan et al. 1995; Bartlet et al. 1999; Merivee et al. 1999; Merivee et al. 2000; Merivee et al. 2001; Merivee et al. 2002; Ploomi et al. 2003; Hu et al. 2009). In the beetles *Hylobius abietis* (Mustaparta 1973), *Agriotes obscurus* (Merivee et al. 1997) and *Psacotheta hilaris* (Castrejón-Gómez et al. 1999), the ts have been shown by electrophysiological methods to be pheromone receptors. The dendrites of ts have been identified as at least 1 of the main sites expressing G-protein  $\alpha$  subunit (Lo G $\alpha$ ), an important signal transduction protein (Kang et al. 2011).

The ssI and ssII, long and filmy with fluted surfaces, occurred on the scape, pedicel and funicular flagellum. The numbers of these sensilla are very few compared to the numbers of ts and th. In some lepidopteran species, ssI and ssII are known to be antennal mechanoreceptors (Schneider 1964; Cuperus 1983; Honda et al. 1983). The ss were also described on antennae of the yellow spotted longhorn beetle, *Psacotheta hilaris* (Dai & Honda 1990). Hix et al. (2003) deduced that the ss on RWW antennae might function in proprioception and mechanoreception.

There is little published information on sensilla hsl and th. The hsl may function in forming a small plastron-like air bubble associated with the club; th may function as hygro- and thermoreceptors when the RWW is out of water (Hix et al. 2003).

The probable function of each type of antennal sensilla, except ts as mentioned above, of *L. oryophilus* described in this paper is mainly based on comparisons with previous SEM investigations of similar sensilla. Future studies of the detailed functions of the antennal sensilla of *L. oryophilus* using transmission electron microscopy coupled with electrophysiological and behavioral experiments are needed to confirm the functions of the different sensilla described in this study.

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