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Sexual dimorphism in the distribution and biometrics of the palpal sensilla of *Coccinella septempunctata*, and a description of a new sensillum

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Abstract: Scanning electron microscopy was used to investigate the palpi and tarsi of *Coccinella septempunctata* to identify the principal chemosensory organs likely to be responsible for pesticide residue detection. The study confirmed that the range of sensilla on the maxillary palps included two types of basiconic sensilla, which are both mechanosensory and chemosensory, and one type of campaniform sensilla. The paper reports the first accurate morphometrics of these sensilla, highlighting sexual dimorphism. Measurements of the terminal segment of the maxillary palp showed a significant interaction between side (left or right lateral) and sex of the insect. A new campaniform sensillum was described for the labial palps, totalling between 12 and 17 located on each labial palp. Biometric measurements established a mean diameter of 2.4 μm for these mechanoreceptors. The only chemoreceptors on the labial palps were confirmed to be the basiconic sensilla described in earlier studies. The numbers of these basiconic sensilla were shown for the first time to be sexually dimorphic, with a mean of 18 in males and 16 in females. Sex differences were also exhibited in the tarsi: in the width of the adhesive pad of the second tarsomere, which was larger in males towards the front of the insect and in females towards the rear of the insect. Explanations for these disparities, and for the function of the newly identified sensilla, are discussed.

Key words: *Coccinella septempunctata*; scanning electron microscopy; ultrastructure; adhesive setae; morphometrics

1 INTRODUCTION

Behavioural responses to pesticide residues have been reported from a number of phytophagous, detritivorous, and predatory arthropods, including hoverflies, parasitic wasps, and ground beetles (Elzen, 1989; Samu and Vollrath, 1992; Wiles and Jepson, 1993; Bayley and Baatrup, 1996; Longley and Jepson, 1996). Such changes have included altered locomotor patterns, searching behaviour, host recognition, and reproductive behaviour including egg deposition, sexual communication and mating behaviour (Banken and Stark, 1998; Salerno *et al*., 2002).

A range of behavioural responses to dimethoate residues has also been recorded from the coccinellid, *Coccinella septempunctata*, which together lead to an avoidance response, characterised by increases in walking rates, decreases in turning rates (Singh *et al*., 2001), and reduced feeding on contaminated prey (Singh *et al*., 2004). Such behavioural modifications have the potential to affect the dispersal and distribution of coccinellids in crop systems, important factors determining the impact of natural enemies on prey populations (Zhu *et al*., 1999; Holland *et al*., 2000). Reduced (sub-lethal) application rates of insecticides have also been shown to affect the distribution of other coleopteran fauna in conventionally managed fields (Jepson and Thacker, 1990; Shah *et al*., 2003). Such behavioural responses are therefore important considerations if coccinellids such as *C. septempunctata* are to be utilised effectively in integrated pest management strategies for aphids (Oakley *et al*., 1996), but the mechanisms by which ladybirds detect the pesticide residues and avoid treated and potentially harmful environments remains poorly understood.

Extensive work has been carried out on the

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searching behaviour and sensory perception of ladybirds with respect to prey location（Stubbs，1980；Shonouda，1999；Ninkovic *et al*.，2001），including their responses to aphid-induced plant volatiles（Zhu *et al*.，1999）. The few studies that have focussed on the physical sensory apparatus involved（Barbier *et al*.，1996）have not examined the role of these organs in the detection of pesticide residues（Yan *et al*.，1982；Barbier *et al*.，1989；Jourdan *et al*.，1995）. However，qualitative descriptions of the sensilla of *C*. *septempunctata* have suggested that most are located on the maxillary palps（Yan *et al*.，1982，1987；Barbier *et al*.，1989；Jourdan *et al*.，1995）. A detailed biometric study is required to identify candidate organs for electrophysiological studies to determine those involved with the detection of pesticides. A limiting factor on the previous work examining the sensilla of coccinellids has been the complicated and time-consuming preparation techniques employed，which have resulted in a low number of specimens（up to five）contributing to each data set（Barbier *et al*.，1996）. As part of an ongoing study into the mechanisms by which coccinellids detect insecticides，this paper reports a morphological study of the palpal sense organs and the tarsi of *C*. *septempunctata* using a technique that speeds up the preparation and reduces the normal distortion that often obscures many of the sensilla.

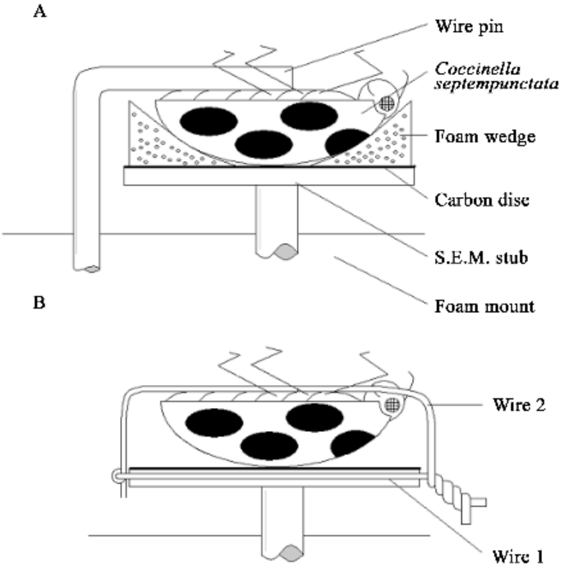

Fig. 1 Specimen mounts for examination under the scanning electron microscope

A：Position of foam wedges and right-angled wire pin to stabilise the insect；B：Position of securing wires.

This study examines the hypothesis that the maxillary palps of *C*. *septempunctata* are the principle sensory organs involved in the detection of pesticide residues and other surface-bound chemicals normally experienced by these animals.

2 MATERIALS AND METHODS

2.1 Insects

C. *septempunctata*（Linnaeus）were cultured using live pea aphids（*Acyrthrosiphon pisum* Harris）at 18℃ – 25℃ under a 16L∶8D photoperiod，following the method of Majerus *et al*.（1989）. Individual insects were anaesthetised using gaseous carbon dioxide for 30 minutes（Symondson and Williams，1997）. Each specimen was then placed in a double-skinned glass vial，lowered into a liquid nitrogen dewar and held 1 cm above the surface for no longer than one minute，killing the insect whilst preventing reflex bleeding.

2.2 Mounting technique

Each specimen was placed on its dorsal surface on a stub，using a double-sided，sticky carbon disc（Agar Scientific）. Several foam wedges were placed around the coccinellid to prevent it rolling（Fig. 1：A），and it was then secured onto the disc using a wire pin，which was anchored into the foam that held the stub. A short length（3 – 7 cm）of 0.22 mm diameter copper wire was wrapped around the stub and the ends were twisted together to secure it（Fig. 1：B，wire one）. The limbs were extended away from the body before a second length of wire（wire two）was then threaded through and around the first，before being stretched over the ladybird on the stub. By positioning wire two under the femuro-tibial joint of each of the three legs on one side of the body，the wire was secured on the opposite side of the stub in such a way that tightening the wire resulted in the ladybird's legs being forced to splay outwards. Hence the undersides of the tarsi were kept clearly visible. The procedure for wire two was repeated on both sides of the ladybird，before the foam wedges and the metal pin were removed.

2.3 Scanning electron microscopy

Specimens were sputter-coated with Ag/Pl using an EMSCOPE 500A sputter-coater for two minutes at 15 mA and examined immediately，using a scanning electron microscope（Philips XL20）. The range of sensilla present were recorded and biometric measurements were taken of the maxillary and labial palps，the tarsal adhesive pads，and any hairs and sensilla present that could be physiologically or chemically responsive（Microscope Control Software for Philips XL20 Scanning Electron Microscope）.

2.4 Analysis

Lengths and diameters of the maxillary and labial palps，the tarsal adhesive pads，and hairs and sensilla were recorded. In addition，densities per mm^2（ρ）were calculated from the mean of five transect counts in both the x plane（c_x）and the y plane（c_y），and from the sample area（xy）μm^2，using equation 1.

$$\rho = \frac{\bar{c}_x \bar{c}_y}{xy} \times 10^6 \qquad (1)$$

A total of 308 measurements were taken of various structures from each specimen examined. The means of these measurements were used for subsequent analysis. Multiple-level full factorial ANOVA and LSD (at $P < 0.05$) was used to identify differences and interactions involving sex, side of insect and in the cases of tarsal measurements, front, middle or rear leg.

3 RESULTS

A mean of 2 684 (± 275) sensilla were found on the ellipsoidal terminal sensory patch (T.S.P.) of the maxillary palps, which had a total area of 28 421.6 (± 1 881.6) μm^2, at a density of 87 456 (± 9 950) mm^{-2}. Seventeen (± 0.262) sensilla were found on the labial palps in a mean total area of 369.3 (± 13.19) μm^2, at a density of 46 165 (± 2 035) mm^{-2} (Table 1). There was no evidence of chemoreceptive sensilla on the tarsi or the tarsal adhesive pads.

3.1 Maxillary palps

In females, the left palpal segments were longer than the right, whereas the left-hand segments were shorter than the right in males (Fig. 2：A). This was demonstrated by a significant negative interaction between sex and side in terminal segment length ($F_{1,18} = 5.131$, $P = 0.039$).

Table 1 Summary of biometric measurements of the palpi and tarsomeres of *Coccinella septempunctata*

Organ	Feature	Sex	Side	Mean length	S.E.M.	Mean breadth	S.E.M.	Number obs/ individual	Number of individuals
Maxillary palp	Terminal segment size			469.76	7.18	380.30	8.99	1	20
	T.S.P.			444.05	8.05	81.70	5.35	1	19
	Bohm sensilla			3.939	0.188	1.708	0.037	20	20
	"Hairs"			25.370	0.869	3.003	0.076	20	20
	Basiconic sensilla Type A (Fig.3b(α))			4.016	0.125	1.847	0.036	20	20
	Basiconic sensilla Type B (Fig.3b(β))	Male		2.862	0.095	$2.000b_1$	0.049	10	10
		Female		2.818	0.137	$1.761b_2$	0.048	10	10
	Campaniform sensilla (Fig.3b(δ))					2.915	0.079	10	20
	Cuticular microtriches (Fig.3b(γ))		Left	2.583	0.141	$2.034a_1$	0.073	10	20
			Right	2.583	0.141	$2.834a_2$	0.089	10	20
Labial palp	T.S.P.					22.129	0.495	1	18
	Basiconic sensilla (Fig.4b(α))			2.991	0.102	1.912	0.041	20	18
	Campaniform sensilla (Fig.4b(β))					2.377	0.089	20	18
Tarsomere 1	Adhesive setal pad		Fore	$596.35c_1$	0.24	$256.094d_1$	0.27	1	20
			Middle	$638.704c_2$	0.24	$219.432d_2$	0.26	1	20
			Hind	$591.562c_1$	0.24	$244.174d_1$	0.24	1	20
Tarsomere 2	Adhesive setal pad	Male		262.40	0.21	$305.8f_1$	0.21	1	29
		Female		284.70	0.20	$309.2f_2$	0.20	1	30

Notes：All measurements are in micrometers (μm) unless otherwise indicated, S.E.M. = Standard error of the mean. Paired measurements followed by the same letter & subscripts within each column were not significantly different ($P < 0.05$).

Each maxillary palp is known to possess a T.S.P., which contains a high concentration of sensilla (Barbier *et al*., 1989；Fig. 3：A). In this study, three different types of sensilla were noted on the terminal segment outwith the T.S.P.: sensilla resembling peg-like Böhm sensilla (*sensu* Jourdan *et al*., 1995)；long, heavily ribbed hairs；long hairs with only faint ribbing. The latter two are considered to be chaetiform and trichoid sensilla respectively (*sensu* Jourdan *et al*., 1995). There was no evidence of a terminal pore on the three sensilla types. For both the hairs and the Böhm sensilla, no size differences were detected between sexes ($F_{1,19} = 3.532$, $P = 0.079$) or side of the body ($F_{1,19} = 0.003$, $P = 0.958$), nor were there interactions considering the sex and side together ($F_{1,19} = 1.531$, $P = 0.234$).

Four distinct structures were located within the marginal and central zones of the T.S.P. of the maxillary palps, of which three were sensilla. In the marginal zone, a non-sensory dentiform cuticular projection with a triangular profile, previously described as a 'microtriche' (Barbier *et al*., 1996), was found. The second structure in the marginal zone was a placoid campaniform sensilla, which was distributed in two or three loosely defined rows embedded amongst the microtriches described above (Fig. 3).

The central zone of sensilla contained two types of basiconic sensilla. The first, basiconic type A, were heavily ribbed, cylindrical, tapered towards the distal end, and had a distinct terminal pore (Fig. 3：B). The second, basiconic type B, was much more cylindrical, with a terminus that was orthogonal in profile (though frequently cambered), in which were a

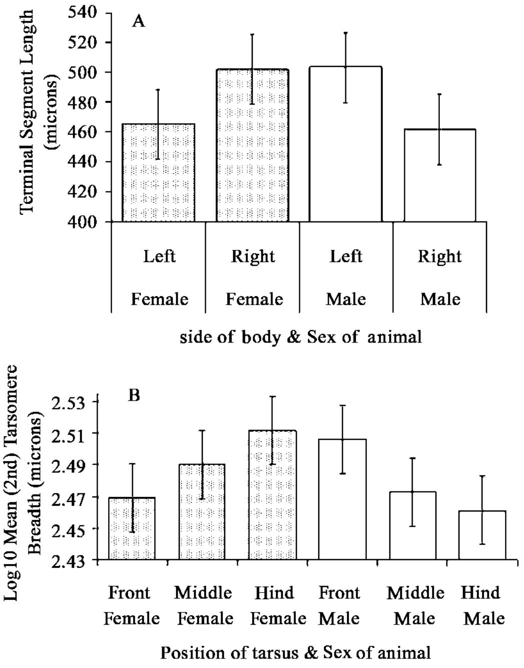

Fig. 2　Examples of sexual， lateral & longitudinal dimorphisms of the sense organs of *Coccinella septempunctata*
A：Length of terminal segment of maxillary palp；
B：Breadth of adhesive pad of second tarsomeres.

number of much smaller pores， separated by structures described as ‘micromamelons’ by Barbier *et al*.（1989）. The protruding portion of the body of the sensilla was situated in a palisaded cuticular base or collar， and the walls of the structure were smooth when compared with basiconic type A.

3.2 Labial palps

The labial palps were elongate， bullet-shaped organs（Fig. 4：A）， with a circular sensory patch at their distal end（Fig. 4：B）. Within the T.S.P. the sensilla were uniformly basiconic in type and of similar appearance to the basiconic type A sensilla of the maxillary palps. However， the basiconic sensilla of the labial palps were significantly smaller than those of the maxillary palps（$F_{1,30} = 18.97$， $P < 0.001$）. Sensilla frequency was also sexually dimorphic（$F_{1,17} = 6.094$， $P = 0.027$）， with significantly more on the male（17.90 ± 0.53， $n = 10$）than the female（16.25 ± 0.25， $n = 8$）labial palps.

A ring of campaniform sensilla， similar in appearance to those on the maxillary palps， bordered the outside edge of the terminal sensory patch（Fig. 4：C）. These organs were significantly smaller than their counterparts on the maxillary palps（$F_{1,37} = 18.97$， $P < 0.000$）. Orientation of the palps restricted establishment of the total number of these structures to three specimens， with 12， 13 and 17 sensilla respectively.

3.3 Tarsi

A large number of setae were distributed over the surfaces of the tarsi. The setae covering the upper surfaces of the first two tarsomeres， and the entirety of the second two tarsomeres， appear to be chaetiform sensilla. There were adhesive pads on the ventral surfaces of the first two tarsomeres， comprised of densely packed setae. Despite differences in the dimensions of the middle pair of tarsal adhesive pads for the first tarsomere（Table 1）， there were no significant differences in the areas of any of the tarsal adhesive pads：all tarsi had a first tarsal adhesive pad area of 142 101.94 mm^2（± 0.1519， $n = 60$）.

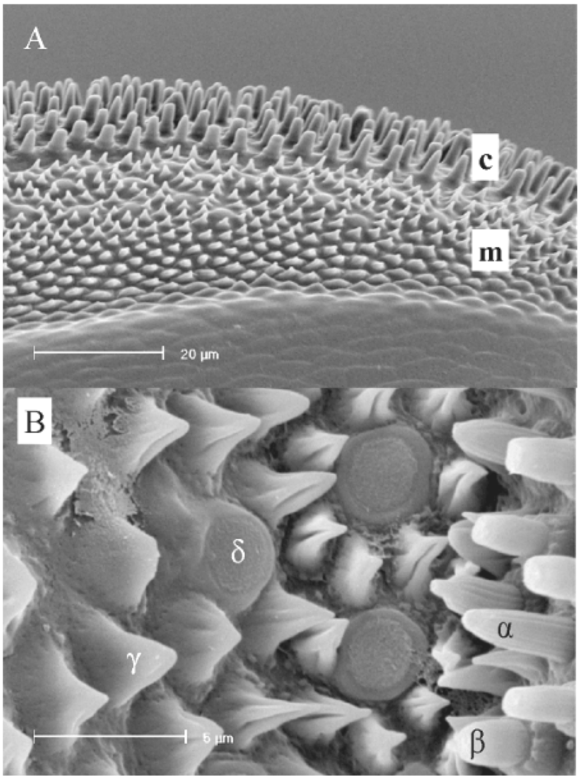

Fig. 3　Maxillary palps of *Coccinella septempunctata*
A：The TSP of the maxillary palps is composed of several distinct zones of sensilla， with bands of dentiform epithelials and campaniform sensilla limited to the marginal zone（m）and circumventing the chemosensitive basiconic sensilla in the central zone（c）；B：（α）：Basiconic Type A sensilla；（β）：Basiconic Type B sensilla embedded in palisaded bases；（γ）：Dentiform epithelials；（δ）：Placoid campaniform sensilla.

Significant differences were found in the lengths（$F_{1,58} = 9.72$， $P = 0.03$）and areas（$F_{1,58} = 6.93$， $P = 0.011$）of the adhesive pads of the second tarsomeres between males and females. The second tarsal adhesive pads of females were larger in both aspects than those of males. The second tarsal adhesive pads of females increased in breadth from the front to the rear， whereas in males， this trend was reversed， manifest in a significant interaction between sex and position（fore， middle or hind）for this variable（$F_{2,58} = 4.27$， $P = 0.020$；Fig. 2：B）.

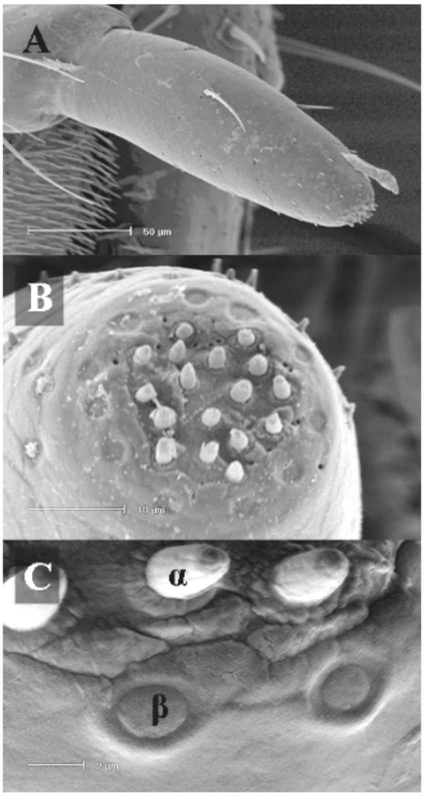

Fig. 4　Labial palps of *Coccinella septempunctata*
A：The terminal segments are bullet-shaped，with a TSP at the distal ends of their terminal segments；B：The TSP is roughly circular，containing basiconic sensilla and numerous pores；C：（α）：The TSP appears to have a single type of chemically responsive basiconic sensilla；（β）：Unlike in the maxillary palps，the associated campaniform sensilla of the labial palps appear in a ring exterior to the TSP.

Within the adhesive pads there were three types of setae：‘adhesive type Ⅰ’setae，‘adhesive type Ⅱ’setae，and‘male setae’（*sensu* Stork，1980）. The ‘male setae’were present on only males in 81.6%（± 4.44%，$n = 76$）of male tarsi. Within males as a group，the setae were present significantly more frequently on the second tarsomere than on the first（C. I. diff. = 24% ± 20.96%，$P < 0.05$）.

The adhesive setae of the first tarsomere were found to be uniformly distributed across all the tarsi（11 230.2 ± 1 553 mm^{-2}，$n = 57$）. The setae of the second tarsal segment however，demonstrated significant differences in their densities in relation to both the side of the body（$F_{1,56} = 4.904$，$P = 0.032$），with the setae on the left being packed tighter than those on the right，and the position of the tarsi，with the setal densities increasing from the rear to the front tarsi（$F_{2,56} = 3.875$，$P = 0.028$）.

Spurs on the tibio-tarsal joint were absent from the first pair of legs（$n = 25$），and present on the middle and hind legs in 90.9%（± 6.3%，$n = 22$）and 100%（$n = 21$）respectively.

4 DISCUSSION

Previous microscopy studies on the palpi and tarsi of *C*. *septempunctata* have provided detailed descriptions of the chemosensilla and adhesive setae，and have given a broad outline of the dimensions of the structures found（Stork，1980；Yan *et al*.，1982，1987；Barbier *et al*.，1989；Jourdan *et al*.，1995）. This study confirms their qualitative findings，has added biometric detail and has extended the range of known sensilla.

The preparation technique used resulted in the ‘highly mobile’（Barbier *et al*.，1996）cuticle of the terminal sensory patch of the maxillary palps being maintained in a convex position. The new technique is more rapid than conventional methods，and results in fewer specimens being spoiled by reflex bleeding. This enabled more accurate population means based on large sample sizes. In making these advances，there was some small trade-off with the fine detail at high magnification and future studies might consider preparing one specimen specifically for qualitative analysis using more traditional methods.

4.1　Sensilla and sexual dimorphism

The ultrastructure of the three sensilla types found on the maxillary palps of aphidophagous coccinellids have been previously described（Yan *et al*.，1987；Barbier *et al*.，1989）. The current study examined the biometrics of both the labial and maxillary palpi of *C*. *septempunctata* identifying new sexually dimorphic features and a degree of bilateral asymmetry. These factors are illustrated through the interaction between sex and side with regard to the length of the maxillary palp terminal segment（Fig. 2：A）. Lateral asymmetry in sensory organs has been previously linked to the evolution of directional sensitivity in birds（e. g. Norberg，1978；Nardi and Bingman，2007）and in nematodes（e. g. Hobert *et al*.，2002；Yu *et al*.，2003）. Were a similar evolutionary pressure at work in coccinellids，it may imply an ability to analyse directional chemical concentration gradients effectively. However，linking such morphological asymmetry to coccinellid sex requires further investigation.

Basiconic type A sensilla showed no evidence of the micro-digitations surrounding the single terminal pore that were described for *S*. *undecimnotata*，*Chilocorus schiodtei*，and *Epilachna chrysomelina*（Barbier *et al*.，1989）.

In the previous study（Barbier *et al*.，1989），the basiconic type B sensilla on the maxillary palps of *S*. *undecimnotata* were considered to be purely chemosensory in nature，and to function in very short-range olfaction. In *C*. *septempunctata*，the external processes of these sensilla were up to 1.55x larger by volume in males than in females. The significance of this volumetric sex difference has yet to be demonstrated.

Possible explanations for the higher number of basiconic sensilla on the labial palps of males found in this study include sexual identification mechanisms employed by coccinellids, and sexually dimorphic dietary preferences. Evidence to support the first explanation is scarce, with no evidence of the use of labial palps in *C. septempunctata* sexual identification, an ability thought to be exclusive to females (Majerus, 1994; Hemptinne *et al*., 1998). Evidence for sexually dimorphic diets in *C. septempunctata* is stronger. Majerus (1994) considered that during periods of egg production and maturation, females feed on a more restricted range of prey. Also, in a laboratory study of feeding intensity in *C. septempunctata*, Wetzel *et al*. (1982) reported that males contained a lower mass of *Sitobion avenae* in their guts than females. Further work is required to link the basiconic frequency to a specific function.

4.2 New structures

Previously undescribed sensilla were discovered on the labial palps that most closely resemble flattened, plate-like (placoid) campaniform sensilla similar to those found on the maxillary palps of aphidophagous ladybirds, and those described for *Calliphora vicina* as ' type 14 sensilla ' (Grunert and Gnatzy, 1987; Krenn and Penz, 1998). These are most likely to be mechanoreceptive. The location of these structures on the labial palp, around the outside of the sensory patch, would allow the sensilla to detect pressure on the palp of sufficient force to deform the tip of the segment. Such pressure may be applied when the palps are used to manipulate food into the buccal opening, or when the terminal sensory patch is placed in direct contact with a substrate being ' tasted '.

The circular shapes of these campaniform sensilla may be indicative of a multipolar firing response. The campaniform sensilla of many insects respond specifically to polarized mechanical stimuli, and their topographies are hence distorted to reflect this and to maximize a unidirectional cuticular deformation, as in the oval campaniform sensilla of the Diptera (Gnatzy *et al*., 1987). The circular appearance of these campaniform sensilla may indicate a non-directional response pattern to deformations in the cuticle. Campaniform sensilla are characterized by a single receptor neurone within each sensillum, and on the palps of *C. septempunctata*, the neurone may generate an action potential in response to any deformation of the sensillum's plate. Directional information would then be obtained by analysing the pattern of firing of all the campaniform sensilla around the tip of the T.S.P. as a group.

4.3 Tarsi

The sexually dimorphic ratio of the breadth of the adhesive pads and density of setae on the second tarsomeres was significant, indicated by the interaction of sex and position. During copulation, the male mounts the female from behind, distributing most of his weight over the rear of the female. Following a latent period of about 45 minutes, males then shake their bodies from side to side (Obata and Johki, 1991; Majerus, 1994). The increase in breadth anteriorly, augmented by the increase in setal density on the second tarsomeres towards the front of the males, will increase their ability to resist dislodgement from the female.

4.4 Maxillary palps as principle sensory organ

The numbers of sensilla on the maxillary palps (> 2 600), suggests that future studies of the sensory abilities of ladybirds should focus on the maxillary palps as the principal chemosensory organs. Comparison of the numbers of sensilla is recognized as a simple and effective way of determining which organs are most sensitive (Symondson and Williams, 1997), and the number of sensilla on the maxillary palps has been found to be more than five times greater than that on other sensory organs, of which, the next closest, the antennae, were found to possess 500 (females) to 540 (males) (Jourdan *et al*., 1995).

By increasing our understanding of the chemical ecology and chemoreception of this ladybird, this investigation provides an essential precursor to mechanistic studies into the behaviour of beneficial arthropods in integrated pest management strategies. Behavioural studies (Singh *et al*., 2001, 2004) indicate that once contact is made with a sprayed substrate, individuals are able to detect the spray residue, before expressing avoidance behaviour. Further electrophysiological work into the range of sensitivities and mechanisms of the maxillary sensilla, coupled with behavioural bioassays, is underway to elucidate this mechanism.

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七星瓢虫唇须感器分布和统计特征的雌雄差异

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摘要：应用扫描电镜观察七星瓢虫 *Coccinella septempunctata* 的唇须和附节，以便确认在感应农药残留时起主要作用的化学感受器。研究证明分布在下颚须上的感器类型包括两种锥形感器（兼有机械感受器和化学感受器的功能）和一种钟形感器。同时本文首次报道了对这些感器精确的形态测量，明确了其性二型性。对下颚须的测量表明其左右末节的长度差异与七星瓢虫的性别之间有明显的相关性。文中还记述了下唇须上一种新的钟形感器，其在每个下唇须上的数量大约为 12～17 个。经测量这些机械感受器的平均直径为 2.4 μm。早期研究中所记述的锥形感器被证实是下唇须上仅有的化学感应器，并且首次证明这些锥形感器的数量与性别相关，雄性平均为 18 个，雌性平均为 16 个。附节上也存在性别差异：第 2 跗节跗垫的宽度在雄性中是从后向前逐渐增大，而在雌性中刚好相反。本文还就这些差异的意义以及新发现感器的功能进行了讨论。

关键词：瓢虫；扫描电镜；超微结构；粘性刚毛；形态测量

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