

Antennal sensilla of grasshoppers (Orthoptera: Acrididae) in relation to food preferences and habits

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The external structure, i.e. number and distribution of sensillae on male and female antennae of 12 species of grasshoppers belonging to Pamphaginae, Catantopinae, Oedipodinae and Gomphocerinae in the grasslands of Inner Mongolia was investigated using scanning electron microscopy. Five major types of antennal sensillae were detected – trichoid, long basiconic, short basiconic, slender and short basiconic, and coeloconic sensillae. Total number of antennal sensillae varied among different sexes, subfamilies, feeding groups, life forms and eco-forms. Males showed significantly more sensillae than females, due to presence of more short basiconic and coeloconic sensillae. Species under Catantopinae showed more long basiconic sensillae than the others. The Oedipodinae had the highest number of slender and short basiconic sensillae and coeloconic sensillae, followed by Catantopinae and Gomphocerinae; while Pamphaginae had the fewest. The total number of sensillae showed the same trend for these two types amongst the subfamilies as well, species which prefer habits on the ground possessed fewer antennal sensillae than species which prefer to stay on plants. The maximal number of antennal sensillae were observed in hygrophytous species, *Chorthippus albomarginatus*, in the 12 grasshopper species investigated, although the data is not statistically significant. The general trend which emerged was that species feeding on grass possessed more antennal sensillae, particularly coeloconic sensillae, compared to other feeding group species.

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1. Introduction

The antennae of insects play an important role in host orientation, food selection and oviposition site selection. It is generally agreed that the sensilla on insect's antennae are not randomly distributed (Zacharuk 1985). Their pattern may reflect the effect of many interacting selection pressures in which size of the individual, sex, developmental stages, feeding habits and habitats are of considerable significance (Chapman 1982). Morphometric studies dealing with distribution and abundance of acridid antennal sensilla have been conducted on *Melanoplus differentialis* (Thomas) (Slifer *et al* 1959), *Melanoplus bivittatus*

(Say) (Riegert 1960), *Hypochlora alba* (Dodge) (Bland 1982), *Locusta migratoria* L. (Greenwood and Chapman 1984; Chapman and Greenwood 1986) and *Schistocerca gregaria* (Forskål) (Ochieng and Hansson 1996; Ochieng *et al* 1998).

The biogeography of the grasshopper fauna, including approximately 150 species in Inner Mongolia, has been studied (Kang *et al* 1991). About 10–15 species are primarily responsible for agricultural damage. The feeding patterns, food selection (Li *et al* 1983, 1987; Li and Chen 1985, 1987) and ecological niches of 12 grasshopper species have been reported (Kang 1990; Kang and Chen 1994a,b). According to these studies grasshoppers in Inner

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Mongolia grasslands can be segregated into five feeding groups (table 1): namely; forbivorous (broad leaf herbs feeders), graminivorous (grasses feeders), mixed-graminivorous (grasses and forbs feeders preferring grasses), mixed-forbivorous (grasses and forbs feeders preferring forbs) and phyto-carnivorous (feed on grasses and/or organic detritus). Their life forms fell into four groups: namely; terricoles (live mostly on the ground and feed on plants – mainly herbs – without climbing them, though they may do so when roosting or perching), plant-terricoles (live in terricoles and plantcoles, preferring terricoles), terri-plantcoles (live in terricoles and plantcoles, preferring plantcoles) and plantcoles (live mainly in herbaceous habitats, including dense thickets of shrubs and herbs with or without an admixture of grasses). Four eco-forms were presented: namely; xerophytous (semi-desert by over grazing), meso-xerophytous (semi-arid, short grasses prairies with much open ground), mesophytous (semi-arid, more uniform and continuous cover of tall grasses) and hygrophytous (humid areas with mixed grass-herb meadows). A previous study has shown the structural adaptation of mandibles and food specificity in grasshoppers in Inner Mongolian grasslands. The mandible structures of graminivorous and forbivorous forms of these grasshopper species entirely agree with their food habits (Kang *et al* 1999). However, the herbivorous mandibles are not distinctly associated with the food habits of these grasshopper species. The difference in number and distribution of various structural and functional types of antennal sensilla may be peculiar to an insect form, and related to its development, habits or habitats as well (Zacharuk

1985). Are there any differences of the antennal sensilla among the grasshoppers that belong to different trophic niches? The research on antennal sensilla of these grasshoppers in relation to their food preferences and habits will further our understanding of the evolution of taxonomic groups with specialized food habits.

In this study, we examined the type, number and distribution of antennal sensilla of the 12 species of grasshoppers, which are categorized into different subfamilies, to elucidate the probable effects of those selection pressures on the sensory equipment. One species each was from subfamilies of Pamphaginae and Catantopinae, two from Oedipodinae and eight from Gomphocerinae. These are co-existing species on grasslands of Inner Mongolia. Each species shows particular characteristics in food habits and adaptation to its habitats as given in table 1.

2. Materials and methods

2.1 Insects

Adult grasshoppers were field collected on the Inner Mongolia grasslands in the summer of 1996. Individuals were processed for scanning electron microscopy (SEM) within less than one day of capture.

2.2 Scanning electron microscopy

Antennae of male and female specimens were removed and placed in 5% KI solution for three days, during which

Table 1. Ecological differentiation of twelve grasshopper species in Inner Mongolia grasslands.

Subfamily/species	Feeding group ^a	Habit		
		Eco-form ^b	Life form ^c	Size ^c
Pamphaginae				
<i>Haplotropis brunneriana</i> (Sauss.)	Forbivorous	Mesophytous	Terricoles	Large
Catantopinae				
<i>Calliptamus abbreviatus</i> (Ikonn.)	Forbivorous	Meso-xerophytous	Terricoles	Small
Oedipodinae				
<i>Oedaleus decorus asiaticus</i> (B.-Bienko)	Gramnivorous	Xerophytous	Terricoles	Medium
<i>Angaracris barabensis</i> (Pall.)	Forbivorous	Xerophytous	Terricoles	Medium
Gomphocerinae				
<i>Mongolotettix japonicus vittatus</i> (Uvr.)	Mixed-forbivorous	Mesophytous	Plantcoles	Small
<i>Omocestus haemorrhoidlis</i> (Charp.)	Phyto-carnivorous	Meso-xerophytous	Mixed-Terricoles	Small
<i>Chorthippus</i> (s.str.) <i>albomarginatus</i> (De Geer)	Gramnivorous	Hygrophytous	Plantcoles	Small
<i>Chorthippus brunneus huabeiensis</i> Xia et Jin	Mixed-gramnivorous	Meso-xerophytous	Mixed-plantcoles	Small
<i>Dasyhippus barbipes</i> (F.-W.)	Mixed-gramnivorous	Meso-xerophytous	Mixed-plantcoles	Small
<i>Myrmeleotettix palpalis</i> (Zub.)	Mixed-gramnivorous	Meso-xerophytous	Mixed-plantcoles	Small
<i>Chorthippus</i> (A.) <i>fallax</i> (Zub.)	Mixed-gramnivorous	Mesophytous	Plantcoles	Small
<i>Pararcyptora microptera meridionalis</i> (Ikonn.)	Gramnivorous	Xerophytous	Terricoles	Medium

^aKang and Chen 1994a; ^bKang and Chen 1992; ^cYan and Chen 1997.

time the solution was refreshed each day. The antennae were then rinsed and air-dried, coated with gold by an ion sputter device (E-102), and the specimen examined in a scanning electron microscope (HITACHI S-2360N).

Since the two antennae of an insect generally symmetrical in the distribution of sensilla, both antennae of an individual were used, one for the investigation of the ventral side and the other for the dorsal side. Numbers of sensilla on both antennae were summed as the sensilla number per antenna. Data of two samples of each sex of a species was averaged, except for the male *Haplotropis brunneriana* due to the shortage of insects.

Antennal sensilla were grouped into five major types: namely; trichoid, long basiconic, short basiconic, slender and short basiconic and coeloconic sensilla, as discussed by Bland (1989). Sensilla lengths (mean and range) were determined by measuring each sensilla type present on eight antennal segments. The sensilla were counted from the region of flagellum, scape and pedicel. The region near the scape and pedicel was regarded as proximal, while near the tip of antenna as distal. Data of sensilla number was analysed by multivariate analysis of variance (MANOVA) and Turkey test (HSD).

3. Results

3.1 Main types of antennae sensilla

Five types of antennal sensilla were observed on the grasshopper antennae. They are long basiconic, short basiconic, slender and short basiconic, coeloconic, and trichoid sensilla (figures 1, 2).

Trichoid sensilla were setiform hairs with a basal insertion on the cuticle. The surfaces of these sensilla were usually ribbed (figure 2) and their length ranged from about 50 μm to 260 μm . These sensilla usually occurred exclusively on the few proximal segments, with the scape and pedicel showing maximum number of these trichoid sensilla. These sensilla are probably mechanoreceptors (Zacharuk 1985; Bland 1989).

Long basiconic sensilla were usually ribbed and their apical pores occasionally visible (figure 3). These sensilla may be contact chemoreceptors (Chapman 1982), and were observed from the first distal segment to the last several proximal segments, and none occurred on the scape or pedicel. Their length ranged from about 20 μm to 120 μm . Instead of the usual peg-like form, finger-shaped long basiconic sensilla were observed on *H. brunneriana* in relatively large numbers (figure 4).

Short basiconic sensilla were stouter than the long basiconic sensilla (figure 5). These are considered olfactory receptors (Chapman 1982; Zacharuk 1985); and ranged from about 8 μm to 30 μm in length and usually occurred

in cuticular depressions. These sensilla were observed on nearly all antennal segments, with a concentration in the middle segments. A typical short basiconic sensillum on *O. decorus asiaticus* is presented in figure 5. We observed variations of this type of sensillum: (i) short basiconic sensillum that is bent to look like an egg on *Ch. albomarginatus*, occurring usually on proximal segments (figure 6); (ii) short basiconic sensilla surrounded by incomplete concentric cuticular depression on *Om. haemorrhoidlis* (figure 7); (iii) short basiconic sensillum surrounded by a ring of cuticle on *M. japonicus* (figure 8); and (iv) short basiconic sensillum with an expanded base on *Ch. albomarginatus* (figure 9) that usually occurred on the several proximal segments.

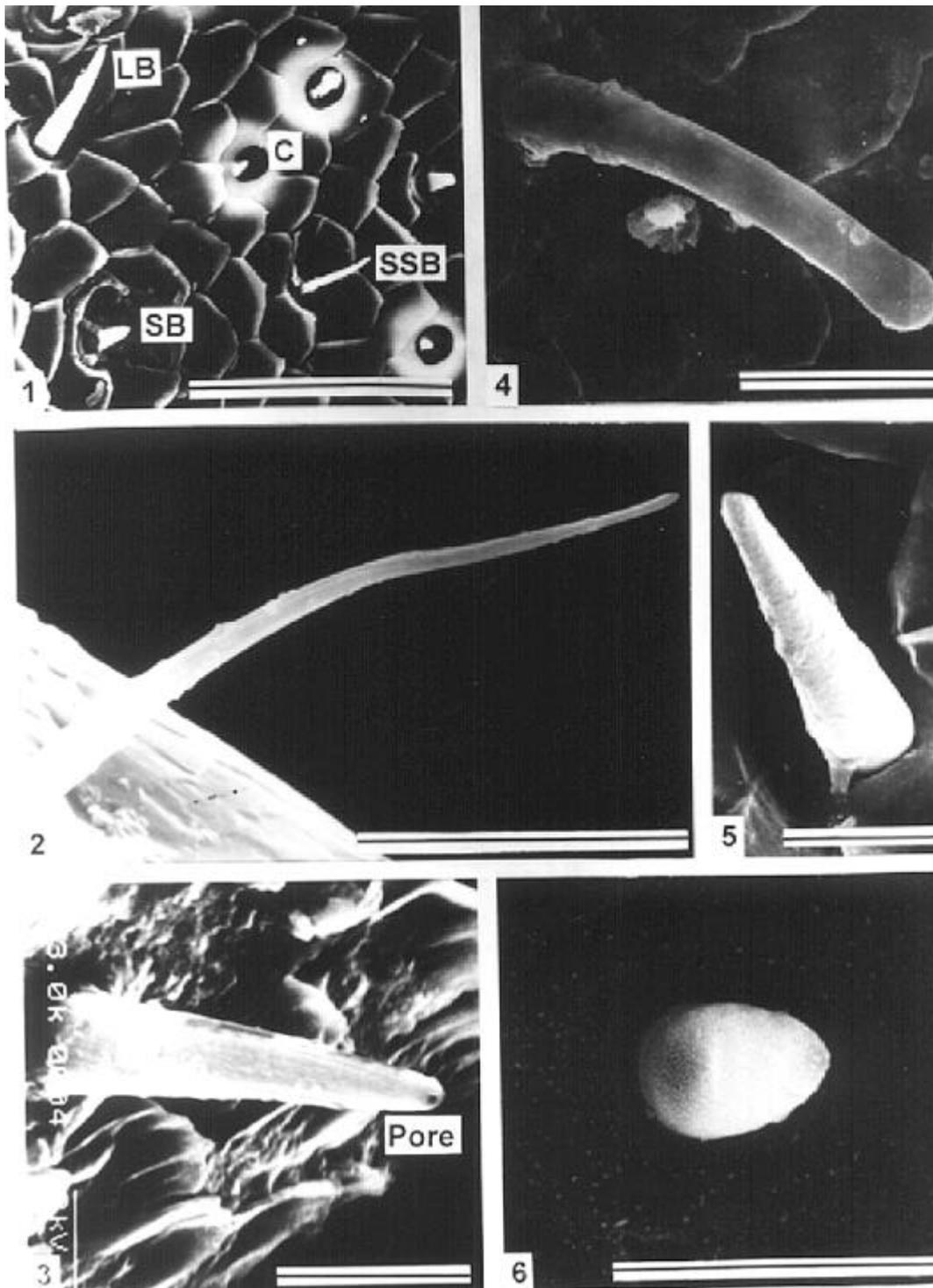
Slender and short basiconic sensilla were thinner in shape than the short basiconic sensilla (figure 10), while the lengths of the two sensilla types were similar. These have a similar distribution to that of short basiconic sensilla; and are considered olfactory receptors (Ameismeier 1987).

Coeloconic sensilla, about 3–5 μm in length, had cavity openings with ribbed pegs sitting on the bottom (figure 11), and apical pores were often observed. These were observed from the first distal segment, occupying most antennal segments, with a concentration in the middle segments. There were few of them on the first several proximal segments. No coeloconic sensilla were observed on the scape and pedicel. These sensilla may be olfactory receptors (Chapman 1982; Zacharuk 1985; Ocheing *et al* 1998).

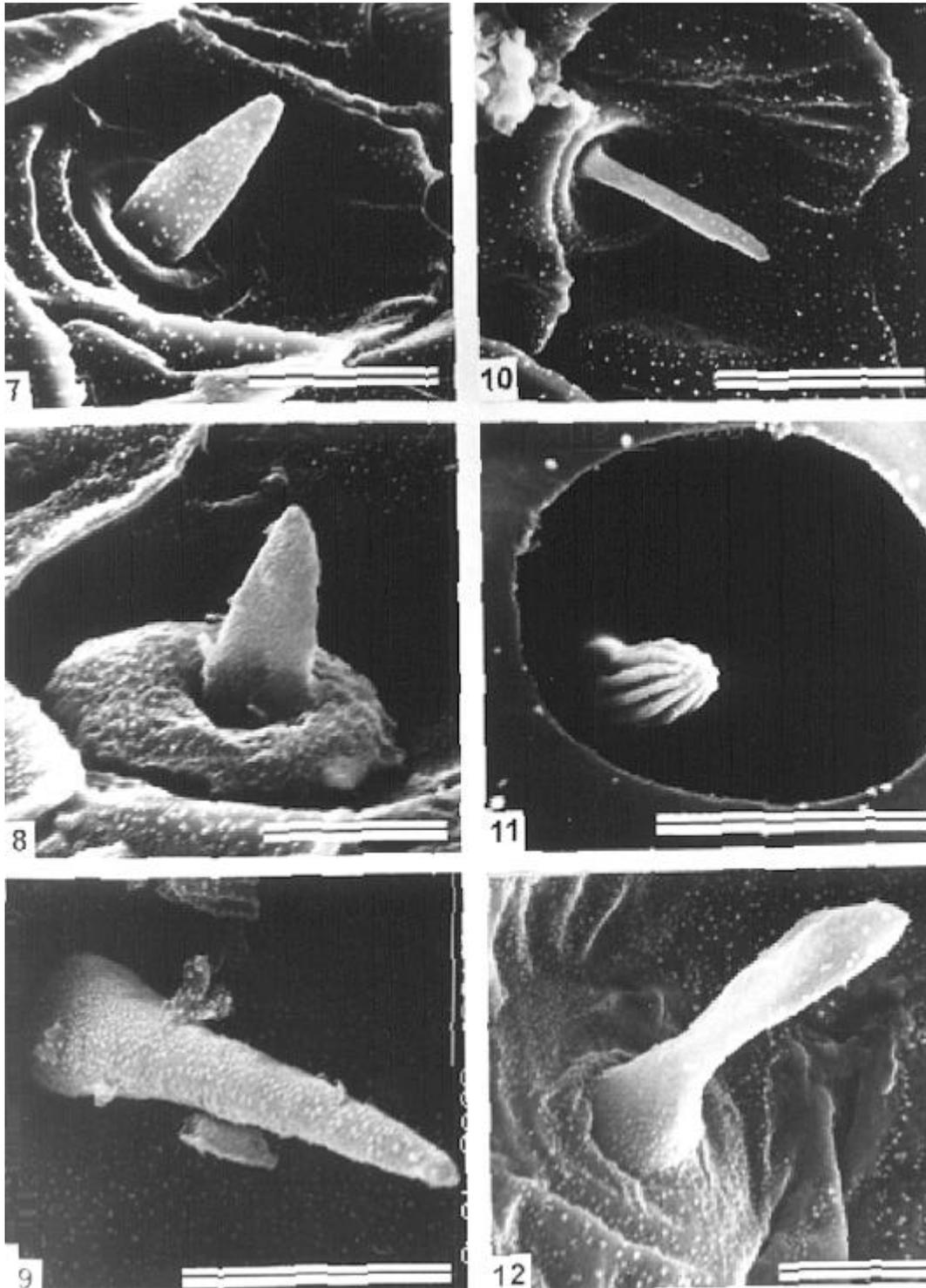
3.2 Other sensilla and structure

In addition to the five major types of sensilla, sensilla with an uncommon shape in relatively low numbers were also observed. More than ten paddle-shaped sensilla, which were 10–20 μm in length, were observed on the middle portion of the antenna of *Ch. brunneus* (figure 12), *Pararcyptora microptera* and *O. decorus asiaticus*. Twelve dome-like sensilla campaniformia were observed on the distal part of antenna of the female *Ch. brunneus* (figure 13). Large pouch-like openings were occasionally present at the joint of scape and pedicel on several species (figure 15). These may be muscle attachments that are involved in antennal movement (Bland 1989).

An irregular oval arrangement of sharply pointed cuticular plates was present on the distal edge of the fifth segment from the apex in most species (figures 14 and 16). The cuticular plates, 90 μm \times 50 μm , generally varied with the size of the species. This structure is widespread in the Acrididea (Key 1985), and has been named as the rosette (Bland 1982), an antennal organ (Blackith and Goto 1974) and lenticular organ (Key 1985) respectively. Their function is unknown.



Figures 1–6. (1) Four major types of antennal sensilla. LB, long basiconic sensillum; SB, short basiconic sensillum; SSB, slender and short basiconic sensillum; C, coeloconic sensillum. Bar = 50 μm . (2) Trichoid sensillum on *O. decorus asiaticus*. Bar = 50 μm . (3) Long basiconic sensillum with ribbed surface and an apical pore on *P. microptera*. Bar = 10 μm . (4) Finger-shaped long basiconic sensillum on *H. brunneriana*. Bar = 20 μm . (5) Typical short basiconic sensillum on *O. decorus asiaticus*. Bar = 10 μm . (6) Egg-shaped short basiconic sensillum on *Ch. albomarginatus*. Bar = 10 μm .

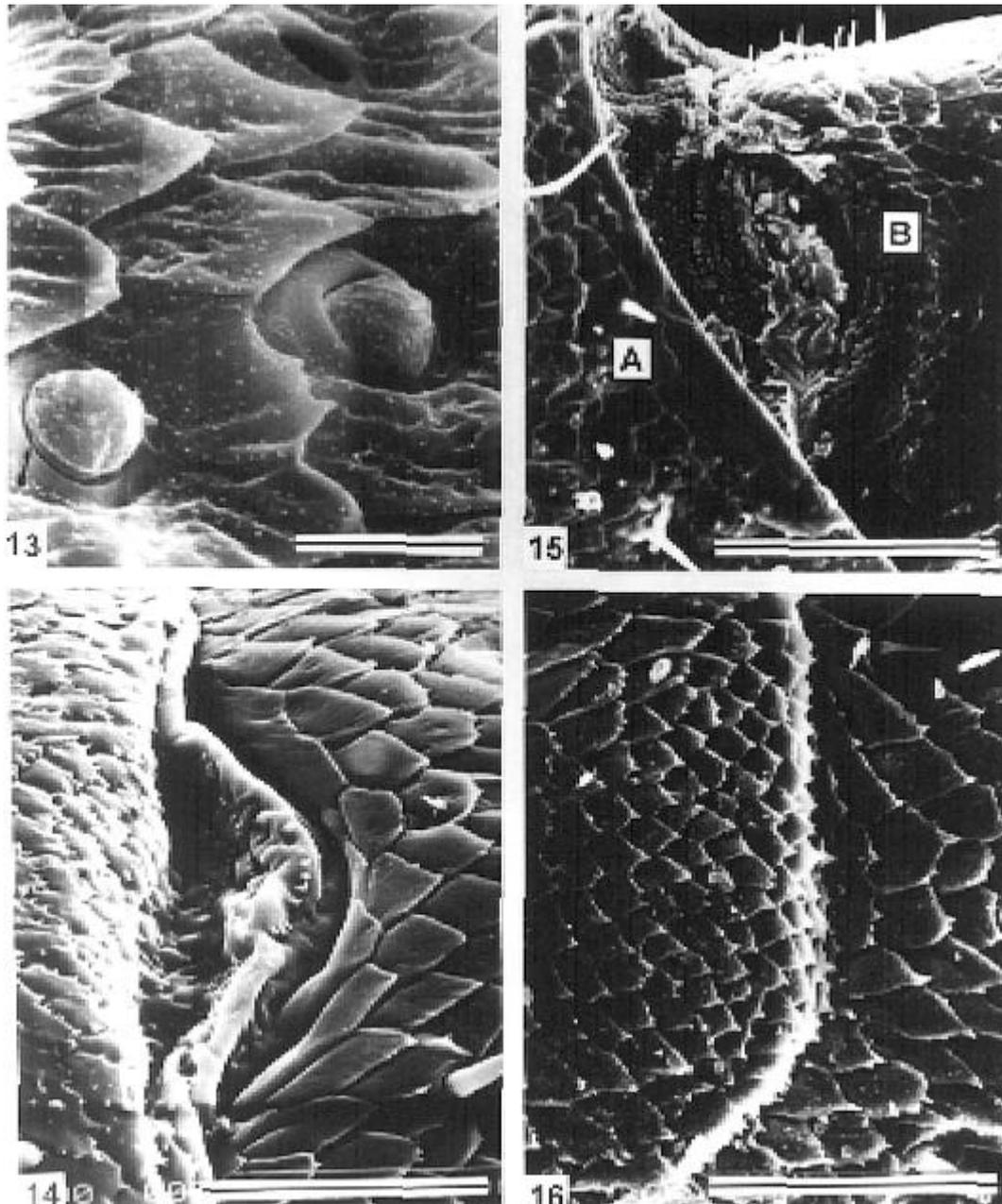


Figures 7–12. (7) Short basiconic sensillum with a wavy cuticular depression on *Om. haemorrhoidlis*. Bar = 10 μ m. (8) Short basiconic sensillum surrounded by a ring of cuticle on *M. japonic*. Bar = 10 μ m. (9) Short basiconic sensillum with an expanded base on *Ch. albomarginatus*. Bar = 5 μ m. (10) Slender and short basiconic sensillum on *M. palpalis*. Bar = 10 μ m. (11) Coeloconic sensillum on *Ch. albomarginatus*. Bar = 5 μ m. (12) Paddle-shaped sensillum on *Ch. brunneus*. Bar = 5 μ m.

3.3 Mean number of sensilla

Mean number of each sensillum type per antenna was different among the 12 grasshopper species (table 2). Trichoid sensilla always had the lowest number amongst the five sensilla types. The fewest trichoid sensilla occurred on *M. japonicus* (F4; M3), the most occurred on *A. barabensis* (F23; M40). The trichoid sensilla of male

Ch. brunneus were much more numerous than female (F3; M20). The largest basiconic sensilla number was on *Ch. brunneus* (F442; M579) and *O. decorus asiaticus* (F529; M479), while the lowest was on *D. barbipes* (F176; M237). Short basiconic sensilla had the highest number among all sensilla types for each subfamily. They were most abundant on *D. barbipes* (F802; M2574) and *Ch. brunneus* (F1083; M1572). *O. decorus asiaticus* (F695;



Figures 13–16. (13) Dome-like sensilla on female *Ch. brunneus*. Bar = 5 μ m. (14) “Lenticular organ” on the distal 5th segment on *C. abbreviatus*. Bar = 50 μ m. (15) Large pouch-like openings positioned at the joint of scape and pedicel on *Om. haemorrhoidalis*. A, scape; B, pedicel. Bar = 10 μ m. (16) “Lenticular organ” on the distal 5th segment on *M. palpalis*. Bar = 50 μ m.

M680) bearing the most abundant slender and short basiconic sensilla and *H. brunneriana* (F102; M197) the fewest. Most coeloconic sensilla occurred on *O. decorus asiaticus* (F524; M1016), and *H. brunneriana* (F190; M490) had the fewest (table 2). No significant differences were found within species for the total number of sensilla.

3.4 Sensilla number of different subfamilies

The number of each type of sensilla, except trichoid and short basiconic sensilla, varied significantly among different subfamilies. Catantopinae bears more long basiconic sensilla than the others. The Oedipodinae had the

highest number of slender and short basiconic sensilla and coeloconic sensilla, followed by Catantopinae and Gomphocerinae; Pamphaginae had the fewest. The total number of sensilla had the same difference with these two types of sensilla among subfamilies. Both sexes have the same trend in sensilla number variation. Males have more abundant short sensilla and coeloconic sensilla than females in Gomphocerinae, which result in the total number difference between sexes in this subfamily ($P < 0.05$).

3.5 Sensilla number of different feeding groups

Mean number of each sensilla type and the total sensilla for species with different food habits was shown among

Table 2. Mean number of each sensillum type per antenna and mean number of sensilla per segment of 12 grasshopper species.

Subfamily/species	Sex	Total number per antenna (Mean \pm SD)						Segment number	Mean/segment
		Trichoid	Long basiconic	Short basiconic	Slender and short basiconic	Coeloconic	Total		
Pamphaginae									
<i>Haplotropis brunneriana</i>	F	5.5	275 \pm 36.8	598.5 \pm 102.5	101.5 \pm 46.0	189.5 \pm 94.0	1170 \pm 206.5	19	61.6 \pm 10.9
	M	5	311	1139	197	490	2142		
Catantopinae									
<i>Calliptamus abbreviatus</i>	F	3.5 \pm 0.7	466.5 \pm 17.7	729 \pm 49.5	406.5 \pm 58.7	388.5 \pm 30.4	1994 \pm 21.2	24	83.1 \pm 4.0
	M	5 \pm 1.4	411.5 \pm 72.8	900.5 \pm 89.8	375 \pm 41.0	371.5 \pm 9.2	2063.5 \pm 68.6		
Oedipodinae									
<i>Oedaleus decorus asiaticus</i> *	F	25 \pm 2.8	529 \pm 31.1	812 \pm 226.3	695 \pm 244.7	524 \pm 60.8	2585 \pm 70.7	25	103.4 \pm 2.8
	M	12.5 \pm 4.9	478.5 \pm 14.8	1543 \pm 65.1	679.5 \pm 92.6	1015.5 \pm 4.9	3729 \pm 12.7		
<i>Angaracris barabensis</i>	F	22.5 \pm 7.8	421.5 \pm 89.8	752.5 \pm 47.4	504.5 \pm 10.6	531 \pm 90.5	2232 \pm 45.3	25	89.3 \pm 1.8
	M	39.5 \pm 3.5	423.5 \pm 20.5	915.5 \pm 40.3	505 \pm 84.9	454.5 \pm 30.4	2338 \pm 118.8		
Gomphocerinae									
<i>Mongolotettix japonicus vittatus</i> *	F	4 \pm 4.2	330 \pm 59.4	641.5 \pm 46.0	400 \pm 50.9	397.5 \pm 105.4	1773 \pm 165.5	20	88.7 \pm 2.0
	M	3 \pm 1.4	303.5 \pm 36.1	1345.5 \pm 251	440.5 \pm 229.8	816.5 \pm 123.7	2909 \pm 140.0		
<i>Omocestus haemorrhoidalis</i>	F	14 \pm 0	314.5 \pm 40.3	726 \pm 26.9	355 \pm 93.3	447 \pm 89.1	1856.5 \pm 195.9	25	74.3 \pm 7.8
	M	7.5 \pm 7.8	352.5 \pm 41.7	963.5 \pm 200.1	359.5 \pm 101.1	435.5 \pm 55.9	2118.5 \pm 204.4		
<i>Chorthippus albomarginatus</i> *	F	12.5 \pm 3.5	375 \pm 82.0	891.5 \pm 275	472 \pm 104.7	566 \pm 83.4	2317 \pm 8.5	25	92.7 \pm 0.3
	M	10.5 \pm 4.9	556.5 \pm 82.7	1941 \pm 134.4	654 \pm 48.1	951 \pm 80.6	4113 \pm 340.8		
<i>Chorthippus brunneus</i>	F	3 \pm 1.4	441.5 \pm 105.4	1083 \pm 123.0	441 \pm 113.1	539 \pm 230.5	2507.5 \pm 570.6	25	100.3 \pm 22.8
	M	19.5 \pm 4.9	578.5 \pm 68.6	1572 \pm 176.8	438 \pm 66.5	786 \pm 97.6	3394 \pm 86.3		
<i>Dasyhippus barbipes</i> *	F	12.5 \pm 4.9	175.5 \pm 21.9	801.5 \pm 113.8	177.5 \pm 31.8	324 \pm 19.8	1491 \pm 152.7	22	67.8 \pm 6.9
	M	23.5 \pm 0.7	237 \pm 52.3	2573.5 \pm 163.3	266.5 \pm 9.2	736.5 \pm 34.6	3837 \pm 189.5		
<i>Myrmeleotettix palpalis</i>	F	14 \pm 2.8	241.5 \pm 60.1	487 \pm 36.8	205.5 \pm 87.0	232.5 \pm 37.5	1180.5 \pm 224.2	23	51.3 \pm 9.7
	M	11.5 \pm 0.7	279.5 \pm 50.2	830.5 \pm 23.3	349.5 \pm 171.8	437.5 \pm 95.5	1908.5 \pm 340.1		
<i>Chorthippus fallax</i>	F	9 \pm 2.8	396.5 \pm 2.1	825 \pm 56.6	595.5 \pm 67.2	434.5 \pm 98.3	2260.5 \pm 88.4	24	94.2 \pm 3.7
	M	5 \pm 4.2	500.5 \pm 85.6	1199 \pm 114.6	451.5 \pm 95.5	572.5 \pm 47.4	2728.5 \pm 147.8		
<i>Pararcyptora microptera meridionalis</i> *	F	9.5 \pm 9.2	371 \pm 90.5	902 \pm 326.7	352.5 \pm 311.8	490 \pm 89.1	2125 \pm 173.9	25	85 \pm 7.0
	M	6 \pm 1.4	340.5 \pm 149.2	1742.5 \pm 166.2	264 \pm 161.2	770 \pm 124.5	3123 \pm 602.5		

*Presents species whose total sensilla number and mean number/segment are significantly different between sexes ($P < 0.05$).

different feeding groups. Graminivorous species possess more number of coeloconic sensilla (statistically significant) than the other feeding groups, also showed the largest total number of sensilla. Statistically significant sexual difference was observed for the total number of sensilla present per antenna in graminivorous, mix-forbivorous and mix-graminivorous species, which are due to more number of short basiconic and/or coeloconic sensilla in males than females.

3.6 Sensilla number of different life forms

Mean number of long basiconic sensilla showed significant differences in females among different life forms. Species of plant-terricoles had significantly shorter basiconic sensilla numbers than those of the other life forms. Males showed more short and coeloconic sensilla than females in terricoles and plantcoles. The total number of the sensilla in males was also more than females in these two life forms species ($P < 0.05$).

3.7 Sensilla number of different eco-forms

Females in xerophytous species possessed more number of trichoid and slender and short basiconic sensilla than the other eco-form species. Males showed more number of short and coeloconic sensilla than females in meso-xerophytous, mesophytous and hygrophytous species. Hygrophytous species had the maximal number of sensilla (F2317, M4113).

4. Discussion

In this study, males had significantly more antennal sensilla than the females. Chapman (1982) and Bland (1989) attributed the dimorphism of insect antennal sensilla number either to the different feeding habits of sexes, or to the attraction of the male by the female pheromone. For instance, both sexes of *O. decorus asiaticus* and *A. barabensis* have the same host plant preference (table 1). However, a sexual dimorphism of body size can be found in *O. decorus asiaticus*. Males are much smaller than females, and they are more vigorous and can travel through a wider range of area than females. More sensilla and higher sensitivity of males to odours may help them locate females and/or host plants as well. In species where the sensilla differences between sexes were small, visual and auditory cues may be more important than olfaction to bring the sexes together. For example, adult *A. barabensis* males hover over 1 to 1.5 m high with great voice for mating. This sound may be one of the attractive cues in their mate finding. Different life forms

(see table 1) between female and male could also be attributed to sexually different antennal sensilla number. In *D. barbipes*, *Ch. brunneus*, and *M. palpalis*, females are mixed-plantcoles, while males are plantcoles due to their smaller size (Yan and Chen 1997). Males had higher sensilla numbers.

Males had significantly more antennal sensilla than the females, mainly due to the abundance of short basiconic and coeloconic sensilla. Both these types are considered olfactory sensilla in some species. Basiconic sensilla were shown to have an olfactory function in the locust *Locusta migratoria* (Ameismeier 1987), *Schistocera gregaria* (Ochieng and Hansson 1996), and other insects such as the white pine weevil *Hylobius abietis* (Mustaparta 1975) and the Colorado potato beetle *Leptinotarsa decemlineata* (Ma and Visser 1987). Coeloconic sensilla have been shown to respond to many host-plant odours in migratory locust *L. migratoria* (Kafka 1970). More basiconic (especially short basiconic) and coeloconic sensilla number on male antennae may indicate that the two sexes have different olfactory sensitivities. For example, the two species of Oedipodinae grasshoppers, *O. decorus asiaticus* and *A. barabensis*, had 44% and 5% more antennal sensilla on males than females respectively. *O. decorus asiaticus* males showed higher electroantennogram (EAG) responses than conspecific females to many plant volatile compounds, while no sexual difference was observed in *A. barabensis* (Chen *et al* 2003). The number of short basiconic and coeloconic sensilla was much more abundant in *O. decorus asiaticus* male than female, while no such sexual difference was found in *A. barabensis* (table 2).

Despite the differences of antennal length and segment number among the 12 grasshopper species, the distribution of sensilla basiconica and coeloconica are observed over the entire antennal flagellum, with a concentration in the middle segments (about segments 7–17). This result is consistent with that of Ochieng *et al* (1998). EAG response to plant volatile compounds were elicited mainly by the sensilla beyond the proximal seven segments. It may also indicate that the basiconica and coeloconic sensilla serve as the major olfactory receptors, and the olfactory perception is mainly accomplished by the distal part of the antenna apart from the seven proximal segments (Chen *et al* 2003).

The total number of antennal sensilla varied greatly among different subfamilies, feeding groups, life forms and eco-forms, which also mainly due to the variation of short basiconic and/or coeloconic abundance. In another words, the abundance of short basiconic and/or coeloconic reflects the grasshoppers' food preference and habitat selection.

A previous study has shown that life form (see table 1) correlated with individual size (Yan and Chen 1997).

Grasshoppers in Inner Mongolia grassland could be divided into three groups: large, medium, and small size groups. The larger were typically terricoles (e.g. *H. brunneriana*), and the smaller were typically planticoles (e.g. *Mongolotettix japonicus vittatus*). In this study, no significant correlation was observed between the number of sensilla and individual size ($P > 0.05$). Besides, males showed statistically significant more number of sensilla than females. Moreover, they were observed to be smaller than females. So the differences in numbers of sensilla could not be accounted for by size differences. However, life form may account for differences in sensilla number. Species that prefer to habitat on ground possess less number of antennal sensilla than species that prefer to stay on plants, although the data was not statistically significant. Therefore, the species preferring to stay on plants may display higher sensitivity to plant odour perception because of the complex surroundings where many plant odours. Grasshoppers on arid grasslands generally have fewer sensilla than those in damp grass forb habitats (Bland 1989). Our studies confirmed this, since species growing in wet habitats showed slightly more number of sensilla than those growing in dry grassland. For example, in the field *H. brunneriana* exclusively inhabits dry desert region. Extremely large body size of *H. brunneriana* makes them difficult to travel around, restricting them to a narrow region, while *Ch. albomarginatus* is the only hygrophytous species in the 12 grasshopper species investigated, preferring damp habitats and it was observed to occupy a wider region. More number of antennal sensilla were found on male *Ch. albomarginatus* than the others (although the difference is not statistically significant) this perhaps reflect the higher sensitivity need more abundant plants than on arid habits. In the field investigation, *Ch. albomarginatus* was the most sensitive to grazing. They could not survive in the grazing grasslands (Kang and Chen 1992).

The external structure of insects reflects their adaptation to food selection. For instance, the mandible structures of graminivorous and forbivorous forms of different grasshopper species entirely agree with their food habits (Kang *et al* 1999). A previous study of the sensilla distribution on mouthpart showed that the graminivorous species tended to have fewer chemoreceptors on mouthparts than forbivorous species of similar size (Chapman and Thomas 1978). In this study, a trend was shown that the number of sensilla per antenna varied; with the graminivorous species showing the maximal number (F2342, M3487) – perhaps because of more number of coeloconic sensilla. This result is consistent with that of Bland (1989). Further, investigations on the difference in distribution of sensilla on antennae and mouthpart are needed. Additionally, the grasshoppers have different food selection ability. *Ch. albomarginatus* and *D. barbipes* have the

most restricted food selection followed by *O. decorus asiaticus* and *M. palpalis*; *M. japonicus vittatus* and *Om. haemorrhoidlis* have the least food selection (Kang and Chen 1994a). Although more number of antennal sensilla were observed on *Ch. albomarginatus* and *D. barbipes* than in *M. japonicus vittatus* and *Om. haemorrhoidlis*, especially in the males (table 2), it is difficult to conclude that more number of antennal sensilla result in restricted food selection. Relatively few specimens per species were used in this study because of the large size of the investigation. We have therefore observed only some particular trends of sensilla distribution of grasshoppers in Inner Mongolia. Further, study is needed to draw more general conclusion.

The olfactory cues received by the antennal sensilla were conducted to the primary olfactory center of the brain, the antennal lobe. A recent study shows that anatomical and physiological properties of the antennal lobe and its neurons to a large extent reflect the changes in olfactory-guided behaviour during development and between phases of the desert locust *Schistocerca gregaria* (Anton *et al* 2002). Thus, a comparative study of the anatomical and physiological characteristics of the antennal lobe in grasshopper species may give us an answer to their host plant preference.

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References

- Anton S, Ignell R and Hansson B S 2002 Developmental changes in the structure and function of the central olfactory system in gregarious and solitary desert locusts; *Microsc. Res. Tech.* **56** 281–291
- Ameismeier F 1987 Ultrastructure of the chemosensitive basiconic single-walled wall-pore sensilla on the antennae in adults and embryonic stages of *Locusta migratoria* L. (Insecta, Orthoptera); *Cell Tissue Res.* **247** 605–612
- Blackith R E and Goto H E 1974 Antennal structures of morabine grasshoppers; *Acrida* **3** 7–17
- Bland R G 1982 Morphology and distribution of sensilla on the antennae and mouthparts of *Hypochlora alba* (Orthoptera: Acrididae) *Ann. Entomol. Soc. Am.* **75** 272–283
- Bland R G 1989 Antennal sensilla of Acrididae (Orthoptera) in relation to subfamily and food preference; *Entomol. Soc. Am.* **82** 368–384
- Chapman R F 1982 Chemoreception: The significance of receptor numbers; *Adv. Insect Physiol.* **16** 247–333

- Chapman R F and Thomas J G 1978 The numbers and distribution of sensilla on the mouthparts of Acridoidea; *Acrida* **7** 115–148
- Chapman R F and Greenwood M 1986 Changes in distribution and abundance of antennal sensilla during growth of *Locusta migratoria* L. (Orthoptera: Acrididae); *Int. J. Insect Morphol. Embryol.* **15** 83–96
- Chen H H, Zhao Y X and Kang L 2003 Comparison of the olfactory sensitivity of two sympatric steppe grasshopper species (Orthoptera: Acrididae) to plant volatile compounds; *Sci. China (Ser. C)* (in press)
- Greenwood M and Chapman R F 1984 Differences in numbers of sensilla on the antennae of solitary and gregarious *Locusta migratoria* L. (Orthoptera: Acrididae); *Int. J. Insect Morphol. Embryol.* **13** 295–301
- Kafka W A 1970 Molekulare wechselwirkungen bei der Erregung einzelner Riechzellen; *Z. Vergl. Physiol.* **70** 105–143
- Kang L 1990 *Influence of grazing activity on the grasshopper community in typical steppe*, Ph.D. dissertation, the Chinese Academy of Sciences, Beijing (in Chinese with English summary)
- Kang L, Li H C and Zhang Z R 1991 Catalogue of grassland insects in Nei Mongol; in *The grassland insects of Inner Mongolia* (eds) Y Ma, H C Li and L Kang (Beijing: Tianze Press) (in Chinese with English summary) pp 91–275
- Kang L and Chen Y L 1992 Temporal and spatial heterogeneity of grassland grasshoppers; *Res. Grassl. Ecosyst.* **4** 109–123 (in Chinese with English summary)
- Kang L and Chen Y L 1994a Trophic niches of grasshoppers within steppe ecosystem in Inner Mongolia; *Acta Entom. Sinica* **37** 178–189 (in Chinese with English summary)
- Kang L and Chen Y L 1994b Multidimensional analysis of resource utilization in assemblages of rangeland grasshoppers; *Entom. Sinica* **1** 178–192
- Kang L, Gan Y L and Li S W 1999 The structural adaptation of mandibles and food specificity in grasshoppers on Inner Mongolian Grasslands; *J. Orth. Res.* **8** 257–269
- Key K H L 1985 Monograph of the Monistriini and Petasidini (Orthoptera: Pyrgomorphidae); *Aust. J. Zool. Suppl. Ser.* **107** 1–213
- Li H C and Chen Y L 1985 Studies on the feeding behaviour of acridoids in the typical steppe subzone of Nei Mongol (Inner Mongolia) Autonomous Region 2. Characteristics of food selection in natural plant communities; *Res. Grassl. Ecosyst.* **1** 154–156 (in Chinese with English summary)
- Li H C, Xi R H and Chen Y L 1983 Studies on the feeding behaviour of acridids in typical steppe subzone of Nei Mongol (Inner Mongolia) Autonomous Region 1. Characteristics of food selection within the artificial cages; *Acta Ecol. Sinica* **3** 214–228 (in Chinese with English summary)
- Li H C, Wang Z and Chen Y L 1987 Food consumption and utilization by three species of acridids (adult stage) in typical steppe; *Acta Ecol. Sinica* **7** 331–338 (in Chinese with English summary)
- Ma W C and Visser J H 1987 Single unit analysis of odor quality coding by the olfactory antennal receptor system of Colorado beetle; *Ent. Exp. Appl.* **24** 520–533
- Mustaparta H 1975 Responses of single olfactory cells in the pine weevil *Hylobius abietis* L. (Col.: Curculionidae); *J. Comp. Physiol.* **97** 271–290
- Ochieng S A and Hansson B S 1996 Morphological types and physiological responses of antennal olfactory receptor neurons in the desert locust, *Schistocerca gregaria* (Orthoptera: Acrididae); *The Proceeding of XX International Congress of Entomology*, Florence, Italy, August 25–31, p 137
- Ochieng S A, Hallberg E and Hansson B S 1998 Fine structure and distribution of antennal sensilla of the desert locust, *Schistocerca gregaria* (Orthoptera: Acrididae); *Cell Tissue Res.* **291** 525–536
- Riegert P W 1960 The humidity reactions of *Melanoplus bivittatus* (Say) (Orthoptera: Acrididae); *Biol. Bull.* **106** 122–128
- Slifer E H, Prestage J J and Beams H W 1959 The chemoreceptors and other sense organs on the antennal flagellum of the grasshopper (Orthoptera: Acrididae); *J. Morphol.* **105** 145–191
- Yan Z C and Chen Y L 1997 Studies on the individual size group and the life form of grasshoppers in typical steppe of Inner Mongolia, China; *Acta Ecol. Sinica* **17** 666–670 (in Chinese with English summary)
- Zacharuk R Y 1985 Antenna and sensilla; in *Comprehensive insect physiology, biochemistry and pharmacology* (eds) G A Kerkut and L I Gilbert (Oxford: Pergamon) Vol. 6, pp 1–69

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