



The larval sensilla on the antennae and mouthparts of five species of Cossidae (Lepidoptera)

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1 **The larval sensilla on the antennae and mouthparts of five species of**

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3 **Running title: Larval sensilla of Cossidae**

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1 **The larval sensilla on the antennae and mouthparts of five species of**
2 **Cossidae (Lepidoptera)**

3

4 Lili Xu^{ab}, Jiahe Pei^a, Tao Wang^c, Lili Ren^{a*}, Shixiang Zong^{a*}

5 **Abstract**

6 Most species in Cossidae family can migrate from one host to a new one in later larval instars,
7 which is different from other bark and wood boring insects. In this study, we selected *Eogystia*
8 *hippohaecolus* (Hua, Chou, Fang and Chen, 1990), *Deserticossus artemisiae* (Chou et Hua,
9 1986), *Deserticossus arenicola* (Staudinger, 1879), *Yakudza vicarious* (Walker, 1865), and
10 *Streltziella insularis* (Staudinger, 1892) to understand how these species locate new hosts in
11 their larval stages. Scanning electron microscopy was used to determine the typology, morphology,
12 number and distribution of sensilla on the antennae, maxillary palps, galeas, and labial palps of
13 these five species. There were no differences in typology, morphology and number of sensilla
14 between the five species. We observed antenna with three to four short sensilla basiconica, two
15 sensilla chaetica, four sensilla basiconica, and one sensillum styloconicum. The maxillary palp had
16 seven short sensilla basiconica, one sensillum digitiformium, and two sensilla placodea. The
17 maxillary galea had three short sensilla basiconica, two sensilla styloconica, and one sensillum
18 chaeticum. The labial palp had one short sensillum basiconicum and one sensillum styloconicum.
19 Our results will provide a basis for further studies on the feeding, host-transfer behaviors, and
20 electrophysiology of this group of forest pests.

21

22 **Key words:** Larva; Host migration; SEM; Carpenter moth; Cossidae.

1 Introduction

2 Bark and wood boring insects reside inside living xylem or the phloem of trees, at least during part
3 of their life cycles. Most of these insects, such as Bark beetles, Bark Weevils, Buprestids, and
4 Longhorn beetles (Lieutier et al. 2004) will not migrate from the tree they bored into during larval
5 stages. Only a minority, such as Cossidae and Aegeriidae, show host migration (Gao and Qin 1983;
6 Hu et al. 1987; Zong et al. 2005; Wang et al. 2011; Yang et al. 2012b; Liu 2013; Sun et al. 2015).
7 *Eogystia hippophaecolus* (Hua, Chou, Fang and Chen, 1990), *Deserticossus artemisiae* (Chou et
8 Hua, 1986), *Deserticossus arenicola* (Staudinger, 1879), *Yakudza vicarius* (Walker, 1865), and
9 *Streltziella insularis* (Staudinger, 1892), are five species in the family Cossidae Leach of
10 Lepidoptera, and were previously classified in the same genus *Holcocerus* Staudinger (Yakovlev
11 2006). The larvae of these species bore into the trunks and roots of foliage trees species, which
12 can weaken and lead to the death of the plants. The larvae of these insects have caused
13 enormous losses to many forestation projects in China, and have adversely affected the
14 implementation of desertification control and the urban greening programs (Hua et al. 1990). *E.*
15 *hippophaecolus* is the major insect of the sea buckthorn (Zong et al. 2005, 2006). The hosts of *D.*
16 *artemisiae* are *Artemisia ordosica* Krasch and *Salix mongolica* Siuzew (Sun et al. 2015). *Y.*
17 *vicarius* infests *Ulmus pumila* L., *Robinia pseudoacacia* L., *S. babylonica* L., *Populus* spp., and
18 other broadleaf trees (Tong 2013; Yang et al. 2012a). The hosts of *S. insularis* are *Broussonetia*
19 *papyrifera* (L.) Vent., *Sophora japonica* L., *U. pumila* L., *Fraxinus chinensis* Roxb., and *Ginkgo*
20 *biloba* L., among others. The above five species, except *Y. vicarius*, are reported to engage in
21 inter-hosts migration, when the host can no longer offer sufficient nutrients or is broken by the
22 wind, the larvae crawl onto the soil or the surface of the ground under the tree and migrate to

1 another host plant. Besides, the larvae of five species, except *S. insularis*, conduct intra-host
2 migration, moving from the trunk to the roots to overwintering (Gao and Qin 1983; Hu et al. 1987;
3 Zong et al. 2005; Wang et al. 2011; Yang et al. 2012b; Sun et al. 2015).

4 The sensilla of insect larvae play a significant role in self-protection, host selection, food
5 searching, and feeding behavior (Zacharuk 1980; Zacharuk and Shields 1991; Cobb 1999). The
6 sensilla of lepidopteran larvae are involved in recognizing food high in nutrient content, and
7 excluding interference from surroundings. (Boer and Hanson 1987; Albert 2003). Sensilla in
8 larvae also provide the larvae with information on temperature, humidity, and danger in the
9 environment. A large number of cephalic sensilla have been observed in lepidopteran larvae,
10 including phytophagous pests such as *Choristoneura fumiferana* (Clemens, 1865) (Albert 1980,
11 2003), *Antheraea assamensis* Helfer, 1837 (Goldsmith et al. 2014), the suborder Ditrysia (Grimes
12 and Neunzig 1986), *Manduca sexta* (L., 1763) (Kent 1987), *Mamestra configurata* Walker, 1856
13 (Shields 1994), *Homoeosoma nebulella* Denis and Schiffermüller, 1775 (Faucheux 1995), and
14 *Lymantria dispar* (L., 1758) (Shields 2009), among others. Previous research on the sensilla of
15 boring insects has primarily focused on fruit borers: for example, *Helicoverpa armigera* (Hübner,
16 1808) (Keil 1996; Tang et al. 2014), *Carposina sasakii* Matsumura, 1900 (Liu et al. 2011), and
17 *Grapholita molesta* (Busck, 1916) (Song et al. 2014), among others. However, there have been no
18 studies of the cephalic sensilla of bark and wood boring insects that engage in host migration.
19 With the aim of gaining a better understanding of the olfaction and gustation mechanisms that
20 affect behavior during trunk host migration, we investigated the typology and distribution of
21 cephalic sensilla on the antennae, maxillary palps, galeas, and labial palps of the larvae of five
22 Cossidae species. The results of this study will provide a theoretical foundation and practical

1 guidance for future electrophysiological and electrochemical experiments on these larvae.

2 **Materials and methods**

3 *Insects*

4 The larvae of *E. hippophaecolus* were collected in Jianping, Liaoning Province. The larvae of *Y.*
5 *vicarius* and *D. artemisiae* were collected in Yanchi, Ningxia Hui Autonomous Region, in January
6 2014. The larvae of *S. insularis* were collected in the Haidian District, Beijing, in May 2014. The
7 larvae of *D. arenicola* were collected in Yulin, Shanxi Province. The larvae were preserved in 75%
8 ethanol. The total larvae developing stage number varied in those five species. However, all the
9 larvae of these five species observed in our study were in their last developing stage.

10 *Scanning electron microscopy*

11 The heads of the larvae were excised under an anatomical microscopy (Leica EZ4D, Germany),
12 and were washed with phosphate buffer solution and 75% ethanol for 3 min each. After washing,
13 the specimens were dehydrated in an ascending series of ethanol (80%, 85%, 90%, 95%, 100%,
14 and 100% for 20 min each). The specimens were fixed on a stub, air-dried in natural conditions for
15 24 h, and then sputter-coated with gold by an E-1010 sputter ion instrument (HITACHI, Japan).
16 After these procedures, the samples were examined with an S-3400N scanning electron
17 microscope (HITACHI, Japan) at an accelerating voltage of 0.5–30 kV.

18 *Data analyses*

19 The types of sensilla were identified according to Schneider (1964), Zacharuk (1980), Zacharuk
20 and Shields (1991), and Sen (1988). The numbers of sensilla on antenna, maxillary palp, galea,
21 and labial palp were low and easily identified, which permitted the direct counting of sensilla. All
22 sensilla were counted and measured for length and diameter, and the means and standard

1 deviations were calculated from at least ten larvae of each species. ImageJ (Broken Symmetry
2 Software, USA) was used for the measurements, and the data calculations and statistical analyses
3 were performed with Microsoft Excel 2003 (Microsoft, USA). The micrographs of the sensilla
4 were processed using Photoshop CS6.0 (Adobe Systems, USA). The schematic representation was
5 rendered using Easy PaintTool SAI (SYSTEMAX Software Development, Japan).

6 **Results**

7 The morphology of the heads of the five species of larvae is shown in Fig. 1. All species had six
8 ocelli and numerous sensilla chaetica.

9 **Antenna**

10 ***General morphology of the antenna***

11 The antennae of the larvae were located on both sides of the head and lateral to the mandibles
12 within sunken antennal sockets, which allowed the antennae to extend and contract (Fig. 1). The
13 antennae had three segments, and the lengths of each segment are shown in Table 1. The longest
14 segment was the first, with a junctional membrane without sensilla, and the second segment,
15 embedded within the first segment, was cylindrical and could retract into the first segment. The
16 third segment was similar to the second in morphology, although shorter, and was located dorsally
17 on the second segment (Fig. 2).

18 ***Typology and morphology of sensilla***

19 The typology of antennal sensilla did not differ between the five species. The sensilla types on the
20 antennae included short sensilla basiconica, sensilla basiconica, sensilla styloconica, and sensilla
21 chaetica (Fig. 3). The morphological characteristics of these sensilla are shown in Tables 2 and 3.

22 ***Short sensilla basiconica***

1 The two types of short sensilla basiconica were similar in morphology with short and upright
2 cones. Those two types, short sensilla basiconica type 1 and short sensilla basiconica type 2, were
3 distinguished based on their length, basal diameter, shape, and whether with a terminal pore.

4 *Short sensilla basiconica type 1.* These sensilla had inconspicuous sockets, rigid and stout basal
5 shafts that gradually narrowed to the tips, which were blunt and without terminal pore. The wall of
6 the shaft was smooth with a comparatively large ecdysial pore that faced the middle of the second
7 segment of the antenna (Fig. 4A).

8 *Short sensilla basiconica type 2.* These sensilla located in the slight elevated sockets and were
9 hemispherical in shape. The surface was smooth, the tip was blunt and without terminal pore, but
10 with an ecdysial pore (Fig. 4B).

11 *Sensilla basiconica*

12 The sensilla basiconica were cones with thick basal shafts, blunt tips, and slightly raised sockets. A
13 large number of tiny sensillar wall pores were observed. The two types of these sensilla, b.1 and
14 b.2, were distinguished based on the length, distribution pattern of the wall pores, and the basal
15 diameter.

16 *Sensilla basiconica type 1.* These sensilla were abundant with wrinkled wall pores and a circle of
17 round ecdysial pores on the basal shaft. Each circle contained four to six round cuticular pores
18 (Fig. 4C).

19 *Sensilla basiconica type 2.* These sensilla were cone-shaped with a round ecdysial pore on the
20 blunt tips and wrinkled wall pores. The basal diameter and length were much smaller than those of
21 b.1 (Fig. 4D).

22 *Sensilla styloconica*

1 These sensilla (sensilla styloconica type 1) were structured in two parts with smooth parts. The
2 upper part of a sensillum styloconicum was the sensory cone with blunt tip without terminal pore
3 and the lower part was the stylus which resembles a circular table in shape. The ratio of the length
4 of the sensory cone and the length of the stylus was approximately 2:1 (Fig. 4E).

5 *Sensilla chaetica*

6 Overall, the characteristics of sensilla chaetica were similar, and these sensilla were slender, tall,
7 and straight, similar to pointed spines with sharp tips, with smooth walls. All these sensilla were
8 without sensory pores. Based on the morphological characteristics of the socket, and the length
9 and basal diameter, these sensilla were separated into two types, i.e., sensilla chaetica type 1 and
10 sensilla chaetica type 2.

11 *Sensilla chaetica type 1.* They had shallow, longitudinal grooves along the shafts and deep, round,
12 flexible sockets (Fig. 2).

13 *Sensilla chaetica type 2.* They had smooth walls and swollen, tight sockets. The bases of the
14 shafts were broad, but the apices were sharp. Compared with sensilla chaetica type 1, the length
15 and basal diameter of sensilla chaetica type 2 were significantly smaller (Fig. 4F).

16 *The distribution of sensilla*

17 The distribution of sensilla on the antenna is shown in Fig. 4, and the schematic representation of
18 the dorsoanterior aspect of the distribution of the sensilla on the antenna is shown in Fig. 10A. No
19 sensilla were found on the first antennal segment. On the second segment, two sensilla chaetica
20 (sensilla chaetica 1 and sensilla chaetica 2), one sensillum basiconicum type 1, one short sensillum
21 basiconicum type 1, and one or two short sensilla basiconica type 2 were observed. The sensillum
22 chaeticum type 1 was on the ventral surface, and the sensillum chaeticum type 2 was on the dorsal

1 surface, of the distal segment. Two sensilla basiconica type 1 located on the distal margin of the
2 segment. The short sensillum basiconicum type 1 located between the sensillum chaeticum type 1
3 and the sensillum basiconicum type 1 on the ventral surface, and the short sensillum basiconicum
4 type 2 distributed between the third segment and the short sensillum basiconicum type 1. On the
5 third segment, one sensillum styloconicum type 1 was on the external, ventral surface, one
6 sensillum basiconicum type 1 was on the ventral surface, and one sensillum basiconicum type 2
7 was on the dorsal surface. One short sensillum basiconicum type 1 was observed in the middle of
8 the segment.

9 **Maxillary palp**

10 *General morphology of the maxillary palp*

11 The maxillary palp located on the palpifer and had two segments. The lengths of the larval
12 maxillary palps of the five species are presented in Table 1. The first segment was cylindrical and
13 the longest, and its shape resembled a conical frustum (Fig. 5).

14 *Typology and morphology of sensilla*

15 The typology of sensilla of the maxillary palps was not different among the five species of larvae.
16 The types of sensilla on the maxillary palp included short sensilla basiconica, sensilla digitiformia,
17 sensilla placodea, and sensilla styloconica (Fig. 6). The morphological characteristics of the
18 sensilla are presented in Tables 2 and 4.

19 *Short sensilla basiconica*

20 *Short sensilla basiconica type 3.* They had inconspicuous sockets and smooth walls. The tips were
21 always flattened and were blunt, with a terminal pore. The basal and apical diameters were
22 approximately equal (Fig. 7A).

1 *Short sensilla basiconica type 4.* The basal shafts of these sensilla were thick and narrowed
2 gradually to the tips, which were blunt and had a round terminal pore. The length of short sensilla
3 basiconica type 4 was shorter than that of the other types (Fig. 7B).

4 *Short sensilla basiconica type 5.* Sensillum of this type had inconspicuous socket and blunt tip
5 with a terminal pore (Fig. 7C).

6 *Sensilla styloconica*

7 The basal regions of these sensilla (sensilla styloconica type 2) were swollen, and the basal shafts
8 were not transparent. The upper part was a cone with a blunt tip bearing a fractured apical pore.
9 The ratio of the lengths of the upper and the lower parts was approximately 5:1 (Fig. 7D).

10 *Sensilla digitiformia*

11 Sensilla digitiformia were plate-like in shape and located on the bottom of a depression in the
12 cuticle. The base was connected to the cuticle but the apex was separated. The walls of the sensilla
13 had abundant, closely spaced, wrinkled wall pores (Fig. 7E).

14 *Sensilla placodea*

15 Sensilla placodea were oval in shape and located on the bottom of a depression in the cuticle, and
16 the walls had closely spaced, wrinkled wall pores (Fig. 7F).

17 ***The distribution of sensilla***

18 On the first segment of the maxillary palp, no sensilla were observed. On the dorsal surface of the
19 second segment, one sensillum digitiformium and two sensilla placodea were observed. On the tip
20 of the second segment, one sensillum styloconicum type 2, one short sensillum basiconicum type
21 3, five short sensilla basiconica type 4, and one sensillum basiconicum type 5 were observed. The
22 sensillum styloconicum type 2 was on the inside of the tip, and the short sensillum basiconicum

1 type 3 was on the ventral surface of the tip. The short sensilla basiconica type 4 distributed in a
2 circle, and the short sensillum basiconicum type 5 was on the outside of the tip (Figs. 6, 10B).

3 **Maxillary galea**

4 *General morphology of the maxillary galea*

5 The maxillary galea had one segment and located on the inner side of the palpifer, with a shape
6 similar to a circular table. The lengths of the maxillary galeas are shown in Table 1.

7 *Typology and morphology of sensilla*

8 The types of sensilla on the galeas of the larvae included short sensilla basiconica, sensilla
9 styloconica, and sensilla chaetica. The morphological characteristics of those sensilla are shown in
10 Tables 2 and 5.

11 *Short sensilla basiconica*

12 *Short sensilla basiconica type 6.* These sensilla had swollen basal regions that gradually narrowed
13 to blunt and rounded tips without apical pores. The surface of the shafts was smooth with no wall
14 pore (Fig. 8A).

15 *Short sensilla basiconica type 7.* The basal regions of these sensilla were rigid and stout, with a
16 round ecdysial pore on the dorsal surface. The tips were blunt and often bifurcated (Fig. 8B).

17 *Short sensilla basiconica type 8.* For these sensilla, the morphological characteristics were
18 identical to those of short sensilla basiconica type 7, although the size was much smaller (Fig. 8C).

19 *Sensilla styloconica*

20 The stylus was a cylinder; the sensory cone had a blunt tip and an apparently round apical pore.
21 The ratio of the lengths of the sensory cone and the stylus was approximately 1:4 (Fig. 8D).

22 *Sensilla chaetica*

1 The sensilla chaetica (sensilla chaetica type 3) was flat and located in a sunken socket, which had
2 a smooth surface. The basal and middle diameters were approximately the same, and gradually
3 narrowed to a sharp tip without terminal pore (Fig. 8E).

4 ***The distribution of sensilla***

5 On the apical portion of the galea, two sensilla styloconica type 3, three short sensilla basiconica
6 (one short sensillum basiconicum type 6, short sensillum basiconicum type 7, and short sensillum
7 basiconicum type 8), and one sensillum chaeticum type 3 were observed. The two sensilla
8 styloconica type 3 distributed in the middle of the lobe, the short sensillum basiconicum type 6
9 was between the two sensilla styloconica type 3. The short sensillum basiconicum type 7 was
10 close to the inner side of the ventral surface, and the short sensillum basiconicum type 8 located
11 on the ventral surface. The sensillum chaeticum type 3 was on the dorsal surface of the lobe (Figs.
12 5, 10C).

13 **Labial palp**

14 ***General morphology of the labial palp***

15 The labial palp located on the spinneret and was cone-shaped with only one segment. The lengths
16 of the labial palps are shown in Table 1.

17 ***Typology and morphology of sensilla***

18 Two types of sensilla were found on the labial palp, i.e., sensilla styloconica and short sensilla
19 basiconica (Fig. 9). The morphological characteristics of them are shown in Tables 2 and 6.

20 ***Sensilla styloconica type 4***

21 In contrast to sensilla styloconica type 3, the distal part of sensilla styloconica type 4 had a longer
22 cone with a blunt tip with an apical pore. The ratio of the lengths of the upper and the lower parts

1 was approximately 3:1.

2 *Short sensilla basiconica*

3 These sensilla (short sensilla basiconica type 9) were cones with smooth surface and round, blunt
4 tips without apical pore.

5 ***The distribution of sensilla***

6 One sensillum styloconicum type 4 was observed on the ventral surface, and one short sensillum
7 basiconicum type 9 was observed on the dorsal surface, on the apical region of the labial palp
8 (Figs. 9, 10D).

9 **Discussion**

10 The sensory equipment is identical in the five species of larvae, despite 4 of them show inter-hosts
11 migration and *Y. vicarius* does not. This might be because of hosts of *Y. vicarius* included elm,
12 poplar, and other broadleaf trees, which have well-developed root systems that provide sufficient
13 nutrition for growth and reproduction of the larvae. Therefore, we speculate that the larvae of *Y.*
14 *vicarius* most likely transfer to a new host after the death of the old host.

15 **Antenna**

16 The typology, distribution, and quantity of larval antennal sensilla of the five species studied were
17 similar to those of other lepidopteran larvae, Tineidae (Faucheux 1984a), *H. nebulella* (Faucheux
18 1995), *G. molesta* (Song et al. 2014), and *C. sasakii* (Liu et al. 2011). However, other free living
19 Lepidoptera such as *M. sexta* have one more type of sensilla, the sensillum campaniformium, on
20 the base of the second segment of the antenna. But *M. sexta* don't have sensillum which is similar
21 to short sensilla basiconica type 2 (Kent et al. 1987). The single sensillum recording of Dethier

1 (1941) have shown that the antennal sensilla chaetica in larvae of Lepidoptera act as
2 mechanoreceptors. They have a similar morphology to that of the sensilla chaetica in our study.
3 When larvae move to a new host via the soil or the ground surface, sensilla chaetica may function
4 to sense and avoid objects that cause damage to the head and antennae (Gao and Qin 1983; Hu et
5 al. 1987; Zong et al. 2005; Wang et al. 2011). Sensilla chaetica type 1 of the five Cossidae species
6 located on the ventral edge of the antenna, and its extreme length would allow the larvae to make
7 initial contact with the external environment. Sensilla chaetica type 1 had loose and sunken
8 sockets, that allowed them to move freely during the mechanoreception and avoid damages to the
9 sensilla; therefore, larval responses to multi-faceted environments are facilitated. The sensilla
10 chaetica type 2 located laterally on the antenna, and the function of these sensilla may be in
11 detection of the lateral environment to avoid damage to the antenna and sensilla. The sensilla
12 basiconica of the antennae of lepidopterans have been studied extensively, and these sensilla are
13 likely to be involved in detecting plant volatiles and carbon dioxide (Dethier 1937; Dethier 1941;
14 Morita and Yamashita 1961). The abundant wall pores on the surface of the sensilla basiconica of
15 these five species suggested that they would be involved in the olfaction, according to Zacharuk
16 and Shields (1991). During host transfer behaviors of these larvae, the sensilla basiconica may
17 detect long-distance plant secondary metabolic substances and nutrients, which play an important
18 role in the process of selecting a suitable host. A study by Schoonhoven (1967) on *Dendrolimus*
19 *pini* (L., 1758), *M. sexta* and a study of Song et al. (2014) on *G. molesta* (Busck) have shown that
20 sensilla morphologically similar to short sensilla basiconica type 1 and sensilla styloconica may
21 react to temperature changes. For these larvae, these sensilla may be involved in the choice of
22 suitable overwintering sites and new hosts, and in the determination of appropriate times to

1 transfer to roots to survive the winter.

2 **Maxillary palp**

3 On the tip of the maxillary palp, seven short sensilla basiconica and one sensillum styloconicum
4 were observed with pores on apical parts. The distribution and quantity of the sensilla were similar
5 to those of Tineidae (Faucheux 1984b), *H. nebulella* (Faucheux 1995), *G. molesta* (Song et al.
6 2014) and *C. sasakii* (Liu et al. 2011). Five short sensilla basiconica with apical pores and three
7 short sensilla basiconica with wall pores have been observed in *H. armigera* (Tang et al. 2014).
8 The differences in the number and morphology of the sensilla indicated that the five species
9 studied might engage in trunk boring. Short sensilla basiconica on the maxillary palp are widely
10 regarded as tactile chemosensilla (Albert 1980; Stange and Stowe 1999; Song et al. 2014). In an
11 electrochemical experiment on the maxillary palp of *C. fumiferana* by Albert (2003), both sensilla
12 styloconica and short sensilla basiconica have been tested to react to carbohydrates, which
13 suggests that these sensilla may be involved in feeding activities. The study of Dethier and Kuch
14 (1971) has suggested that the sensilla on the maxillary palp play an important role in determining
15 plant nutritional status and identifying secondary substances, such as sugars, amino acids, and
16 salts. When the host is in a state of extreme weakness, the maxillary sensilla of the larvae may
17 evaluate the nutritional status of the plant to determine whether to stay or migrate to a new host.
18 Sensilla digitiformia, which had consistent structures, were similar to those of other lepidopterous
19 larvae (Faucheux 1984b, 1995, 1999; Grimes and Neunzig 1986; Keil 1996; Song et al. 2014).
20 Based on the research of Stange and Stowe (1999), sensilla digitiformia act as receptors for CO₂,
21 although Albert (1980) has suggested that these sensilla may function in mechanoreception.
22 According to Stange and Stowe (1999), sensilla placodea may also be receptors for CO₂ and

1 function in olfaction. These sensilla may be important for host-migration behavior and for
2 selecting a suitable host.

3 **Maxillary galea**

4 Grimes and Neunzig (1986) have studied the distribution and quantity of sensilla on the galeas of
5 41 species of lepidopteran larvae, including *Prionoxystus* sp., *C. niponensis*, and *G. molesta*. By
6 contrast, the larvae of the five Cossidae species have one sensillum chaeticum, whereas the other
7 species have three; however, the distribution and quantity of the other sensilla types are similar. In
8 many other larvae, transmission electron microscopy of sensilla styloconica with apical pores has
9 revealed four gustatory sensory neurons and a neuron for mechanoreception, which function in
10 chemoreception and mechanoreception, respectively, and may play important roles in larval
11 feeding (Albert 1980; Shields 2009; Tang et al. 2014). In electrophysiological studies of Albert
12 (1980) on *C. fumiferana*, the sensilla have been shown to detect sugars, salt, amino acids, and
13 plant secondary substances, which would allow a nutritional evaluation of the plant material and a
14 subsequent adjustment of insect feeding behavior. Therefore, these sensilla may have a role in
15 feeding and the reselection of a host for the larvae. Short sensilla basiconica, located between the
16 two sensilla styloconica, have been referred to as sensilla basiconica CSB in the study of Grimes
17 and Neunzig (1986). These might function in mechanoreception and in other interactions with the
18 environment. In the study of *Mamestra configurata*, Shields (1994) has named the sensilla of this
19 types “basiconic sensilla S”, and suggested they have the ability to detect temperature changes.
20 short sensilla basiconica type 2 and short sensilla basiconica type 3 have located ventral to the two
21 sensilla styloconica, and, according to Shields (1994), they have tubular bodies that are assumed
22 to act as mechanoreceptors for the detection of mechanical vibrations during feeding and eating,

1 and changes in the environment to protect them from mandibles. Additionally, short sensilla
2 basiconica type 2 and short sensilla basiconica type 3 of the five Cossidae larvae might adjust the
3 location of the sensilla styloconica to avoid injury during the processing and ingestion of food.
4 Sensilla chaetica of the five Cossidae larvae might be mechanoreceptors that participate in
5 detecting the environment and the hardness of the food to protect the galeas, and adjust the
6 movement of the mandibles according to previous studies (Zacharuk and Shields 1991; Liu et al.
7 2011).

8 **Labial palp**

9 Sensilla quite similar with sensilla styloconica and short sensilla basiconica of the five
10 Cossidae larvae have been also observed on the labial palps of *C. niponensis* and *G. molesta*, and
11 named “sensillum styloconicum” and “sensillum chaeticum”, but their ultrastructure and function
12 have not been defined (Liu et al. 2011; Song et al. 2014). Based on electrophysiological
13 experiments with *C. fumiferana* and *H. nebullella*, the sensilla of these types, which are similar to
14 these two sensilla in the present report, may act as mechanoreceptors (Albert 1980; Faucheux
15 1995). On the larvae of the five species, the labial palp was dorsal to the spinneret and located on
16 the upper side of the throat; therefore, it might be used to detect the hardness of food before eating,
17 and coordinate the movement of the mandible and the spinneret.

18 **Conclusion**

19 In the present paper, we investigated the distribution, typology, and quantity of sensilla on the
20 antennae, maxillary palps, galeas, and labial palps of the five Cossidae species larvae. We also
21 discussed the putative function of different sensilla in larval behaviors such as host migration:
22 short sensilla basiconica might be gustatory receptors that act mostly as mechanoreceptors;

1 sensilla styloconica on antennae (which are aporous) might function as thermoreceptors, while
2 those on the other appendages (which are uniporous) might have a gustatory function; sensilla
3 basiconica might function as olfactory receptors. Our study could serve as a basis for further
4 studies on the feeding, self-protection, host-transfer behaviors, and electrophysiology of these
5 forest pests. Our study has showed that the sensillum equipment of larval antennae and mouthparts
6 is identical in the phytophagous insects (Albert 1980; Shields 1994, 2009; Faucheux 1995;
7 Goldsmith et al. 2014), the keratinophagous insects (Faucheux 1994a, 1999) and the wood boring
8 insects (this paper).

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1 **Figure Legends**

2 **Figure 1. Ventral view of the heads of the five species**

3 *A. Eogystia hippophaecolus. B. Deserticossus artemisiae. C. D. arenicola. D. Yakudza vicarius.*
4 *E. Streltziella insularis.* A = antenna; L = labrum; LP = labial palp; Mx = maxilla; S =
5 stemmata; Sp = spinneret.

6 **Figure 2. General morphology of the antennae of the five species**

7 *A. Eogystia hippophaecolus, left antenna. B. Deserticossus artemisiae, right antenna. C. H.*
8 *arenicola, right antenna. D. Yakudza vicarius, left antenna. E. Streltziella insularis, right*
9 *antenna.* I = 1st segment; II = 2nd segment; III = 3rd segment; ch.1 = sensilla chaetica type 1.

10 **Figure 3. Distribution of sensilla on the antennae of the five species**

11 *A. Eogystia hippophaecolus, left antenna. B. Deserticossus artemisiae, right antenna. C. D.*
12 *arenicola, right antenna. D. Yakudza vicarius, right antenna. E. Streltziella insularis*
13 *Staudinger, left antenna.* 1-2 = short sensilla basiconica type 1-2; b.1 = sensilla basiconica type 1;
14 b.2 = sensilla basiconica type 2; ch.1 = sensilla chaetica type 1; ch.2 = sensilla chaetica type 2;
15 sty.1 = sensilla styloconica type 1.

16 **Figure 4. SEM micrograph of sensilla on the antenna**

17 *A. Short sensilla basiconica type 1 with a subterminal pore. B. Short sensilla basiconica type 2*
18 *with a terminal pore. C. Sensilla basiconica type 1 with wall pores and ecdysial pores. D. Sensilla*
19 *basiconica type 2 with wall pores and an ecdysial pore. E. Sensilla styloconica type 1. F. Sensilla*
20 *chaetica type 2. In figures A, B, C and D, white arrows show ecdysial pore. In figures C and D,*
21 *black arrows show wall pores.*

22 **Figure 5. General morphology of the maxillae, and the distribution of sensilla on maxillary**
23 **galeas of the five species**

1 **A.** *Eogystia hippophaecolus*, right maxilla. **B.** *Deserticossus artemisiae*, right maxilla. **C.** *D.*
2 *arenicola*, right maxilla. **D.** *Yakudza vicarius*, left maxilla. **E.** *Streltzoviella insularis*, right
3 maxilla. I = 1st segment; II = 2nd segment; G = maxillary galea; MP = maxillary palp; 6–8 =
4 Short sensilla basiconica type 6–8; sty.3 = sensilla styloconica type 3; ch.3 = sensilla chaetica type
5 3. D = sensilla digitiformia; P = sensilla placodea.

6 **Figure 6. Distribution of sensilla on the maxillary palps of the five species**

7 **A.** *Eogystia hippophaecolus*, left maxillary palp. **B.** *Deserticossus artemisiae*, left maxillary palp.
8 **C.** *D. arenicola*, left maxillary palp. **D.** *Yakudza vicarius*, left maxillary palp. **E.** *Streltzoviella*
9 *insularis*, right maxillary palp. 3–5 = short sensilla basiconica type 3–5; sty.2 = sensilla
10 styloconica type 2; D = sensilla digitiformia; P = sensilla placodea.

11 **Figure 7. Sensilla on the maxillary palp**

12 **A.** Short sensilla basiconica type 3 with terminal pore. **B.** Short sensilla basiconica type 4 with
13 terminal pore. **C.** Short sensilla basiconica type 5 with terminal pore. **D.** Sensilla styloconica type
14 2 with terminal pore. **E.** Sensilla digitiformia with cuticular pores. **F.** Sensilla placodea with
15 cuticular pores. In figures A, B, C and D, white arrows show ecdysial pore. In figures E and F,
16 black arrows show wall pores.

17 **Figure 8. Sensilla on maxillary galea**

18 **A.** Short sensilla basiconica type 6. **B.** Short sensilla basiconica type 7, the white arrow shows the
19 ecdysial pore. **C.** Short sensilla basiconica type 8, the white arrow shows the ecdysial pore. **D.**
20 Sensilla styloconica type 3, the black arrow shows the terminal pore. **E.** Sensilla chaetica type 3.

21 **Figure 9. Distribution of sensilla on the labial palps of the five species**

22 **A.** *Eogystia hippophaecolus*. **B.** *Deserticossus artemisiae*, left labial palp. **C.** *D. arenicola*, left

1 labial palp. **D.** *Yakudza vicarius*, right labial palp. **E.** *Streltziella insularis*, left labial palp. 9 =

2 Short sensilla basiconica type 9; sty.4 = sensilla styloconica type 4.

3 **Figure 10. Schematic representation of the antenna, maxillary palp, galea and labial palp**

4 **A.** Dorsoanterior aspect of the right mesal antenna. **B.** Dorsoanterior aspect of the right mesal

5 maxillary palp. **C.** Dorsoanterior aspect of the left mesal maxillary galea. **D.** Dorsoposterior aspect

6 of the left mesal labial palp. 1-9 = short sensilla basiconica type 1-9; b.1 = sensilla basiconica type

7 1; b.2 = sensilla basiconica type 2; ch.1 = sensilla chaetica type 1; ch.2 = sensilla chaetica type 2;

8 sty.1-4 = sensilla styloconica type 1-4; D = Sensilla digitiformia; P = sensilla placodea.

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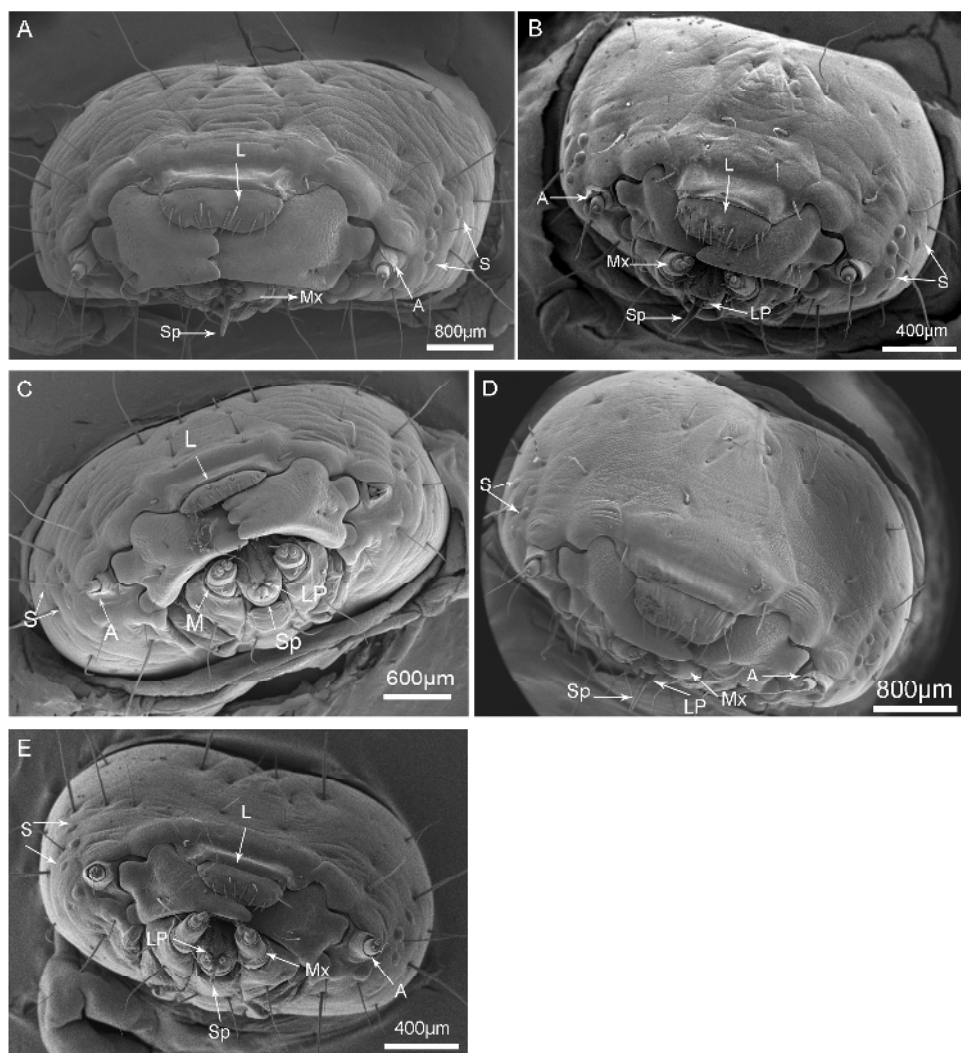


Figure 1. Ventral view of the heads of the five species

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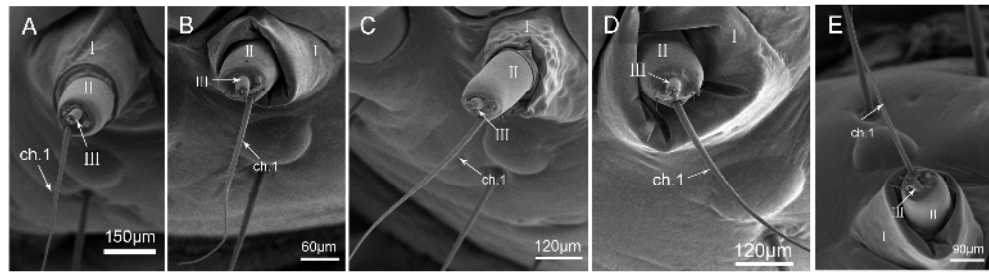


Figure 2. General morphology of the antennae of the five species
209x59mm (300 x 300 DPI)

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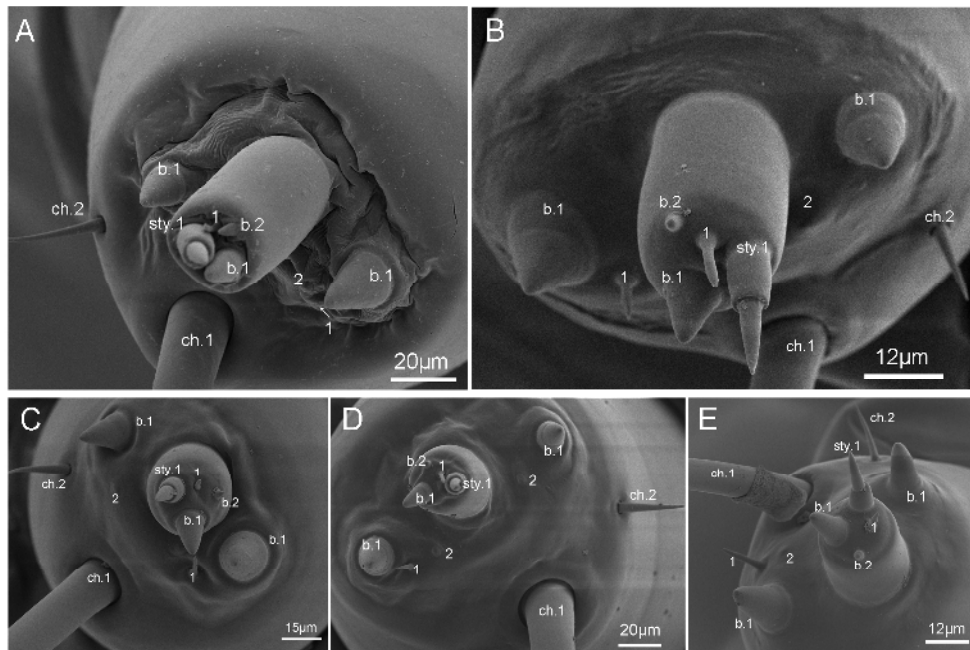


Figure 3. Distribution of sensilla on the antennae of the five species

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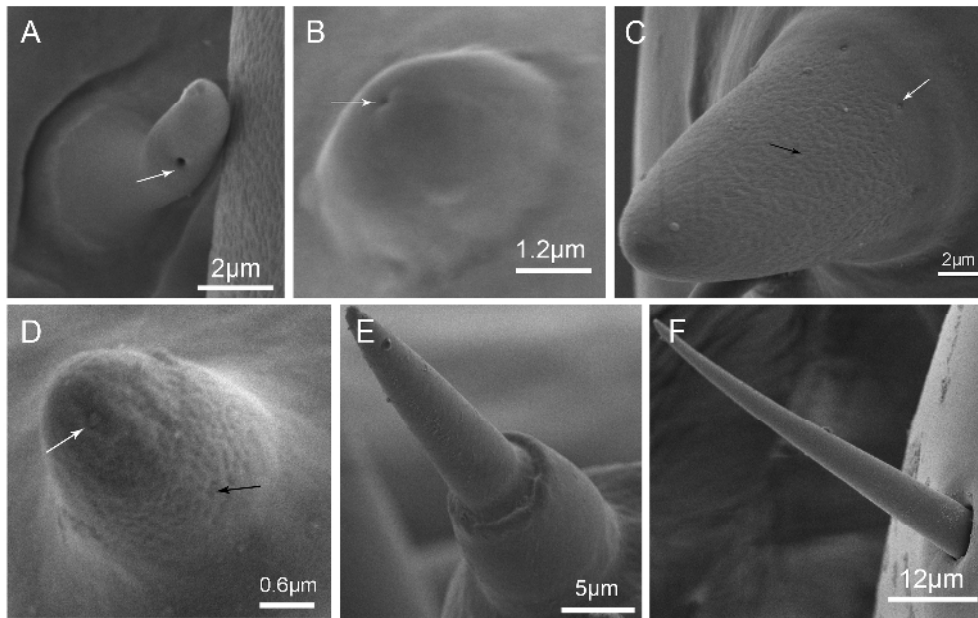


Figure 4. SEM micrograph of sensilla on the antenna

209x133mm (300 x 300 DPI)

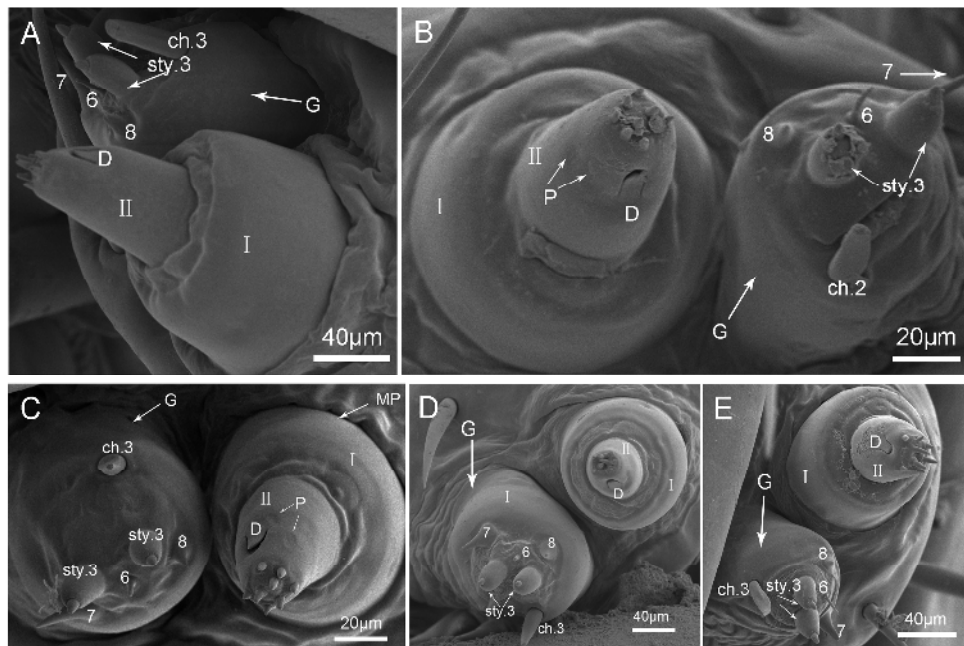


Figure 5. General morphology of the maxillae, and the distribution of sensilla on maxillary galeas of the five species

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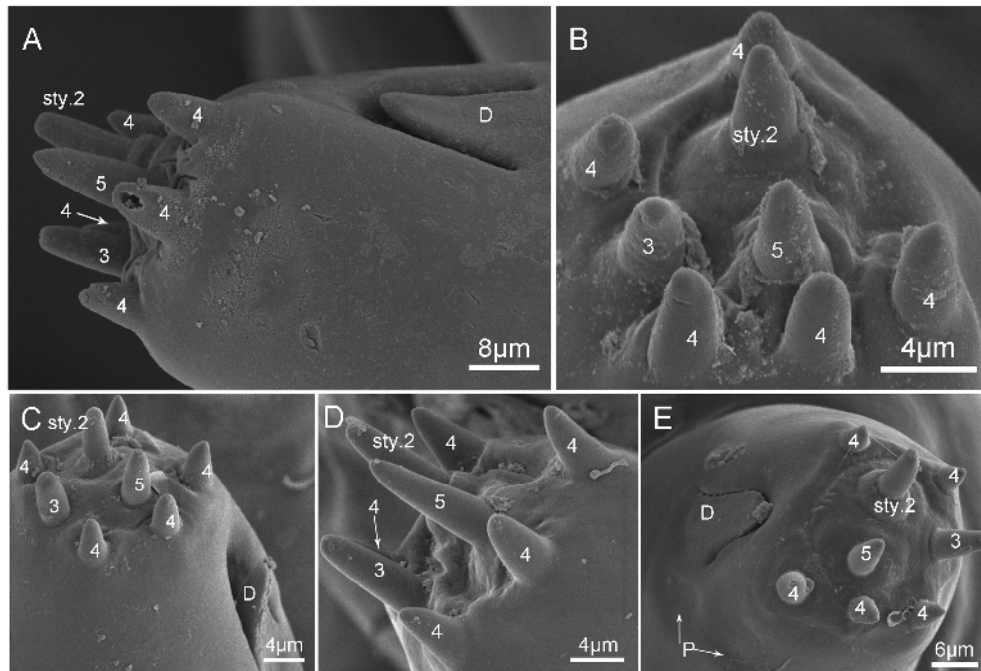


Figure 6. Distribution of sensilla on the maxillary palps of the five species
209x143mm (300 x 300 DPI)

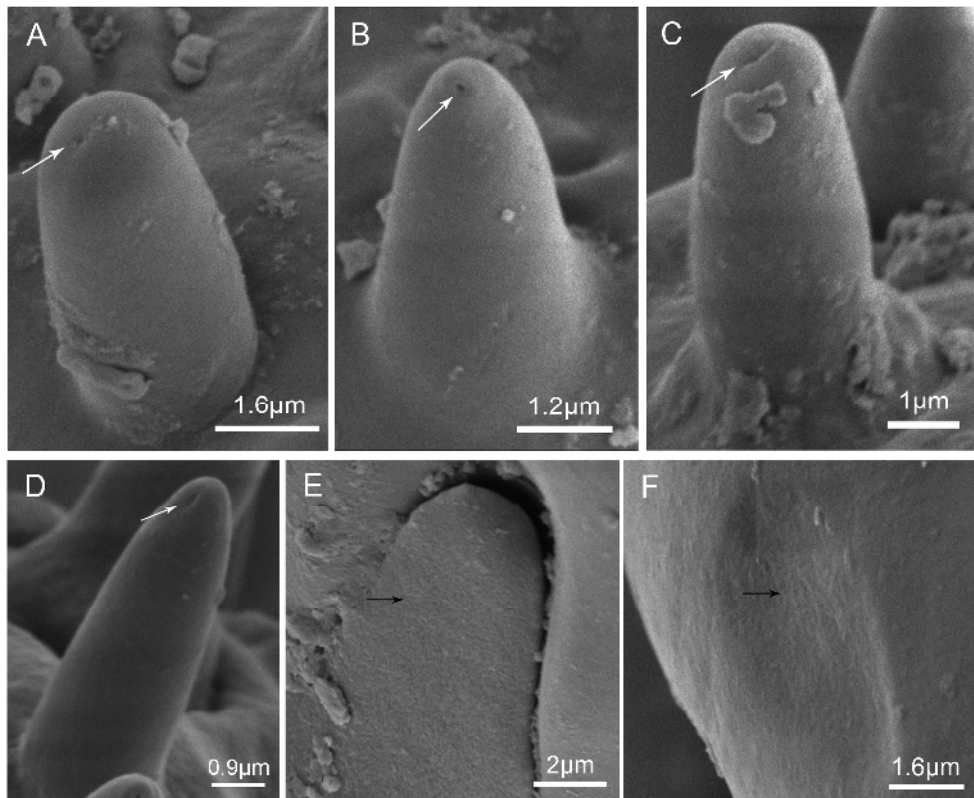


Figure 7. Sensilla on the maxillary palp

209x171mm (300 x 300 DPI)

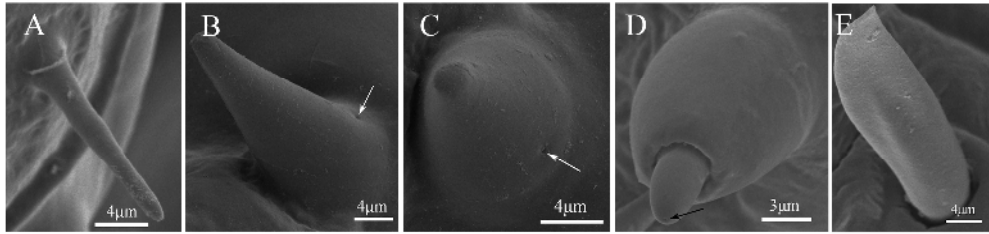


Figure 8. Sensilla on maxillary galea
209x50mm (300 x 300 DPI)

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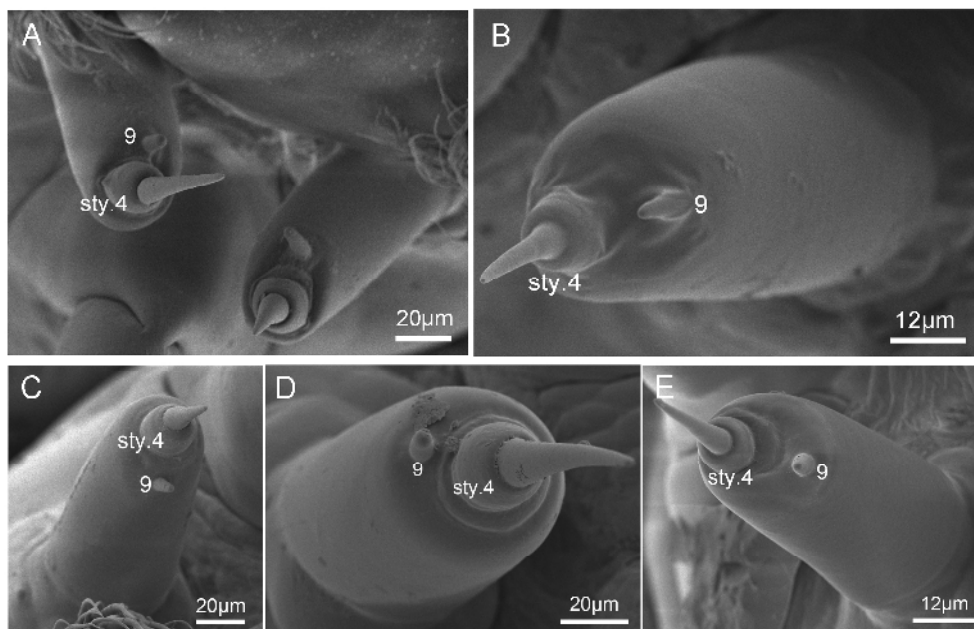


Figure 9. Distribution of sensilla on the labial palps of the five species

209x135mm (300 x 300 DPI)

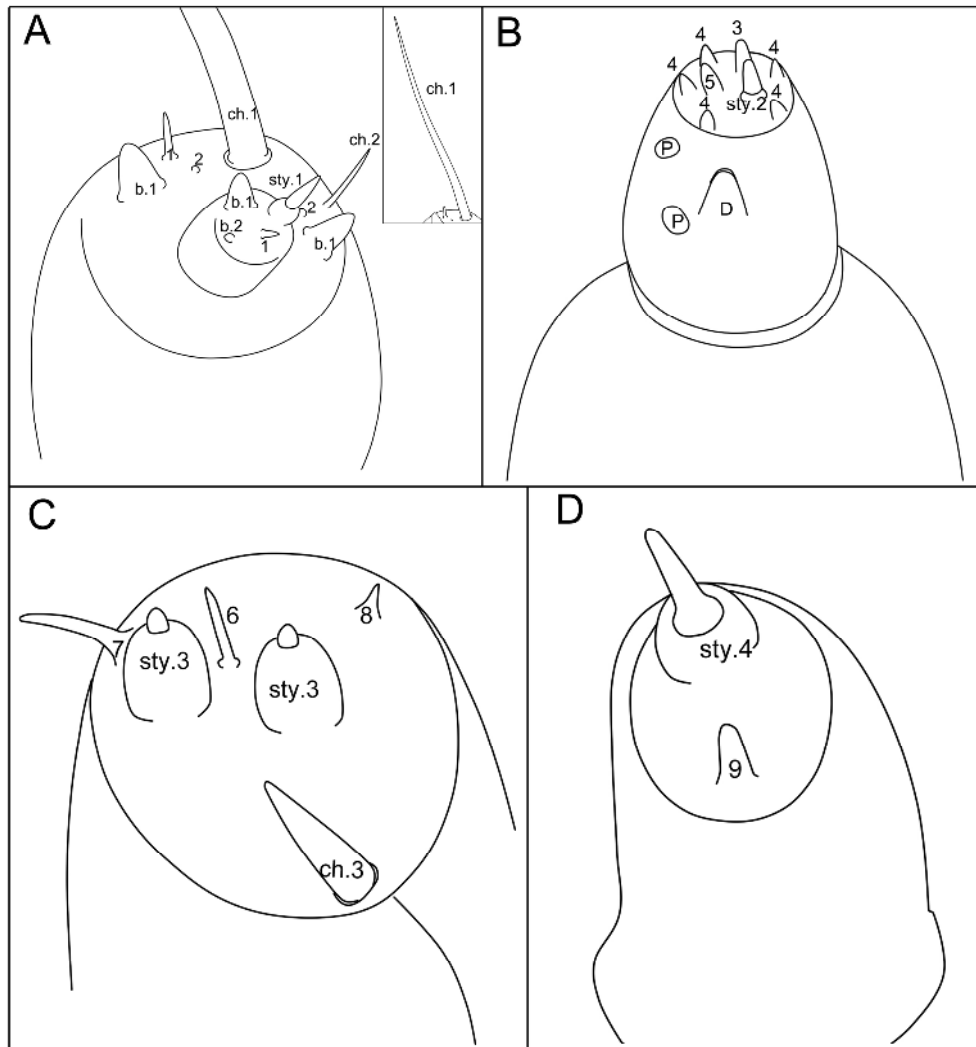


Figure 10. Schematic representation of the antenna, maxillary palp, galea and labial palp

224x241mm (300 x 300 DPI)

Tables

Table 1 The lengths (μm) of antennae, maxillary palps, galeas, and labial palps of five species

Species	Lengths of appendages ¹						
	A-I	A-II	A-III	M-I	M-II	L	G
<i>E. hippophaecolus</i>	134.2 \pm 17.4	109.2 \pm 19.9	27.1 \pm 5.8	69.1 \pm 8.0	84.2 \pm 2.1	74.7 \pm 3.9	125.8 \pm 3.5
<i>D. artemisiae</i>	116.9 \pm 10.6	96.1 \pm 8.7	36.4 \pm 1.7	36.4 \pm 5.4	45.0 \pm 1.1	43.8 \pm 4.1	70.8 \pm 6.5
<i>D. arenicola</i>	110.2 \pm 5.4	97.3 \pm 0.3	31.9 \pm 3.7	43.9 \pm 4.0	56.6 \pm 4.8	54.1 \pm 5.1	63.2 \pm 8.3
<i>Y. vicarius</i>	109.6 \pm 15.4	86.9 \pm 6.1	24.3 \pm 0.7	53.0 \pm 0.8	60.6 \pm 5.2	63.9 \pm 3.7	107.1 \pm 17.1
<i>S. insularis</i>	101.2 \pm 9.1	97.9 \pm 8.7	33.7 \pm 3.0	34.5 \pm 1.9	42.8 \pm 3.9	31.6 \pm 2.9	84.0 \pm 8.9

¹ A-I, A-II, and A-III are segments 1–3 of the antenna, respectively; M-I and M-II are segments 1 and 2 of the maxillary palp; G is the maxillary galea; and L is the labial palp.

Table 2 Comparative morphology and distribution of all types of sensilla on the antennae, maxillary palps, galeas, and labial palps of the five species

Type	Distributed on body part	Morphological characteristics of sensilla			
		Wall	Tip	Socket	
Short sensilla basiconica	s.b.1	antenna	Ecdysial pore	Blunt	No obvious socket
	s.b.2	antenna	Smooth	Terminal pore	Tight
	s.b.3	maxillary palp	Smooth	Terminal pore	No obvious socket
	s.b.4	maxillary palp	Smooth	Terminal pore	No obvious socket
	s.b.5	maxillary palp	Smooth	Terminal pore	No obvious socket
	s.b.6	maxillary galea	Smooth	Blunt	No obvious socket
	s.b.7	maxillary galea	Ecdysial pore	Blunt	No obvious socket
	s.b.8	maxillary galea	Ecdysial pore	Blunt	No obvious socket
	s.b.9	labial palp	Smooth	Blunt	No obvious socket
Sensilla basiconica	b.1	antenna	wall pores and ecdysial pores	Blunt	Tight
	b.2	antenna	Wall pores and one ecdysial pore	Blunt	Tight
Sensilla styloconica	sty.1	antenna	Smooth	Blunt	No obvious socket
	sty.2	maxillary palp	Smooth	Terminal pore	No obvious socket
	sty.3	maxillary galea	Smooth	Terminal pore	No obvious socket
	sty.4	labial palp	Smooth	Terminal pore	No obvious socket
Sensilla digitiformia	s.d	maxillary palp	Wall pores	Blunt	Sunken and flexible
Sensilla placodea	s.p	maxillary palp	Wall pores	Blunt	No obvious socket
Sensilla chaetica	ch.1	antenna	Shallow grooves	Sharp	Sunken and flexible
	ch.2	antenna	Smooth	Sharp	Tight
	ch.3	maxillary galea	Smooth	Sharp	Sunken and flexible

Table 3 The lengths and diameters (μm) of all sensilla types on the antennae

Type ²	Lengths and diameters of sensilla ¹									
	<i>E. hippophaecolus</i>		<i>D. artemisiae</i>		<i>D. arenicola</i>		<i>Y. vicarius</i>		<i>S. insularis</i>	
	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter
s.b.1	10.2±1.6	3.1±0.2	10.3±3.0	3.1±0.9	9.0±2.5	3.0±0.4	12.2±3.4	3.2±0.5	10.1±3.2	3.0±0.5
s.b.2	3.7±0.9	4.1±0.6	2.4±0.6	3.7±0.6	3.1±0.7	4.7±1.1	3.1±0.6	4.1±1.0	1.8±0.5	2.8±0.8
b.1	19.6±3.6	13.5±3.0	16.2±3.9	13.3±3.0	18.7±3.6	14.2±2.9	23.2±4.4	13.1±3.1	19.1±3.6	11.3±2.9
b.2	25.7±0.8	22.4±0.4	3.3±0.9	2.8±0.5	3.6±0.7	3.3±0.3	4.2±0.8	3.6±0.4	3.2±0.9	3.0±0.6
sty.1	28.6±4.3	10.2±1.1	23.8±5.9	8.1±1.3	20.0±5.7	10.0±1.0	27.0±1.9	9.2±1.5	21.7±1.3	7.7±1.1
ch.1	545.0±47.4	19.7±2.0	492.6±97.1	12.7±2.0	516.5±32.9	16.9±1.8	535.5±69.8	17.5±2.8	471.0±55.1	12.3±3.8
ch.2	29.6±4.6	4.7±0.4	16.4±6.1	3.1±0.7	18.6±4.5	4.1±0.7	25.4±6.2	3.7±0.9	16.8±4.0	3.0±1.1

¹ All sensilla of each type on the antenna of at least ten larvae were measured; means \pm standard deviations are shown. ² s.b.1 = short sensilla basiconica type 1; s.b.2

= short sensilla basiconica type 2; b.1 = sensilla basiconica type 1; b.2 = sensilla basiconica type 2; sty.1 = sensilla styloconica type 1; ch.1 = sensilla chaetica type 1;

ch.2 = sensilla chaetica type 2.

Table 4 The lengths and diameters (μm) of all sensilla types on the maxillary palps

Type ²	Lengths and diameters of sensilla ¹									
	<i>E. hippophaecolus</i>		<i>D. artemisiae</i>		<i>D. arenicola</i>		<i>Y. vicarious</i>		<i>S. insularis</i>	
	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter
s.t.b.3	9.0±0.6	4.1±0.7	4.7±0.9	2.9±0.4	6.5±1.2	3.3±0.3	7.7±1.2	3.5±0.5	7.3±1.6	3.0±0.6
s.t.b.4	6.8±0.8	4.6±0.5	4.5±0.9	3.1±0.3	5.3±0.8	3.6±0.5	5.5±0.8	3.7±0.5	4.3±0.5	2.6±0.2
s.t.b.5	10.9±0.9	4.5±0.4	5.9±1.2	3.1±0.3	8.0±1.6	3.3±0.2	8.9±2.0	3.7±0.6	7.2±1.4	2.8±0.5
sty.2	11.3±1.1	5.1±0.4	6.1±1.5	5.0±0.7	8.2±1.2	5.7±0.6	9.5±1.2	5.5±1.0	9.6±1.8	5.3±1.0
s.d	6.5±1.2	12.8±1.1	7.9±1.0	6.8±1.5	9.8±2.3	9.1±1.4	11.9±1.2	11.1±1.5	9.3±0.4	8.3±1.2
s.p	4.6±0.3	5.4±0.4	3.5±0.8	5.3±0.1	3.4±0.7	5.0±0.4	3.9±0.3	7.1±1.2	3.1±0.5	6.5±0.9

¹ All sensilla of each type on the maxillary palp of at least ten larvae were measured; means \pm standard deviations are shown. ² s.b.3-5 = short sensilla basiconica type

3-5; sty.2 = sensilla styloconica type 2; s.d = sensilla digitiformia; s.p = sensilla placodea.

Table 5 The lengths and diameters (μm) of all sensilla types on the maxillary galeas

Types ²	Lengths and diameters of sensilla ¹									
	<i>E. hippophaecolus</i>		<i>D. artemisiae</i>		<i>D. arenicola</i>		<i>Y. vicarious</i>		<i>S. insularis</i>	
	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter
s.t.b.6	16.2 \pm 1.8	3.9 \pm 0.6	13.7 \pm 1.9	4.4 \pm 0.1	13.4 \pm 3.4	4.0 \pm 0.5	11.4 \pm 1.7	4.1 \pm 0.5	11.1 \pm 2.9	3.3 \pm 0.6
s.t.b.7	30.8 \pm 1.6	14.6 \pm 1.3	23.2 \pm 5.0	9.1 \pm 2.2	27.0 \pm 4.0	13.1 \pm 3.4	32.1 \pm 5.5	16.4 \pm 2.9	18.0 \pm 2.8	8.2 \pm 1.8
s.t.b.8	16.5 \pm 1.8	12.2 \pm 1.4	10.5 \pm 3.5	7.7 \pm 1.6	13.3 \pm 3.6	10.8 \pm 2.1	12.6 \pm 2.5	9.4 \pm 1.6	7.1 \pm 2.1	6.8 \pm 1.9
sty.3	35.0 \pm 0.8	18.1 \pm 2.0	22.9 \pm 3.4	13.4 \pm 1.7	25.0 \pm 4.2	16.0 \pm 1.8	31.0 \pm 4.0	18.8 \pm 2.3	18.4 \pm 3.9	11.8 \pm 2.3
ch.3	48.7 \pm 5.5	12.9 \pm 1.2	21.7 \pm 2.9	6.5 \pm 2.4	43.8 \pm 5.4	11.6 \pm 2.1	48.1 \pm 8.2	13.0 \pm 3.3	22.2 \pm 4.1	5.8 \pm 1.0

¹All sensilla of each type on the maxillary galea of at least ten larvae were measured; means \pm standard deviations are shown. ² s.b.6-8 = short sensilla basiconica

type 6-8; sty.3 = sensilla styloconica type 3; ch.3 = sensilla chaetica type 3.

Table 6 The lengths and diameters (μm) of all sensilla types on the labial palps

Types ²	Lengths and diameters of sensilla ¹									
	<i>E. hippophaecolus</i>		<i>D. artemisiae</i>		<i>D. arenicola</i>		<i>Y. vicarious</i>		<i>S. insularis</i>	
	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter	Length	Diameter
s.t.b.9	12.1 \pm 1.8	6.1 \pm 1.1	8.0 \pm 1.0	4.8 \pm 0.5	10.9 \pm 3.0	5.3 \pm 0.6	10.5 \pm 2.8	6.5 \pm 2.0	7.3 \pm 2.9	4.4 \pm 1.0
sty.4	59.9 \pm 8.9	24.1 \pm 4.7	40.6 \pm 6.0	13.4 \pm 1.5	48.5 \pm 9.3	18.8 \pm 3.0	75.2 \pm 11.1	25.5 \pm 3.5	48.1 \pm 9.6	13.6 \pm 3.8

¹All sensilla of each type on the labial palp of at least ten larvae were measured; means \pm standard deviations are shown. ²s.b.9 = short sensilla basiconica type 9;

sty.4 = sensilla styloconica type 4.