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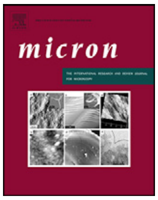

A SEM study of antennal and maxillary sensilla in *Zema gressitti* Fennah (Hemiptera: Fulgoromorpha: Tropiduchidae)

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ABSTRACT

The sensory organs on the antennae and maxillary plates of *Zema gressitti* Fennah (Hemiptera: Fulgoromorpha: Tropiduchidae) are studied using scanning electron microscopy. Four types of antennal sensilla are reported: trichoid sensilla on the antennal scape and antennal pedicel, plate organs on the antennal pedicel, campaniform sensilla on the antennal scape and antennal pedicel, and coeloconic sensilla in Bourgoin's organ on the antennal flagellum. Cuticular denticles and cuticular microtubercles are also present on the antennal pedicel. On the maxillary plates, three campaniform sensilla are discovered. Additionally, Evans' organs are described as placoid sensilla sunk into deep cuticular cavities on the maxillae below the antennae. The morphology of the sensory equipments in this species is provided for possible use in taxonomic and phylogenetic studies within the Tropiduchidae and Fulgoromorpha.

1. Introduction

Despite the studies of comparative morphology (Bugnion, 1908) and ultrastructures (Lewis and Marshall, 1970; Stroiński et al., 2011), still very little is known about the characteristic of different antennal sensory of the Fulgoromorpha. However, a remarkable disparity across the same sensory equipments is observed, which may have potential value for taxonomic and phylogenetic analyses (Bourgoin, 1986; Bourgoin and Deiss, 1994; Liang, 2001; Hamilton, 2011; Stroiński et al., 2011). Besides the antennal sensilla, Evans' organs have been found on the maxillary plates below the antennae (Evans, 1973; Bourgoin, 1986). Although they are of major importance in understanding the origin of the head capsule in Hemiptera (Evans, 1973; Bourgoin, 1986), these structures have surprisingly attracted very little attention (Bourgoin, 1986; Liang, 2005).

Currently, there is a paucity of the anatomical and molecular data on Fulgoromorpha, let alone the morphoanatomy information of Tropiduchidae. This situation prevents a deeper understanding of the phylogenetic relationships within the Tropiduchidae, and their monophyly and position relative to the other lineages of Fulgoromorpha are still to be resolved. Subsequently, this study investigated, through scanning electron microscopy (SEM) observations, the antennal sensory equipments and the maxillary Evans' organs in *Zema gressitti* Fennah, 1956 as potential new characteristics to include for future comparative morphological studies in Tropiduchidae and Fulgoromorpha.

2. Materials and methods

The samples of *Z. gressitti* used in this study and the corresponding collection information are listed in Table 1. All specimens are deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZCAS).

To prepare for observation with SEM, the specimens were first rinsed in chloroform bath or lukewarm 10% KOH bath in an ultrasonic cleaner for 1 min to remove the cuticular waxy powder. Thereafter, for further cleaning, the head with antennae was dissected from the body and cleaned twice with 75% alcohol (2 min for each case). The samples were then dehydrated through increasing concentrations of alcohol, critical point dried, mounted on stubs with double-side adhesive tape, and coated with a film of gold–palladium. Observations were made with a HITACHI S34Q SEM (Hitachi Corp., Tokyo, Japan) at the Microscopy Core Facility, Biological Technology Center, Beijing Forestry University.

Terminology for the sensilla description follows Bourgoin and Deiss (1994), completed in Stroiński et al. (2011).

3. Results

3.1. Gross morphology of the antennae

As in other planthoppers, adult *Z. gressitti* are equipped with a pair of antennae located laterally on the head capsule and inserted

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Table 1
Collection information for samples of *Zema gressitti* used in this study.

Number of specimens[a]	Locality	Collection date	Method of preservation
2 m, 2f	China, Sichuan, Wushan, Liziping, 1850 m	18-V-1994	Dried
1 m, 1f	China, Sichuan, Mt. Emei, Baoguosi, 550–750 m	4-VI-1957	Dried
1 m	China, Sichuan, Mt. Emei, Baoguosi, 600 m	5-V-1957	Dried
1 m	China, Xizang, Chayu, Hongwei Village, 2100 m	28-VI-1978	Dried
1 m	China, Xizang, Chayu, Dongchong, 1570 m	23-VI-1978	Dried
1 m, 1f	China, Hubei, Shennongjia, Songban, 900 m	12-VI-1981	Dried
1 m	China, Yunnan, Xiaguan to Yongping, 1800 m	4-V-1955	Dried

[a] m, male; f, female.

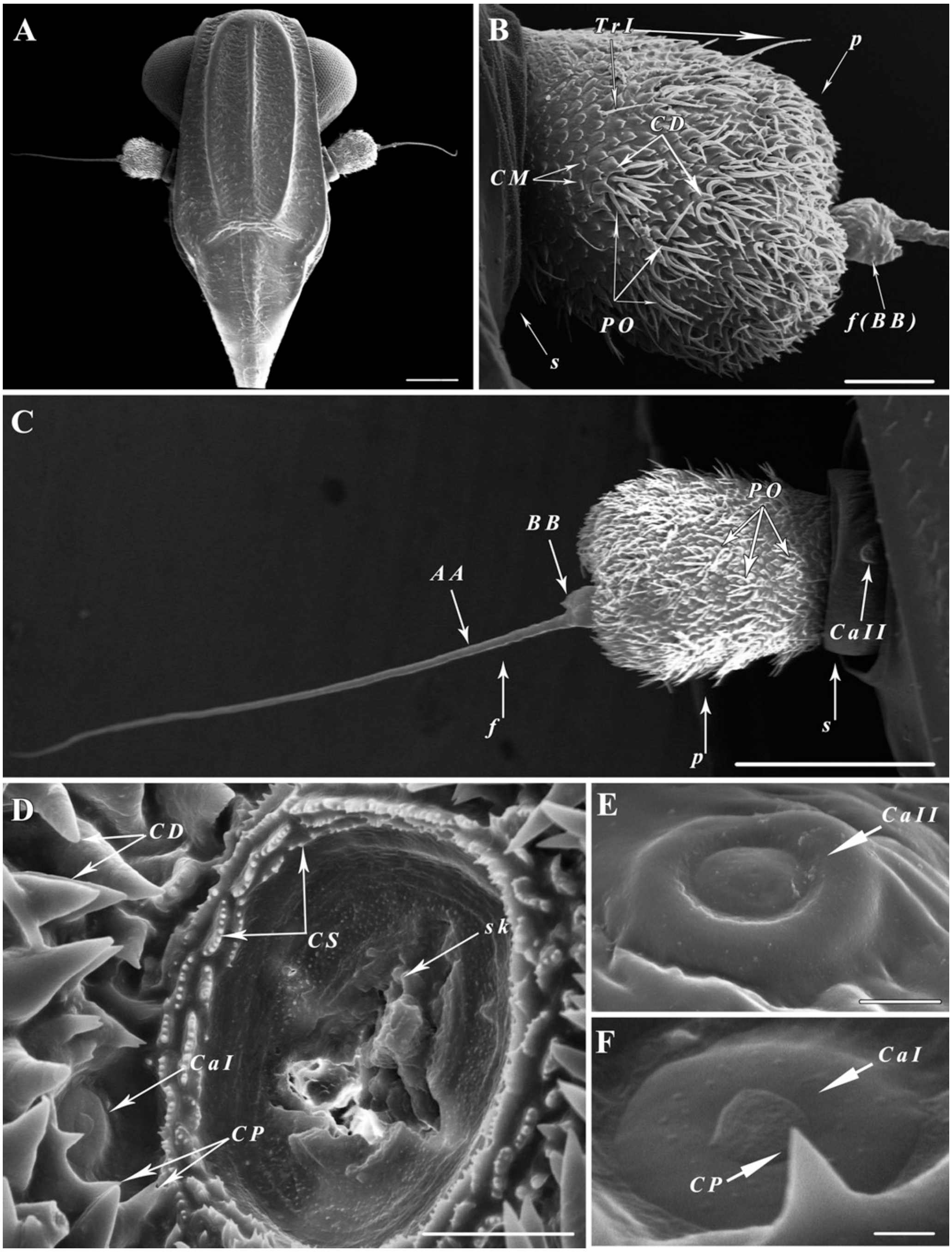

Fig. 1. SEM images of *Zema gressitti.* (A) Head capsule of *Z. gressitti* showing the position of the antennae. (B) General view of the antennal scape (s), antennal pedicel (p) and basal bulb (BB) of the antennal flagellum (f), showing the position of the cuticular microtubercles (CM), plate organs (PO), cuticular denticles (CD) and trichoid sensilla (TrI). (C) General view of the antenna showing the antennal scape (s) with a campaniform sensillum subtype II (CaII), the antennal pedicel (p) with plate organs (PO), and the antennal flagellum (f) with apical arista (AA) and basal bulb (BB). (D) The top of the antennal pedicel, showing the socket (sk), cuticular spines (CP), a campaniform sensillum subtype I (CaI) and cuticular denticles (CD). (E) Enlarged view of the campaniform sensillum subtype II (CaII) on the antennal scape. (F) Enlarged view of the campaniform sensillum subtype I (CaI) on the antennal pedicel. Scale bars: A = 300 μm; B = 50 μm; C = 200 μm; D = 10.0 μm; E = 5.00 μm; and F = 1.00 μm.

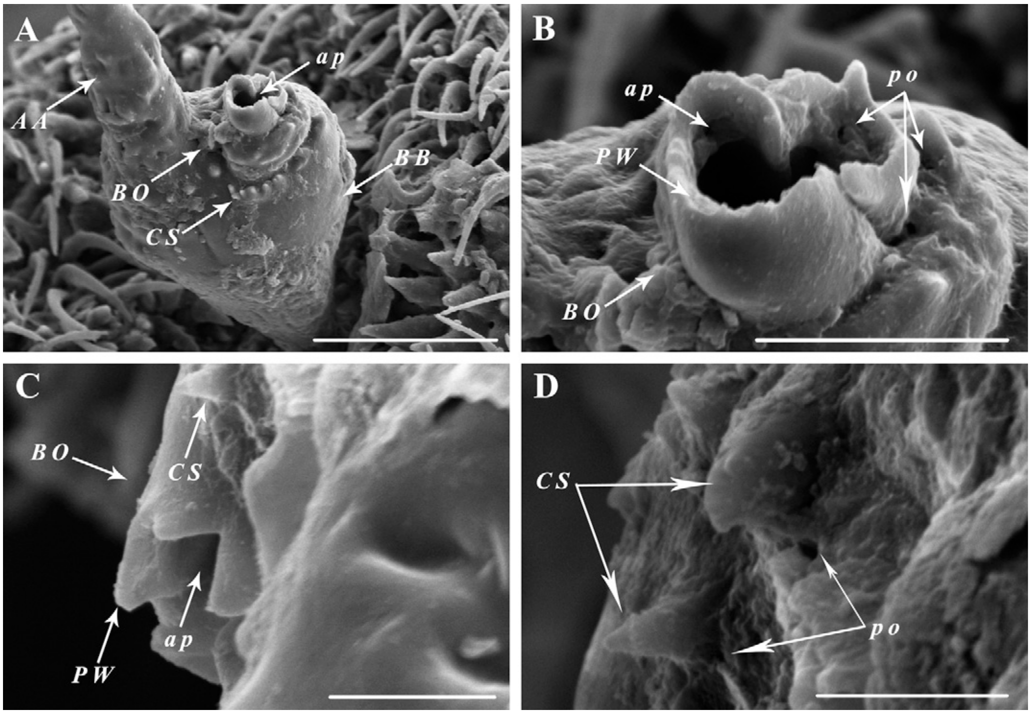

Fig. 2. SEM images of expanded flagellar base in *Zema gressitti*. (**A**) General view of the flagellar bulb base (BB) with part of apical arista (AA), showing the Bourgoin's organ (BO), aperture (ap) and cuticular spines (CS); (B, C) Apical view of the Bourgoin's organ (BO), showing the aperture (ap), petal-like walls (PW), pores (po) and the cuticular spines (CS). (D) Lateral view of cuticular spines (CS) and the small pores (po) on the expanded flagellar base. Scale bars: A = 30.0 μm; B = 10.0 μm; C = 5.00 μm; and D = 3.00 μm.

beneath the eyes (Fig. 1A). In both adult male and female, the antennae are 880–1040 μm long (Fig. 1A). Each antenna consists of three segments: a short ring-like antennal scape connecting the antenna with the head capsule, a stout cylindrical antennal pedicel and a long bristle-like antennal flagellum (Fig. 1C). The antennal scape is 52–71 μm long, bearing few sensilla (Figs. 1C and 3E), and the antennal pedicel is about 200–242 μm long and is covered with sensory equipments (Fig. 1B and C). The antennal flagellum is composed of two distinct portions, a basal bulb and an apical arista (Figs. 1C and 2A). The basal bulb is an expanded flagellar base which inserted in a socket on the apex of the antennal pedicel at the level of a disk-like, concave area (Fig. 1D). This area is encircled by series of concentrically arranged cuticular spines (Fig. 1D). A single campaniform sensillum is proximally situated near the socket (Fig. 1D). The distal part of the basal bulb gives rise to a long, thread-like arista, which is 628–727 μm long and ended with a sharp apex (Fig. 1C).

3.2. Antennal and maxillary sensilla types and distribution

Four types of antennal sensory equipments are discovered: trichoid sensilla, plate organs, campaniform sensilla and coeloconic sensilla. Trichoid sensilla and plate organs are widely distributed on the antennal pedicel (Fig. 1B and C) while the coeloconic sensilla occur only inside the Bourgoin's organ at the expanded flagellar base (Fig. 2A). Two campaniform sensilla are situated near the apical socket of the antennal pedicel (Fig. 1D and F) and on the antennal scape (Fig. 1C and E) respectively. This type of sensilla can also be found on the maxillary plates near the antennal scape. Besides, an evident Evans' organ is present on each maxillary surface.

3.2.1. Trichoid sensilla (Tr)

Tr observed on the antennae of *Z. gressitti* can be divided into three subtypes referred here as TrI, TrII and TrIII.

TrI are uniporous sensilla, separately distributed on the antennal pedicel (Fig. 1B): 5–10 at the base, 3–5 at the middle and 3–7 at the proximal apex. They are 22–63 μm long, 1.6–2.6 μm in basal diameter and are acute-tipped (Fig. 3A), with straight longitudinal grooves on the surfaces (Fig. 3B). Each TrI is found inserted into an evident raised socket (3.4–4.4 μm in diameter) with a tiny pore beside the socket, and protruding between 30° and 40° from the antenna (Fig. 3B).

TrII are usually confined to the dorsal–lateral apex of the antennal pedicel. They are 17.5–26 μm in length, 2.2–2.9 μm in basal diameter and blunt-tipped, with irregularly netted patterns on the surfaces (Fig. 3D). Each of them inserts into a depression (3.4–4.4 μm in diameter) with several shallow pits on the surface (Fig. 3D), and is hollow (Fig. 3C) and curved toward the antennal shaft (Fig. 3D).

A single TrIII is identified on the lateral surface of the antennal scape in *Z. gressitti* (Figs. 3E and 5C). It is 32–36 μm long, with a diameter that measures 2.5 μm near the base, and is acute-tipped with a smooth surface (Figs. 3E, F and 5C). It is inserted vertically into a raised socket (about 3.9 μm in diameter) and bends slightly at the apex (Fig. 3F).

3.2.2. Plate organs (PO)

PO, the dominant type of sensilla on the antennal pedicel of *Z. gressitti*, are belonging to the setae-like projected type. They are distributed unevenly on the antennal pedicel surface (50–60 PO in total), and are more densely concentrated on the distal region of the antennal pedicel (Fig. 1B and C). Each PO consists of a cluster of 10–17 setae-like projections (7–35 μm long) surrounded by 5–11 cuticular denticles (Fig. 4A and B). These setae-like projections are tapering from flat bases into blunt tips (Fig. 4C), and surround concentrically on a flat central multiporous area (5–7 pores) of 8–15 μm diameter (Fig. 4C). Some setae-like projections are longer than the cuticular denticles (Fig. 4A), while others are as long as those denticles (Fig. 4B). They are of the multiporous type.

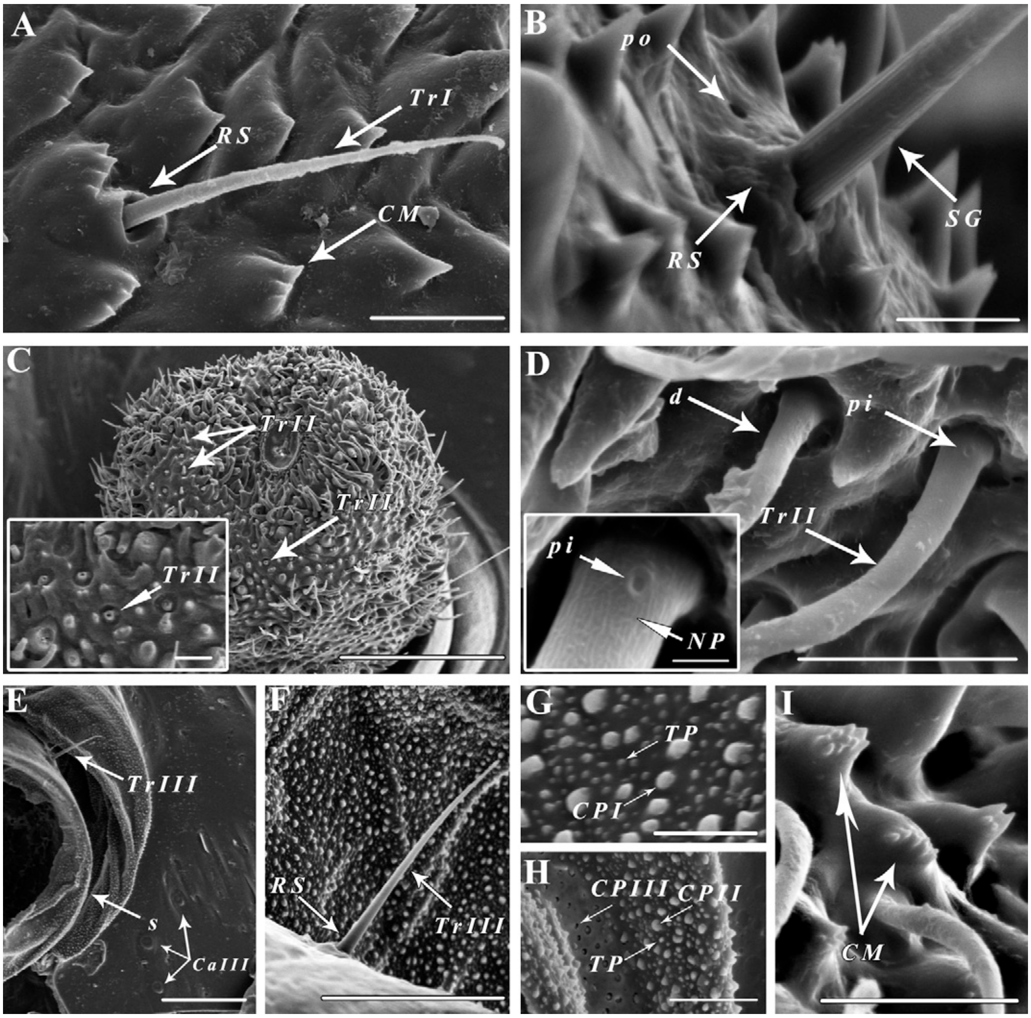

Fig. 3. SEM images of trichoid sensilla, cuticular microtubercles and cone-shaped processes on the antennae and maxillae of *Zema gressitti*. (A, B) Trichoid sensilla subtype I (TrI). (C, D) Trichoid sensilla subtype II (TrII). (E, F) Trichoid sensilla subtype III (TrIII). (G) Cone-shaped processes subtype I (CPI) and tiny projections (TP) on the antennal scape; (H) Cone-shaped processes subtype II (CPII) and tiny projections (TP) on the maxillary plate with cone-shaped processes subtype III (CPIII) sunk in depressions; (I) Cuticular microtubercles (CM). CaIII (campaniform sensillum subtype III); d (depression); RS (raised socket); CM (cuticular microtubercles); NP (netted patterns); po (pore); pi (pit); s (antennal scape); SG (straight grooves). Scale bars: A = 10.0 μm; B = 5.00 μm; C = 100 μm (inset: 10.0 μm); D = 10.0 μm (inset = 1.00 μm); E = 50 μm; F = 20.0 μm; G = 5.00 μm; H = 10.0 μm; and I = 30.0 μm.

3.2.3. *Campaniform sensilla (Ca)*

Three subtypes of Ca (CaI, CaII and CaIII) have been observed on the surfaces of the antennal pedicel, antennal scape and maxilla respectively.

A single CaI is found near the apical socket of the antennal pedicel near the expanded flagellar base (Figs. 1D and 5A). CaI is a dome-shaped sensory structure (5–7 μm in diameter) set in a deep cavity encircled by rings of cone-shaped projections (Fig. 1D and F).

Only a CaII, with similar shape to CaI, is detected on the ventral surface of each antennal scape (Figs. 1C and 5A). However, CaII (about 18 μm in diameter) is larger than CaI and not set in a depression, but rises up from the surface by 2–3 μm lacking cuticular denticles surrounding it (Figs. 1C, E and 5A).

Three CaIII (6.1–9.2 μm in diameter), with structures similar to CaII, are present on the maxillary plate near the antennal scape (Figs. 3E and 5C).

3.2.4. *Coeloconic sensilla (Co) and Bourgoin's organ (BO)*

At the base of the flagellar arista, an evident BO opens (about 7.8 μm in diameter of the aperture) on the anterior part of the basal bulb (Fig. 2A), with 4–5 petal-like walls (4.2–5.9 μm long) surrounding the aperture (Fig. 2B and C). The antennal second projections (Shih and Yang, 1996), also called basal flagellar processes (Liang, 2001) are absent in this species. Around the surface of BO, a row of 7–15 cuticular spines are observed (Fig. 2A). Each spine is cone-shaped with a pore situated at the base (Fig. 2C and D). Co are usually sheltered by BO (Bourgoin, 1986; Romani et al., 2009) and cannot be detected here.

3.2.5. *Evans' organ (EO)*

EO can be discovered at the dorsal margins of the maxillary plates in both male and female specimens (Fig. 5A and C). Specifically, the sensilla are situated at a distance of roughly 80 μm above the frontoclypeal structure and below the antennae and eyes (Fig. 5A and C). Each EO is formed by a deep cavity (8–16 μm deep), with 4 petal-like cuticular infoldings in the center (Fig. 5B and D). The cavity measures 25.3–37.2 μm in diameter and has a thick rim, which is crinkled inside (Fig. 5B and D).

3.3. *Other antennal and maxillary structures*

3.3.1. *Cuticular denticles (CD)*

CD are found around the setae-like projections in PO (Figs. 1D and 4A–D). Depending on the plate diameter, the number

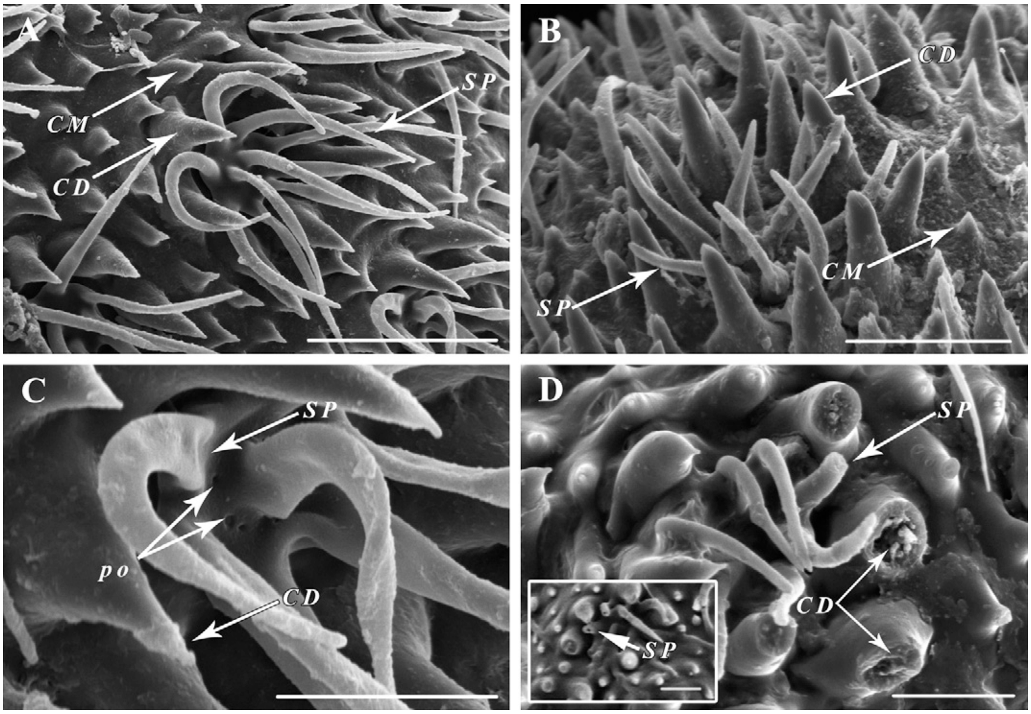

Fig. 4. SEM images of plate organs of *Zema gressitti*. (A) General view of a plate organ (PO), showing setae-like projections (SP) which are longer than cuticular denticles (CD). (B) General view of a plate organ (PO), showing setae-like projections (SP) which are shorter than or as long as cuticular denticles (CD). (C) The bottom of a plate organ (PO) with several small pores (po) and basal-flattened setae-like projections (SP) on the flattened plate. (D) Hollow setae-like projections (SP) and cuticular denticles (CD). CM (cuticular microtubercles). Scale bars: A = 30.0 μm; B = 20.0 μm; C = 10.0 μm; and D = 10.0 μm (inset = 10.0 μm).

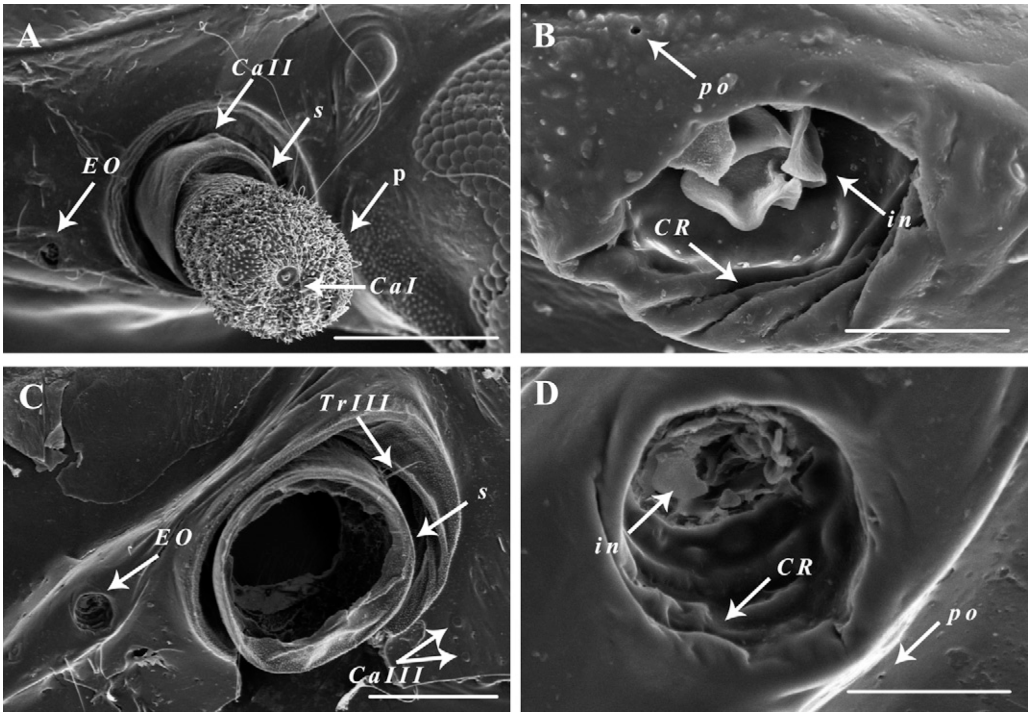

Fig. 5. SEM of Evans' organ of *Zema gressitti*. (A, C) General view of different types of Evans' organs (EO) near the antennal scape (s). (B, D) Different type of Evans' organs with infoldings (in) and crinkled rim (CR) inside and a pore (po) outside. CaI (campaniform sensillum subtype I); CaII (campaniform sensillum subtype II); CaIII (campaniform sensillum subtype III); p (antennal pedicel). Scale bars: A = 200 μm; B = 10.0 μm; C = 20.0 μm; and D = 20.0 μm.

of the denticles surrounding each PO varies from 5 to 11. Each CD is cone-shaped with a sharp apex, measures 9.7–16.6 μm in length and 6.3–9.4 μm in diameter at the base, and it is hollow with a smooth surface (Fig. 4A–D). These structures are more sclerotized and straighter than the setae-like projections (Fig. 4A–D).

3.3.2. *Cuticular microtubercles (CM)*

CM are a kind of cuticular structures present in great numbers on the surface of the antennal pedicel, with increasing density from the base to apex (Fig. 1B). Most of them are cone-shaped, 4.7–10.8 μm in length, and tapering to sharp tips (Fig. 4A and B).

Some CM appear like small cones and divide distantly into 2–10 blunt-tipped pegs across different area on the antennal pedicel (Fig. 3A and I). However, some CM on the extreme base appear to be shorter (4.7–7.2 μm long), scale-like and seem to be fused with each other (Fig. 1B).

3.3.3. *Cone-shaped processes (CP)*

Three subtypes of CP (CPI, CPII and CPIII) have been revealed on the antennal scape and maxilla. Numerous CPI are situated on the surface of the antennal scape ridges (Fig. 3G). Each of them (0.6–1.2 μm in length) rises from a depression surrounded by several tiny projections (about 0.2 μm in length) and has a blunt tip (Fig. 3G). CPII with similar structures and sizes can be seen on the border of the maxillary plates surrounding the antennal scape (Fig. 3H). Numerous CPIII sink in depressions between the circular ridges on the maxillary plates (Fig. 3H).

4. Discussion

The antennal morphology of *Z. gressitti* is similar to that in other fulgoromorphan groups, with three segments of a short antennal scape, a cylindrical antennal pedicel and a thread-like antennal flagellum (Fig. 1C), and *Z. gressitti* share similar kinds of antennal sensilla with most fulgoromorphan species (Stroiński et al., 2011).

Sensilla. TrI (Fig. 3A and B) and TrII (Fig. 3C and D) on the antennal pedicel are identified as chemoreceptors (Aljunid and Anderson, 1983). TrIII (Figs. 3E, F and 5C) on the antennal scape are extremely similar to Böhm bristles, which are probably present in analogous locations in various insects (Heran, 1959; Markl, 1962; Schneider, 1964). The Böhm bristles at the two proximal joints of the antennae in honey bee could electrophysiologically be shown to be phasic-tonic mechanoreceptors (Schneider, 1964). Data from silk moths and butterflies suggests that the Böhm bristles encode the gross changes in antennal position (Sane et al., 2007). As such, this kind of sensilla is considered to be mechanoreceptors on the antennae, and presumably function as proprioceptors which perceive antennal position (Pringle, 1938; Thurm, 1962; Schneider, 1964; Sane et al., 2007).

Ca have been reported in a variety of places on insects such as halters, palps, legs, bases of wings, and even the eyes (Schneider, 1964; Bromley et al., 1980), and also have been found in planthoppers (Schneider, 1964; Bourgoin, 1985; Romani et al., 2009). However, only a few cases of CaII have been reported on the antennal scape (Bartlett and Hamilton, 2011), and CaIII on the maxillae have rarely been discovered. They are generally few in number, usually located near the segmental joints, and are considered as mechanoreceptors (Schneider, 1964; McIver, 1985; Zacharuk, 1985; Liang and Fletcher, 2002). Here they probably act as antennal proprioceptors (Bromley et al., 1980), and respond to the stresses arising from the movement of the flagella as already reported in aphids (Dunn, 1978). The inner structure must be studied further to provide evidence of this.

PO are known on the antennae in different insect groups, such as Hymenoptera, Coleoptera and Hemiptera (Snodgrass, 1926; Slifer, 1970). PO of Fulgoromorpha exhibit important structural variations which have been classified into 5 main morphological types, two of which have been reported from Tropiduchidae: the setae-like projected plate and the folded flattened plate (often clover leaf-like) (Stroiński et al., 2011). As in many other fulgoromorphan species, PO on the antennal pedicel in *Z. gressitti* are of the setae-like projected plate type (Fig. 4A and B) and are similar to those of some other tropiduchids already studied: *Kusuma* sp. (Marshall and Lewis, 1971: Fig. 1), *Trypetimorpha japonica* Ishihara (Huang and Bourgoin, 1993: Fig. 2), and *Teramnon stenopteryx* Fennah (Hamilton, 2011), but are different from those in *Ossoides lineatus* Bierman (Marshall and Lewis, 1971: Fig. 1), in which the clover-leaf type projections (4 infoldings) replace the digitate ones. According to the intra-group repetition criterion (Wiley, 1981), which says that the character that is most widely distributed within a taxon is probably the plesiomorphic one, Bourgoin and Deiss (1994) suggested that the digitate plate might be the plesiomorphic form in Fulgoromorpha. Based on previous electronic microscopic studies, PO in planthoppers are considered evolving from clusters of basiconic receptors which are becoming reduced and aggregating into a meta-placoid structure, and then evolving from a still multi-digitate plate toward a fully integrated flattened plate (Lewis and Marshall, 1970; Altner and Prillinger, 1980; Rojas-Rousse and Palevody, 1983). Accordingly, PO in *O. lineatus*, showing a trend to be less indented, reveal an apomorphic condition for this character regarding to other tropiduchid species.

Bourgoin's organ. BO seems to be present in all planthoppers families and is proposed to have a sensory function (Bourgoin, 1985; Cobben, 1988; Liang, 2001). This role has been confirmed by Romani et al. (2009) in a very complete study and confirmed the presence of two coeloconic sensilla (Co) in *Hyalesthes obsoletus* (Cixiidae). Its aperture is surrounded by a ridge that can take different shapes: single ring, petal-like wall, fringed or digitate wall. In *Z. gressitti*, it looks like the petal-like wall (Fig. 2B and C). In Achilixiidae, Derbidae, Meenoplidae, Kinnaridae, Tettigometridae, Ricaniidae, part of Cixiidae and Flatidae, digitiform tips have been found around the aperture (Bourgoin, 1985; Shih and Yang, 1996; Liang, 2001; Romani et al., 2009). Co also occur in other Auchenorrhyncha lineages such as in some Australian cercopid species. They exhibit a simple rim with a smooth margin, and are sunken below the cuticular surface at the base of the flagellum (Liang and Fletcher, 2002: Figs. 1–9). The antennal second projections (Shih and Yang, 1996), also called basal flagellar processes (Liang, 2001), are absent as in many other planthoppers. Further studies on the distribution of this structure within the lower Fulgoromorphan families are necessary.

Evans' organ. EO are first reported by Evans (1973) who considered this structure to be homologous with the maxillary palps of the other Hexapoda according to the appendicular theory, which claims that the maxillary plates in Hemiptera are originated from the ancestral transformed maxillary cardo/stipes or even the galea. This theory is challenged by Parsons (1964, 1974) who recognized a subgenal origin to these maxillary plates (the parietal theory). Analysis of the distribution and disparity of EO in the Hemiptera have confirmed this last point of view of Parsons (Bourgoin, 1985). The position of EO on the maxillary plates varies according to the taxa: dorsally or ventrally to the maxillary sulcus when present, very posteriorly on the gena or very anteriorly under the antennal socket (Bourgoin, 1986). It was reported on the subantennal process as the 'subantennal plaque sensillum' in Cixiidae *Borysthenes maculata* Matsumura and *Euryphlepsia papuaensis* Muir (Liang, 2005). In *Z. gressitti*, its position is similar to the one observed in most fulgoromorpha taxa at the basal marge of the gena. EO seems absent in Sternorrhyncha and Heteroptera, but present in Auchenorrhyncha and Coleorrhyncha. Each EO in Auchenorrhyncha is reported as 'a finger-like lobe contained in a pit' (Evans, 1973) or 'a subantennal plaque sensillum' (Liang, 2005), whereas that in Coleorrhyncha is placoid-like (Bourgoin, 1986). It is suspected that the evolution and the morphology of this structure accords with the evolution of PO or the labial subapical sensory organs (Brozek and Bourgoin, submitted). Further studies may lead to observations of other morphological types. Therefore, the flattened structure reported in Tettigometridae (Bourgoin, 1986) or the thrown-folded type one reported in Cixiidae (Liang, 2005) and here Tropiduchidae should be considered as advanced characteristics, and multi-digitate type is expected to be found in other taxa. Being of the multiporous type, EO are probably olfactory receptors.

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