



Research paper

Fine morphology of the antennae and mouthparts of *Dentatissus damnosa* (Chou & Lu) (Hemiptera: Issidae)

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ABSTRACT

The ultrastructural morphology of the antennae and mouthparts of *Dentatissus damnosa* (Chou & Lu) (Hemiptera: Issidae) was examined using scanning electron microscopy. Eight types of sensilla were found on antennal segments, including a Böhm bristle on the scape, sensillum trichoideum and plaque organ on the pedicel, sensillum chaeticum and two subtypes of sensilla campaniformia on these two segments; Bourgoïn's organ and sensillum basiconicum were observed on the basal bulb of the flagellum. The mouthparts of *D. damnosa* conform to the typical piercing-sucking type in Hemiptera. The mandible styles bear 7 protuberances on the distal extremity, including sensilla chaetica, sensilla basiconica and a pair of sub-apical labial sensilla at different positions on the labium. The labial tip forms three sensory fields and each dorsal sensory field consists of 9 uniporous peg-like sensilla, 1 multiporous peg-like sensillum and 7 long sensilla basiconica. The ventral sensory field has two dome-shaped sensilla and two pairs of different sensilla basiconica.

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1. Introduction

Insect antennae and mouthparts possess a series of sensilla which endow an insect with a range of sensory functions and play significant roles in ecological behavior, such as host plant detection, feeding and mating (Backus, 1988; Schneider, 1964; Zacharuk, 1985). The sensory structures and function of sensilla can be deduced from their structure (Schneider, 1964). Confirmation of the structures and clarification of the sensory mechanisms on insect antennae and mouthparts can help us understand their phylogeny and ecology.

The primary function of antennae is to carry exterosensilla and to extend these ahead of the body and bilaterally in approximately equal proportions (Zacharuk, 1985). Most of these antennal sensilla are generally distributed on the flagellum, and present a variety of forms and characteristics in relation to their various functions in contact chemoreception, mechanoreception and thermohygroreception (Chapman, 1998; Zacharuk, 1985). With regard to Fulgoromorpha, the sensilla of a flagellum are less in number than in many other insects, and ultrastructure observations of antennal sensilla in planthoppers have so far mostly focused on

Delphacidae and Tropiduchidae (Fu et al., 2012, 2013; Sun et al., 2006; Wang et al., 1997; Wang et al., 2012, 2013). Antennal structures are indeed demonstrated in some taxonomic papers (Liang, 2001a,b; Liang, 2002a,b; Stroiński et al., 2011) and plaque organs on the pedicel have been considered as a potential characteristic for taxonomic and phylogenetic analysis (Bourgoïn, 1985; Bourgoïn and Deiss, 1994; Cheng and Yang, 1996a,b; Hamilton, 2011; Lewis and Marshall, 1970; Marshall and Lewis, 1971; Shih and Yang, 1996, 1997).

Mouthparts are structurally modified among insects primarily in relation to their mode of feeding (Zacharuk, 1985). The similar piercing-sucking mouthparts of auchenorrhynchs are presumably due to strong structural and functional constraints on their evolution, a resemblance due to adapting to various food resources and feeding habits (Backus, 1985, 1988; Backus and McLean, 1982, 1983, 1985). However, limited anatomical studies of mouthparts structures and sensilla have interfered with understanding of sensory mechanisms and mediation of feeding in the Auchenorrhyncha. In Fulgoromorpha, research on mouthparts has focused on labial sensilla (Backus, 1985; Brožek and Bourgoïn, 2013a; Foster et al., 1983b; Liang, 2005; Mora et al., 2001; Sōgawa, 1977; Wang et al., 2012), the interlocking mechanism of maxillae and mandibles (Brožek et al., 2006; Brožek and Bourgoïn, 2013b), or description of mouthpart morphology just for delphacids (Dai et al., 2014; Mora et al., 2001).

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The issid species *Dentatissus damnosus* was originally established as a *Sivaloka* species in the Issidae by Chou et al. (1985). It was transferred to the genus *Kodaianella* (Gnezdilov, 2013) and now it has been assigned to the genus *Dentatissus* (Chen et al., 2014). This species is widely distributed in the Chinese fauna and injurious to many kinds of woody plants (Chen et al., 2014). Although the biometrics, internal reproductive organs and mitochondrial genome have been well documented in *D. damnosa* (Meng et al., 2010; Song et al., 2010; Yan et al., 2005), the ultrastructural information remains obscure. Furthermore, the types and distribution of sensilla of the antennae and mouthparts, and the relationship between mouthpart structure and function in feeding of issids are not yet known. The aim of this study is to investigate the ultrastructure of the mouthparts and antennae of *Dentatissus damnosus* through scanning electron microscopy (SEM) observations, to demonstrate the sensory system and infer the feeding behavior of the family Issidae.

2. Materials and methods

2.1. Sample preparation for scanning electron microscopy

Adults of *D. damnosa* were collected from the north campus of Northwest A&F University in Yangling, Shaanxi, China, in June 2014 and 2015. Voucher specimens were deposited in the Entomological Museum of Northwest A&F University. The heads together with antennae and labium were removed from seven randomly selected specimens. They were then serially dehydrated in a graded ethanol, replaced by tertiary butanol, freeze-dried for 3 h in a VFD-21S freeze dryer (Hitachi, Tokyo, Japan), and sputter-coated with gold in a MSP-1S high resolution sputter coater (Hitachi, Tokyo, Japan). Observations and micrographs were carried out under a Hitachi S-3400N scanning electron microscope (Hitachi, Tokyo, Japan) at 15 kV.

2.2. Terminology

For classification of sensilla, we follow Schneider (1964) and Zacharuk (1985). The terminology of the sensilla on the antennae is

based on the criteria established by Bourgoïn and Deiss (1994) and Stroiński et al. (2011). The nomenclature for connecting systems between maxillae and mandibles and the sensilla on the labial tip follows Brožek et al. (2006) and Brožek and Bourgoïn (2013a).

3. Results

3.1. Antennae

3.1.1. General description of antennae

As in other planthoppers, adult *D. damnosa* have a pair of setaceous antennae laterally situated on the head capsule and inserted beneath the eyes (Fig. 1A, B). Each antenna comprises three segments: a short ring-like scape connecting the antenna with the head capsule, an enlarged cylindrical pedicel that possesses most of the sensilla and a long bristle-like flagellum with a swollen sensory region near its junction with the pedicel (Figs. 1A, 2A). Both male and female adults have the antennae 1090–1120 μm long (Fig. 1A).

The flagellum comprises a basal bulb and a thread-like arista that is inserted into the apical socket of the pedicel (Fig. 2A–C). The basal bulb appears wrinkled on the surface and the arista is about 815 μm long and ends with a pointed apex (Figs. 1A, 2C, 3C). Subsegments of the flagellum were not visible.

The pedicel is about 200 μm long (Fig. 2B). It is covered with a variety of sensilla and also a mass of cuticular microtubercles (Cm) which become increasingly dense from the base to apex of pedicel (Fig. 2D, F–H). Most Cm are cone-shaped, 0.8–2.7 μm in length, and tapering to sharp tips. Some Cm on the extreme base of the pedicel seem blended with others and appear scale-like although some of them resemble small cones and distally divide into 2–6 blunt-tipped pegs (Fig. 2F–H). The pedicel apex possesses a socket (sk) and is encircled by rings of concentrically-arranged short cuticular spines (Cs) (Fig. 2D).

The scape is 84.6–87.2 μm long (Fig. 2F). It bears few sensilla (Figs. 2F; 3A, B, G). The scape ridges are wrinkled with numerous papillae (pa) on the surface, each of them 0.8–1.4 μm in diameter (Fig. 3A, B). Some Cm are also present on the anterior and lateral surface of the scape (Fig. 3B).

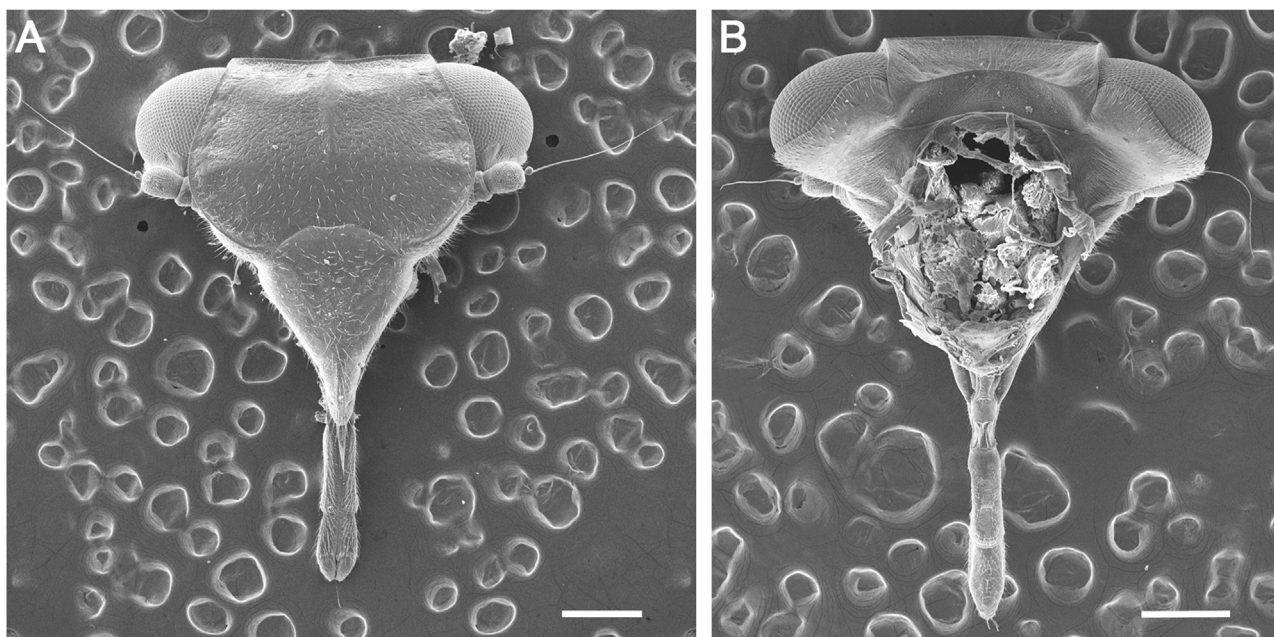


Fig. 1. Head of adult *D. damnosa* including the antennae and mouthparts. (A) Anterior view. (B) Posterior view. Scale bars: (A) and (B) = 400 μm .

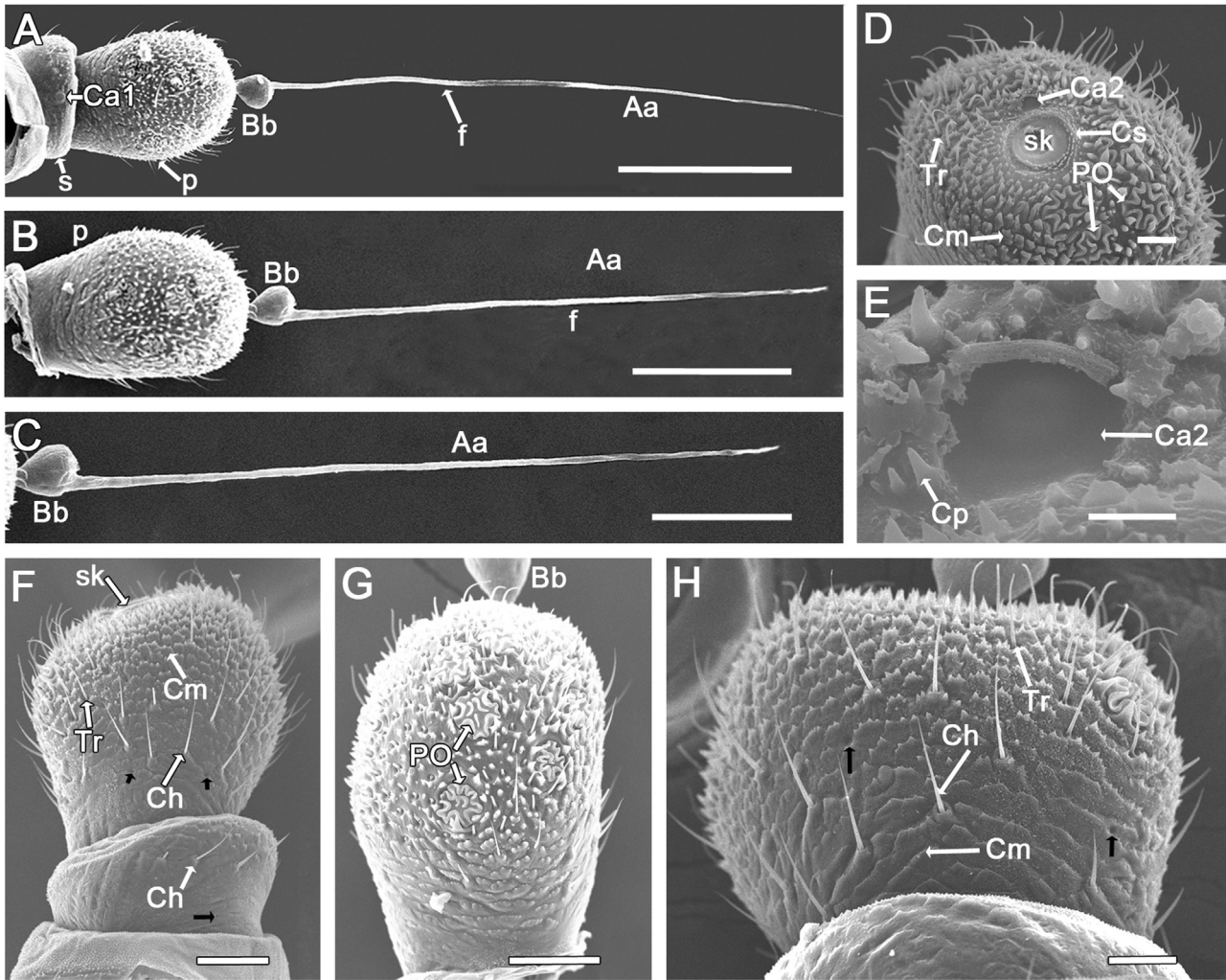


Fig. 2. Antennae of *D. damnosa*. (A) Posterior view of the scape, pedicel and flagellum. (B) Anterior view of the pedicel and flagellum. (C) Anterior view of the flagellum with apical arista and basal bulb. (D) The top of the pedicel. (E) Sensillum campaniformium II with cone-shaped projections on the pedicel. (F) Lateral view of the scape and pedicel, the black arrows show the pits. (G) Anterior view of the pedicel. (H) Lateral view of the pedicel, the black arrows show the pits. Abbreviations: Aa, apical arista; Bb, basal bulb; Ca2, sensillum campaniformium subtype II; Ch1, sensilla chaetica subtype I; Cm, cuticular microtubercles; Cp, cone-shaped projections; Cs, cuticular spines; f, flagellum; p, pedicel; pa, papillae; PO, plaque organs; s, scape; sk, socket; Tr, sensilla trichodea. Scale bars: (A) = 200 μm ; (B) = 150 μm ; (C) = 100 μm ; (D) and (H) = 25 μm ; (E), (F) and (G) = 50 μm .

3.1.2. Types and distribution of antennal sensilla

3.1.2.1. Sensillum Chaeticum (Ch). Sensilla chaetica are sparsely distributed on the surface of the scape and pedicel (Figs. 2F, H; 3G). Each of them is inserted into a flexible socket which is slightly elevated above the antennal surface. They were found to be 21.3–28.5 μm in length, 2.1–2.4 μm in basal diameter, with longitudinal grooves on surface (Fig. 3I). Ch are slender, aporous and with pointed apices (Figs. 2H; 3H, I).

3.1.2.2. Böhm Bristle (BB). A single Böhm bristle is present on the dorsolateral surface of the scape (Fig. 3G). The BB is nearly vertical to the surface of scape and emerges from a flexible socket. The straight bristle (about 12.4 μm long) is aporous, and blunt-tipped with straight longitudinal grooves on the surface (Fig. 3J).

3.1.2.3. Sensillum Trichoideum (Tr). Sensilla trichodea are only found and largely identified on the pedicel (Fig. 2F–H). They are hollow (about 26.4 μm in length, 2.4 μm in basal diameter), slender, curved, tapered to a relatively blunt-tip and set into individual pits (3.5 μm in diameter) (Fig. 3H, L). Tr is with irregularly netted patterns on the surface and an obvious basal pore (Fig. 3K). Tr was the most abundant type of antennal sensilla observed (Fig. 2G, H).

3.1.2.4. Plaque Organ (PO). Plaque organs are observed only on the pedicel. They are distributed unevenly and are more densely concentrated on the distal region of the pedicel (Fig. 2D, G). Each PO consists of a sclerotized plate (20.1–22.0 μm in diameter) externally surrounded by 6–8 cuticular denticles (Cd) (Fig. 3H, L). The edge of the plate is turned up in 6–8 places, surrounding 1–3 small ridges (Figs. 2D, G; 3H). Some shallow pores have been detected on the flat central area of plate (Fig. 3M). The raised edge is shorter than the cuticular denticles (Cd). Each Cd is cone-shaped with a sharp apex, and measures 5.2–5.7 μm in length and 4.2–5.7 μm in diameter at the base (Fig. 3H, L).

3.1.2.5. Sensilla Campaniformia (Ca). Two subtypes of Ca are arranged singly on the scape and pedicel (Figs. 2A, D; 3B). Ca are hemispherical formations of the cuticle and have no pores or openings (Figs. 2E; 3B, D). A sensillum campaniformia subtype I (Ca1) (~13.9 μm in diameter) is detected on the ventral surface near the distal rim of the scape, rises up from the surface and lacks any cuticular denticles surrounding it (Fig. 3B, D). A sensillum campaniformia subtype II (Ca2) (~11.2 μm in diameter) is located near the apical socket within the cuticular spines on the apical surface

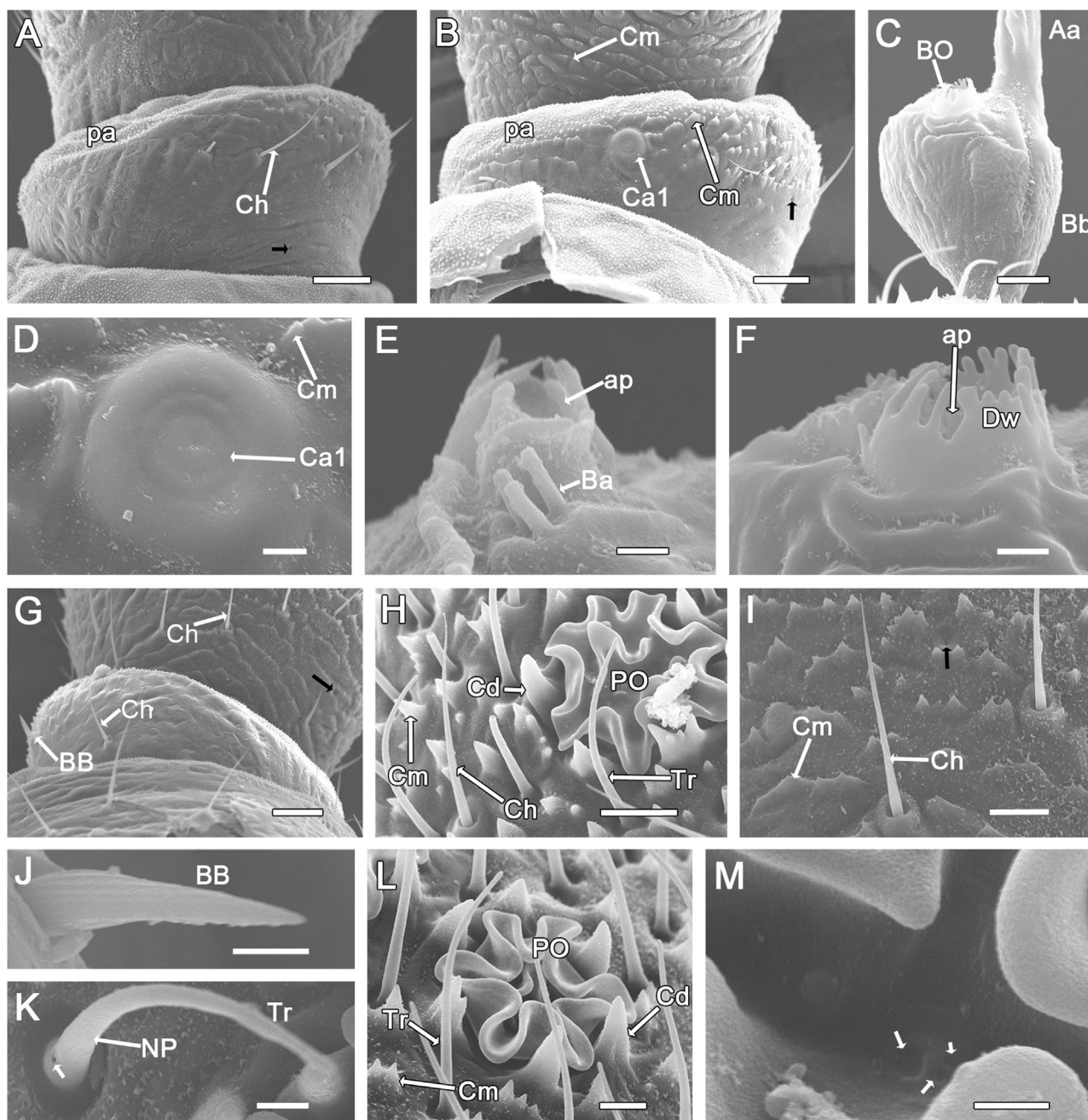


Fig. 3. Antennae of *D. damnosa*. (A) Posterior view of the scape and pedicel. (B) Anterior sides of the scape and pedicel, the black arrow shows the pit. (C) General view of the flagellar basal bulb. (D) Sensillum campaniformium subtype I on the scape. (E) 3 sensilla basiconica on the aperture ventrally. (F) Bourgoin's organ. (G) Lateral view of the scape and pedicel, the black arrow shows the pit. (H) Sensillum chaeticum, sensilla trichodea and plaque organ on the pedicel. (I) Sensilla chaetica on the basal scape, the black arrow shows the pore. (J) Böhm bristle on the scape. (K) Sensillum trichodeum on the pedicel, the white arrow shows the pore. (L) Plaque organ and cuticular denticles on the scape. (M) Shallow pores (white arrows) on the central flat of the plaque organ. Abbreviations: Aa, apical arista; ap, aperture; Bb, basal bulb; BB, Böhm bristle; BO, Bourgoin's organ; Ca1, sensillum campaniformium subtype I; Cd, cuticular denticles; Ch, sensillum chaeticum; Cm, cuticular microtubercles; Dw, digitate wall; NP, netted patterns; pa, papillae; PO, plaque organ; Tr, sensillum trichodeum. Scale bars: (A) and (G) = 25 μm ; (B) = 20 μm ; (C), (H) and (I) = 10 μm ; (D), (E), (J) and (K) = 2.5 μm ; (F) = 2 μm ; (L) = 5 μm ; (M) = 1.5 μm .

of the pedicel (Fig. 2D) and is set in a cavity encircled by rings of cone-shaped projections (Cp) (Fig. 2E).

3.1.2.6. Bourgoin's organ (BO) and Sensillum basiconicum (Ba). At the base of the flagellar arista, an evident BO opens on the anterior surface of the basal bulb (Figs. 2C, 3C), with a digitate wall (3.1–5.9 μm long) surrounding the aperture (Fig. 3E, F). The surface of the BO is wrinkled and furrowed (Fig. 3C). On the aperture ventrally, 3 sensilla basiconica emerge from a cuticular fold

(7.8–8.8 μm long). The Ba has a smooth shaft and a blunt apex (Fig. 3E).

3.2. Mouthparts

3.2.1. Gross morphology of mouthparts

As in other auchenorrhynchan insects, the mouthparts of *D. damnosa* arise from the posterior part of the head capsule (Fig. 1A, B) and are composed of a cone-shaped labrum (Lm) (Fig. 5A), a tube-like labium (Lb) (Fig. 4A, B) and a stylet fascicle (Sf) (Fig. 7A).

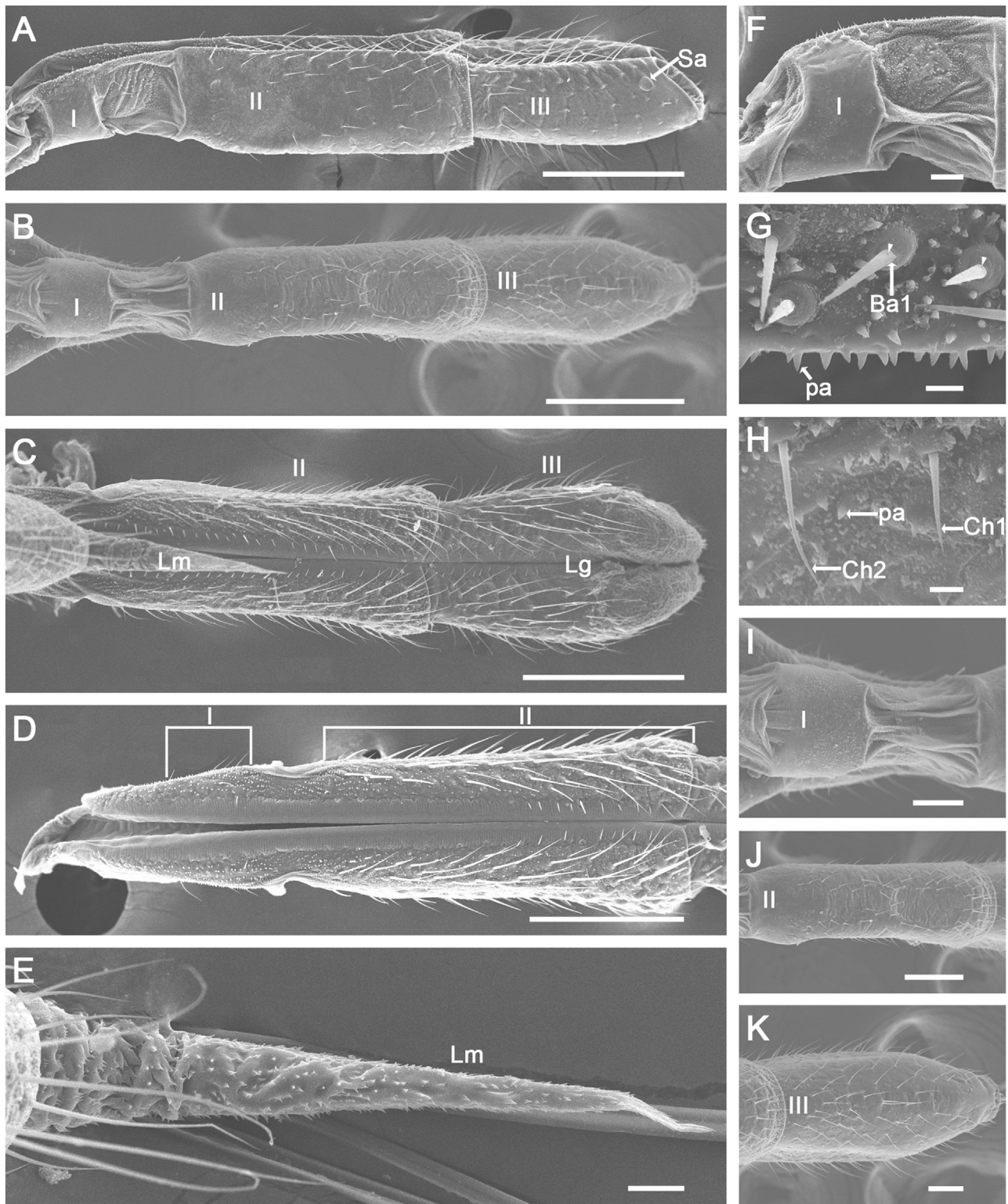


Fig. 4. SEM of labrum and labium of *D. damnosa*. (A) Lateral view of three-segmented labium. (B) The dorsal view of labium. (C) The anterior view of labrum and labium. (D) The anterior view of the first and second labial segments. (E) The anterior view of labrum. (F) Lateral view of the first labial segment. (G) Sensilla basiconica subtype I (white triangles showing the pores) and papillae on the lateral margin of the first labial segment. (H) Sensillum chaeticum subtype I and sensillum chaeticum subtype II on the membrane between the first and second labial segment. (I) The dorsal view of the first labial segments. (J) The dorsal view of the second labial segment. (K) The dorsal view of the third labial segment. Abbreviations: Ba1, sensilla basiconica subtype I; Ch1, sensillum chaeticum subtype I; Ch2, sensillum chaeticum subtype II; I, the first labial segment; II, the second labial segment; III, the third labial segment; Lg, labial groove; Lm, labrum; pa, papillae; Sa, sub-apical labial sensillum. Scale bars: (A) and (B) = 200 μm ; (C) and (D) = 150 μm ; (E) = 20 μm ; (F), (G) and (H) = 5 μm ; (I) and (K) = 50 μm ; (J) = 100 μm .

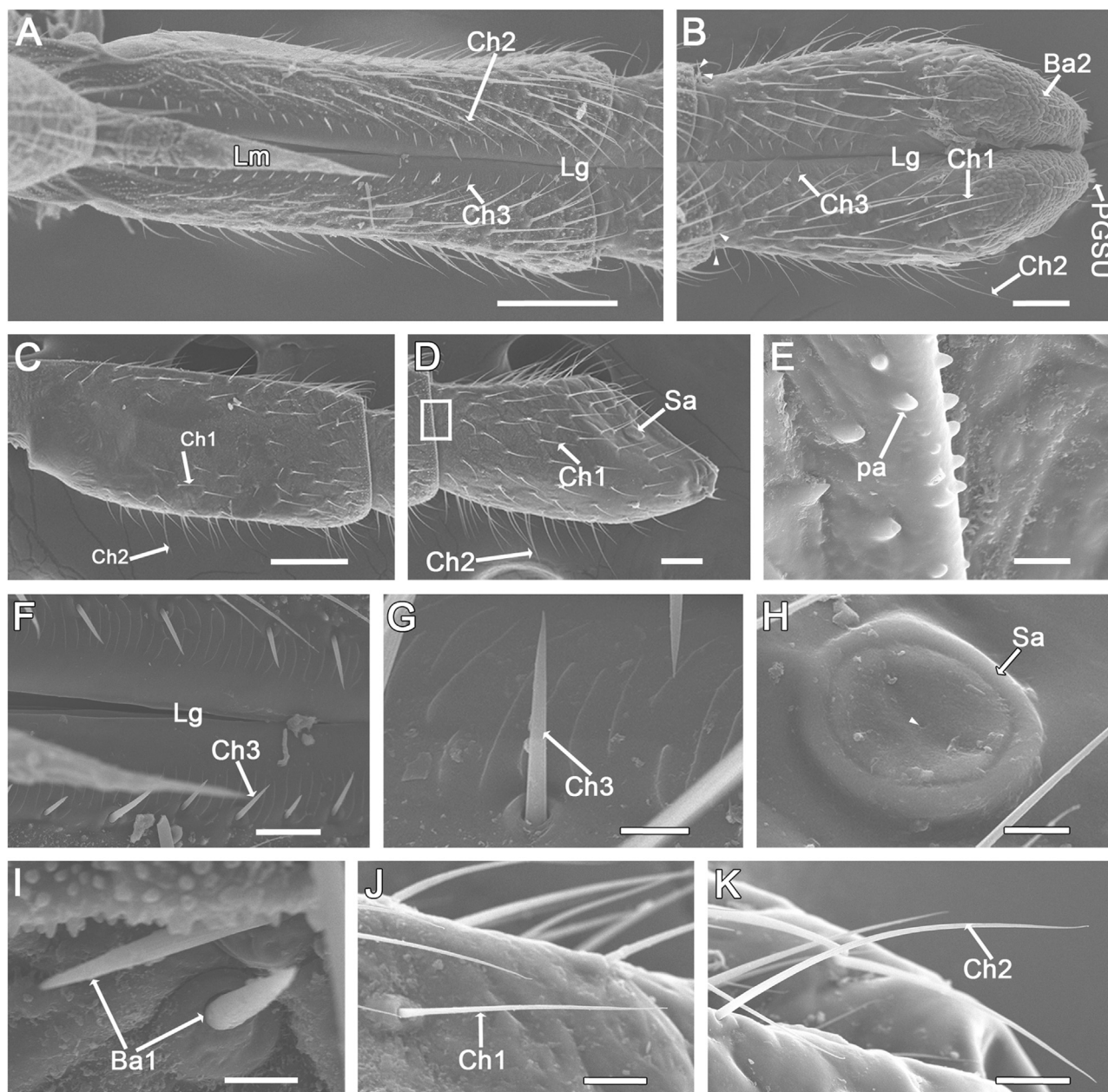


Fig. 5. SEM images of labium and the labial sensilla of *D. damnsa*. (A) The anterior view of labrum and the second labial segment. (B) The anterior view of the third labial segment, showing sensilla basiconica subtype I (white triangles) at junction of second and third segment. (C) The lateral surface of the second labial segment. (D) The lateral surface the third labial segment. (E) The outlined box of Fig. 5D, showing papillae. (F) Sensilla chaetica subtype III and wrinkles symmetrically located on each side of the labial groove. (G) Sensillum chaeticum subtype III. (H) Sub-apical labial sensillum, the white triangle showing the pore. (I) Two sensilla basiconica subtype I at base of the third segment. (J) Sensillum chaeticum subtype I. (K) Sensillum chaeticum subtype II. Abbreviations: Ba1, sensilla basiconica subtype I; Ba2, sensilla basiconica subtype II; Ch1, sensillum chaetica subtype I; Ch2, sensillum chaetica subtype II; Ch3, sensillum chaetica subtype III; Lg, labial groove; Lm, labrum; PGSU, uniporous peg-like sensilla; Sa, sub-apical labial sensillum. Scale bars: (A) = 100 μm ; (B) and (C) = 50 μm ; (D), (E), (G), (H) and (I) = 5 μm ; (F) = 15 μm ; (J) and (K) = 10 μm .

The three-segmented labium has a deep longitudinal labial groove (Lg) on the anterior surface (Fig. 4C), which wraps around the stylet fascicle which consists of two inner maxillary (Mx) stylets incompletely surrounded by two relatively shorter mandibular (Md) stylets, and is partially sheltered by the small conical labrum. The surface of labium and labial tip covered with different types of sensilla (Figs. 4A–C, 6).

3.2.2. Labrum (Lm)

The upmost and conical labrum is short ($\sim 255 \mu\text{m}$), is attached along the posterior margin to the anteclypeus, and overlays half of the labial groove of the second labial segments (Fig. 5A). The labrum

is relatively straight and gradually tapers to the tip. The tip of the labrum is extended. The anterior surface of the labrum is wrinkled, with small spines of $< 2.8 \mu\text{m}$ in length; the basal part of the labrum has more wrinkles but fewer spines (Fig. 4E).

3.2.3. Labium (Lb)

The labium is modified as a rostrum and contains three segments (Fig. 4A, B). The anterior surface of the labium is bisected by a labial groove which extends the entire length (Fig. 4C). Sensilla are widely distributed on each side of the labial groove, and relatively fewer are present on the dorsal and lateral surfaces (Fig. 4A–C). The tip

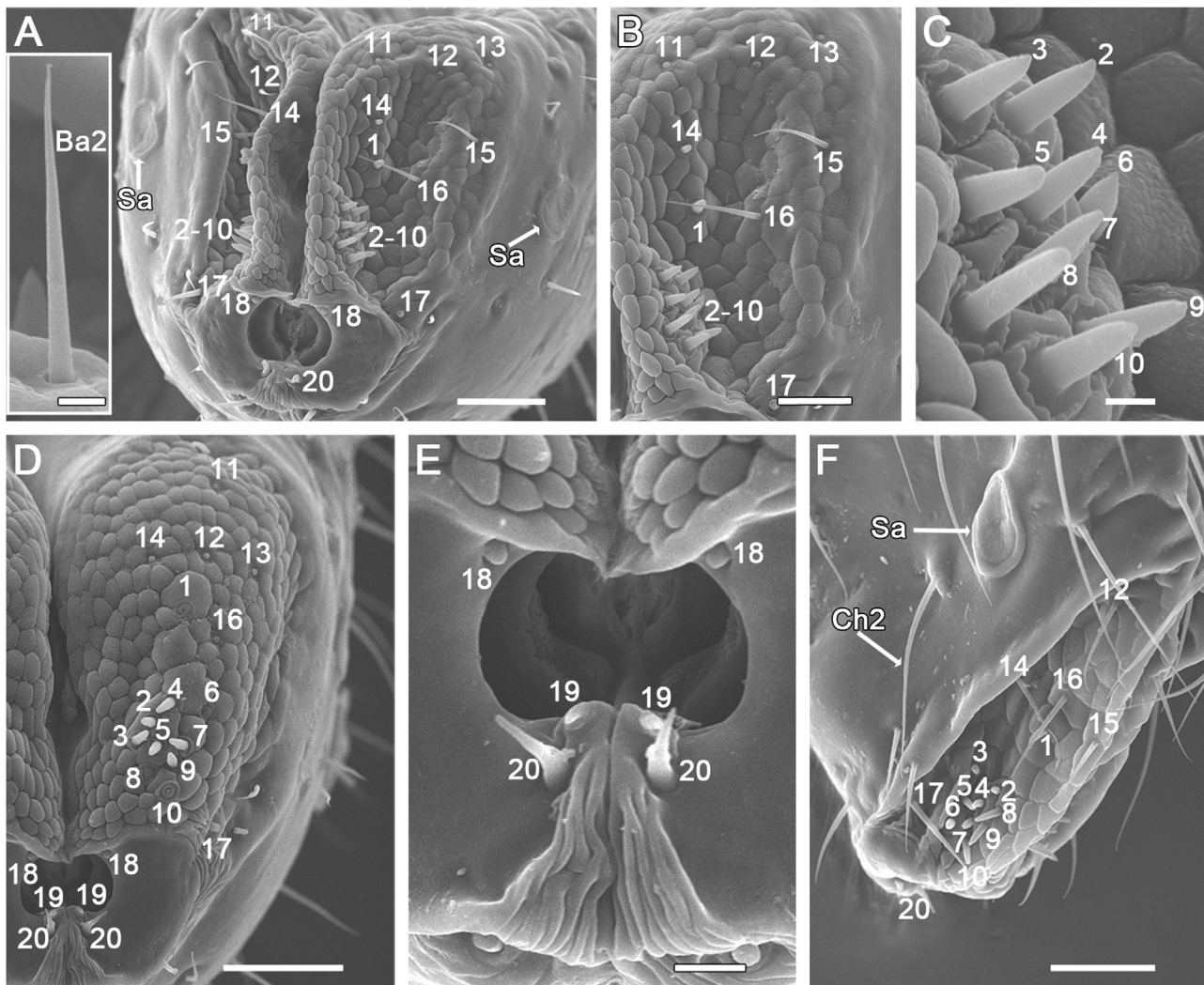


Fig. 6. SEM images of the sensilla on the labial tip of *D. damnosa*. (A) The labial tip from anterior view. (B) Left side of the dorsal sensory field. (C) View of 9 slender uniporous peg-like sensilla. (D) The left side of the labial tip. (E) View of ventral sensory field. (F) The right side of the labial tip. Abbreviations: Ba2, sensillum basiconica subtype II; No. 1, multiporous peg-like sensillum; Nos. 2–10, uniporous peg-like sensilla; Nos. 11–17, sensilla basiconica subtype II; No. 18, dome-shaped sensillum; Nos. 19–20, sensilla basiconica subtype III. Scale bars: (A) = 25 μm (inset: 2.5 μm); (B) = 15 μm ; (C) = 2.5 μm ; (D) = 25 μm ; (E) = 5 μm ; (F) = 20 μm .

of the labial segment has an opening from which the apices of the stylets protrude (Figs. 5B, 6).

The total length of the labium is about 900 μm (Fig. 4A). The entire labium has a relatively uniform width through most of its length with the distal segment narrowing to the tip (Fig. 4B).

Three subtypes of sensilla chaetica have been observed on the labial surfaces. Sensilla chaetica subtype I (Ch1) are slender, relatively straight with pointed tips, and inserted into flexible sockets (16.2–60.7 μm in length); their surface has longitudinal grooves (Figs. 4H, 5J). Sensilla chaetica subtype II (Ch2) resemble Ch1 in their morphology but they are slightly curved in the apical half (28.1–108.7 μm in length) (Figs. 4H, 5K). Sensilla chaetica subtype III (Ch3) (6.8–15.8 μm in length) are short and straight, with a blunt tip and sunken into a flexible socket (Fig. 5F, G). Sensilla basiconica observed on the labium can be divided into three subtypes. Sensilla basiconica subtype I (Ba1) are short, straight, arising from an obviously inflexible socket, with sharp tips and basal pore, and are about 12 μm in length (Figs. 4G, 5I). Two subtypes of sensilla basiconica are found on the labial tip. Sensilla basiconica subtype II (Ba2) (~19 μm in length) are long, with pointed tips and a smooth cuticular wall (Fig. 6A, inset). Sensilla basiconica subtype III (Ba3)

(~6 μm in length) resemble Ba2 in their morphology but are shorter and curved (Fig. 6E).

The first labial segment is short (~86 μm) and concealed by the overlapping anteclypeus (Fig. 4B, C). When the labium is removed from the head, the anterior surface of this segment can be observed, the labial surface has prominent transverse ridges on each side of the labial groove and laterally to them the surface is covered with numerous papillae (Fig. 4D). The lateral and posterior surface is smooth, only some papillae and Ba1 are present on the lateral margins (Fig. 4F, G, I). The membranous joint between the first and second labial segments is excessively constricted, and possesses wrinkles, papillae, with few of Ch1 and Ch2 (Fig. 4F, H, I).

The second labial segment is the longest (~400 μm) of the three segments (Fig. 4A, B). Some papillae are scattered on the anterior margin (Fig. 5E), and a small number of Ch1 and Ch2 are present in the area of the lateral and posterior surfaces of the segment (Figs. 4J, 5C), but more wrinkles emerge on the relatively flat posterior surface (Fig. 4J). On the anterior surface of this segment, a row of Ch3 and a line of transverse ridges approach the two sides of the labial groove (Fig. 5A, F); a large number of Ch1 and Ch2 are symmetrically located on each side of the labial groove (Figs. 4D, 5A).

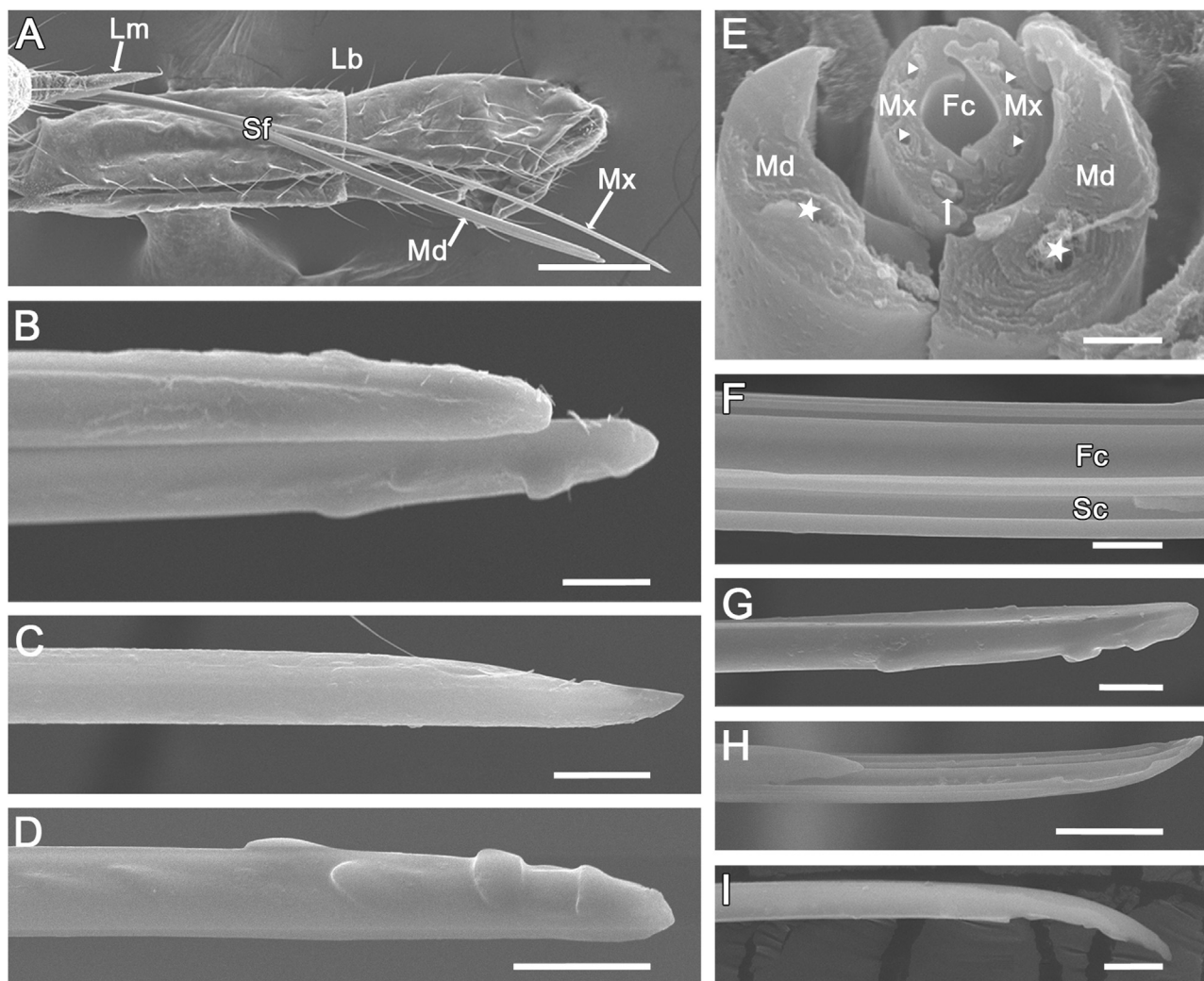


Fig. 7. SEM of *D. damnosa* stylets. (A) Whole stylet fascicle. (B) Apices of mandibular stylets. (C) Apices of maxillary stylets. (D) Tip of mandibular stylet, showing protuberance on the convex external surface. (E) Cross-section of stylet fascicle showing mandibular stylets and maxillary stylets, the interlocking between the maxillary stylets, food canal, salivary canal (white arrow), two dendritic canals in each maxillary stylet (white triangle) and one dendritic canal in each mandibular stylet (white pentacle). (F) One of the maxillary stylets showing inner surface. (G) The smooth hollow inner surface in mandibular stylet. (H) Tip of maxillary stylets, showing inner and outer surface. (I) Tip of maxillary stylet. Abbreviations: Fc, food canal; Md, mandibular stylets; Mx, maxillary stylets; Sc, salivary canal; Sf, stylet fascicle. Scale bars: (A) = 100 μm ; (B), (C), (G) and (I) = 5 μm ; (D) and (H) = 10 μm ; (E) and (F) = 2.5 μm .

The third labial segment is about 350 μm long, of uniform width from base to apical 1/4 then narrowing to the labial tip (Figs. 4K, 5B). The distribution of sensilla on the third segment resembles the second segment. At the junction with the second segment, there are two pairs of Ba1 located on both sides of the labial groove (Fig. 5B, I). On each lateral surface of the third segment and close to the labial tip, a deformed placoid sub-apical labial sensillum ($\sim 21.1 \times 17.1 \mu\text{m}$ in diameter) which has a tiny pore was found (Figs. 5D, H; 6F).

The labial tip possesses two dorsal sensory fields symmetrically located on each side of the stylet groove and a ventral sensory field is located behind the stylet groove (Fig. 6A, D). Each dorsal sensory field consists of 9 slender uniporous peg-like sensilla (PGSU, Nos. 2–10) which are grouped together, 1 multiporous peg sensillum (PGSM, No. 1), and 7 long sensilla basiconica subtype II (Ba2, Nos. 11–17) (Fig. 6). The peg-like sensilla with petaliform inflexible sockets vary in length from 6.6 to 7.6 μm with a diameter of about 1.9 μm (Fig. 6C). The multiporous peg sensillum inserts into a raised inflexible socket (Fig. 6B). On each side of the ventral sensory field is a dome-shaped sensillum (No. 18) on the upper area between the dorsal sensory field and the opening of the maxillae

and mandibles, in contrast with a long sensillum basiconica subtype III (Ba3, No. 20) and a relatively shorter sensillum basiconica subtype III (Ba3, No. 19) on the under area; these are in close contact with the stylets at the point at which they protrude from the labium (Fig. 6A, D, E).

3.2.4. Stylet fascicle

The needle-like stylet fascicle contains two mandibular and two maxillary stylets wrapped in the labium and protruding from the labial tip (Fig. 7A). The diameter of the stylet fascicle is approximately 13.9 μm and the average length of the mandibular and maxillary stylets is about 816 and 900 μm respectively (Fig. 7A, E).

The mandibular stylets are comma-shaped in cross-section respectively, located on each outer side of the maxillary stylets and slightly shorter than the maxillary stylets (Fig. 7A, E). The mandibular stylets envelop two curved maxillary stylets, which are tightly held together (Fig. 7E). The inner surfaces of the mandibular stylets are smooth (Fig. 7G), making it convenient for free movement of the maxillary stylets to probe plant tissue. The convex ventral surface of the mandibular stylets contains 7 protuberances which are

located at the extreme tip of the stylet (Fig. 7B, D). The cross-section of the stylet fascicle shows that each mandibular stylet has a dendritic canal (Fig. 7E), which is a large duct that runs the length of the stylet and is located centrally in the thickest portion of each stylet.

In contrast to the mandibles, the maxillary stylets are asymmetrical and complex (Fig. 7C, H). The external surface of the maxillary stylets is smooth (Fig. 7C, H, I). The two interlocking maxillary stylets in cross-section are approximately elliptical due to the joining of the two crescent-shaped stylets (Fig. 7E). The two maxillary stylets are held together by internal longitudinal grooves and their interlocking mechanism along their length, and are incompletely enveloped by the mandibular stylets (Fig. 7E). The apical part of the maxillary stylets is sharply pointed and incurved (Fig. 7C, H, I). The two internal longitudinal grooves interlock with each other forming a food canal used to suck plant juice, and a salivary canal that directs saliva to the plant (Fig. 7E, F). The hollow food canal is approximately oval in cross-section and located in the center due to the symmetrical concave inner walls of the two stylets (Fig. 7E, F). The salivary canal is located laterally on the inner side as the stylets interlock and is approximately circular (Fig. 7E, F). The diameter of the food canal is about 2.5 μm , which is much larger than the salivary canal at 1.1 μm in diameter (Fig. 7E, F). The food and salivary canals extend proximal to the stylet tip (Fig. 7H). Within each maxillary stylet there are two approximately circular dendritic canals, smaller than the salivary canal (Fig. 7E).

4. Discussion

4.1. Antennae

This study found the flagellum of *D. damnosa* is long and inserted into the apical socket of the pedicel. This is accord with the characteristic of a socketed mechanoreceptor bristle illustrated by Keil (1997) and may respond to direct touch, be receptive to air currents and monitor the relative position of the head. *D. damnosa* share similar kinds of antennal sensilla with most fulgoromorphans (Stroiński et al., 2011).

4.1.1. Sensillum Chaeticum (Ch)

The Ch of *D. damnosa* highly accord with the characteristics of the “trichoid sensilla of type I” of the tropiduchids *Kallitaxila granulata* and *Zema gressitti* which are identified as chemoreceptors (Wang et al., 2012, 2013). Ch are the longest antennal sensilla in *D. damnosa* as they will be the first sensilla to contact external objects, and may function as tactile mechanoreceptors also mentioned by Fu et al. (2012).

4.1.2. Böhm Bristle (BB)

The characteristics of the BB on *D. damnosa* is extremely similar to the Böhm bristle described by Fu et al. (2012) on the delphacid *Laodelphax striatellus* but visibly differs from the “trichoid sensilla of type III (BB)” of the tropiduchids *K. granulata* and *Z. gressitti* (Wang et al., 2012, 2013). BB at the two proximal joints of the antennae were considered to be mechanoreceptors on the antennae, and presumably function as proprioceptors which perceive antennal movement and position (Fu et al., 2012; Schneider, 1964). The function of the BB in *D. damnosa* would be to detect the relative position of the scape to the head.

4.1.3. Sensillum Trichodeum (Tr)

Tr detected on *D. damnosa* appears to be analogous to the “sensilla trichoidea” of Fu et al. (2012) on the delphacid *L. striatellus* which are suggested to be olfactory. The textured surface (Aljunid and Anderson, 1983), reticulated surface (Fu et al., 2012) and netted pattern surface (*D. damnosa*) of Tr may be analogous. The Tr of *D. damnosa* conform to the “trichoid sensilla of type II” of the

tropiduchids *K. granulata* and *Z. gressitti* which are identified as chemoreceptors (Wang et al., 2012, 2013).

4.1.4. Plaque Organ (PO)

Plaque organs on the pedicel in *D. damnosa* are similar to some other issids described in Hamilton (2011) by their folded flattened plate type. PO in *D. damnosa* may function as olfactory sensilla (Aljunid and Anderson, 1983; Bourgoïn and Deiss, 1994; Youn, 2002). The olfactory function of plaque organ is reflected in the pores on the flat central area of the plate in *D. damnosa*. *D. damnosa* and *Z. gressitti* (Wang et al., 2012) share a similar morphology of PO, but those on *D. damnosa* have more small ridges. We are not certain if the decrease in the amount of small ridges is an evolutionary trend in this folded flattened plate type (Bourgoïn and Deiss, 1994; Stroiński et al., 2011). The cuticular denticles of *D. damnosa* are similar to those of some planthoppers, and are considered to protect the plaque organs (Aljunid and Anderson, 1983; Fu et al., 2012; Wang et al., 2012, 2013).

4.1.5. Sensilla Campaniformia (Ca)

Ca have been reported in various insects including planthoppers (Bourgoïn, 1985; Keil, 1997; McIver, 1975, 1985; Schneider, 1964; Zacharuk, 1985). In *D. damnosa*, Ca were singly found on the distal rim of the scape and on the apical part of the pedicel; this form was also found in some planthoppers (Fu et al., 2012; Romani et al., 2009; Wang et al., 2012, 2013). Ca found near the junction of antennal segments are considered to be mechanoreceptors to respond to the stresses due to the movement of flagella and are probably involved in the perception of movement and position of the antennal segments (Bromley et al., 1980; Fu et al., 2012; Wang et al., 2012, 2013).

4.1.6. Bourgoïn's organ (BO) and Sensillum basiconicum (Ba)

BO seems to be present in all planthoppers (Bourgoïn, 1985; Stroiński et al., 2011). The aperture of BO in *D. damnosa* is surrounded by a digitate wall; this form has been found in most planthoppers (Bourgoïn, 1985; Bourgoïn and Deiss, 1994; Fu et al., 2013; Liang, 2001b; Stroiński et al., 2011; Wang et al., 2012). The BO appears as a small utricle sheltering a few sensilla in two distinct chambers (Bourgoïn, 1985; Romani et al., 2009), suggesting that the BO of *Hyalesthes obsoletus* might be involved in the perception of thermo-hygroreception, olfactory reception and CO₂ concentration detection (Romani et al., 2009; Stroiński et al., 2011). It is likely the BO of *D. damnosa* play a similar role as in *H. obsoletus* as they belong to homologous structures, but we are not certain about this. The presence of 3 Ba on flagellum in *D. damnosa* was also reported in *L. striatellus* (Fu et al., 2012, 2013). The flagellar sensilla basiconica of *D. damnosa* appears to be homologous to the “spur consisting of three sensilla styloconica” in *H. obsoletus* which is considered to be thermo-hygroreceptive (Fu et al., 2012; Romani et al., 2009).

The distribution pattern of sensilla on the antennae of *D. damnosa* is different from the briefly explained pattern presented by Zacharuk (1985). In *D. damnosa*, the pedicel becomes the main sensory area and bears the most numerous and widest varieties of sensilla while the flagellum is specialized into a long mechanoreceptive structure and bears few other sensilla (Romani et al., 2009). Olfactory receptors (Tr and PO) are the most numerous sensilla on the antenna of *D. damnosa* suggesting that olfaction likely plays an important role in their behavioral ecology, and may play a role in detecting and locating host plants. The ultrastructure, arrangement, and/or number of plaque organs on the pedicel and the morphology of Bourgoïn's organs on the flagellum might be reliable enough to be of taxonomic value.

4.2. Mouthparts

The gross morphology of mouthparts of *D. damnosa* are similar to some other described auchenorrhynchs (Cobben, 1978; Dai et al., 2014; Leopold et al., 2003; Mora et al., 2001; Tavella and Arzone, 1993; Wang et al., 2015; Wiesenborn, 2004; Zhao et al., 2010).

4.2.1. Labrum

A possible role for the labrum in *D. damnosa* is to support the labium and protect the labial groove during walking and resting, which is inferred from the relative position of the labrum and labium. When they feed, because of the relative position of the labrum and the fact that wrinkles are only located on the basal labrum, the labrum may follow the bend of the labium although Dai et al. (2014) and Wang et al. (2015) believe that the labrum is probably not moveable. The pattern, density and arrangement of the cuticular processes on the surface of labrum are relatively different among auchenorrhynchs; however, we are uncertain whether they have a unique function or not.

4.2.2. Stylet fascicle

Although the morphology of the stylets and the interlocking mechanism of maxillae and mandibles in Issidae have been poorly described, the primary morphology of the stylets in *D. damnosa* are similar to other auchenorrhynchs, which have a sharp end to their maxillary stylets and an abundance of teeth on the mandibular stylets for piercing plant tissues. For example, leafhoppers, psyllids and aphids have relatively more teeth (Forbes, 1969; Garzo et al., 2012; Leopold et al., 2003; Liang et al., 2013; Tavella and Arzone, 1993; Ullman and McLean, 1986; Zhao et al., 2010), whereas there are only 5 teeth on the mandibular stylet in spittlebugs and delphacids (Dai et al., 2014; Mora et al., 2001; Wang et al., 2015). *D. damnosa* have 7 relatively unapparent protuberances on their mandibular stylets which is different from other auchenorrhynchs. The denticulate apex shares only a small portion (about 1/18) of whole length of the mandibular stylet in *D. damnosa*, which suggests that they can only insert it a short distance into the host. Moreover, *D. damnosa* have a longer stylet bundle but the mandibular stylets-to-maxillary stylet ratio is low (91%), which varies among auchenorrhynchs (Dai et al., 2014; Foster et al., 1983a; Leopold et al., 2003; Zhao et al., 2010). This relatively low ratio may account for the increase in teeth and protrusion of the mandibular stylets. The interlocking mechanism of the maxillae and mandibles of *D. damnosa* displays a great similarity to the daliscelid *Ommatidiotus dissimilis* (Brožek et al., 2006; Brožek and Bourgoïn, 2013b) where they have a short middle lock and a ventral lock.

4.2.3. Labial sensilla

The sensory apparatus in planthoppers, studied by Brožek and Bourgoïn (2013a), consists of mechanoreceptor sensilla chaetica plus specialized structures/areas. The labial sensilla in *D. damnosa* likely have mechanoreceptive and chemosensory functions, which probably detect plant surface factors and may help guide the stylets to the surface of the plant. The sensilla chaetica subtype II (Ch2) are the longest of the labial sensilla, and may be the first and main mechanoreceptive sensilla to make contact with external objects. The sensilla chaetica subtype III (Ch3) are closely arranged on each side of the whole labial groove and may detect and lead the inner stylet fascicle to run through the labial segment. Two pairs of sensilla basiconica subtype I (Ba1) located at the joint of the second and third segment, and their location suggests they are proprioceptors to monitor relative positions of the two segments (Gullan and Cranston, 2005). The paired sub-apical labial sensilla are homologous in all planthopper taxa and can evolve into different shapes

(Brožek and Bourgoïn, 2013a). Those in *D. damnosa* are of the placoid flattened type and are extremely similar to those found in the Tropicuchidae, and are presumed to have olfactory and thermoreceptive functions (Brožek and Bourgoïn, 2013a).

The labial tip possesses a moderate number of pored sensilla and sensilla basiconica. The uniporous peg-like sensilla (PGSU) of *D. damnosa* that extremely protrude from the tip perhaps also have a tactile function and are involved in together locating the puncture position of the stylet fascicle as noted by Brožek and Bourgoïn (2013a). The sensilla basiconica subtype II (Ba2) in *D. damnosa* is long and surrounds PGSU and PGSM; they are considered mechanoreceptive structures and probably assist in positioning the labium during feeding (Brožek and Bourgoïn, 2013a). The multiporous peg sensillum (PGSM) is relatively short and far away from the rostrum opening; it probably only has an olfactory function as studied by Cobben (1978). The sensilla on the ventral sensory field in *D. damnosa* are closely located to the rostrum opening and may support and lead the inner stylet fascicle to pierce the surface of the host plant. *D. damnosa* is relatively similar to tropiduchids *Trienopa paradoxa* (which was incorrectly classified by Brožek and Bourgoïn (2013a) as representative of the family Issidae, but now belongs to Tropicuchidae) and *Tropicuchus arisba* in the arrangement of sensilla on the labial tip (Brožek and Bourgoïn, 2013a); this suggests the Issini and Tropicuchini may have a closer phylogenetic relationship. The distribution of the apical sensilla of *D. damnosa* is of “the lophopid pattern” type (Brožek and Bourgoïn, 2013a). Two dome-shaped sensilla located in the ventral sensory field in *D. damnosa*, were found to have a similar position of multiporous oval plate sensilla in the Nogodinidae and long sensilla basiconica in Lophopidae (Brožek and Bourgoïn, 2013a).

The feeding mechanism of *D. damnosa* resembles other auchenorrhynchs based on their mouthpart morphology. The feeding commences with the arrival of *D. damnosa* on a potential host plant. They stretch out the labial segment and appress the labial tip to repeatedly touch the plant surface using the mechanoreceptive or chemoreceptive sensilla. After locating the feeding site using sensilla, the labium telescopes upward with the membranous joint between the first and second labial segments; then the stylet fascicle protrudes to ingest plant fluids and eventually finishes its probing by retracting the stylets from the plant (Backus, 1985, 1988; Foster et al., 1983b).

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