

## **Fine Structure of Sensory Apparatus on the Head of *Cixiopsis punctatus***

Authors: Wang, Rong-rong, Wan, Xin-yi, and Liangc, Ai-ping

Source: Journal of Insect Science, 14(99) : 1-15

Published By: Entomological Society of America

URL: <https://doi.org/10.1673/031.014.99>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



## Fine structure of sensory apparatus on the head of *Cixiopsis punctatus*

Rong-rong Wang<sup>a</sup>, Xin-yi Wan<sup>b</sup>, and Ai-ping Liang<sup>c\*</sup>

Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang District, Beijing 100101, P.R. China

### Abstract

The external morphology of the heads of adult male and female *Cixiopsis punctatus* (Matsumura) (Hemiptera: Fulgoromorpha: Tropiduchidae) was studied using scanning electron microscopy. Eleven types of sensilla or sensory organs were identified: trichoid sensilla on the pedicel, scape, maxillae, and labium; campaniform sensilla on the antennal pedicel, antennal scape, maxillae, and labium; plate organs on the antennal pedicel; coeloconic sensilla in Bourgoin's organ and styloconic sensilla on the expanded flagellar base; Evans' organ and button-like sensilla on the maxillary plates; basiconic sensilla, peg sensilla, and coin-shaped sensilla on the labium. Styloconic sensilla on the expanded flagellar base and peg sensilla located between the dorsal sensory field and the opening of the maxillae and mandibles were first reported in Tropiduchidae. The external morphology, distribution, and abundance of sensilla located on antennae, maxillae, and labium in *C. punctatus* were illustrated.

**Keywords:** Hemiptera, Tropiduchidae, antenna, maxillae, labium, ultrastructure

**Abbreviations:** **Ba**, basiconic sensilla; **Bl**, button-like sensilla; **BO**, Bourgoin's organ; **BSNI**, sensillum basiconicum, nonporous, long; **Ca**, campaniform sensilla; **CM**, cuticular microtubercle; **Co**, coeloconic sensillum; **CP**, cone-shaped process; **Cs**, coin-shaped sensilla; **EO**, Evans' organ; **OPSM**, oval plate sensillum, multiporous; **Pe**, peg sensilla; **PGSM**, peg sensillum, multiporous; **PGSUI**, peg sensillum, uniporous, long; **PGSU2**, peg sensillum, uniporous, short; **PO**, plate organs; **SF-D**, dorsal sensory field; **SF-V**, ventral sensory field; **Tr**, trichoid sensilla

**Correspondence:** <sup>a</sup> [wangrr\\_2008@163.com](mailto:wangrr_2008@163.com), <sup>b</sup> [joywxy@163.com](mailto:joywxy@163.com), <sup>c</sup> [liangap@ioz.ac.cn](mailto:liangap@ioz.ac.cn), \*Corresponding author

**Editor:** Andrew Deans was editor of this paper.

**Received:** 19 March 2013 **Accepted:** 24 September 2013 **Published:** 22 July 2014

**Copyright:** This is an open access paper. We use the Creative Commons Attribution 3.0 license that permits unrestricted use, provided that the paper is properly attributed.

**ISSN:** 1536-2442 | Vol. 14, Number 99

### Cite this paper as:

Wang R-r, Wang X-y, Liang A-p. 2014. Fine structure of sensory apparatus on the head of *Cixiopsis punctatus*. *Journal of Insect Science* 14(99). Available online: <http://www.insectscience.org/14.99>

## Introduction

The Fulgoromorpha, commonly named planthoppers, constitute a large group of phytophagous insects in the order Hemiptera, including about 14,000 described species and 30 recent or fossil families worldwide. It is an old group of Hemiptera, known from fossils of the lower Permian (ca. 258 million years ago), and their phylogeny is still not well understood (Bourgoin 2013).

Although molecular characters are now widely used to reconstruct the phylogeny of Fulgoromorpha (Bourgoin et al. 1997; Yeh et al. 1998, 2005; Yeh and Yang 1999; Bourgoin and Campbell 2002; Urban and Cryan 2007; Song and Liang 2013) and to test existing phylogenetic hypotheses (Muir 1923, 1930; Asche 1987; Emeljanov 1990; Bourgoin 1993; Chen and Yang 1995), several recent studies have also used morphological characters with varying degrees of success (Bourgoin and Deiss 1994; Hamilton 2011; Brožek and Bourgoin 2012). Evidence that morphology is a source of information is far from exhausted in Fulgoromorpha systematics.

Based on studies of comparative morphology (Bugnion 1908) and ultrastructure (Lewis and Marshall 1970; Stroński et al. 2011; Brožek and Bourgoin 2012) of different antennal (plate organs, Bourgoin's organ), labial (labial sensilla), and maxillary (Evans' organ) sensillae of the Fulgoromorpha, a remarkable disparity in the same sensory equipment is observed, which has value for taxonomic and phylogenetic analyses (Bourgoin 1986; Bourgoin and Deiss 1994; Liang 2001; Hamilton 2011; Stroński et al. 2011; Brožek and Bourgoin 2012). However, there is still a paucity of the anatomical data on Fulgoromorpha, let alone the anatomy of Tropicuchidae.

The family Tropicuchidae is the keystone group for understanding evolutionary processes within the higher Fulgoroidea. Our present state of knowledge does not allow unambiguous indication of the ancestral group for the tropiduchids, and thereby at least part of the higher Fulgoroidea. Fennah (1982) revised the higher classification of the Tropicuchidae and recognized 15 tribes in the family. The genus *Cixiopsis* was included in the tribe Cixiopsini. Subsequently, this study investigated, through scanning electron microscopy (SEM) observations, sensory equipment on the head of *Cixiopsis punctatus* (Matsumura) (Hemiptera: Fulgoromorpha: Tropicuchidae) as potential sources for new characters for future comparative morphological studies in Tropicuchidae and Fulgoromorpha.

## Materials and Methods

The external morphology of adult *C. punctatus* (one male and three females) was studied using SEM. All the samples were obtained from Fujian Province, China, and were deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZCAS). For SEM observation, the heads together with antennae were first removed from the specimens. They were then cleaned in a chloroform bath or a lukewarm 10% KOH bath in an ultrasonic cleaner (1 min), followed by twice cleaning in 75% alcohol (2 min for each case) to remove the cuticular waxy powder on the samples' surface. They were then dehydrated in a graded ethanol series, after which they were dried at critical point drying, mounted on stubs with double-sided adhesive tape, and coated with a film of gold-palladium. Finally, observations were made with a Hitachi S34Q SEM ([www.hitachi.com](http://www.hitachi.com)) at the Microscopy Core Facility, Biological Technology Center, Beijing Forestry University.

Terminology for the antennal sensilla description follows Bourgoin and Deiss (1994) and Wang et al. (2013).

## Results

### General description of the antenna

In *C. punctatus*, antennae are situated on the lateral region of the head capsule beneath the compound eyes, as in other planthoppers (Figure 1). In both male and female, each antenna is about 1268  $\mu\text{m}$  long and consists of three segments: a short basal scape, a cylindrical pedicel, and a thread-like flagellum (Figure 2A). The scape is about 59–108  $\mu\text{m}$  long and directly attached to the head capsule, bearing few sensilla (Figure 2A, B). The antennal pedicel is about 230  $\mu\text{m}$  long and is covered by numerous trichoid sensilla and plate organs (Figures 2B, 3B), on the top of which a campaniform sensillum is revealed (Figure 2C). The flagellum (about 955  $\mu\text{m}$  in length) is composed of two distinct portions: a basal bulb with a short petiole at the extreme base and an apical arista (Figure 2A). The basal bulb, a swollen base of the flagellum, is proximally inserted on the pedicel at the level of a disk-like area (Figure 3A). The area is encircled by concentrically arranged cuticular spines (Figure 3A). On the top of the basal bulb, the Bourgoin's organ can be observed (Figure 3A), surrounded by three conspicuous blunt-tipped peg-like styloconic sensilla, dome-like processes (Figure 3C), and cuticular microdigitations (Figure 3D). The distal part of the basal bulb gives rise to a long, thread-like arista and ends with a sharp apex (Figure 2A).

### Types and distribution of the antennal and maxillary sensilla

SEM images show eight major types of sense organs on the antennae and maxillae: trichoid sensilla, plate organs, campaniform sensilla,

coeloconic sensilla, styloconic sensilla, Bourgoin's organ, button-like sensilla, and Evans' organ. Details of each sensillum or organ are described below.

**Trichoid sensilla (Tr).** Tr are common on the antennal and the maxillary surfaces of insects. The Tr on antennae can be divided into three types, referred to here as TrI, TrII, and TrIII. TrI (Figure 2A, B) are bristle-like and scattered on the surface of the antennal pedicel. They are 46–96  $\mu\text{m}$  long, 3.0–3.2  $\mu\text{m}$  in basal diameter, with blunt tip and straight longitudinal grooves on the surfaces (Figure 4A, B). Each TrI is found inserted into an evident raised socket and protrude 30–45° from the antenna (Figure 4A, B). TrII (Figure 4C, D) of 28–37  $\mu\text{m}$  length are usually limited on the antennal pedicel and about 2.4  $\mu\text{m}$  in basal diameter. They are blunt-tipped and curved towards the antennal shaft (Figure 4C) and this type is occasionally observed with forked apex (Figure 4D). Each of them have straight longitudinal patterns and are inserted into a depression, which is about 5.2  $\mu\text{m}$  in diameter (Figure 4C, D). TrIII (Figures 2A, 4E) are distributed on the base of the antennal scape (21–49  $\mu\text{m}$  long, 2.5  $\mu\text{m}$  in basal diameter). This type, which might be the Böhm bristle, morphologically resembles TrI, but is smaller in size.

In addition, Tr are widely distributed on the maxillae (48–74  $\mu\text{m}$  long, 1.9  $\mu\text{m}$  in basal diameter, Figures 2D, 4F). Similar to TrI, they insert into raised sockets and have straight longitudinal grooves on their surfaces (Figure 4F).

**Plate organs (PO).** Seta-like PO were founded in *C. punctatus* of both sexes (Figures 2B, C, 3B, E). They are scattered on the antennal pedicel (Figures 2B, 2C, 3B). Each PO consists of approximately 10 seta-like projections

encircled by rings of cuticular denticles, which are shorter than those projections or as long as them (Figure 3E). These seta-like projections are solid inside (Figure 3F), curved concentrically, and tapering from flat bases into blunt tips (Figure 3E, F). The cuticular microtubercles (CM) are randomly distributed around, not part of the PO, and not circularly arranged (Figure 3E).

**Campaniform sensilla (Ca).** Ca are very few in number, usually located on the antennal and the maxillary surfaces, which are ubiquitous in insects. Based on the position, Ca can be distinguished as CaI, CaII, CaIII. A single CaI (Figure 2C) (8.1–10.0  $\mu\text{m}$  in diameter) is presented on the apical surface of the antennal pedicel. CaI is a dome-shaped structure located in a cavity, which is surrounded by thick walls and cone-shaped projections (Figure 2C). Only one of the CaII (Figure 2B) (17–19  $\mu\text{m}$  in diameter) is founded on the antennal scape. Different from the CaI, CaII rise up from the surface and are surrounded by cuticular microtubercles (Figure 2B). A CaIII (Figure 2D) (15–17  $\mu\text{m}$  in diameter), similar to CaII, occurs on the maxilla, with 106  $\mu\text{m}$  away from the base of antennal scape.

**Bourgoin's organ (BO).** On the top of bulb base of the antennal flagellum, there is an evident BO with an elliptical aperture (about 8  $\mu\text{m}$  in long shaft, about 4  $\mu\text{m}$  in short shaft) (Figure 3A, B, C). The aperture is surrounded by denticle-like walls with 5–11  $\mu\text{m}$  of height (Figure 3C). Next to the denticle-like walls, three blunt-tipped, peg-like styloconic sensilla (St, 1  $\mu\text{m}$  in diameter, 2–3  $\mu\text{m}$  in height) of triangular arrangement were identified (Figure 3C, D). Additionally, two dome-like processes are separately distributed near the denticle-like walls (Figure 3C), and some cuticular spines are located on BO's surface (Figure 3D). Coeloconic sensilla (Co) are usually

shielded by BO, and one of them can be seen directly here (Figure 3C).

**Evans' organ (EO).** A single EO (29–34  $\mu\text{m}$  in diameter) is detected at each geno-maxillar sulcus, with a distance of roughly 170  $\mu\text{m}$  from the base of the antennal scape (Figure 2D). Each EO is formed by a deep cavity, which is surrounded by cone-shaped projections and has four petal-like infoldings inside (Figure 2E).

**Button-like sensilla (BI).** Six BI (2–9  $\mu\text{m}$  in diameter) are discovered on the maxilla near the antennal scape (Figure 2F). This type of sensory equipments is composed of a deep cavity with a raised, irregular plate in the center, looking like a button (Figure 2F).

### Gross morphology and sensilla of the labium

Every *C. punctatus* has a three-segmented labium, which is highly adapted to piercing and sucking, including a shortest proximal segment, the longest middle segment, and the shorter distal segment (Figure 5A). The outer mandibular and the inner maxillary mouthparts form the stylet bundle, which lies within a groove in the labium. Dorsal sensory field concave is more extended and reaches laterally to the mandibular and maxillary stylets. Four types of sensilla are observed on the labium: trichoid sensilla (Tr), peg sensilla (Pe), basiconic sensilla (Ba), and coin-shaped sensilla (Cs). In addition, cone-shaped processes (CP, 1.8–5.5  $\mu\text{m}$  in height, 1.5–4.0  $\mu\text{m}$  in basal diameter) are widely distributed on the surface of the proximal segment (Figure 5A). Above the ventral sensory field (SF-V), there is a pair of basiconic sensilla (PeII, 2.2–3.0  $\mu\text{m}$  in diameter) placed slightly between the dorsal sensory field (SF-D) and the maxillary and mandibular stylets (Figure 5C, F, G).



**Tritoid sensilla (Tr).** Tr can be found on the middle and the distal segment (Figure 5A, B). On the back and lateral surface of the middle segment, Tr (66.1–94.6  $\mu\text{m}$  in length, 2.8–4.3  $\mu\text{m}$  in basal diameter) are inserted into evident sockets, bending towards the labial apex. On the ventral surface of the middle segment, two rows of Tr (about 29.0  $\mu\text{m}$  in length) are located on both side of the labial groove, inserting into shallow pits. The Tr (46.1–116.9 in length, 1.9–2.7  $\mu\text{m}$  in basal diameter) scattered on the distal segment curve towards the distal part, insert into unobvious sockets, and have straight longitudinal grooves on the surface (Figure 5B).

**Peg sensilla (Pe).** Two types of Pe are identified on the labial apex, being regarded as PeI and PeII. Each dorsal sensory field on each lateral lobe possesses a terminal field of 10 PeI, varying in length from 2.1–6.2  $\mu\text{m}$  with a basal diameter of 1.8–2.9  $\mu\text{m}$  (Figure 5C, D, E). They are inserted in depression on wrinkled surface of labial tip, with smooth surface and sharp apex and hollow inside (Figure 5C, D, E). Two PeII (3.2–4.3  $\mu\text{m}$  in length, 1.8–2.6  $\mu\text{m}$  in basal diameter) located between the SF-D and the opening of the maxillae and mandibles (Figure 5C, F, G).

**Basiconic sensilla (Ba).** Five pairs of Ba (10.3–23.3  $\mu\text{m}$  in length, 1.4–2.2  $\mu\text{m}$  in basal diameter) are located in apex of labium, of which three pairs are located in the SF-D and two pairs situated below the SF-V (Figure 5C, D).

**Coin-shaped sensilla (Cs).** Two Cs are identified on the lateral surfaces of the distal segment, with one at each side. Each of them is located with 116.9–124.6  $\mu\text{m}$  away from the labial apex, and its diameter is measured as 18.4–22.2  $\mu\text{m}$  (Figure 5C).

## Discussion

The antennal morphology of *C. punctatus* is similar to that in other fulgoromorphan species. Trichoid sensilla III (TrIII) on the antennal scape (Figure 4E) are similar to Böhm bristles, which are present in analogous locations in various insects (Heran 1959; Markl 1962; Schneider 1964) and might function as mechanoreceptors or proprioceptors (Pringle 1938; Thurm 1962; Schneider 1964; Sane et al. 2007).

Bourgoin's organ (BO) seems to be present in all fulgoromorphan families, including an aperture surrounded by a ridge on the top, coeloconic sensilla (Co) inside, and sometimes styloconic sensilla (St) (in Cixiidae, Achilixiidae) beside the ridge (Bourgoin 1985; Cobben 1988; Shih and Yang 1996; Liang 2001; Liang and Fletcher 2002; Romani et al. 2009). The ridge has been revealed as three different types: single ring, petal-like wall (*Kallitaxila granulata*, *Zema gressitti* in Tropicuchidae), fringed or digitate wall (Achilixiidae, Derbidae, Meenoplidae, Kinnaridae, Tettigometridae, Ricanidae, part of Cixiidae and Flatidae) (Bourgoin 1985; Shih and Yang 1996; Liang 2001; Romani et al. 2009; Wang et al. 2012, 2013). In *C. punctatus*, the ridge is single ring type with several denticles on it, and a Co can be identified easily through the aperture (Figure 3C). The morphology of St (Figure 3C, D) in *C. punctatus* is consistent with those in previous records and is the first found in Tropicuchidae.

Campaniform sensilla (Ca) are present in various places, usually near the segmental joints on insects, such as halteres, palps, legs, bases of wings, and eyes (Schneider 1964; Bromley et al. 1980), and have been reported in Fulgoroidea as well (Schneider 1964; Bourgoin

1985; Romani et al. 2009; Bartlett and Hamilton 2011). However, only a few cases of campaniform sensilla II (CaII) are found on the antennal scape (Bartlett and Hamilton 2011), and campaniform sensilla III (CaIII) on the maxillae have rarely been discovered, except for in *Kallitaxila granulata* and *Z. gressitti* (Wang et al. 2012, 2013). In addition, comparing with *K. granulata* and *Z. gressitti*, with three campaniform sensilla III (CaIII) (Wang et al. 2012, 2013), *C. punctatus* only have one campaniform sensilla III (CaIII) on each side of maxillae (Figure 2D).

Plate organs (PO) in Fulgoromorpha, with structural variations, are divided into five main morphological types, two types of which have been reported in Tropicuchidae: the seta-like projected and the folded flattened plate (often clover leaf-like) (Bourgoin and Deiss 1994; Wang et al. 2012, 2013). The PO of *C. punctatus* are in seta-like projected form (Figure 3E, F), similar to some tropicuchid species, e.g. *Kusuma* sp. (Marshall and Lewis 1971), *Trypetimorpha japonica* (Huang and Bourgoin 1993), *Teramnon stenopteryx* (Hamilton 2011), and *Z. gressitti* (Wang et al. 2013). However, they are different from those with a folded flattened form in *Ossoides lineatus* and *K. granulata* in Tropicuchidae, *Microflata stictica* in Flatoidae, and *Lophops carinatus* in Lophopidae (Marshall and Lewis 1971; Bourgoin and Deiss 1994; Stroiński et al. 2011; Wang et al. 2012).

Evans' organ (EO) were first reported as 'a finger-like lobe contained in a pit' in Auchenorrhyncha by Evans (1973), and are considered to be important in understanding the origin of the head capsule in Hemiptera (Evans 1973; Bourgoin 1986). 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). Additionally, EO was named as 'subantennal plaque sensillum' on the subantennal process in *Borysthenes maculata* and *Euryphlepsia papuaensis* of Cixiidae (Liang 2005a). In *C. punctatus*, its position resembles that observed in most fulgoromorpha taxa, such as *Z. gressitti* of Tropicuchidae, at the basal margin of the gena (Figure 2D). EO is apparently absent in Sternorrhyncha and Heteroptera, whereas it is present in Coleorrhyncha as a placoid-like sensillum (Bourgoin 1986).

Peg sensilla (Pe) on labial tip in *C. punctatus* are quite common on the labium in other Fulgoromorpha, e.g., *Nilaparvata lugens* (Delphacidae) (Foster et al. 1983: Figure 1b) and *Andes marmorata* (Cixiidae) (Liang 2005b: Figure 2A), and they vary in number. Brožek and Bourgoin (2012) regarded peg sensilla I (PeI) as uniporous peg sensilla (PGSU1/2) and multiporous peg sensilla (PGSM), and basiconic sensilla (Ba) as long sensilla basiconica (BSN1). However, to accurately define the uniporous peg sensilla (PGSU1/2) and multiporous peg sensilla (PGSM) in *C. punctatus*, further study on the inner structure of Peg sensilla I (PeI) is still necessary. What make this species special are the distinct structures and new morphological characteristics. Peg sensilla II (PeII) were discovered in the tropicuchid labium. The location of PeII (Figure 5C, F, G) is similar to the region of oval plate sensillum, multiporous (OPSM), described in *Nogodina reticulata* (Nogodinidae), and a similar position of the long sensilla basiconica (BSN1) is also found in Lophopidae (Brožek and Bourgoin 2012). The BSN1 in Lophopidae is supposed to represent a specialized pattern (lophopid pattern) that has probably evolved from the issid one (Brožek and Bourgoin 2012). The distribution patterns of the sensilla on the labial tip there-

fore may contribute to the clarification of evolutionary relationship within Fulgoromorpha.

We found coin-shaped sensilla (Cs) in *C. punctatus* on the distal labial segment, similar to *Z. gressitti*, *K. granulata*, and *Lavora ricanoides* of Tropicuchidae (Rong-rong Wang, unpublished data). Cs correspond to special sensory organs known as subapical sensory organs (Backus 1985) and latero-subapical labial sensilla (Liang 2005b), and have been reported in other planthoppers taxa in multifarious forms: peg-like in *Borysthenes maculata* and *Andes marmorata* of Cixiidae (Liang 2005b), multilobed in *Nilaparvata lugens* and other Delphacidae (Foster et al. 1983: Figure 1a; Sōgawa 1981). Moreover, Brožek and Bourgoin (2012) named several different types of these analogous sensilla.

## Acknowledgements

The authors wish to express sincere thanks to the reviewers for valuable comments on the manuscript. This study was supported by the National Natural Science Foundation of China (grant nos. 31270043 and 30900145), awarded to RRW, and the National Basic Research Program of China (973 Program) (2011CB302102), the National Natural Science Foundation of China (grant nos. 30970400, 31172128), the Key Laboratory of the Zoological Systematics and Evolution of the Chinese Academy of Sciences (grant no. O529YX5105), and the National Science Fund for Fostering Talents in Basic Research (Special subjects in animal taxonomy, NSFC-J0630964/J0109), all awarded to APL.

## References

- Asche M. 1987. Preliminary thoughts on the phylogeny of Fulgoromorpha (Homoptera Auchenorrhyncha). In: Vidano C, Arzone A, Editors. *Proceedings of the 6<sup>th</sup> Auchenorrhyncha Meeting, Turin, Italy, 7–11 September 1987*. pp. 47–53. Consiglio Nazionale delle Ricerche.
- Backus EA. 1985. Anatomical and sensory mechanisms of planthopper and leafhopper feeding. In: Nault LR, Rodriguez JG, Editors. *The leafhopper and planthoppers*. pp. 163–194. Wiley Interscience.
- Bartlett CR, Hamilton KGA. 2011. *Aethodelphax prairianus* gen. et sp. nov. (Hemiptera: Delphacidae) and seven congeneric species from North American Delphacodes. *Zootaxa* 2837: 48–66.
- Bourgoin T. 1985. Morphologie antennaire des Tettigometridae (Hemiptera, Fulgoromorpha). *Nouvelle Revue d'Entomologie* 2: 11–20.
- Bourgoin T. 1986. Valeur morphologique de la lame maxillaire chez les Hemiptera; remarques phylogénétiques. *Annales de la Société entomologique de France* 22: 413–422.
- Bourgoin T. 1993. Female genitalia in Fulgoromorpha (Insecta, Hemiptera): morphological and phylogenetical data. *Annales de la Société entomologique de France* 29: 225–244.
- Bourgoin T. 2013. *FLOW (Fulgoromorpha Lists on The Web): A World Knowledge Base Dedicated to Fulgoromorpha*. Version 8. Available online: <http://hemiptera-databases.org/flow/>
- Bourgoin T, Campbell BC. 2002. Inferring a phylogeny for Hemiptera: falling into the ‘autapomorphic trap’. *Denisia* 4: 67–82.

Asche M. 1987. Preliminary thoughts on the phylogeny of Fulgoromorpha (Homoptera Auchenorrhyncha). In: Vidano C, Arzone A,



- Bourgoin T, Deiss V. 1994. Sensory plate organs of the antenna in the Meenoplidae–Kinnaridae group (Hemiptera: Fulgoromorpha). *International Journal of Insect Morphology and Embryology* 23: 159–168.
- Bourgoin T, Steven-Campbell JD, Campbell BC. 1997. Molecular phylogeny of Fulgoromorpha (Insecta, Hemiptera, Archaeorrhyncha). The enigmatic Tettigometridae: evolutionary affiliations and historical biogeography. *Cladistics* 13: 207–224.
- Bromley AK, Dunn JA, Anderson M. 1980. Ultrastructure of the antennal sensilla of aphids. *Cell and Tissue Research* 205: 493–511.
- Brožek J, Bourgoin T. 2012. Morphology and distribution of the external labial sensilla in Fulgoromorpha (Insecta: Hemiptera). *Zoomorphology* 132: 33–65.
- Bugnion E. 1908. Le système nerveux et les organes sensoriels du Fulgore tacheté des Indes et de Ceylan (*Fulgora maculata*). *Journal of Psychology and Neurology* 13: 326–354.
- Chen S, Yang CT. 1995. The metatarsi of the Fulgoroidea (Homoptera: Auchenorrhyncha). *Chinese Journal of Entomology* 15: 257–269.
- Cobben RH. 1988. What do we really know about host selection in Auchenorrhyncha. In: Vidano C, Arzone A, Editors. *Proceedings of the 6<sup>th</sup> Auchenorrhyncha Meeting, Turin, Italy, 7–11 September 1987*. pp. 81–92. Consiglio Nazionale delle Ricerche.
- Emeljanov AF. 1990. An attempt of construction of the phylogenetic tree of the planthoppers (Homoptera, Cicadina). *Entomologicheskoe Obozrenie* 69: 353–356.
- Evans JW. 1973. The maxillary plate of Homoptera-Auchenorrhyncha. *Journal of Entomology Series A* 48: 43–47.
- Fennah RG. 1982. A tribal classification of the Tropiduchidae (Homoptera: Fulgoroidea), with the description of a new species on tea in Malaysia. *Bulletin of Entomological Research* 72: 631–643.
- Foster S, Goodman LJ, Duckett JG. 1983. Ultrastructure of sensory receptors on the labium of the rice brown planthopper. *Cell and Tissue Research* 230: 353–366.
- Hamilton KGA. 2011. Making sense of Fulgoroidea (Hemiptera): new phylogenetic evidence. *Cicadina* 12: 57–79.
- Heran H. 1959. Wahrnehmung und Regelung der Flugeigengeschwindigkeit bei *Apis mellifera* L. *Zeitschrift Fur Vergleichende Physiologie* 42: 103–163.
- Huang J, Bourgoin T. 1993. The planthopper genus *Trypetimorpha*: systematics and phylogenetic relationships (Hemiptera: Fulgoromorpha: Tropiduchidae). *The Journal of Natural History* 27: 609–629.
- Lewis CT, Marshall AT. 1970. The ultrastructure of the sensory plaque organs of the antennae of the Chinese lantern fly, *Pyrops candelaria* L. (Homoptera, Fulgoridae). *Tissue and Cell* 2: 375–385.
- Liang AP. 2001. Morphology of antennal sensilla in *Achilixius sandakanensis* Muir (Hemiptera: Fulgoromorpha: Achilixiidae) with comments on the phylogenetic position

of the Achilixiidae. *Raffles Bulletin of Zoology* 49: 221–225.

Liang AP, Fletcher JM. 2002. Morphology of the antennal sensilla in four Australian spittlebug species (Hemiptera: Cercopidae) with implications for phylogeny. *Australian Journal of Entomology* 41: 39–44.

Liang AP. 2005a. A new structure on the subantennal process of *Borystenes* species (Hemiptera: Fulgoromorpha: Cixiidae: Borysteninae). *Proceedings of the Biological Society of Washington* 118: 809–814.

Liang AP. 2005b. Occurrence of the Latero-subapical labial sensillum in *Borystenes maculata* and *Andes marmorata* (Hemiptera: Fulgoromorpha: Cixiidae). *Journal of Entomological Science* 40: 428–437.

Markl H. 1962. Borstenfelder an den Gelenken als Schweresinnesorgan bei Ameisen und anderen Hymenopteren. *Zeitschrift Fur Vergleichende Physiologie* 45: 475–569.

Marshall AT, Lewis CT. 1971. Structural variation in the antennal sense organs of fulgoroid Homoptera (Insecta). *Zoological Journal of the Linnean Society* 50: 181–184.

Matsumura S. 1900. Uebersicht der Fulgoriden Japans. *Entomologische Nachrichten* 26 (13,14): 205–213.

Matsumura S. 1910. Monographie der dictyophorinen Japans. *Transactions of Sapporo Natural History Society* 3: 99–113.

Matsumura S. 1914. Beitrag zur kenntnis der Fulgoriden Japans. *Annales Musei Nationalis Hungarici* 12: 261–305.

Muir F. 1923. On the classification of the Fulgoroidea (Homoptera). *Proceedings of the Hawaiian Entomological Society* 5: 205–247.

Muir F. 1930. On the classification of the Fulgoroidea (Homoptera). *The Annals and Magazine of Natural History* 10: 461–478.

Pringle JWS. 1938. Proprioception in insects. III. The function of hair sensilla at the joints. *The Journal of Experimental Biology* 15: 467–473.

Romani R, Rossi Stacconi MV, Riolo P, Isidoro N. 2009. The sensory structures of the antennal flagellum in *Hyalesthes obsoletus* (Hemiptera: Fulgoromorpha: Cixiidae): a functional reduction. *Arthropod Structure and Development* 38: 473–483.

Sane SP, Dieudonné A, Willis MA, Daniel TL. 2007. Antennal mechanosensors mediate flight control in moths. *Science* 315: 863–866.

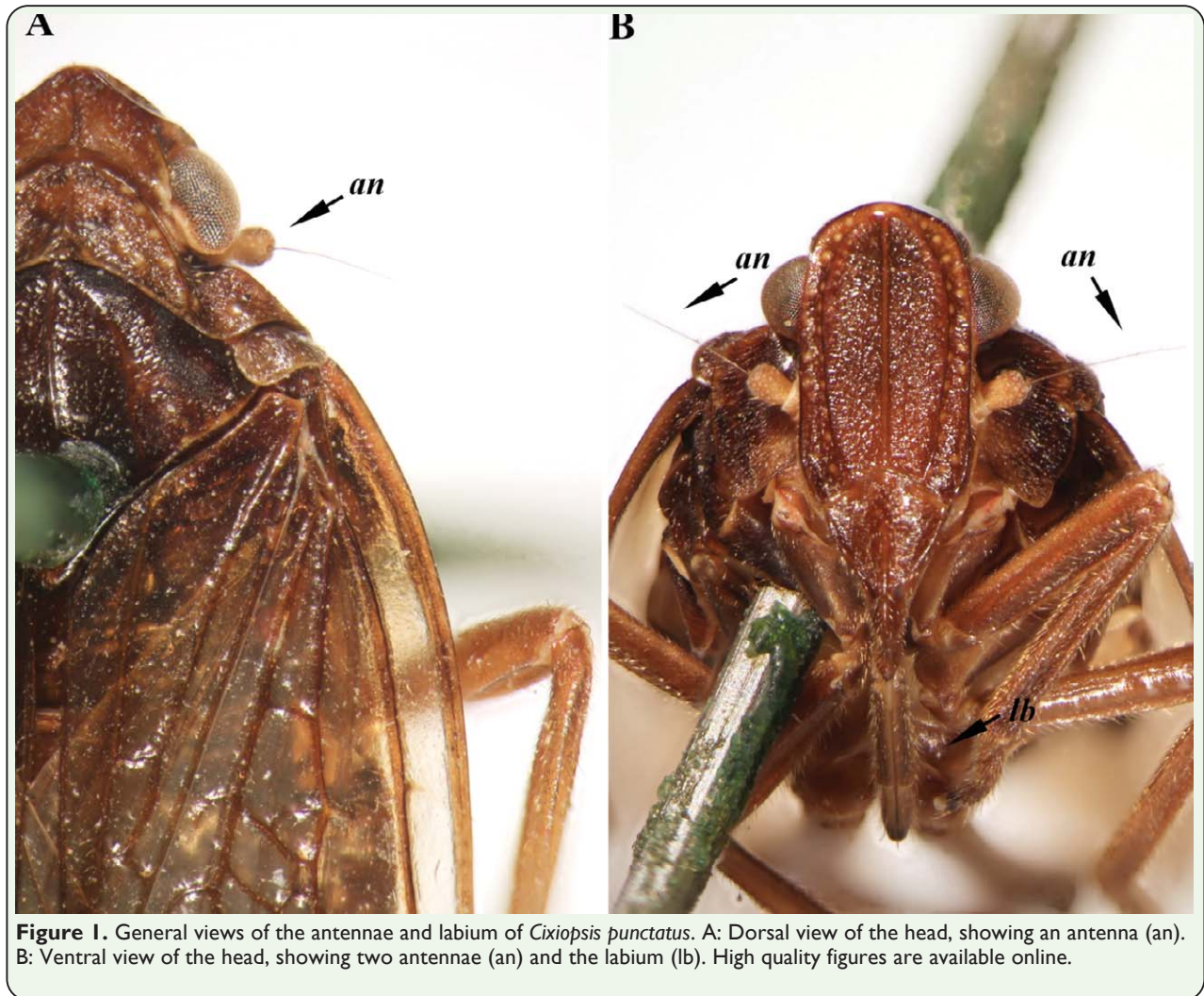
Schneider D. 1964. Insect antennae. *Annual Review of Entomology* 9: 103–122.

Shih HT, Yang CT. 1996. The antennal second projection of Cixiidae (Homoptera: Fulgoroidea). *Chinese Journal of Entomology* 16: 279–285.

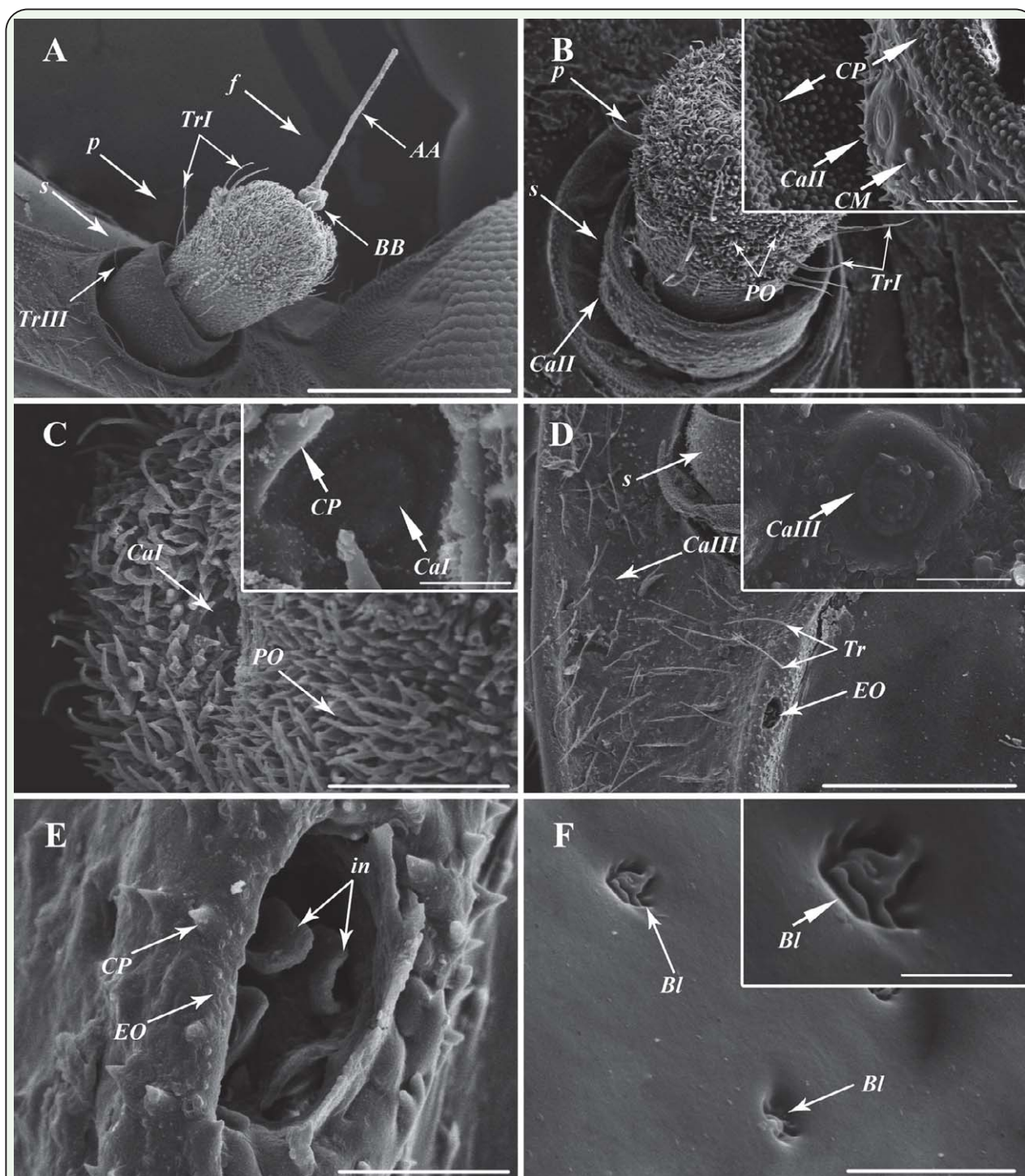
Sōgawa K. 1981. Scanning electron microscopy of the labial tip, feeding mark, and stylet sheath of the brown planthopper. *Proceedings of the Association for Plant Protection of Hokuriku* 29: 32–35.

Song N, Liang AP. 2013. A preliminary molecular phylogeny of planthoppers (Hemiptera: Fulgoroidea) based on nuclear and mitochondrial DNA sequences. *PLOS ONE* 8(3): e58400. doi: 10.1371/journal.pone.0058400.

- Stroiński A, Gnezdilov VM, Bourgoïn T. 2011. Sub-brachypterous Ricaniidae (Hemiptera: Fulgoromorpha) of Madagascar with morphological notes for these taxa. *Zootaxa* 3145: 1–70.
- Thurm U. 1962. Ableitung der Rezeptor-potentiale und Nervenimpulse einzelner Cuticula-Sensillen bei Insekten. *Zeitschrift für Naturforschung* 17: 285–286.
- Urban JM, Cryan JR. 2007. Evolution of the planthoppers (Insecta: Hemiptera: Fulgoroidea). *Molecular Phylogenetics and Evolution* 42: 556–572.
- Wang RR, Wan XY, Liang AP, Bourgoïn T. 2012. Ultrastructure of Sensory Equipments on the Heads of *Kallitaxila granulata* (Stål) (Hemiptera: Fulgoromorpha: Tropiduchidae). *Microscopy Research and Technique* 75: 1659–1665.
- Wang RR, Wan XY, Liang AP, Bourgoïn T. 2013. A SEM study of antennal and maxillary sensilla in *Zema gressitti* Fennah (Hemiptera: Fulgoromorpha: Tropiduchidae). *Micron* 44: 261–267.
- Yeh WB, Yang CT. 1999. Fulgoromorpha phylogeny based on 28S rDNA nucleotide sequence. *Chinese Journal of Entomology* 11: 87–111.
- Yeh WB, Yang CT, Hui CF. 1998. Phylogenetic relationships of the Tropiduchidae-group (Homoptera: Fulgoroidea) of planthoppers inferred through nucleotide sequences. *Zoological Studies* 37: 45–55.
- Yeh WB, Yang CT, Hui CF. 2005. A molecular phylogeny of planthoppers (Hemiptera: Fulgoroidea) inferred from mitochondrial 16S rDNA sequences. *Zoological Studies* 44: 519–535.

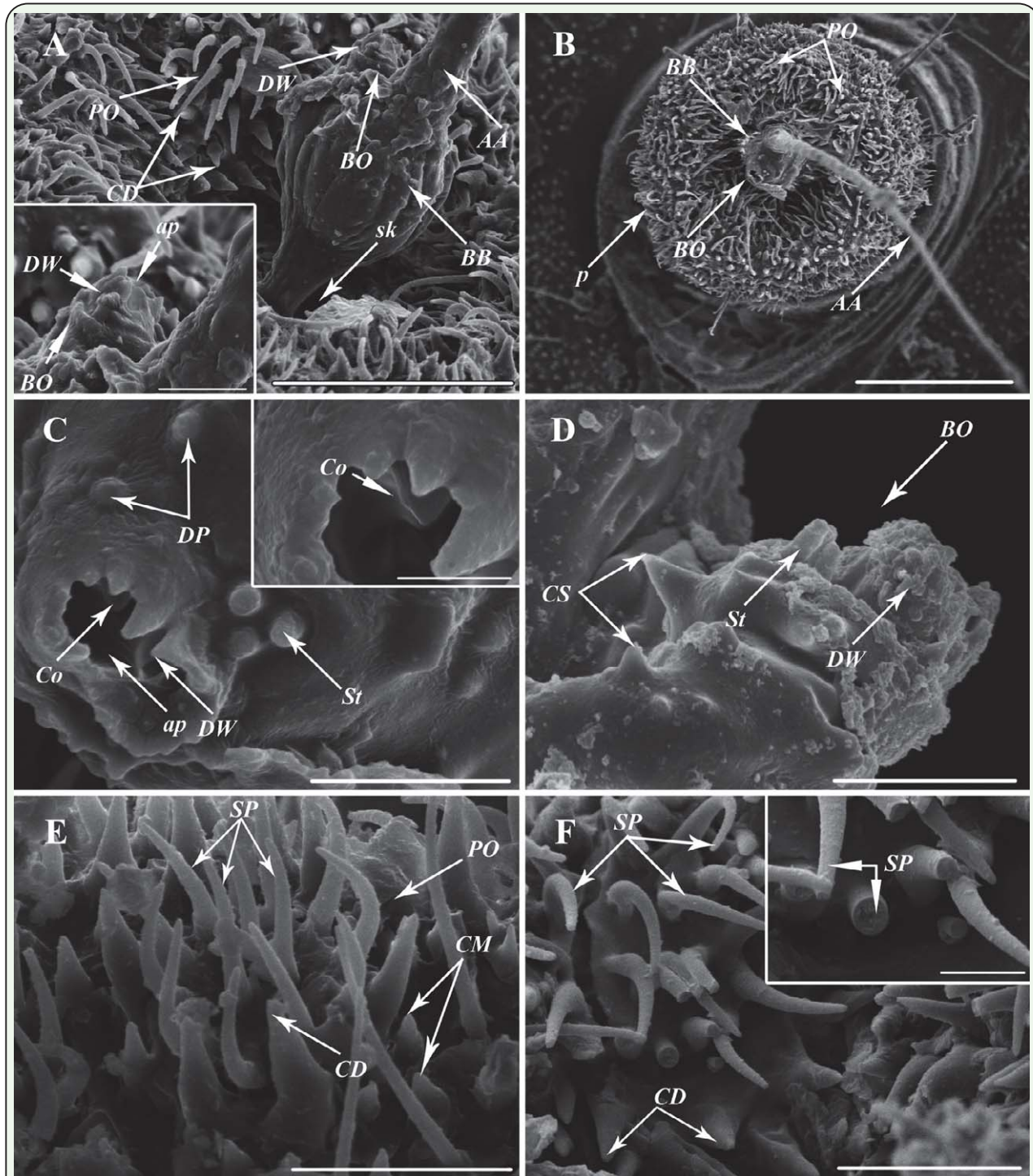




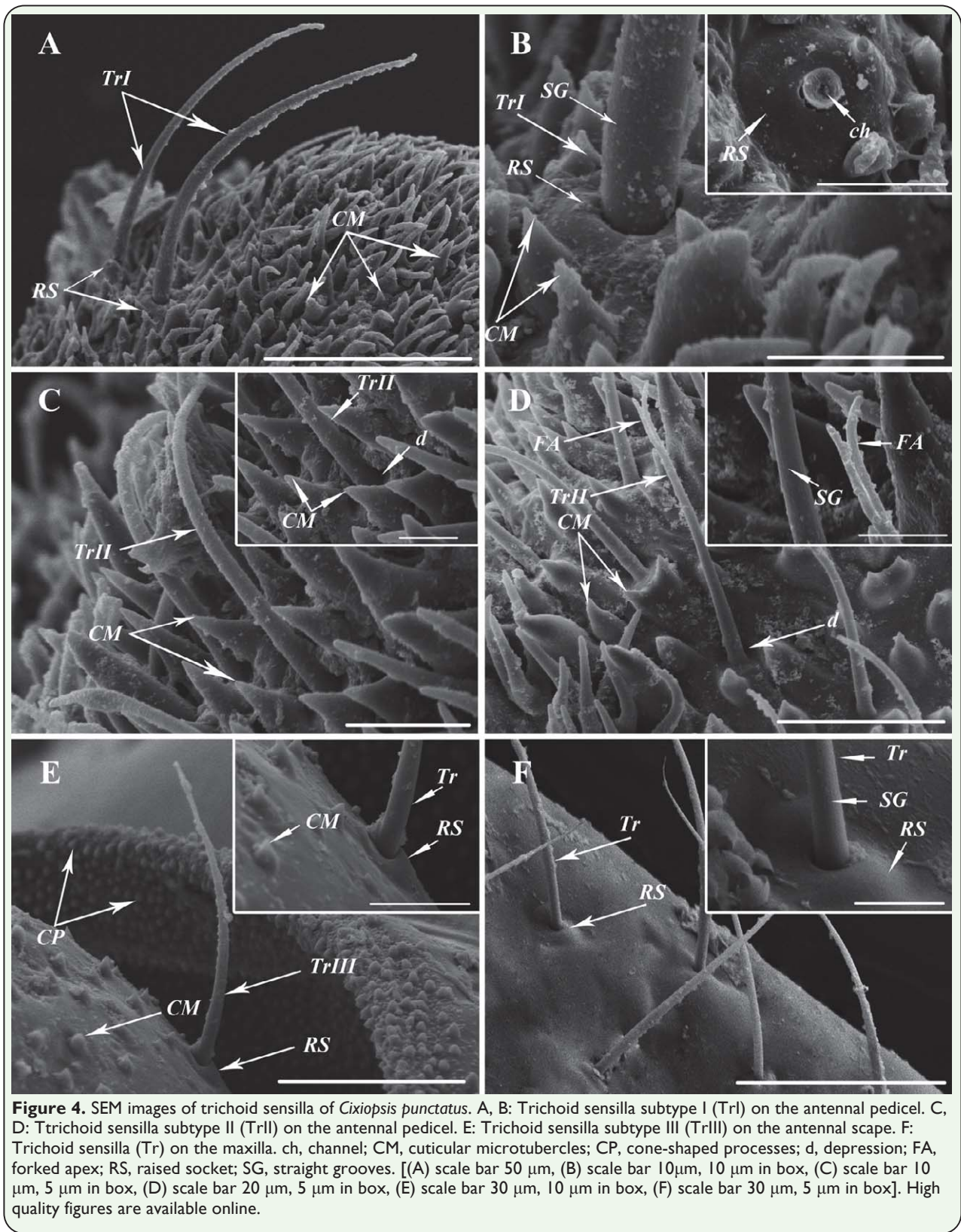


**Figure 2.** SEM images of *Cixiopsis punctatus*. A: General view of the antenna showing the antennal scape (s) with trichoid sensilla subtype III (TrIII), antennal pedicel (p) with trichoid sensilla subtype I (TrI) and the antennal flagellum (f) including the apical arista (AA) and basal bulb (BB). B: General view of the campaniform sensilla subtype II (CalII) and cuticular microtubercles (CM) on the antennal scape (s), the trichoid sensilla subtype I (TrI) and plate organs (PO) on the antennal pedicel (p). C: The top of the antennal pedicel, showing the campaniform sensilla subtype I (Cal), the plate organs (PO) and the cone-shaped processes (CP). D: Maxillary plate under the antennal scape, showing the Evans' organ (EO), trichoid sensilla (Tr) and campaniform sensilla subtype III (TrIII). E: Enlarged view of the Evans' organ (EO), with infoldings (in) inside. F: Button-like sensilla (Bl) on the maxillary plate. [(A) scale bar 300  $\mu$ m, (B) scale bar 200  $\mu$ m, 20  $\mu$ m in box, (C) scale bar 50  $\mu$ m, 5  $\mu$ m in box, (D) scale bar 200  $\mu$ m, 10  $\mu$ m in box, (E) scale bar 20  $\mu$ m, (F) scale bar 10  $\mu$ m, 3  $\mu$ m in box]. High quality figures are available online.

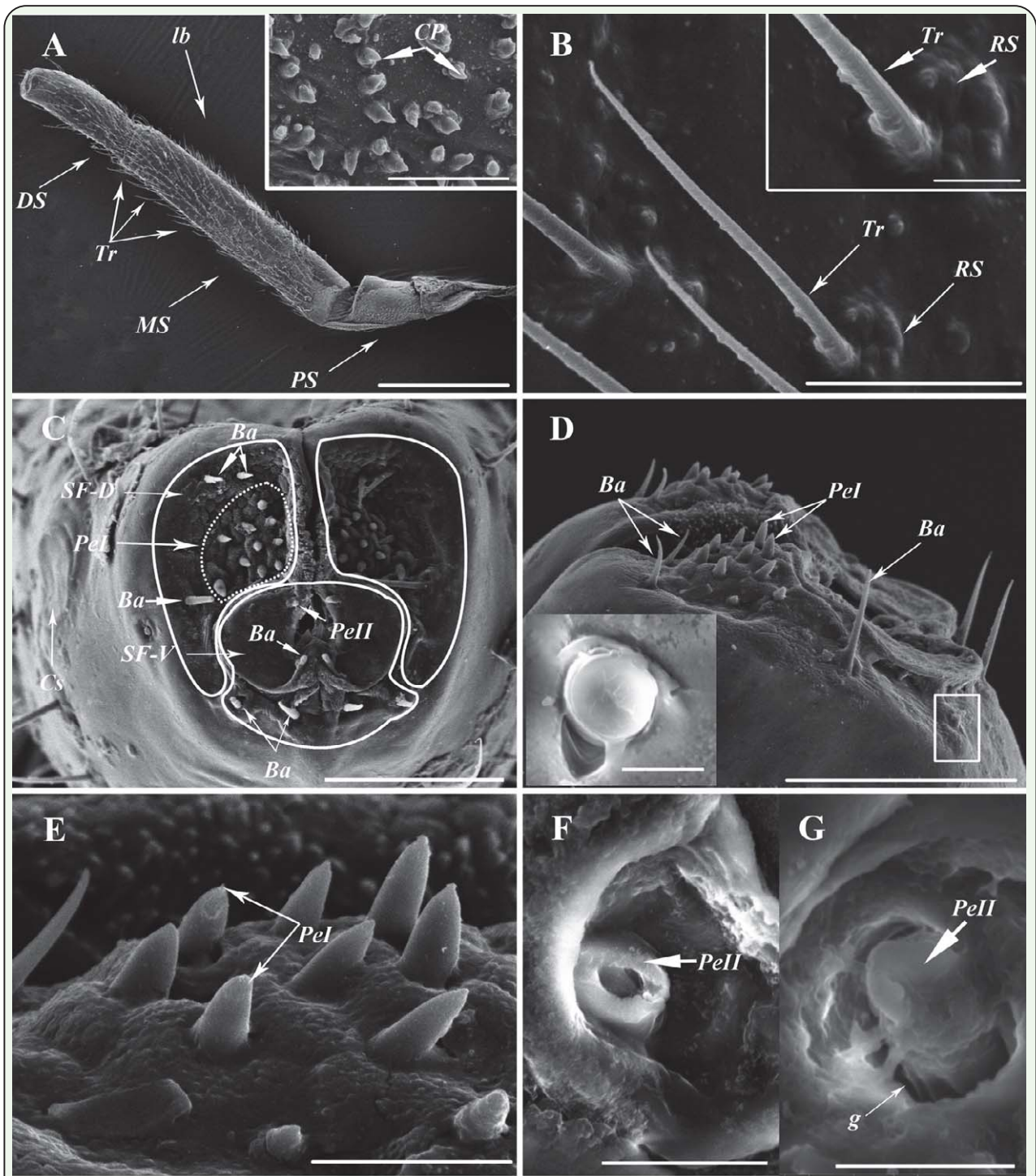




**Figure 3.** SEM images of the antennal pedicel and antennal flagellum of *Cixiopsis punctatus*. A: Bourgoin's organ (BO) surrounded by denticle-like walls (DW) on the flagellar basal bulb (BB), which is inserted into a socket (sk). B: General view of the antenna showing the Bourgoin's organ (BO). C: Top view of the Bourgoin's organ (BO) showing a coeloconic sensillum (Co), an aperture (ap), three styloconic sensilla (St), denticle-like walls (DW) and dome-like processes (DP). D: Lateral view of the Bourgoin's organ (BO), showing the cuticular spines (CS), styloconic sensilla (St) and denticle-like walls (DW). E: Plate organs (PO) with seta-like projections (SP), surrounded by cuticular denticles (CD) and cuticular microtubercles (CM). F: Solid seta-like projections (SP) and cuticular denticles (CD). [(A) scale bar 50  $\mu\text{m}$ , 10  $\mu\text{m}$  in box, (B) scale bar 100  $\mu\text{m}$ , (C) scale bar 10  $\mu\text{m}$ , 5  $\mu\text{m}$  in box, (D) scale bar 10  $\mu\text{m}$ , (E) scale bar 20  $\mu\text{m}$ , (F) scale bar 20  $\mu\text{m}$ , 5  $\mu\text{m}$  in box]. High quality figures are available online.







**Figure 5.** SEM images of the labium of *Cixiopsis punctatus*. A: General view of the labium (lb) with trichoid sensilla (Tr), showing the distal segment (DS), middle segment (MS), proximal segment (PS) and cone-shaped processes (CP) on the proximal segment. B: Trichoid sensilla (Tr) on the distal segment. C: Labial tip, showing the sensory fields with the basiconic sensilla (Ba), peg sensilla (Pel, Pell), and coin-shaped sensilla (Cs). D: The top of the distal segment, showing the basiconic sensilla (Ba) and peg sensilla (Pel). E: Enlarged view of the hollow peg sensilla (Pel). F and G: Enlarged view of the Pell located between the dorsal sensory field (SF-D) and the opening of the maxillae and mandibles, showing the hollow inside and grooves (g) on the surfaces. RS, raised socket; SF-V ventral sensory field. [(A) scale bar 500  $\mu$ m, 20  $\mu$ m in box, (B) scale bar 20  $\mu$ m, 5  $\mu$ m in box, (C) scale bar 50  $\mu$ m, (D) scale bar 50  $\mu$ m, 2  $\mu$ m in box, (E) scale bar 10  $\mu$ m, (F) scale bar 5  $\mu$ m, (G) scale bar 4  $\mu$ m]. High quality figures are available online.