Zoomorphology (2026) 145:37
https://doi.org/10.1007/s00435-026-00789-9

RESEARCH

Morphology and distribution of mouthpart sensilla in *Halyomorpha halys* (Hemiptera: Pentatomidae): insights into feeding biology

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Received: 19 November 2025 / Revised: 29 April 2026 / Accepted: 10 May 2026

Abstract

The brown marmorated stink bug *Halyomorpha halys* (Hemiptera: Pentatomidae) is a globally invasive pest, but detailed information on the ultrastructure and sensory organization of its mouthparts remains incomplete. Using scanning electron microscopy, we examined the piercing-sucking apparatus of *H. halys* adults, focusing on sensilla morphology, number, and distribution. The mouthparts consist of the labrum, four-segmented labium, and paired mandibular and maxillary stylets. Twelve types of sensilla were identified and classified into six categories: basiconica, campaniformia, chaetica, coeloconica, styloconica, and trichodea. The labrum and labium emerged as primary sensory regions, integrating mechanical, chemical, and physical inputs. Sensilla campaniformia, chaetica, and trichodea are mainly interpreted as mechanoreceptors. Sensilla coeloconica have been associated with thermo- and hygroreception, contributing to the detection of physical parameters. The apical sensory fields host basiconica, styloconica, and specialized chaetica, likely mediating gustatory, olfactory, and thermo-hygroreceptive functions during host evaluation. Based on the characteristics observed at the II-III and III-IV transition areas, an alternative labial position was hypothesized, potentially facilitating stylet cleaning and allowing modulation of insertion angle into plant tissues. This study provides the first comprehensive account of the mouthpart sensilla of *H. halys*, emphasizing their functional significance and species-specific traits. The morphological and functional insights gained here contribute to a deeper understanding of feeding biology in Pentatomidae and may support the development of innovative approaches for monitoring and managing this invasive pest.

Keywords *Halyomorpha halys* · Piercing-sucking mouthparts · Scanning electron microscopy · Sensilla morphology · Feeding behavior · Invasive pest

Introduction

The brown marmorated stink bug (BMSB), *Halyomorpha halys* (Stål, 1855) (Hemiptera: Pentatomidae), is an invasive species that has rapidly expanded from its native range in eastern Asia (including China, Japan, Taiwan and Korea) to North America and Europe, where it has become a serious agricultural and urban nuisance pest (Hoebeke and Carter 2003; Haye et al. 2015). Its wide polyphagy, encompassing more than 170 host plants including orchard, vegetable, and ornamental crops, accounts for its severe economic impact (Lee et al. 2013; Leskey and Nielsen 2018). Damage is mainly associated with feeding activity: by piercing plant tissues and sucking sap, *H. halys* can cause local lesions, cell rupture, tissue necrosis, and enzymatic maceration, that lead to fruit discoloration, scarring, pitting, and deformation, as well as abscission of fruits, leaves, stems, flowers, and seeds (Lee et al. 2013; Rice et al. 2014; Lucini and Panizzi 2018).

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Published online: 19 June 2026

Moreover, such injuries frequently promote secondary or postharvest infections, further limiting the marketability of the product (Rice et al. 2014). Major outbreaks in the USA and Europe have demonstrated the capacity of this pest to cause multimillion-dollar losses in fruit production (Bergmann et al. 2016; Leskey and Nielsen 2018).

As in other Pentatomidae, *H. halys* possesses specialized piercing-sucking mouthparts, including a labrum, a segmented labium, and a stylet bundle formed by modified mandibles and maxillae (Parveen et al. 2015; Lucini and Panizzi 2018; Li et al. 2021). These structures not only enable stylet penetration and sap ingestion but also host a wide diversity of cuticular sensilla, which often occur in species-specific combinations and arrangements (Zacharuk 1980, 1985; Brożek and Chłond 2010). In piercing–sucking insects, including stink bugs, cuticular sensilla can function as mechano-, chemo-, thermo-, and/or hygroreceptors, mediating key activities such as host plant recognition, probing, and the assessment of food quality (Backus 1988; Usha Rani and Madhavendra 2005; Wiman et al. 2014; Parveen et al. 2015; Serteyn et al. 2020; Li et al. 2021).

Despite the growing literature on biology, ecology and pest status of *H. halys* (Lee et al. 2013; Rice et al. 2014; Leskey and Nielsen 2018), detailed investigations of its mouthpart morphology and sensory structures remain limited compared to other heteropterans, where morphological and ultrastructural studies of mouthparts and sensilla have proven highly informative, elucidating feeding specialization and trophic adaptations and providing a robust framework for comparative and functional morphology (Brożek 2013; Parveen et al. 2015; Wang et al. 2019, 2020a, b; Taszakowski et al. 2019; Li et al. 2021).

The present study provides a detailed scanning electron microscopy (SEM) analysis of the external mouthpart morphology in adult *H. halys*, with particular emphasis on the distribution, diversity, and putative functions of labral and labial sensilla. By documenting and classifying the types of sensilla and their organization, this work contributes to a better understanding of the sensory basis of feeding in *H. halys* and provides comparative morphological data relevant to both applied pest management and the functional morphology of Hemiptera. Specifically, we aimed to provide the first comprehensive account of sensilla morphology and distribution in *H. halys*, highlighting species-specific traits with potential functional implications for its feeding biology.

Materials and methods

Insect collecting

Adults of *Halyomorpha halys* (males and females) were obtained from laboratory colonies maintained at the University of Perugia (Umbria, Italy). Individuals were sexed under a stereomicroscope (Leica® EZ4W, Heerbrugg, Switzerland) based on external morphological traits and preserved in 70% ethanol until processing. For SEM analyses, 20 specimens of each sex were prepared.

Sample preparation and scanning electron microscopy

Heads were detached in 50% ethanol (Sigma Aldrich®; Milan, Italy) under a stereomicroscope (Leica® EZ4W, Heerbrugg, Switzerland) using fine forceps and micro-scissors. Some heads were left intact, while others were dissected to isolate the complete mouthparts, the labrum, the apical portion of the labium, and individual mandibular and maxillary stylets. All samples were dehydrated through a graded ethanol series (50–99%, three steps of 15 min each) and transferred to hexamethyldisilazane (HMDS; Sigma Aldrich®; Milan, Italy) for final dehydration. Specimens were allowed to evaporate overnight under a fume hood, following protocols successfully applied for sensilla ultrastructure in insects (Ruschioni et al. 2015). Dehydrated preparations were mounted on aluminum stubs with double-sided conductive tape, oriented in multiple views (dorsal, ventral, and lateral), and sputter-coated with gold (10 nm; Union SCD 040, Balzers, FL, Liechtenstein). Observations were performed using three scanning electron microscopes: a Tescan® Vega3 (Brno, Czech Republic) for general head and rostrum morphology, a Zeiss® Supra 40 (Oberkochen, Germany) and a JEOL® JSM-IT800 (Tokyo, Japan) for high-resolution analyses of mouthparts and sensilla. Imaging was carried out under high vacuum using a secondary electron detector, at 3–10 kV accelerating voltage and 6–12 mm working distance. Digital micrographs were captured at variable magnifications depending on the structures examined.

Sensilla classification

Sensilla were identified and classified based on their external morphology (shape, size, socket type, and cuticular ornamentation), following the criteria and the terminology proposed in the literature.

Short, peg-like sensilla emerging from flexible or inflexible sockets were identified as sensilla basiconica (Snodgrass 1935; Zacharuk 1985; Nowińska and Brożek 2017).

Dome-shaped cuticular structures, slightly raised above the surrounding cuticle and characterized by a single external pore, were attributed to sensilla campaniformia (Ca) (Snodgrass 1935; Schneider 1964; McIver 1975; Zacharuk 1985; Shields 2010; Nowińska and Brożek 2017).

Bristle- or spine-like structures inserted into flexible sockets were classified as sensilla chaetica (Ch) (Snodgrass 1935; Schneider 1964; Zacharuk 1985; Shields 2010; Nowińska and Brożek 2017).

Small pegs sunken into a cuticular pit and displaying a smooth surface were classified as sensilla coeloconica (Co) (Snodgrass 1935; Schneider 1964; Altner and Prillinger 1980; Zacharuk 1985; Nowińska and Brożek 2017).

Pegs arising from an elevated cylindrical projection were identified as sensilla styloconica (Schneider 1964; Zacharuk 1985; Shields 2010).

Finally, slender, hair-like sensilla inserted into a flexible socket and tapering from base to apex were assigned to sensilla trichodea (Snodgrass 1935; Zacharuk 1985; Nowińska and Brożek 2017).

For each sensillum type, length, basal diameter and pit diameter (when measurable and present) were recorded from SEM images. The diameter of pore-like structures was also measured using the same approach.

Measurements were obtained using the SEM built-in software after calibration on the scale bar. A minimum of 5–20 replicates per sensillum type were analyzed, depending on their abundance and accessibility.

Data management

Morphometric data were tabulated and analyzed using Microsoft® Excel 365 (Redmond, USA). Distribution patterns of sensilla were described in terms of presence, number, and arrangement on the labrum and each labial segment.

Results

General morphology of the mouthparts

Adults of *H. halys* bear typical piercing-sucking mouthparts composed of a triangular labrum, a four-segmented labium, and a stylet bundle formed by paired mandibular and maxillary stylets (Fig. 1a). At rest, the entire rostrum is held parallel to the body axis, with the stylets protected within the dorsal groove of the labium and secondarily by the labrum. During feeding, the labrum elevates and the labium folds, allowing stylet extrusion, maintaining stylet vertical orientation, and providing continuous protection of the stylets throughout feeding (Fig. 2). The stylets are darkly pigmented along their entire length, whereas the labrum and labium are pale yellow with varying degrees of brownish darkening.

Labrum. The labrum is elongated, with a broad basal region articulated to the anteclypeus and a tapered distal tip (Figs. 1a; 3a,b). A single ventral groove (Fig. 3b) accommodates the proximal section of the stylet bundle, while the dorsal and lateral surfaces exhibit a combination of wrinkles (Fig. 3a) and scale-like patterns (Fig. 3b,c), especially distally. The labrum is slightly longer than the first labial segment (Fig. 3a) and remains aligned with it in the resting position. Pore-like cuticular openings are distributed throughout the surface of the labrum (usually less than 2.5 µm in diameter) (Fig. 3d).

Labium. The labium is cylindrical and segmented into four parts (I-IV) separated by transition areas (Fig. 1a). A distinct articulation is clearly visible between segments I and II (Fig. 1b), whereas the transition areas between the remaining parts are marked mainly by superficially flexible lines (Fig. 1c). A longitudinal dorsal groove extends along the labium, open proximally and gradually closed by appressed margins distally (Figs. 1a; 4). The surface is generally smooth, with pore-like cuticular openings as observed in the labrum and cuticular hairs and sensilla that increase in density toward the distal tip (Fig. 4). Segment I features two lateral prominences flanking the groove (Fig. 4a, b), whereas segments II and III show characteristic rows of setae and surface depressions (Fig. 4c-f). In addition, segment III exhibits dorsal proximal prominences, as highlighted in Fig. 4e. Segment IV (Fig. 4g,h) ends in a rounded tip divided into two symmetrical kidney-shaped sensory fields (SF), each bearing a dense array of sensilla (Fig. 1d,e). Around the terminal opening, cuticular projections (CP) of variable rigidity are also present (Fig. 1d).

Stylet bundle. The stylet bundle is slender and elongated and consists of paired mandibular and maxillary stylets (Fig. 1a, 5). Each mandibular stylet bears blunt teeth, decreasing in size proximally, and several ridges and surface elevations (Fig. 5a-c). The maxillary stylets are spear-shaped, with tridentate tips and a double internal groove (Fig. 5 d-f). A tongue-and-groove locking mechanism ensures the interlocking and the stabilization of the bundle (Fig. 5f) and, in the case of the maxillary stylets, contributes to the formation of the food and salivary canals.

Sensilla categories and types

Twelve types of sensilla were identified (Figs. 6, 7; Table 1), grouped into six morphological categories: basiconica (type 1 and 2), campaniformia, chaetica (type 1, 2, 3 and 4), coeloconica (type 1 and 2), styloconica (type 1 and 2), and trichodea.

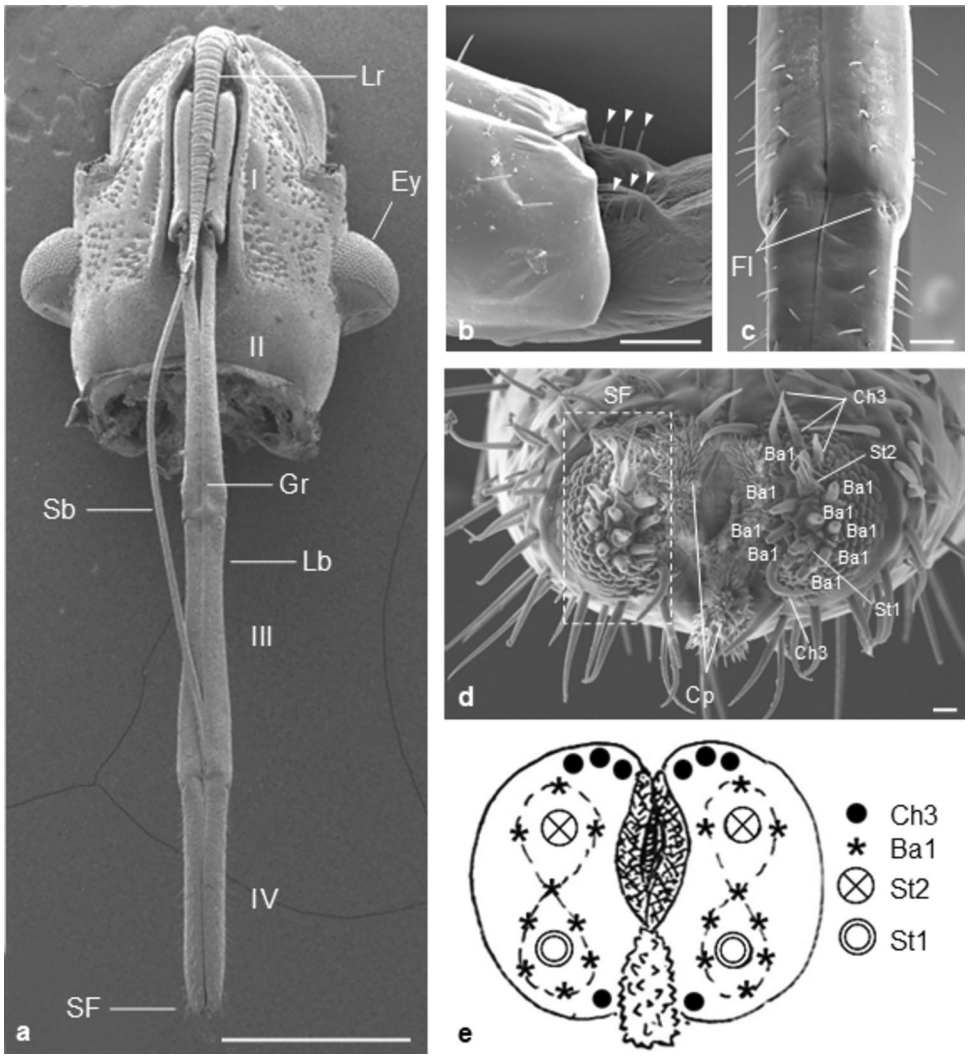

Fig. 1 SEM images of the mouthparts of *Halyomorpha halys*. **a** Ventral view of the adult head showing the four-segmented labium (segments I-IV). (b) Articulation at the I–II labial transition, with three sensilla trichodea (Tr) visible on each side (white arrows). **c** Dorsal view of the transition area between labial segments III and IV, showing the flexible lines. **d** Apical view of the labial tip showing the two sensory fields (SF). **e** Schematic representation of the sensory fields illustrating the arrangement of the four sensilla types: sensilla basiconica type 1 (Ba1); sensilla chaetica type 3 (Ch3); sensilla styloconica type 1 (St1); sensilla styloconica type 2 (St2). *Ey* eye, *Lr* labrum, *Lb* labium, *Sb* stylet bundle, *Gr* longitudinal groove, *Fl* flexible lines, *CP* cuticular projection. Scale bars: 1 mm (**a**); 100 µm (**b, c**); 10 µm (**d**)

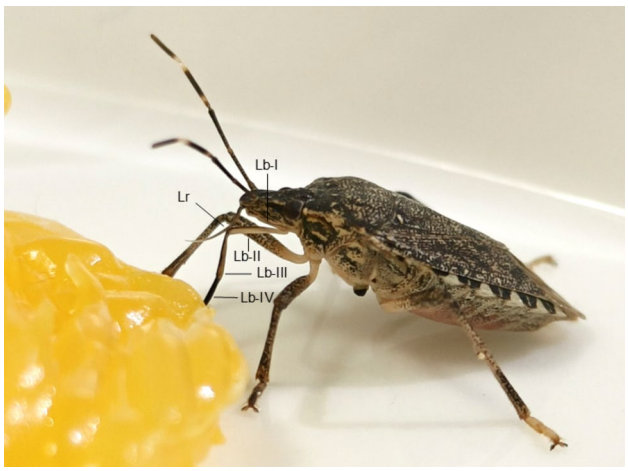

Fig. 2 Position of the mouthpart of an adult *Halyomorpha halys* during feeding. The labrum is raised and contacts the labium at the folding point between segment II and III. Labial folding ensures stylet extrusion, maintains stylet verticality, and provides continuous protection of the stylet bundle throughout feeding. *Lr* labrum, *Lb* labium (segments I–IV)

Sensilla basiconica (Ba) (Figs. 6a,b; 7). Two types of sensilla basiconica were identified. Ba1 were cone-shaped with a rounded tip, smooth surface (Figs. 6a; 7). They measured 18.1 ± 1.7 µm in length and 4.6 ± 0.4 µm in basal diameter, and were restricted to the sensory fields at the tip of the labium, nine per field (Fig. 1d,e; Table 1). Ba2 were shorter, with a straight shaft, evident basal socket, and smooth surface except for a few grooves at the apex (Figs. 6b; 7). They measured 10.9 ± 3.4 µm in length and 2.0 ± 0.3 µm in basal diameter, and were located on the labrum and the proximal segment of the labium (Fig. 7; Table 1).

Sensilla campaniformia (Ca) (Figs. 6c; 7). These sensilla were rounded and slightly elevated, with an ellipsoidal outline and a central dimple. They measured 7.2 ± 0.9 µm in length and 6.2 ± 1.6 µm in width and were distributed throughout the labium, without evident clustering (Fig. 7; Table 1).

Sensilla chaetica (Ch) (Figs. 6d-l; 7). Four morphotypes of sensilla chaetica were distinguished. All were inserted into flexible sockets and terminated in a pointed apex. Ch1

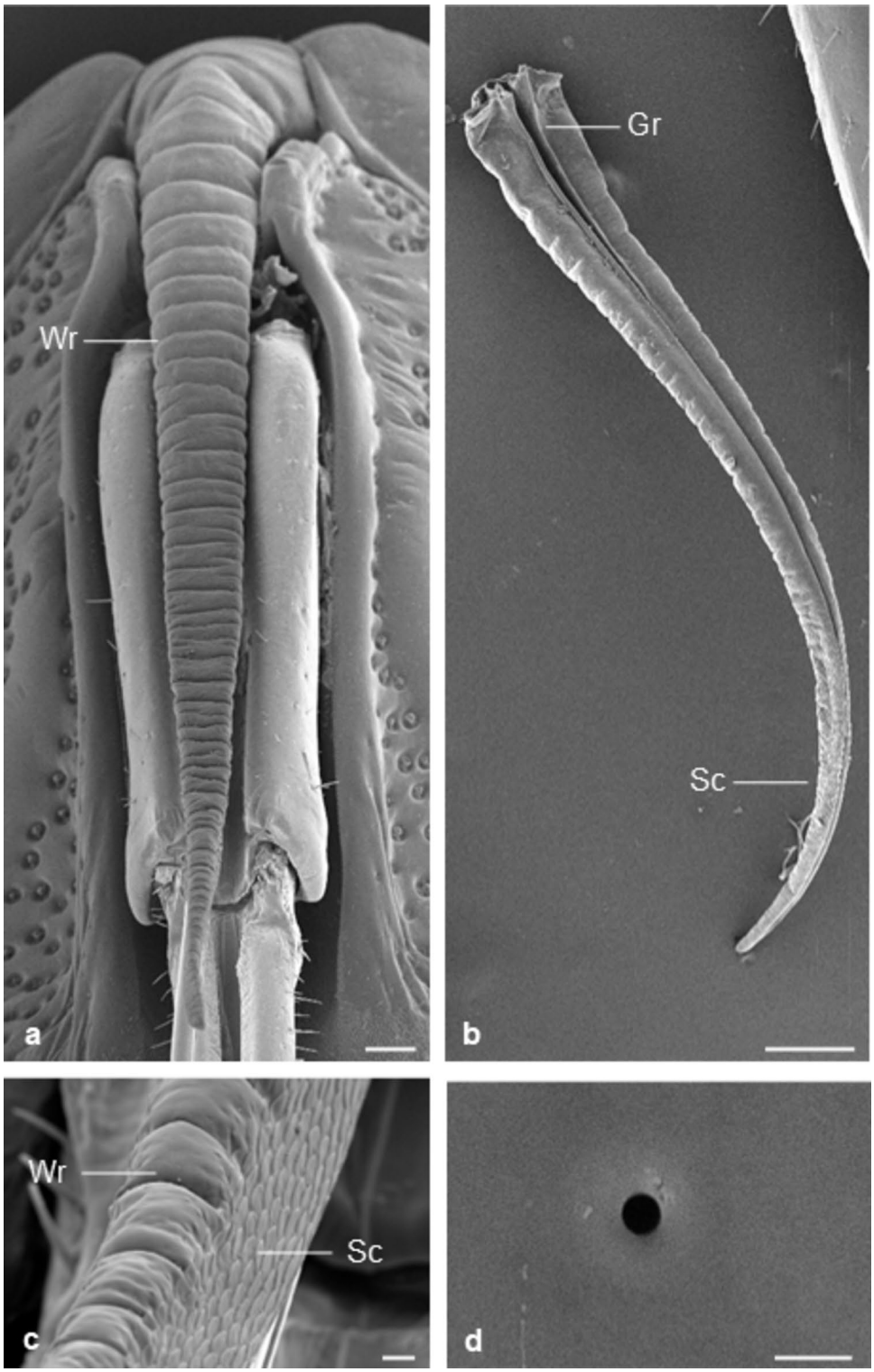

Fig. 3 SEM images of the labrum of *Halyomorpha halys*. **a** Dorsal view showing the elongated, triangular shape of the labrum and the numerous cuticular wrinkles. **b** Ventrolateral view of the labrum showing the longitudinal groove and the scale-like pattern on the distal lateral surface. **c** Magnification of the distal lateral surface of the labrum, showing the scale-like pattern and dorsal wrinkles. **d** Detail of a pore-like cuticular opening. *Wr* wrinkles, *Gr* longitudinal groove, *Sc* scale-like pattern. Scale bars: 100 µm (**a**); 200 µm (**b**); 10 µm (**c**); 1 µm (**d**)

were short, smooth bristles measuring 9.7 ± 3.3 µm in length and 1.6 ± 0.2 µm in basal diameter (Figs. 6d; 7), mainly located on the proximal labrum and occasionally present on the labium (Fig. 7; Table 1). Ch2 were longer (19.5 ± 3.9 µm in length; 2.8 ± 0.6 µm basal diameter) (Figs. 6e; 7), with smooth surface, occurring on both the labrum and, more markedly, on the labium, where they were arranged in longitudinal lines (Fig. 7; Table 1). Ch3 were characterized by a longitudinally grooved surface and measured 45.5 ± 2.3 µm in length and 3.8 ± 0.1 µm in basal diameter (Figs. 6f-h; 7). They were confined to the sensory fields at the labial tip, where three occurred dorsally and one ventrally in each field

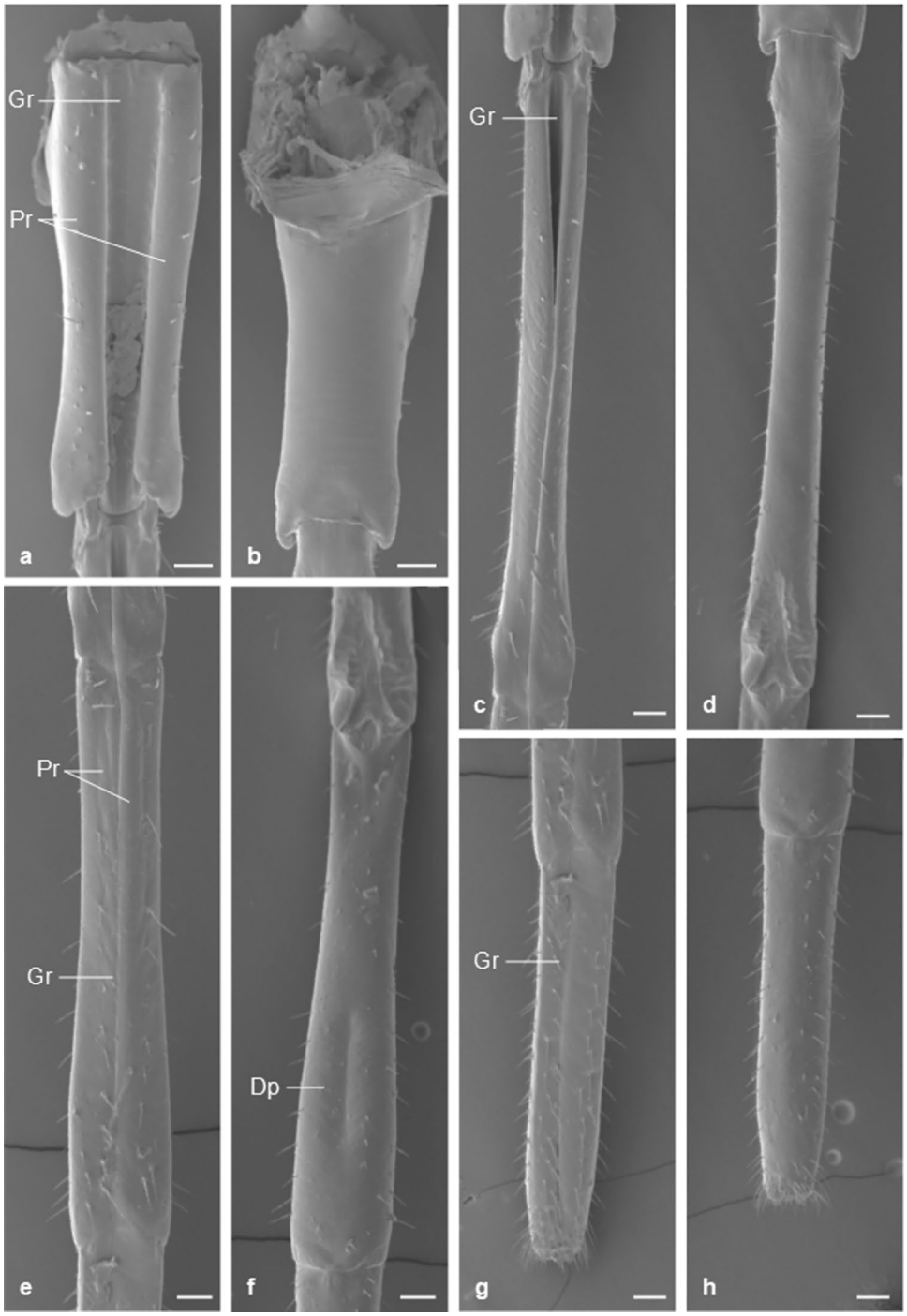

Fig. 4 SEM images of the four labial segments of *Halyomorpha halys*: segment I (**a, b**), segment II (**c, d**), segment III (**e, f**), and segment IV (**g, h**). Dorsal views (**a, c, e, g**) showing the longitudinal groove, the arrangement of chaetic lines along the labial surface, and the prominences observed on segments I and III. Ventral views (**b, d, f, h**) highlighting the chaetic lines and the depression present on segment III. *Gr* longitudinal groove, *Pr* prominence, *Dp* depression. Scale bars: 100 µm (**a**–**h**)

(Fig. 1d,e; Table 1). Ch4 were elongate sensilla with a longitudinally grooved surface, similar in general morphology to Ch3 but considerably longer (177.5 ± 5.3 µm; 8.4 ± 0.8 µm at the base) (Figs. 6i,l; 7). They occurred as two dorsal pairs on segment II, precisely at the contact points between labrum and labium (Fig. 7; Table 1).

Sensilla coeloconica (Co) (Figs. 6m,n; 7). Two types of sensilla coeloconica were observed. Co1 consisted of a small conical peg inserted in a circular pit, slightly protruding above the cuticular surface (Figs. 6m; 7). Pit and cone diameter measured 3.4 ± 0.4 µm. They were located ventrally on the distal part of segment IV (Fig. 7; Table 1). Co2 were smaller, with a pit diameter of 2.5 ± 0.1 µm and cone diameter of 1.6 ± 0.2 µm, not protruding (Figs. 6n; 7), and positioned dorsally at the transition area III–IV (Fig. 7; Table 1). Only a few sensilla of each type were found.

Sensilla styloconica (St) (Figs. 6o,p; 7). Two morphotypes were recognized. St1 consisted of a central cone

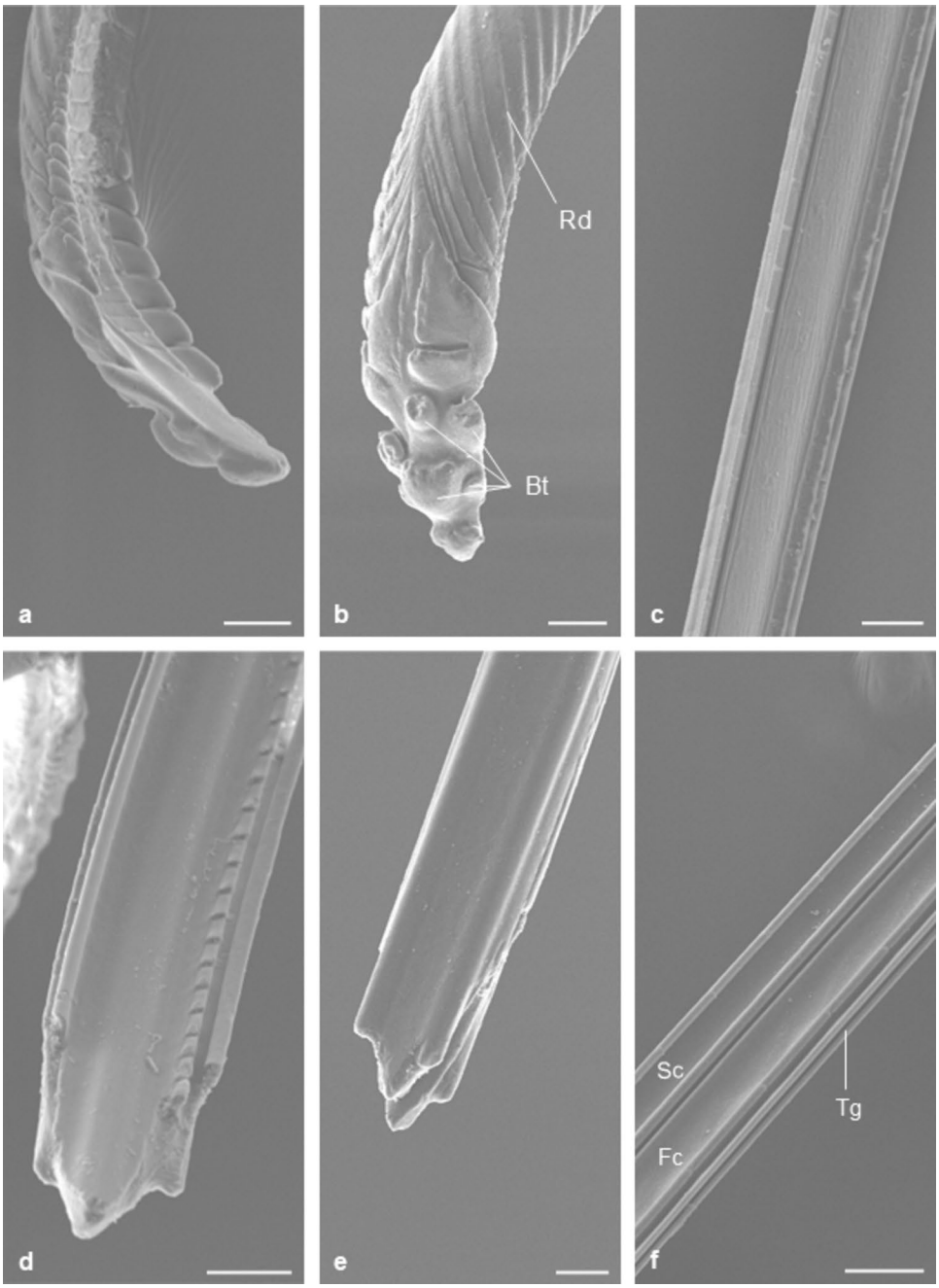

Fig. 5 SEM images of the stylets of *Halyomorpha halys*: **a** internal and **b** external views of the tip of the mandibular stylet, showing blunt teeth and several ridges on the external surface; **c** internal view at mid-length of a mandibular stylet, showing the single internal groove; **d** internal and **e** external views of the tridentate tip of the maxillary stylet; **f** internal view at mid-length of a maxillary stylet showing structures involved in the tongue-and-groove locking mechanism. *Rd* ridges, *Bt* blunt teeth, *Sc* groove forming the salivary canal, *Fc* groove forming the food canal, *Tg* tongue-and-groove structures. Scale bars: 20 µm (**a-f**)

partially enveloped by an external chitinous structure, which covered the basal half and then divided into three short extensions remaining close to the cone. The ventral side of the cone was uncovered, with three basal protrusions visible. The overall basal diameter was 7.5 ± 0.9 µm (Figs. 6o; 7). St2 had an external chitinous structure fully surrounding the base, branching into numerous long, thin extensions that exceeded the length of the central cone. The overall basal diameter was 9.0 ± 1.0 µm (Figs. 6p; 7). Both types were confined to the apical sensory fields of the labium, with one St1 and one St2 per field (Fig. 1d,e; Table 1).

Sensilla trichodea (Tr) (Figs. 6q; 7). Sensilla trichodea were hair-like structures arising from circular, flexible sockets, with a pointed apex and smooth shaft. They had a basal diameter of 4.3 ± 0.6 µm and a length of 39.4 ± 12.1 µm. A basal notch was evident at the insertion point. Tr were located dorsally at two labial folding points: three arranged in a proximal–distal line at the I–II transition on each side, and a single pair at the III–IV transition (Fig. 7; Table 1).

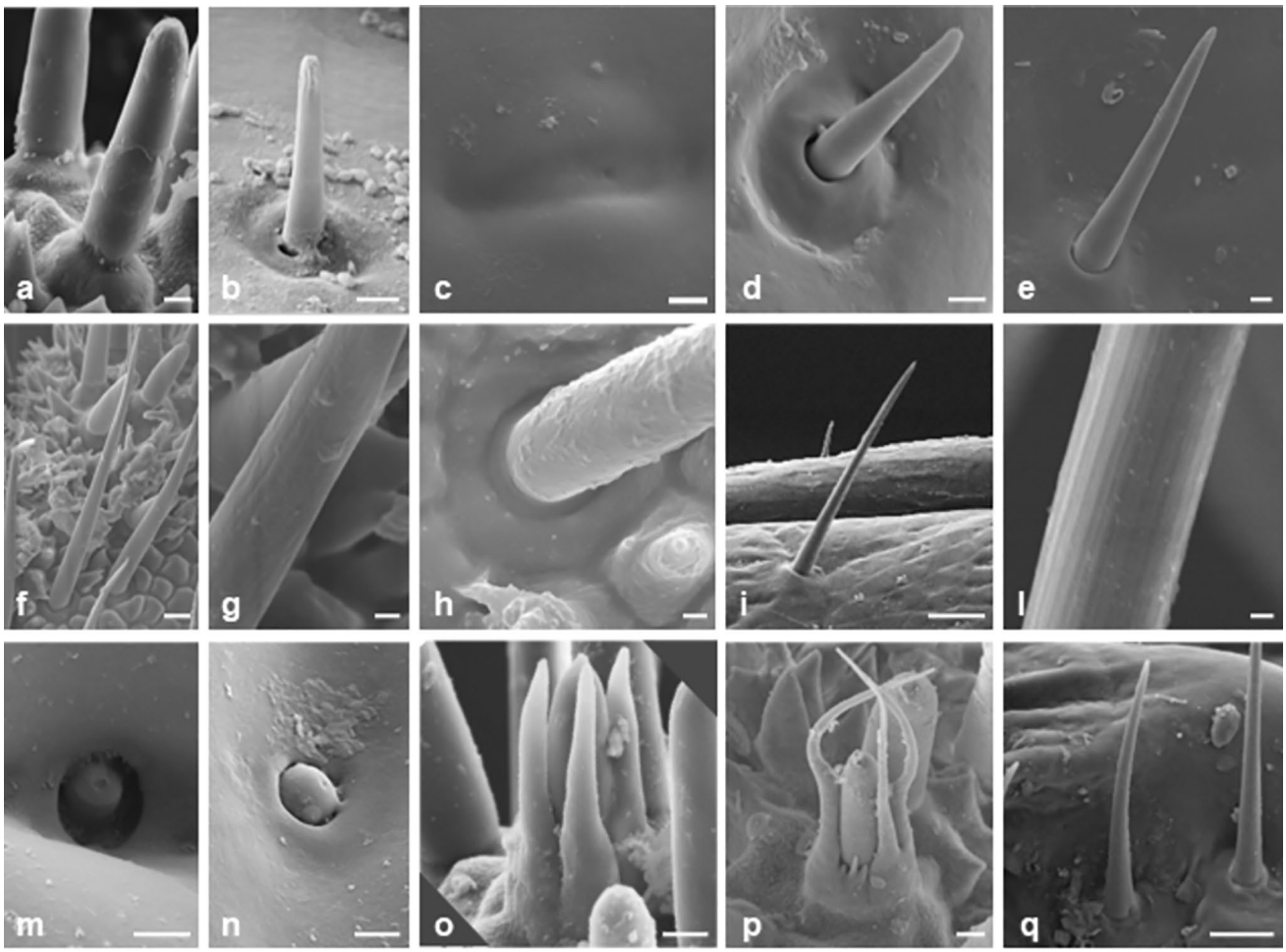

Fig. 6 SEM images of the sensilla identified on the mouthparts of *Halyomorpha halys*. **a** Sensillum basiconicum Ba1; **b** sensillum basiconicum Ba2; **c** sensillum campaniforme Ca; **d** sensillum chaeticum Ch1; **e** sensillum chaeticum Ch2; **f–h** sensillum chaeticum Ch3: whole sensillum (**f**), mid-shaft (**g**), socket (**h**); **i, l** sensillum chaeticum Ch4: whole sensillum (**i**), mid-shaft (**l**); **m** sensillum coeloconicum Co1; **n** sensillum coeloconicum Co2; **o** sensillum styloconicum St1; **p** sensillum styloconicum St2; **q** sensillum trichodeum Tr. Scale bars: 1 µm (**c-e, g, h, l**); 2 µm (**a**, **b**, **m-p**); 5 µm (**f**); 10 µm (**q**); 20 µm (**i**)

Distribution of sensilla types on the mouthparts

On the labrum, sensilla were observed exclusively on the dorsal surface and on the upper portions of the lateral surfaces. They included sensilla basiconica and chaetica (Fig. 7; Table 1). Ba2 were concentrated proximally, mainly along the edge of the wrinkled area, while Ch1 and Ch2 were distributed along the dorsal margins, accompanied by numerous pore-like cuticular openings. Toward the distal end, sensilla chaetica and basiconica progressively decreased, disappearing at the tip. A distinctive feature of the labrum was the presence of dense clusters of Ch1 in the proximal part of each lateral surface, forming well-defined "chaetic areas" (Fig. 7).

Along the labium, sensilla were distributed continuously from the base to the apex, increasing in density distally. In the first segment, Ba2, Ca, Ch1, and Ch2 were identified, although their distribution was irregular and not perfectly symmetrical between the two lateral prominences (Fig. 7; Table 1). Ca were located dorsally, Ba2 were mainly positioned along the dorsal margins, while Ch1 and Ch2 occurred both on the marginal zones and on the lateral and ventral surfaces. In the second segment, the sensilla present included Ca, Ch2, Ch4, and Tr (Fig. 7; Table 1). Ca were scattered across the surface, whereas Ch2 were arranged in seven longitudinal lines: six symmetrically paired along the dorsal, lateral-dorsal, and lateral-ventral regions, and a seventh line isolated on the ventral side. The two pairs of Ch4 were positioned dorsally, one near the appressed margins of the dorsal groove and the other at the distal end of the segment. In addition, three Tr were aligned on each side of the I–II transition area (Fig. 1b).

The third segment bore Ca and Ch2 (Fig. 7; Table 1). Ca were randomly distributed, while Ch2 continued to form

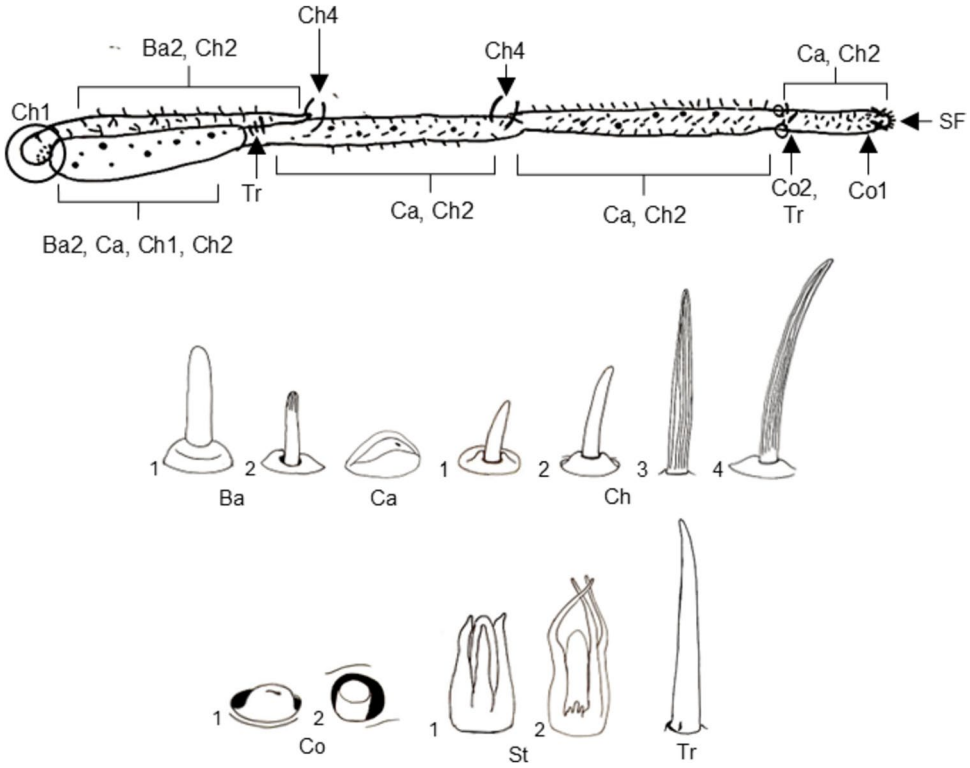

Fig. 7 Schematic representation of the mouthparts of *Halyomorpha halys*, showing the distribution of sensilla along the labrum and the four labial segments, and a comparative illustration of the sensilla types. Sensory fields (SF) at the labial tip and the location of each sensillum type are indicated. Sensilla are classified as follows: Ba, sensilla basiconica (two types: Ba1 and Ba2); Ca, sensilla campaniformia; Ch, sensilla chaetica (four types: Ch1-Ch4); Co, sensilla coeloconica (two types: Co1 and Co2); St, sensilla styloconica (two types: St1 and St2); Tr, sensilla trichodea

longitudinal chaetic lines, accompanied by cuticular hairs of variable length and thickness. The fourth segment displayed the greatest variety of sensilla, with Ca, Ch2, Co1, Co2, and Tr present on the main body (Fig. 7; Table 1). At the III–IV transition, one Tr and one Co2 were located dorsally on each side (Fig. 7; Table 1). On the remaining surface, Ch2 were scattered, whereas cuticular hairs were arranged in longitudinal rows that became denser and more irregular toward the distal end. The tip of the segment hosted numerous Ca, together with a single pair of Co1 located ventrally.

The apical sensory fields of segment IV showed a highly specialized symmetrical organization (Fig. 1d,e; Table 1). Each field contained nine Ba1 arranged in two vertically aligned circles, with one St2 positioned in the center of the dorsal circle and one St1 in the center of the ventral circle. Four Ch3 completed the arrangement, with three sensilla located dorsally and one ventrally.

No sexual dimorphism was detected in sensilla type or distribution.

Discussion

General organization of mouthparts in *Halyomorpha halys*

Adults of *H. halys* possess piercing-sucking mouthparts typical of Pentatomidae, composed of the labrum, the four-segmented labium, and the stylet bundle formed by paired mandibular and maxillary stylets (Parveen et al. 2015; Wang et al. 2020b; Li et al. 2021). As in other heteropterans, sensilla are distributed on different mouthpart structures, and are generally interpreted as mediators of host probing, food acceptance, and feeding (Backus 1988; Usha Rani and Madhavendra 2005; Parveen et al. 2015; Li et al. 2021). Based on their morphology, position, and distribution (Snodgrass 1935; Altner and Prillinger 1980; Zacharuk 1985; Ibrahim et al. 2019), twelve types of sensilla were identified in *H. halys*, potentially functioning as mechano-, chemo-, thermo-, hygroreceptors, or bimodal sensilla (Table 1). No sexual dimorphism was observed in the mouthpart sensilla of *H. halys*, consistent with previous observations in other pentatomid species (Parveen et al. 2015). Although the general morphology and functional roles of piercing–sucking mouthparts have been described for several species within Pentatomidae (Miles 1972; Backus 1988; Usha Rani 2009; Parveen et al. 2015; Lucini and Panizzi 2018; Wang et al. 2020b; Li et al. 2021), detailed ultrastructural studies remain essential to expand our understanding and to highlight species-specific features.

Functional interpretation of sensilla types

Mechanoreceptive sensilla included sensilla trichodea, campaniformia, and three morphotypes of chaetica (Table 1). Sensilla trichodea have been reported as mechanoreceptive

Table 1 Morphological classification, location, and presumed function of sensilla types observed on the mouthparts of *Halyomorpha halys*

Morphological category	Sensilla type	Location	Presumed function	References
Basiconica	Ba1	Lb IV (sensory field)	Gustation	Parveen et al. 2015; Wang et al. 2020a
	Ba2	Lr; Lb I	Mechano-olfaction	Ibrahim et al. 2019; Wang et al. 2020b
Campaniformia	Ca	Lb I-IV	Mechanoreception	McIver 1975; Parveen et al. 2015
Chaetica	Ch1	Lr; Lb I (occasionally)	Mechanoreception	Snodgrass 1935; Backus 1988; Catalá 1996
	Ch2	Lr, Lb I-IV	Mechanoreception	Snodgrass 1935; Backus 1988; Ahmad et al. 2016
	Ch3	Lb IV (sensory field)	Mechano-olfaction	Snodgrass 1935; Ibrahim et al. 2019
	Ch4	Lb II	Mechanoreception	Snodgrass 1935
Coeloconica	Co1	Lb IV (distally)	Hygroreception/ Thermo-hygroreception	Altner and Prillinger 1980; Ibrahim et al. 2019; Nowińska et al. 2020
	Co2	Lb IV (proximally)	Hygroreception/ Thermo-hygroreception	Altner and Prillinger 1980; Ibrahim et al. 2019; Nowińska et al. 2020
Styloconica	St1	Lb IV (sensory field)	Thermo-hygroreception	Usha Rani 2009
	St2	Lb IV (sensory field)	Thermo-hygroreception	Usha Rani 2009
Trichodea	Tr	Lb II, IV	Mechanoreception	Zacharuk 1985; Wang et al. 2020b

in various heteropteran species (Ahmad et al. 2016), although they may also perform chemosensory functions (Snodgrass 1935; Zacharuk 1985). Given their morphology and position on the mouthparts of *H. halys*, these sensilla are hypothesized to be exclusively mechanoreceptive, as also proposed by Wang et al. (2020b) for similarly positioned sensilla in predatory stink bugs.

Chaetica sensilla on the labrum and labium (Ch1, Ch2) are also likely mechanoreceptors, detecting relative movements of the mouthparts and stylet displacement within the dorsal groove. This interpretation aligns with Backus (1988), who indicated that poreless mechanosensory hairs (sensilla chaetica) located along the labial margins in other hemipterans function in sensing the degree of labial bending during probing (Parveen et al. 2015). Similar Ch1 sensilla have been reported also by Catalá (1996) in *Triatoma infestans* (Hemiptera: Reduviidae) (named "Sensilla chaetica type 4"), whereas comparable Ch2 sensilla were reported by Ahmad et al. (2016) on the antennae of *Dolycoris indicus* (Hemiptera: Pentatomidae); in both cases reported with mechanoreceptive functions. The elongated Ch4, located at the contact points between labrum and labium during both resting and feeding phases (Fig. 2), therefore reinforce their role in positional feedback.

Campaniform sensilla are dome-shaped structures typically involved in detecting cuticular strain and mechanical stress within the exoskeleton (McIver 1975). Similar sensilla to those observed in *H. halys* have been described in other Pentatomidae, including Pentatominae and Asopinae, where they are consistently interpreted as mechanoreceptors responsible for monitoring cuticular deformation (Parveen et al. 2015; Ahmad et al. 2016; Wang et al. 2020b). In *H. halys*, their widespread occurrence on the labium may reflect a conserved role in detecting cuticular strain and possibly other physical parameters, such as temperature.

Some sensilla may respond to more than one type of stimulus, thereby acting as bimodal sensilla (McIver 1975; Altner and Prillinger 1980). The mechano-olfactory function of Ba2 was previously hypothesized by Ibrahim et al. (2019) for sensilla with the same morphology and size described on the antennae of *H. halys* (named "Sensilla basiconica type B"). Morphological characteristics of Ba2 correspond well with structures described by Wang et al. (2020b) as sensilla basiconica 1 (Sb1) on the labrum and labial segments I-II of predatory stink bugs, for which only a mechanoreceptive function had been reported. Ch3, restricted to the sensory fields at the labial tip, are long enough to be the first to contact plant surfaces and may simultaneously provide mechanical and chemical information. Their bimodal nature is supported by TEM evidence from an analogous type of sensilla on the antennae of *H. halys*, referred to as sensilla chaetica type "A" (SCh-A), which was demonstrated to have a mechano-olfactory function (Ibrahim et al. 2019).

Together with Ch3, three additional types of sensilla were found on the tip of the mouthparts of *H. halys*: Ba1, St1, and St2. Given the functional importance of the tip during labial dabbing, these sensilla are most likely involved in food evaluation and host selection. Based on their shape and position, Ba1 can be interpreted as gustatory sensilla. The same function has been proposed for morphologically comparable sensilla located on the labial tip of other pentatomid (e.g. *Dolycoris indicus*, *Piezodorus hybneri*, and *Plautia crossota*) (Parveen et al. 2015) and pyrrhocoid species

(Wang et al. 2020a). St1 and St2 are morphologically consistent with thermo-hygroreceptors, as suggested for similar sensilla on the tip of the labium of *Eocanthecona furcellata* by Usha Rani (2009). A possible gustatory function has also been proposed for sensilla with similar shape by Wang et al. (2020b) and Parveen et al. (2015), based on the presence of an apical pore. As no apical pore was observed on St1 and St2, thermo-hygroreception is considered the most probable function.

Sensilla coeloconica (Co) were rarely found on the mouthparts of *H. halys*. Similar morphological characteristics have been reported for sensilla on the antennae of this species, as well as on those of other pentatomids, such as *Eocanthecona furcellata*, *Plautia crossota* and *Scotinophara lurida* (Ibrahim et al. 2019; Li et al. 2021). According to the literature, the function of coeloconic sensilla is usually hygro- or thermo-hygroreceptive, especially when no pores are present on the sensillum wall (Altner and Prillinger 1980; Nowińska and Brożek 2017; Ibrahim et al. 2019; Nowińska et al. 2020). Given the aporous surface of the Co observed in *H. halys*, the thermo-hygroreceptive function is the most plausible. Their limited number and specific distribution, with Co1 occurring ventrally on the distal part of the labium and Co2 occurring dorsally at the III–IV transition, suggest that they are not directly involved in food evaluation but rather in detecting physical parameters (wetness, dryness and changes in air temperature). The reason for their scarcity and their particular position on the mouthparts of *H. halys* remains unclear.

Overall, the sensilla equipment of *H. halys* encompasses chemoreceptors (gustatory and olfactory), thermo- and hygroreceptors, and mechanoreceptors, often with proprioceptive roles. While chemosensory, thermo-, and hygroreceptive sensilla are mainly involved in detecting physical conditions and plant-derived stimuli, mechanoreceptors are essential for guiding and coordinating the movements of the mouthpart elements during probing and feeding.

Mechanical aspects of feeding and stylet protection

The morphological description of the mouthparts of *H. halys* presented here provides new insights into the function and coordinated movement of the mouthparts during the transition from the resting to the feeding phase. The stylets, being the most delicate elements of the mouthparts yet indispensable for tissue penetration and sap uptake, are carefully protected by the labrum and the labium in both phases.

In the resting position, they are double-sheathed: proximally housed in the ventral groove of the labrum, which itself is lodged in the dorsal groove of the labium. Distally, they remain enclosed solely by the labial groove up to their terminal portion. This dual protection ensures stylet integrity, especially during feeding, when both vertical positioning of the stylets and labial folding are required for deep penetration and efficient liquid uptake. The scale-like cuticular surfaces on both labrum and labium appear to form a locking mechanism that increases contact surface and friction. This arrangement is expected to prevent the accidental displacement of the stylets.

During feeding, the labrum moves vertically away from the labium, while the labium folds at the I-II and II-III transition areas to maintain stylet protection and continuity with the vertical axis, simultaneously allowing their extrusion from the apical opening. The magnitude of the folding angles depends on the penetration depth required, the structural limits of the joints, and the nature of the food source. The articulation at TA I-II acts as a true joint, enabling greater mobility compared to the more limited hinge-like movements at II-III and III-IV (Fig. 2). The folding lines observed at TA II–III and III–IV may indicate the possibility of an alternative labial position, potentially facilitating distal stylet cleaning and enabling fine adjustments of the insertion angle to minimize resistance during penetration.

In this context, the two cuticular thickenings on the dorsal surface of labial segment III may function to stabilize the stylets during suction, whereas the ventral recess at the distal part of the same segment likely serves as the internal attachment site of a muscle involved in the voluntary movement of segment IV.

Structural specializations at the labial tip

At the tip of the labium, four main structural components can be distinguished: the sensilla, the wrinkled floor, and two types of cuticular projections. The wrinkled floor likely provides elasticity to accommodate cuticular deformation during stylet extension and retraction, thereby protecting the adjacent sensory fields.

The cuticular projections, considered non-receptive (Parveen et al. 2015), may have distinct functions: more rigid ones acting as brushes for stylet cleaning, and the thinner ones serving both cleaning and friction roles, enhancing the grip on the stylets at the terminal part of piercing-sucking mouthparts (Wang et al. 2020b). This interpretation is supported by observations in Nepoidea and Reduviidae, where the region containing similar cuticular projections has been described as a “brush zone” (Cobben 1978).

Limitations and future perspectives

The present study is based on scanning electron microscopy observations, which allow detailed morphological characterization but do not provide direct evidence of sensory function. Consequently, the functional interpretations

proposed here rely on morphological features and comparisons with previously studied species. Future investigations integrating transmission electron microscopy, electrophysiological approaches, or behavioral assays would be necessary to validate the sensory roles of the different sensilla types. Despite these limitations, the present work provides a comprehensive morphological framework that can support future functional and applied studies on feeding biology in *H. halys*.

Conclusion

The piercing-sucking mouthparts of *Halyomorpha halys* consist of the labrum, the four-segmented labium, and paired mandibular and maxillary stylets. The two typical positions of the labrum and labium ensure continuous protection of the stylets during both resting and feeding, while an additional position of the labium at the II–III and III–IV transitions may facilitate stylet cleaning and allow variation in the insertion angle into plant tissues.

The labrum and labium represent the main sensory regions of heteropteran mouthparts. In the present study, twelve types of sensilla were identified on the labrum and labium of *H. halys*, grouped into six categories: basiconica (Ba1, Ba2), campaniformia (Ca), chaetica (Ch1, Ch2, Ch3, Ch4), coeloconica (Co1, Co2), styloconica (St1, St2), and trichodea (Tr). Their number and distribution differed between the labrum and labium and among the four labial segments, with sensillar density increasing distally.

Morphological features, position, and abundance suggest distinct functional roles. Sensilla distributed over the labrum and labium are presumed to be mainly involved in detecting physical parameters such as temperature and humidity (Ca, Co) and in guiding rostral movements through tactile feedback (Ch1, Ch2, Ch4, Tr). In contrast, sensilla at the apical sensory fields are likely specialized for food evaluation, contributing olfactory (Ch3), gustatory (Ba1), and thermo-hygroreceptive (St1, St2) functions. The functional interpretations proposed here, based on SEM-derived morphological evidence, provide a valuable first framework for understanding the sensory organization in *H. halys* mouthparts. However, further investigations into the neuronal organization of these sensilla are needed to confirm their functional roles. A deeper understanding of the sensory basis of host evaluation in *H. halys* may ultimately support the development and the implementation of control strategies, contributing to more effective integrated management of this invasive pest.

Acknowledgements The authors would like to thank the University of Perugia (Umbria, Italy) for providing the specimens and supporting research.

Author contributions M.C.B.: Writing—original draft, Investigation, Formal analysis. L.C.: Methodology, Investigation, Formal analysis, Writing – review and editing. P.R.: Resources, Writing – review and editing. N.I.: Resources, Writing – review and editing. S.R.: Conceptualization, Methodology, Investigation, Formal analysis, Supervision, Writing – review and editing.

Funding Open access funding provided by Università Politecnica delle Marche within the CRUI-CARE Agreement.

Data availability All obtained data are published in this article.

Declarations

Conflict of interest The authors declare no competing interests.

Human and animal rights All procedures involving insects were performed in accordance with Italian and European legislation on experimental animals. According to Italian Legislative Decree 26/2014, which implements EU Directive 2010/63/EU, invertebrates other than cephalopods are not considered laboratory animals for regulatory purposes. Therefore, no specific authorization was required for the collection, rearing, and experimental use of *Halyomorpha halys* in this study.

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