



Functional morphology of mouthparts and antennal sensillae of two co-generic aphidophagous ladybirds

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Abstract

Functional morphology of sensillae on the antennae and mouthparts of two co-generic aphidophagous ladybird species, viz. *Coccinella septempunctata* and *Coccinella transversalis* (Coleoptera: Coccinellidae) were studied using scanning electron microscopy to determine their structure, functions and sex-specific variations. Their mouthparts comprise of mandible, maxilla, maxillary palps, labrum, labium and labial palps. Sensillae were present on different mouthparts, viz. maxillary palp, labial palps, and the clypeus. Maxillary palps were the main prey-holding apparatus with three distinct regions, viz. proximal, middle, and distal segments. Labial palps provide initial gripping of the prey with three similar regions as that of maxillary palps. Six different types of sensillae were identified on the mouthparts of *C. septempunctata*, viz. chaetica, trichoidea, coeloconica, placoidea, basiconica, and styloconica, while those on *C. transversalis* had seven different sensillae with the inclusion of sensilla campaniformia. The female antennae were greater in length than the male ones in both species. The scape and pedicel segments of the male antennae were greater in length, while flagellomeres were shorter in length than those of the female antennae of the two species. Six types of sensillae, viz. chaetica, trichoidea, basiconica, coeloconica, ampullacea, and campaniformia were identified on *C. septempunctata* antennae, while those of *C. transversalis* had eight with the addition of sensillae sporangia, and styloconica. These sensillae on mouthparts and antennae of both the ladybird species have crucial functional roles in foraging, prey-location, and prey capture.

Keywords *Coccinella septempunctata* · *Coccinella transversalis* · Antenna · Coccinellidae · Mouth-parts · Morphology · Sensillae

Introduction

Predatory ladybirds (Coleoptera: Coccinellidae) are biocontrol agents of numerous phytophagous insects and acarine pests (Hodek et al. 2012; Pervez et al. 2020a). These ladybirds locate, recognize, capture, and consume prey that is primarily modulated by chemoreception (Pettersson et al. 2008; Omkar and Pervez 2016). A wide range of sensillae

distributed all over the body (Hallberg and Hansson 1999), including antennae and mouthparts, facilitate them in foraging and mate-search (Park et al. 2001; Omkar and Pervez 2008; Pervez et al. 2020b). Insect mouthparts are diversely evolved into different forms and functions (Krenn and Aspöck 2012), and have evolved according to the prey-type (Samways et al. 1997; Hao et al. 2019a). Aphidophagous ladybirds possess mandibulate mouthparts that comprise of labrum, mandible, maxillae, labium, and hypopharynx (Hao et al. 2016, 2019a, b) and they use maxillary palpi and labial palpi for contact receptions (Seo and Youn 2000), while only the latter for chewing prey (Wang et al. 1999). Diverse forms of sensillae on their mouthparts provide chemo- and thigmoreceptions thereby evolving them as better predators (Ma et al. 2013; Hao et al. 2016).

Seven spot ladybird, *Coccinella septempunctata* Linnaeus is a eurytopic, cosmopolitan aphidophagous ladybird with a wide prey range (Omkar and Pervez 2004). It preferably preyed upon aphid, *Lipaphis erysimi* (Kaltenbach) (Omkar

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and Srivastava 2003), and is considered as a potential biocontrol agent (Pervez and Omkar 2005). Despite its wide occurrence and biocontrol potential, little is known on the morphology of its mouthparts and sensillae associated with them for prey capture. Baoyu et al. (2000) noted two sensillae, viz. trichodea and basiconica on its antennae. Srivastava and Omkar (2003) found female antenna to be greater in length than that of male with the presence of eight types of antennal sensillae. Thornham et al. (2007) studied its sensory structures on the palpi and tarsi and found two types of sensilla basiconica (for mechano- and chemo-reception) and sensilla campaniformia on the labial palpi.

Coccinella transversalis Fabricius is also a major aphidophagous ladybird species of the Oriental region with a wide prey range (Omkar and Pervez 2004). It predares upon aphid, *Aphis gossypii* (Glover) (Omkar and James 2004) and could be a potential candidate for this aphid biocontrol (Pervez and Omkar 2005). It is a highly potential biocontrol agent in terms of foraging and feeding efficiency (Omkar and James 2003). Despite it being an important biocontrol agent of aphids, there is a dearth of information available on the structure of antennae, mouthparts and feeding habits of *C. transversalis*. However, its co-generic species, *Coccinella transversoguttata* Faldermann contains four chemo-sensitive sensillae, viz. sensilla chaetica, sensilla basiconica, sensilla styloconica and sensilla placoidea on the mouthparts, which are directly associated with prey-recognition and capturing (Hao et al. 2019a). Similarly, the seven sensillae on mouthparts of a ladybird, *Hippodamia variegata* (Goeze) provide ease in prey-location and prey-handling (Hao et al. 2019b). Such information on the functional morphology of mouthparts and antennal sensillae may provide an insight into the foraging and feeding mechanisms of the two co-generic *Coccinella* species.

Rogers and Simpson (1997) found that insects feeding on synthetic diets had a lesser number of sensillae than those feeding on natural foods, suggesting that sensillae had a major role in the foraging insects in terms of food location and identification. Thus, the aggregation and types of sensillae on the mouthparts are directly associated with feeding habits. Information regarding their arrangement on various mouthparts and antennae may provide a better understanding of their functions and utility in locating-prey and habitats along with their role in mate-location and reproduction. Such information on their functional morphology may provide an insight into the foraging and feeding mechanisms of *C. septempunctata* and *C. transversalis*, which will further be helpful in their utilization in biological control programme. Given this, we performed the scanning electron microscopy of mouthparts and antennae of males and females of both the above two co-generic *Coccinella* species, to identify

sex-dependent functional morphology of their mouthparts and antennal sensillae.

Materials and methods

Stock culture

Adults of *C. septempunctata* and *C. transversalis* were collected from Kashipur, Uttarakhand, India (29°2104'N, 78°9619'E) preying on aphid, *L. erysimi* infested on mustard (*Brassica campestris*) crops and aphid, *Aphis craccivora* (Koch) infested on cowpea (*Lablab purpureus* (L.) Sweet), respectively, and brought to the laboratory. The adults of the two co-generic species were sexually identified based on genitalia under the Stereoscopic Trinocular (*Lyzer*) at 40X and 100X magnifications connected to a personal computer (DELL). Thereafter, the adult male and female of each species were paired in Petri dishes (9.0 cm diameter × 2.0 cm height) consisting of a sufficient quantity of aphids (prey and host plant as above), which were placed in the Environmental Test Chamber (*REMI*, Remi Instruments) under constant abiotic conditions (27 ± 2 °C; 65 ± 5% RH; 14L: 10D). Adults mated and females laid eggs in clusters that were collected and reared from egg-hatch till adult emergence (space and food as above). The emerging F₁ adults were isolated in Petri dishes and reared on the above food for the next 20 days to attain sexual maturity, and were used for the scanning electron microphotography of mouthparts and antennae.

Scanning electron microscopy

We selected healthy 20-day-old adult males and females of the two co-generic ladybird species and anesthetized them by keeping cotton swabbed in 90% alcohol in their Petri dishes. Thereafter, the mouthparts and antennae were excised carefully using a microblade and microneedle while observing them under a Stereomicroscope (*Lieca S8APO*). We immersed the mouthparts and antennae in 10% KOH for an hour to clear the unwanted tissues from them. Thereafter, the mouthparts and antennae were dehydrated by treating them in the alcohol grades of 30%, 50%, 70%, 90%, and 100% concentration for 10 min. The processed body-parts were air-dried for 30 min at 30 °C and coated with a thin layer of gold by *Polaron SC 502* sputter coater. Thereafter, each mouthpart/ antenna was mounted on a stub consisting of double-sided sticky tapes and coated with the gold-palladium. We inserted the mouthpart/ antenna containing stub in the scanning electron microscope (Jeol JSM 5600) and, viewed and clicked microphotographs at different magnifications at 15 kV. We replicated this experiment six times (n = 6).

Statistical analyses

The morphometric analysis of the body lengths and widths of various mouthpart components, viz. labrum, maxillary palp, labium, clypeus along with antenna and flagellomeres of both the sexes of the two co-generic ladybird species were determined (in μm) using the scale mentioned on each scanning electron microphotograph. The lengths of certain sensillae were also measured using the scales mentioned in scanning electron microphotographs. The morphometric data of the two sexes of the ladybird species were compared by a two-sampled 't' test and the means were compared using Tukey's HSD test using statistical software, MINITAB 13.0 on the personal computer (DELL). The maxillary palp and labial palps were compared at three distinct levels of their body lengths, viz. proximal, middle and distal using Three-way ANOVA using "sex", "palp" and "distribution" as independent variables and 'body lengths' as a dependent variable using a statistical software SAS 9.0 (2002). The means were compared using Bonferroni (Dunn) Tests on SAS 9.0 (2002).

Results

Mouthparts and concomitant sensillae of the two co-generic ladybird species

Mouthparts of males and females of *C. septempunctata* (Fig. 1) and *C. transversalis* (Fig. 2) consisted of clypeus (CLP), mandible (MD), maxilla (MX), maxillary palp (MP), labium (LB), labial palp (LP) and labrum (LM). The body length ($t = -15.42$; $P < 0.0001$, d. f. = 9) and width ($t = -3.15$; $P = 0.012$, d. f. = 9) of labrum of *C. septempunctata* were significantly greater in the adult female than the male (Table 1). Similarly, its maxillary palp at proximal ($t = -3.25$; $P < 0.001$, d. f. = 7), middle ($t = -2.24$; $P < 0.05$, d. f. = 6) and distal ($t = -22.67$; $P < 0.0001$, d. f. = 6) ends, and the labial palp at the proximal ($t = -4.34$; $P < 0.01$, d. f. = 9) and middle ($t = -2.80$; $P < 0.023$, d. f. = 8) regions were significantly longer in the female. On the contrary, clypeus of adult male *C. septempunctata* was significantly greater in length than that of the adult female ($t = 3.10$; $P = 0.015$, d. f. = 8).

Fig. 1 Scanning Electron Microphotographs of the heads consisting of mouthparts of male and female *C. septempunctata*. (A) Dorsal view of Male; (B) Ventral view of Male; (C) Dorsal view of Female; (D) Ventral view of Female ladybird. CE- Compound eye; CLP – clypeus; AN – antenna; LR- labrum; MD – Mandible; MX- maxilla; MP- maxillary palp; LB- labium; LP- labial palp; (The circles show chemosensory field in the maxillary palp)

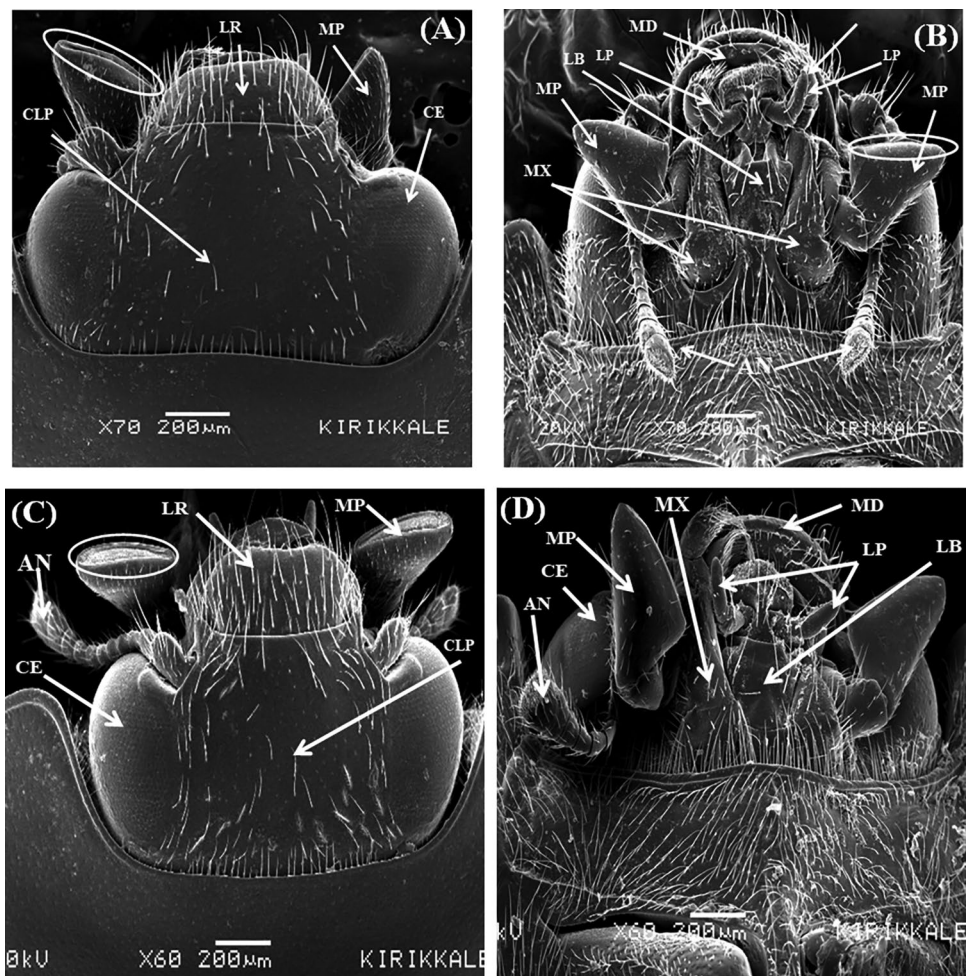
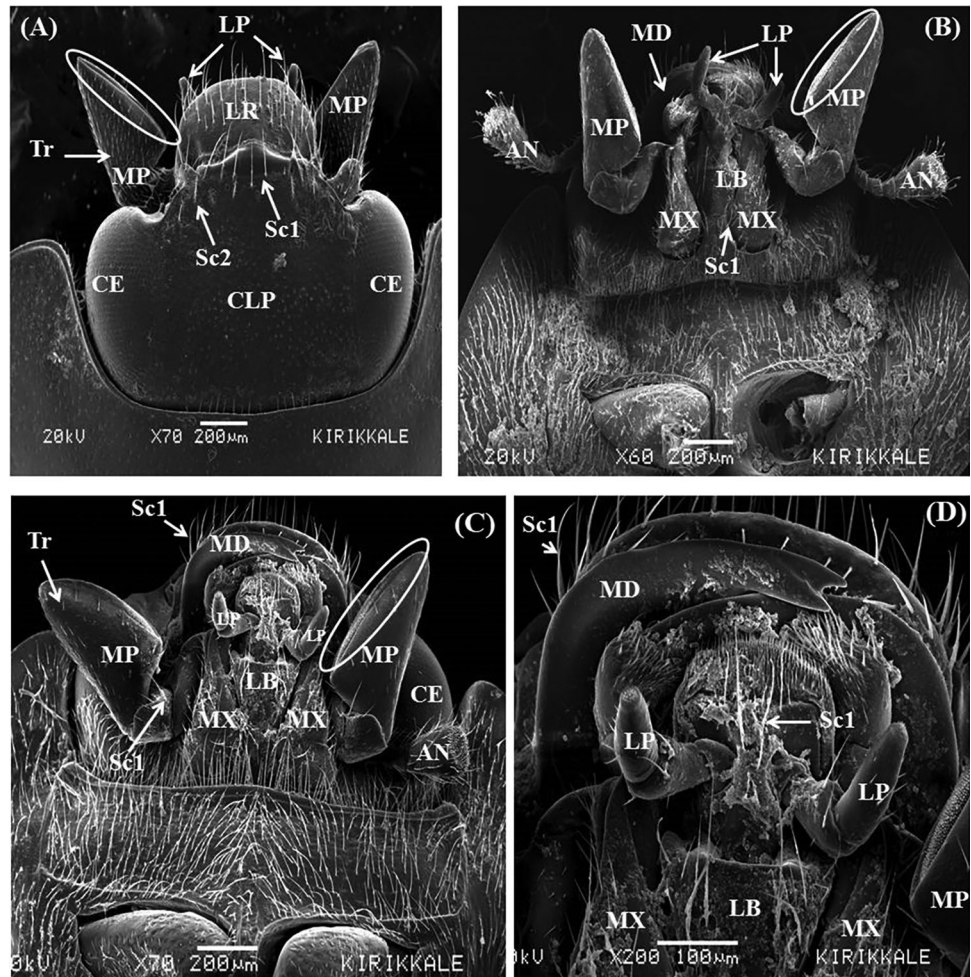


Fig. 2 Scanning Electron Microphotographs of the heads consisting of mouthparts of male and female *C. transversalis*. (A) Dorsal view of Male; (B) Ventral view of Male; (C) Ventral view; (D) Magnified ventral View. CE- Compound eye; CLP – clypeus; AN – antenna; LR- labrum; MD – Mandible; MX- maxilla; MP- maxillary palp; LB- labium; LP- labial palp; Sc-sensilla chaetica; Tr-sensilla trichoidea (The circles show chemosensory field in the maxillary palp)



The body lengths of clypeus ($t = -8.99$; $P < 0.001$; d. f. = 7), labrum ($t = -24.39$; $P < 0.0001$; d. f. = 7), maxillary palp at the proximal end ($t = -12.65$; $P < 0.0001$; d. f. = 8) along with its sensory field of adult male, *C. transversalis* were significantly lesser than those of its conspecific female (Table 2). Similarly, the width labrum ($t = -11.23$; $P < 0.0001$; d. f. = 8) and clypeus ($t = -16.76$; $P < 0.0001$; d. f. = 8) of adult male, *C. transversalis* were also significantly shorter than those of its conspecific female. On the contrary, middle part of maxillary palp ($t = 9.82$; $P < 0.0001$; d. f. = 7) along with proximal ($t = 2.51$; $P < 0.05$; d. f. = 8), middle ($t = 10.72$; $P < 0.0001$; d. f. = 9) and the distal ($t = 4.57$; $P < 0.01$; d. f. = 6) parts of labial palp of adult male, *C. transversalis* were significantly greater in length than that of the adult female.

The clypeus in males of *C. septempunctata* (Fig. 1) and *C. transversalis* (Fig. 2) had fewer sensilla chaetica at the distal region than that of females. Sensilla chaetica were the longest sensilla with thick wall and located mainly on the entire surface of labrum, maxillae and labium of both ladybird species (Figs. 3 and 4). Trichoidea (Tr) with slender and pointed tips were the second-longest sensilla in

both species. The proximal and middle segments of maxillary palps of the two species possessed both chaetica and trichoidea (Tr; 25–38 μm), while their distal segment has trichoidea in abundance with fewer chaetica. The chemosensory field of maxillary palp of *C. transversalis* had aggregation of sensilla basiconica (Ba) with blunt-tips and stout pegs. Sensilla styloconica (St) and placoidea (Pl) were found on the chemosensory region of the labial palps of both species. St appeared cylindrical and had blunt tips (Figs. 3 and 5). The labial palps of both species had sensillae, viz. chaetica (Sc), coeloconica (Co), campaniformia (Ca), placoidea (Pl), basiconica (Ba) and styloconica (St) (Figs. 2, 4, 5 and 6). At the periphery of the chemosensory field of labial palps of both species, there were sensillae placoidea (Pl) arranged in the form of a ring and an aggregation of sensillae basiconica (Ba; 1–2 μm) and styloconica (St; 2–4 μm) at the middle. Sensilla placoidea (Pl) appeared as sunken-plate like structures with a diameter of 1–3 μm (Figs. 4 and 6). The distal segments of labial palps of both species also had scattered sensilla campaniformia (Ca) and coeloconica (Co). Sensilla campaniformia appeared as dome shaped structures in a socket while sensilla coeloconica appeared as

Fig. 3 Scanning Electron Microphotographs of the heads exhibiting maxillary palps and chemosensory fields of (A) male and (B) female *C. septempunctata*. Labial palps and chemosensory fields of (C) male and (D) female *C. septempunctata*

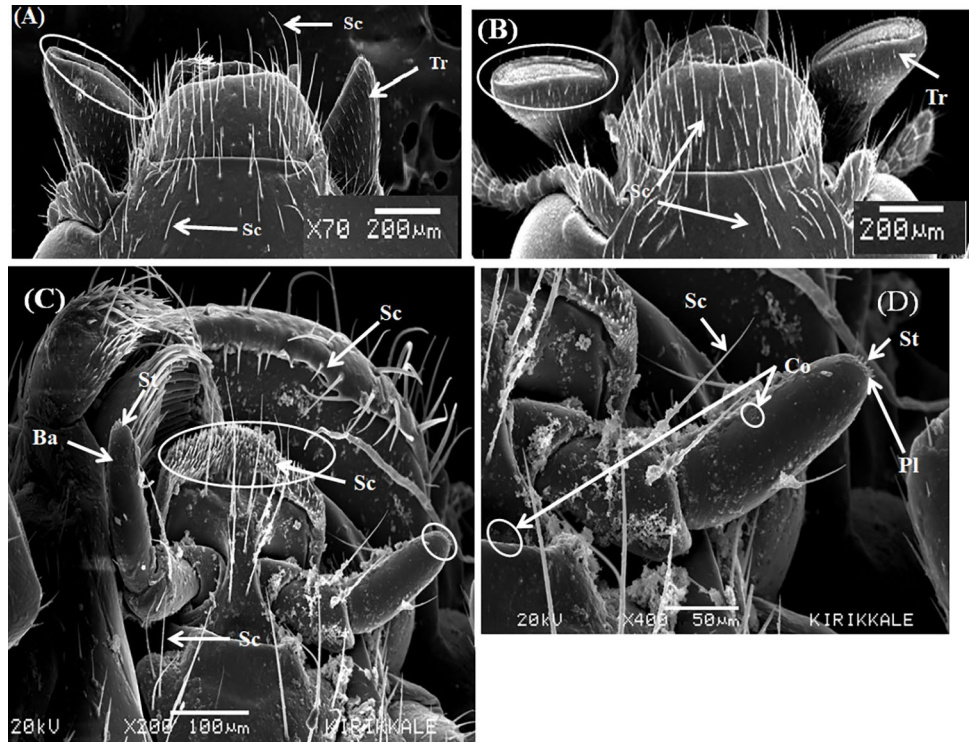


Fig. 4 Diagrammatic representation of various sensilla, viz. (a) Am = ampullacea, (b) Co = coeloconica, (c) Ca = campaniformia, (d) Pl = placoidea, (e) St = Styloconica, (f) Ba1 = basiconica 1, (g) Ba2 = basiconica 2, (h) Tr = trichoidea, and (i) Sc = chaetica

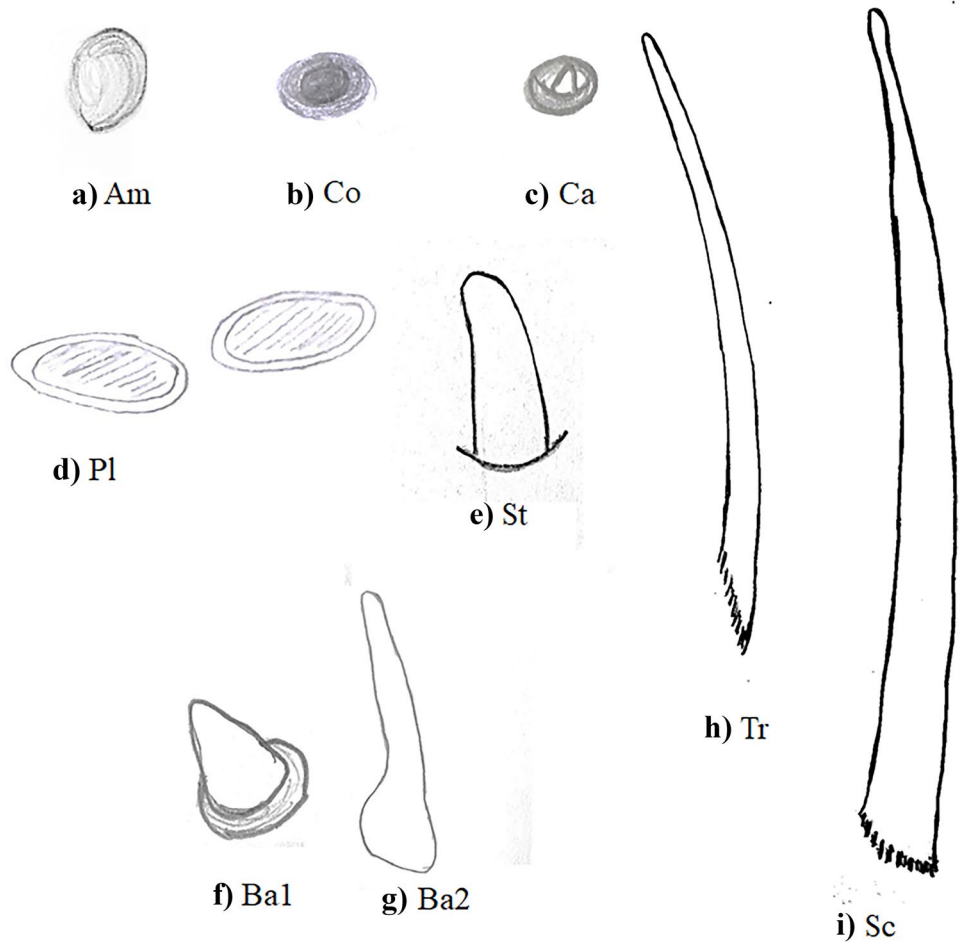
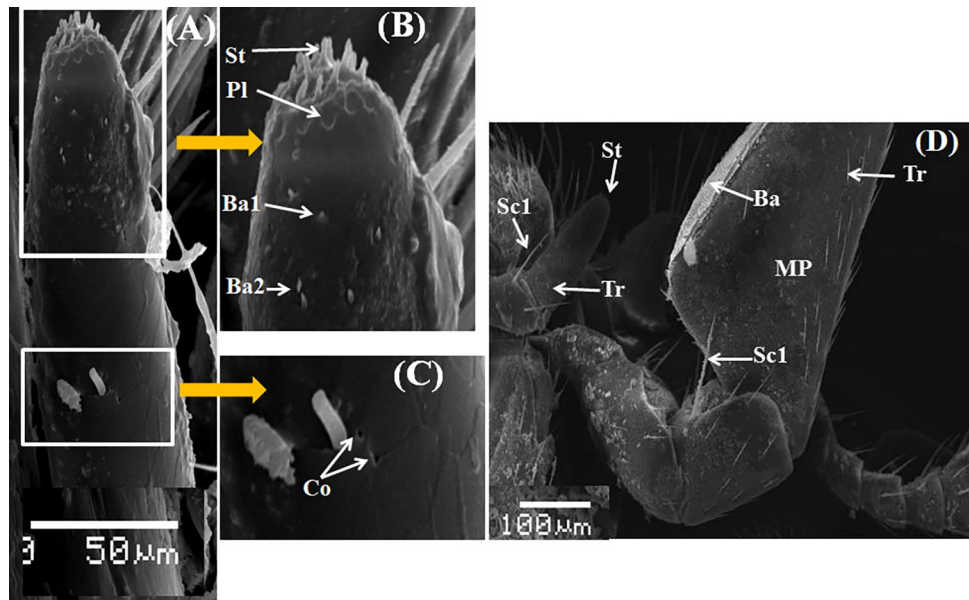


Fig. 5 Scanning Electron Microphotographs showing (A) different types of sensilla, viz. Pl=Placoidea, St=Styloconica, Ba1 & Ba2=Basiconica 1 & 2, and Co=Coeloconica on the labial palp of male *C. septempunctata*, (B) labial palp of male *C. septempunctata* showing Pl and St, and (C) labial palp of male *C. septempunctata* showing Co, (D) labial and maxillary palps of male *C. transversalis* showing sensilla St, Ba, Sc=chaetica and Tr=trichoidea

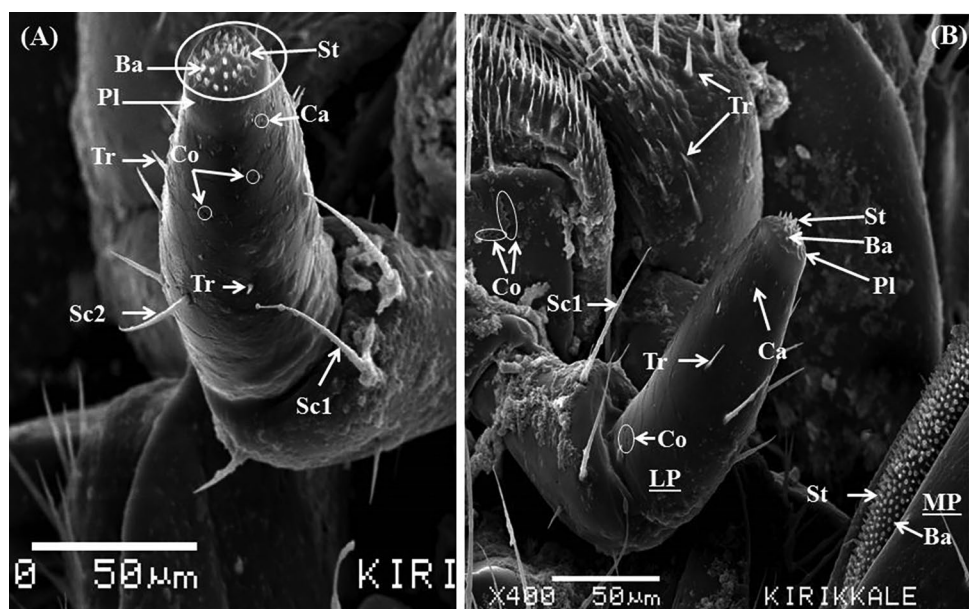


small pit-like structures resembling pores. Sensilla Tr were found only in labial palps of *C. transversalis*. A few chaetica (Sc1; 41–45 μm) were observed in the middle segment and some sensillae chaetica (Sc2; 19–25 μm) and trichoidea (Tr; 7–11 μm) in the distal segment of *C. transversalis*.

The maxillary palps of the two ladybird species were larger than labial palps with three distribution segments, viz. proximal, middle and distal. In *C. septempunctata*, the three-way ANOVA revealed significant main effects of “palp” ($F = 14,806.3$; $P < 0.0001$; d.f. = 1) and its “distribution” ($F = 8322.68$; $P < 0.0001$; d.f. = 2) on the body lengths. The

main effect of “sex”, however, was not significant ($F = 0.38$; $P = 0.53$; d. f. = 1). The interactions between “sex” \times “palp” ($F = 3.94$; $P < 0.05$; d. f. = 1), “sex” \times “distribution” ($F = 598.02$; $P < 0.0001$; d. f. = 2), “distribution” \times “palp” ($F = 3681.25$; $P < 0.0001$; d. f. = 2) and “sex” \times “palp” \times “distribution” ($F = 634.90$; $P < 0.0001$; d. f. = 2) were also found to be statistically significant. In *C. transversalis*, the three-way ANOVA revealed significant main effects of “sex” ($F = 36.69$; $P < 0.0001$; d.f. = 1), “palp” ($F = 40,879.7$; $P < 0.0001$; d.f. = 1) and its “distribution” ($F = 10,430.3$; $P < 0.0001$; d.f. = 2) on the body lengths. The interactions

Fig. 6 Sensilla on the palps of female *C. transversalis*. (A) Labial palp; (B) Labial and maxillary palps (The circle shows the chemosensory field in the labial palp)



Main Effects Plot - Data Means for LENGTH

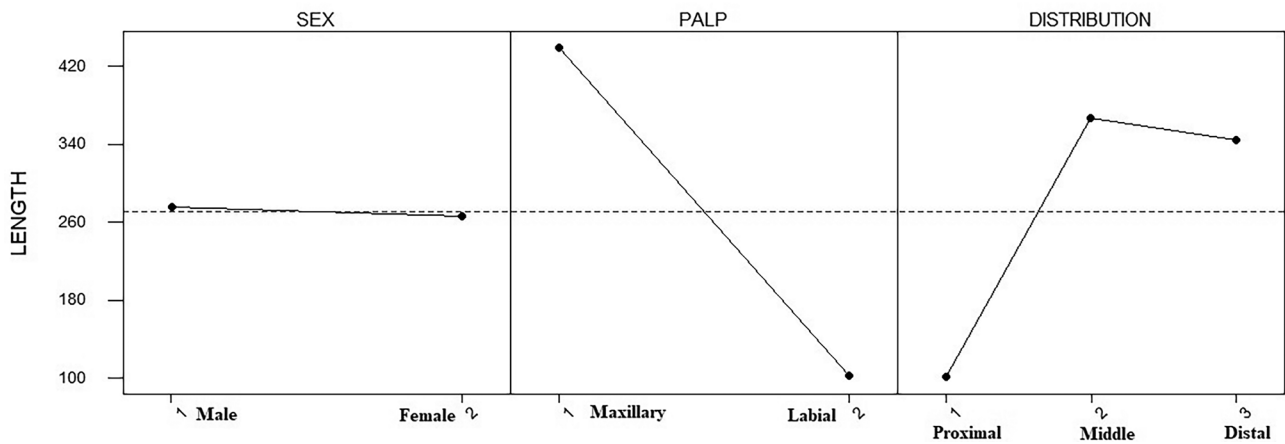


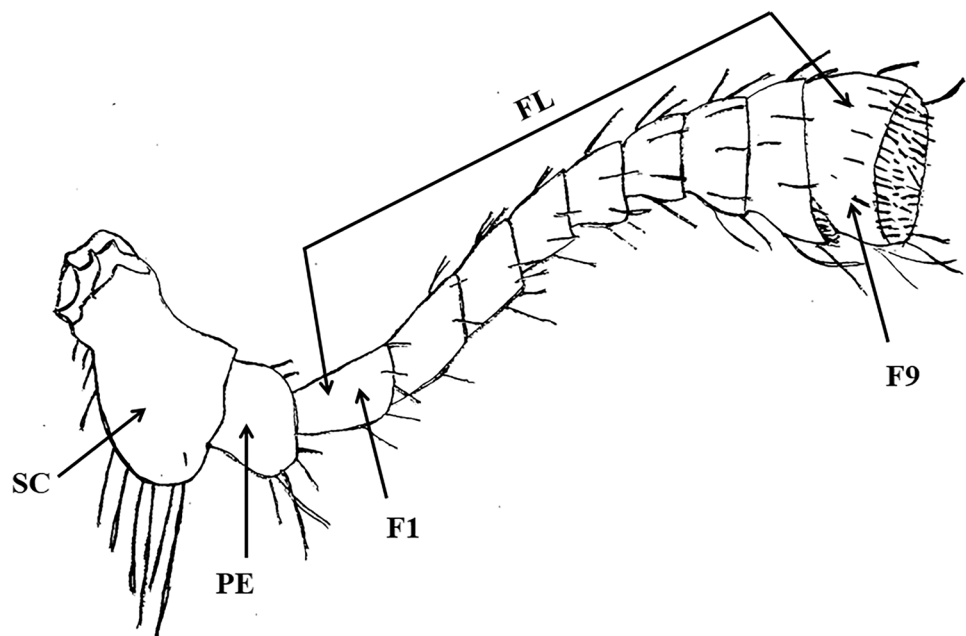
Fig. 7 Plot showing the main effects of sex, palp and distribution on the lengths of maxillary and labial palps of male and female, *C. transversalis*

between “sex” × “palp” ($F = 14.65$; $P < 0.0003$; $d.f. = 1$), “sex” × “distribution” ($F = 53.64$; $P < 0.0001$; $d.f. = 2$), “distribution” × “palp” ($F = 5517.25$; $P < 0.0001$; $d.f. = 2$) and “sex” × “palp” × “distribution” ($F = 108.60$; $P < 0.0001$; $d.f. = 2$) were also found to be statistically significant. These differences can be easily observed in the Main Effects Plot (Fig. 7). Within the ‘distribution’, the distal segment of the maxillary ‘palp’ of both the sexes of the two *Coccinella* species appeared more receptive as it contained aggregation of sensillae in the form of a chemosensory field at the terminal part.

Antennae and the concomitant sensillae of the two co-generic ladybird species

A pair of antennae, each comprised of a scape (SC), pedicel (PE) and nine segmented flagellum (FL) were found anterior to the compound eyes of both *Coccinella* species (Fig. 8). The scape ($t = 16.66$; $P < 0.0001$; $d.f. = 9$) and pedicel ($t = 9.74$; $P < 0.0001$; $d.f. = 9$) of adult male, *C. septempunctata* were significantly greater in length than those of female (Table 3). The flagellomeres F1 to F8 of male, *C. septempunctata* were significantly shorter ($P < 0.0001$) and

Fig. 8 Diagrammatic representation of a typical antenna of *Coccinella* showing various segments, viz. SC = Scape, PE = Pedicel, FL = Flagellum, and F1–F9 = nine flagellar segments



F9 was significantly greater ($t=7.38$; $P<0.001$; d. f. = 8) in length than those of its conspecific female. In *C. transversalis*, the scape ($t=-14.49$; $P<0.0001$; d. f. = 9) and pedicel ($t=-12.68$; $P<0.0001$; d. f. = 7) in the antenna of adult male was significantly shorter in length than that of female (Table 2). The proximal and distal regions of the scape and pedicel were broader in the female (Table 4). All the flagellomeres on the antenna of the male ladybird were significantly ($t=-20.43$; $P<0.0001$; d. f. = 5) shorter in length than those of the adult female. Thus, antennal lengths of adult males of *C. septempunctata* ($t=-3.80$; $P<0.01$; d. f. = 9) and *C. transversalis* ($t=-19.77$; $P<0.0001$; d. f. = 5) were significantly shorter than those of their conspecific adult females (Fig. 9).

Six and eight types of sensillae were found on the antennae of *C. septempunctata* and *C. transversalis*, respectively, viz. sensillae chaetica (Sc), trichoidea (Tr), basiconica (Ba), campaniformia (Ca), coeloconica (Co) and ampullacea (Am) in both species, while additional sensilla styloconica (St) and sporangia (Sp) in *C. transversalis*. Based on their lengths, various sensillae can be arranged in descending order as: $Sc > Tr > Ba > St > Sp > Ca$. Fewer Sc and Ca were found on the scapes of males and females of *C. septempunctata* (Fig. 10A, B) and *C. transversalis* (Fig. 10C, D). Two subtypes of chaetica, viz. Sc1 (63.64 μm) and Sc3 (21.28 μm) were present on the antennae of *C. transversalis*. It also contained 3–4 sensillae campaniformia. However, pedicel had only Sc2 (29.1 μm) and Sc3 (23.64 μm) (Fig. 10). The female antenna had numerous sensillae chaetica (Sc) and

two campaniformia (Ca) on the scape. Three subtypes of chaetica were observed on scape, viz. Sc1 (156.67 μm), Sc3 (33.33 μm) and Sc4 (13.33 μm). Sc4 were present as a group in the most proximal region of scape. However, the pedicel only had Sc2 (46.67 μm) and Sc3 (34.28 μm) (Fig. 10). The sensillae on F8 and F9 were in abundance more in number and diversity in both the species. Four and five types of sensillae were identified in the F8-F9 flagellomeres male and female, *C. septempunctata* respectively, while five and eight types of sensillae in those of male and female, *C. transversalis*, respectively.

1. **Sensilla chaetica (Sc):** These were the longest sensilla present on the entire antennae and the mouthparts of both ladybird species (Figs. 3 and 11). They possessed longitudinally arranged furrows and were of different sizes at the lateral and middle parts of each flagellomere. The lateral side of flagellomeres contain Sc of lengths 67.95 ± 0.9 and 86.61 ± 2.87 μm on male and female antennae of *C. septempunctata*, respectively ($t=-13.86$; $P<0.0001$; d. f. = 5). Their centre portions contain Sc of length 39.10 ± 0.90 and 61.61 ± 0.89 μm on male and female antennae, respectively ($t=-39.53$; $P<0.0001$; d. f. = 9). The antenna of the adult male, *C. transversalis* contained 10–12 Sc, primarily Sc1 (65–90 μm) and Sc2 (27–45 μm) on F9 (Fig. 7). Similarly, antenna of adult females of *C. transversalis* contained both Sc1 (90–95 μm) and Sc2 (37–47 μm) (Fig. 8). Sc1 and Sc2 were

Fig. 9 Morphology of antennae of adults of (A) Male and (B) Female, *C. septempunctata*, and (C) Male and (D) Female *Coccinella transversalis*

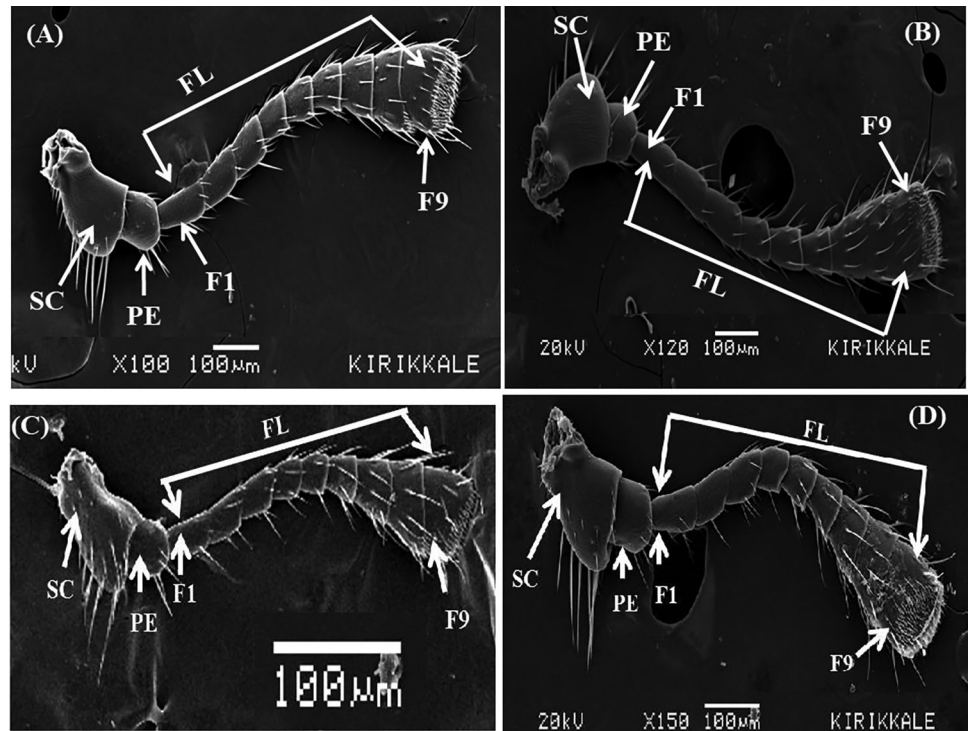
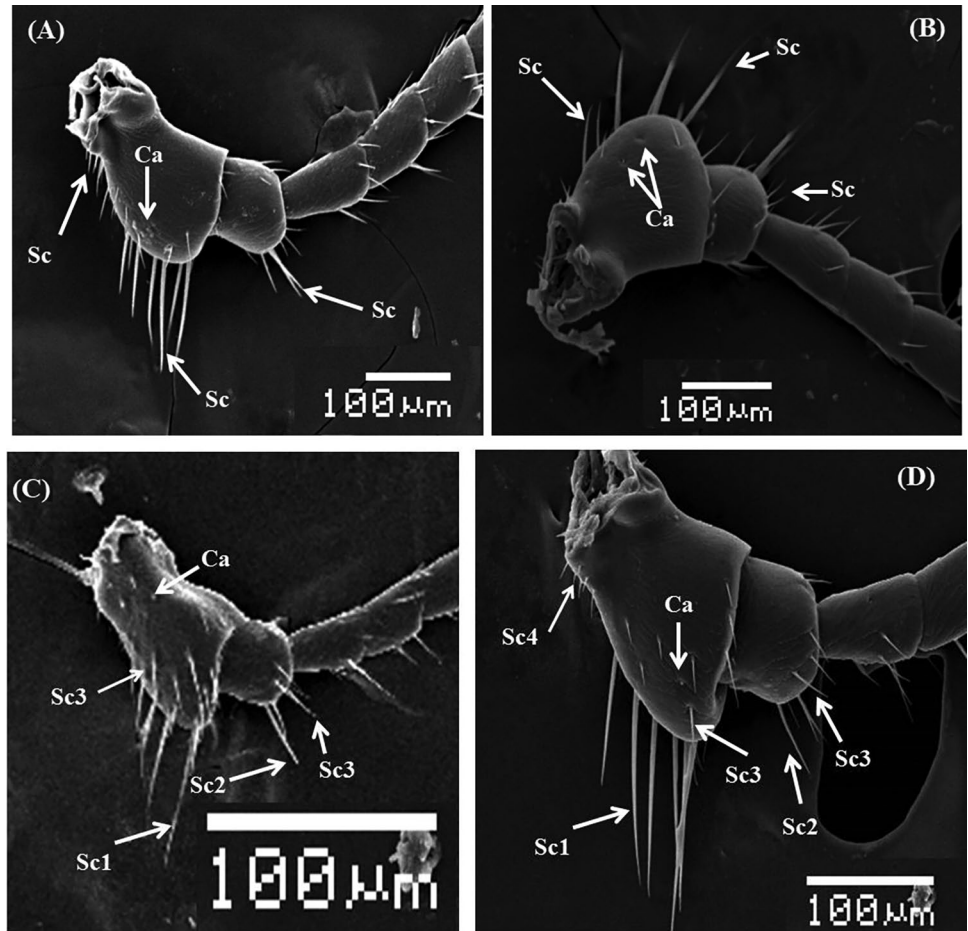


Fig. 10 Sensilla on scape and pedicel of (A) Male and (B) Female, *C. septempunctata*, and (C) Male and (D) Female, *C. transversalis*; Sc- sensilla chaetica; Ca-sensilla campaniformia



present in fewer numbers on F9 than the other sensillae but these are in high numbers on F1 to F8 (Fig. 12).

2. **Sensilla Trichoidea (Tr)**

Trichoidea was the second-longest sensilla located on F9 flagellomere in round concave sockets. They were slender hair-like structures, tapered from base to top, and were slightly longer and thinner than basiconica. Tr were

whirled at the circumference of the terminal surface of F9 (Fig. 11) and on the distal region of maxillary palp (Fig. 5) of both the sexes in *C. septempunctata*. The lengths of Tr were of 13.78 ± 1.72 and 23.21 ± 3.26 μm on male and female antennae, respectively ($t = -5.75$; $P < 0.001$; d. f. = 7). In males of *C. transversalis*, three types of Tr were identified, i.e. Tr1 (30–33 μm), Tr2

Fig. 11 Sensilla on F8-F9 flagellomeres of male (A) and female (B) *Coccinella septempunctata*. Sc- chaetica; Tr- trichoidea; Ba- basiconica; Co- coeloconicum; Am – ampullacea; The circle shows the congregation of sensilla at the F8-F9 junction

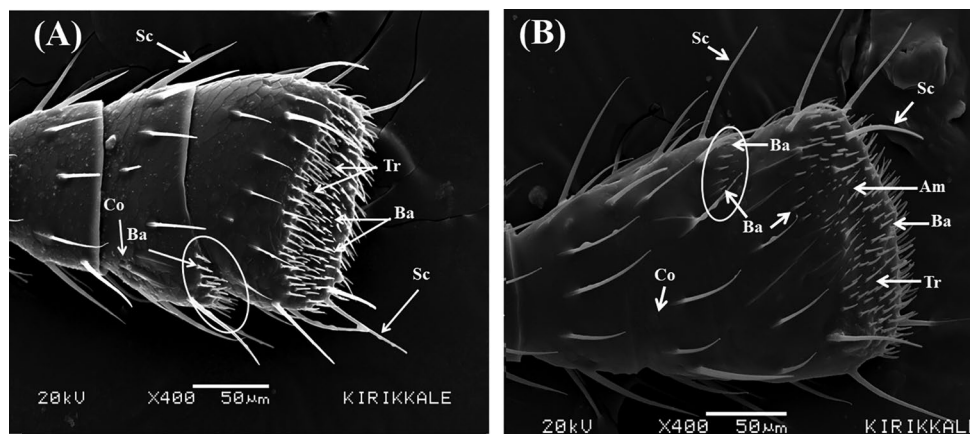


Fig. 12 Sensilla on distal flagellomeres of male (A) and female (B) *C. transversalis*. Sc- sensilla chaetica; Tr- sensilla trichoidea; Ba- sensilla basiconica; Co-sensilla coeloconicum; St-sensilla styloconicum; Ca-sensilla campaniformia; Am-sensilla ampullacea (The circle shows the congregation of sensilla at the F8-F9 junction)

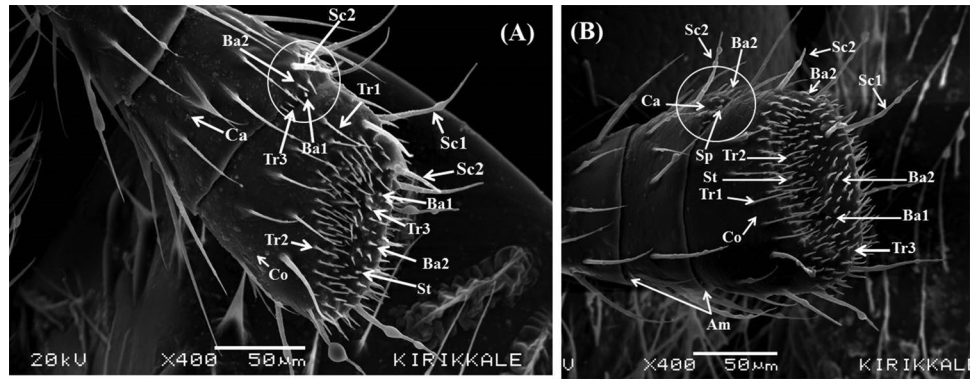


Table 1 Morphometric analysis of the mouthparts of male and female, *C. septempunctata*. The data (length and width) of various components is in μm, i.e. 10⁻⁶ m

Mouth parts	Dimension	Male	Female	t-value
Labrum	Length	234.2 ± 7.9	311.00 ± 7.9	t = -15.42; P < 0.0001, d.f. = 9
	Width	544.0 ± 11.3	565.0 ± 9.6	t = -3.15; P = 0.012, d.f. = 9
Maxillary Palp	Proximal	100.0 ± 11.9	133.5 ± 6.32	t = -3.25; P < 0.01, d.f. = 7
	Middle	153.7 ± 3.5	162.8 ± 8.5	t = -2.24; P < 0.05, d.f. = 6
	Distal	524.7 ± 5.1	675.0 ± 14.5	t = -22.67; P < 0.0001, d.f. = 6
Labial Palp	Proximal	35.7 ± 1.6	41.0 ± 2.2	t = -4.34; P < 0.01, d.f. = 9
	Middle	96.2 ± 6.1	104.5 ± 4.1	t = -2.80; P < 0.023, d.f. = 8
	Distal	162.2 ± 3.9	162.3 ± 8.8	t = -0.04; P = 0.97, d.f. = 6
Clypeus	Length	900.2 ± 10.4	877.3 ± 14.8	t = 3.10; P = 0.015, d.f. = 8
	Width	777.2 ± 18.9	777.8 ± 15.9	t = -0.07; P = 0.95, d.f. = 9

Data is Mean ± S.D

(9–12 μm) and Tr3 (5–7 μm) (Fig. 12). A whirl of Tr, particularly that of Tr2, was found at the circumference of the terminal surface of F9 antennal segment of adult male. Tr3 were found at the centre of the F9 along with basiconica (Ba) and styloconica (St). The antenna of adult female contained, three types of Tr on F9 flagellomere. Sensilla Tr1 (32–35 μm) were present at the periphery of F9, followed by Tr2 (15–17 μm) and Tr3 (5–10 μm) towards the centre (Fig. 12).

3. Sensilla Basiconica (Ba)

Sensilla basiconica appeared as stout peg-like structure that was broader and thicker than Tr and lied at an angle of 50°–70° to the antennal axis. The sensillae Ba were of 8.65 ± 0.78 and 10.12 ± 0.84 μm (t = -2.84; P = 0.019; d. f. = 9) on male and female antennae of *C. septempunctata*, respectively on the distal-most surface of F9 (Fig. 11). These were also congregated at the lateral juncture point of F8 and F8 in both sexes. In males

Table 2 Morphometric analysis of the mouthparts of male and female, *C. transversalis*. The data (length and width) of various components is in μm, i.e. 10⁻⁶ m

Mouth parts	Dimension	Male	Female	t-value
Labrum	Length	265.0 ± 5.0	361.5 ± 2.5	t = -24.39; P < 0.0001, d.f. = 7
	Width	563.0 ± 17.0	637.0 ± 8.5	t = -11.23; P < 0.0001, d.f. = 8
Maxillary Palp	Proximal	236.7 ± 7.4	304.2 ± 9.6	t = -12.65; P < 0.0001, d.f. = 8
	Middle	193.0 ± 7.0	132.5 ± 13.6	t = 9.82; P < 0.0001, d.f. = 7
	Distal	637.7 ± 4.1	650.0 ± 6.5	t = -2.51; P < 0.05, d.f. = 6
	Sensory Field	493.8 ± 0.8	530.8 ± 8.3	t = -9.82; P < 0.0001, d.f. = 5
Labial Palp	Proximal	41.2 ± 2.0	37.0 ± 2.3	t = 2.51; P < 0.05, d.f. = 8
	Middle	104.7 ± 3.6	76.7 ± 5.5	t = 10.72; P < 0.0001, d.f. = 9
	Distal	185.3 ± 3.6	168.0 ± 9.4	t = 4.57; P < 0.01, d.f. = 6
	Sensory Field	25.5 ± 1.7	33.0 ± 0.8	t = -10.43; P < 0.0001, d.f. = 8
Clypeus	Length	1142.5 ± 24.6	1401.7 ± 69.5	t = -8.99; P < 0.001, d.f. = 7
	Width	802.7 ± 12.3	957.5 ± 14.4	t = -16.76 P < 0.0001, d.f. = 8

Data is Mean ± S.D

Table 3 Lengths and widths of various antennal segments of adult male and female of *C. septempunctata*. The data (length and width) of various components is in μm , i.e. 10^{-6} m

	Male			Female			T-test*
	Length (μm)	Width (μm)		Length (μm)	Width (μm)		
		Proximal	Distal		Proximal	Distal	
Scape	199.8±3.53	105.31±2.36	89.2±3.20	157.7±4.42	126.3±5.50	184.2±5.23	t = 16.66; P < 0.0001; d.f. = 9
Pedicel	78.8±2.48	100.0±3.0	110.5±4.25	63.2±2.61	121.1±4.5	115.8±6.15	t = 9.74; P < 0.0001; d.f. = 9
F1	105.2±6.47	52.6±1.76	68.4±3.25	115.7±5.28	47.3±2.14	73.9±2.50	t = -2.81; P < 0.05; d.f. = 9
F2	63.5±2.57	68.4±3.75	78.9±6.52	84.3±3.09	68.4±3.20	78.9±6.40	t = -11.60; P < 0.0001; d.f. = 9
F3	73.5±4.43	73.7±3.30	84.21±5.40	100.0±6.22	68.4±3.20	78.9±6.40	t = -7.76; P < 0.0001; d.f. = 9
F4	63.7±2.62	63.2±2.45	84.21±5.40	73.7±3.68	68.4±3.20	84.2±3.50	t = -4.95; P < 0.001; d.f. = 9
F5	57.8±1.07	68.4±1.80	84.21±5.40	73.7±3.69	63.1±2.15	84.2±5.45	t = -9.24; P < 0.0001; d.f. = 5
F6	57.3±1.37	63.2±2.45	105.3±5.50	68.5±2.63	63.1±2.80	94.7±4.50	t = -8.41; P < 0.0001; d.f. = 9
F7	68.3±2.05	89.5±2.90	110.5±5.35	68.5±2.63	84.2±4.50	136.8±5.65	t = -0.12; P = 0.905; d.f. = 9
F8	57.8±1.67	136.8±5.25	178.9±5.85	68.4±2.62	136.8±5.40	178.9±485	t = -7.65; P < 0.0001; d.f. = 8
F9	78.8±2.48	173.9±6.00	184.2±5.65	63.3±3.99	178.9±6.25	189.5±6.30	t = 7.38; P < 0.001; d.f. = 8
Flagellum length	626.0±9.95			716.2±10.02			t = -14.28; P < 0.0001; d.f. = 9
Total length of antenna	904.7±13.08			937.0±13.8			t = -3.80; P < 0.01; d.f. = 9

The data are Mean ± S.D

*Only the lengths of various antennal components of adult male and female, *C. septempunctata* were subjected to t-test

of *C. transversalis*, three types of Ba were identified on the distal-most surface of F9, viz. Ba1 (1.16 μm), Ba2 (2.33 μm) and Ba3 (5.81 μm). They lied at the centre of the whirl formed by Tr and St at the terminal surface of F9 (Fig. 12). The adult females of *C. transversalis* contained numerous Ba1 (3–4 μm) and Ba2 (8–10 μm) at

the distal region of F9 distributed intermittently between Tr (Fig. 12).

4. **Sensilla Campaniformia (Ca)**

Sensilla campaniformia appear as a knob-like, dome-shaped structure at the centre with a circular depression. A few Ca were found on the scapes of adult male

Table 4 Lengths and widths of various antennal segments of adult male and female of *C. transversalis*. The data (length and width) of various components is in μm , i.e. 10^{-6} m

	Male			Female			T-test*
	Length (μm)	Width (μm)		Length (μm)	Width (μm)		
		Proximal	Distal		Proximal	Distal	
Scape	103.2±3.24	62.1±1.65	86.2±3.20	137.5±4.19	93.1±3.21	155.2±4.25	t = -14.49; P < 0.0001; d.f. = 9
Pedicel	52.0±1.29	51.7±3.50	44.8±2.25	68.8±2.67	100.0±4.25	100.0±4.15	t = -12.68; P < 0.0001; d.f. = 7
F1	54.3±2.87	24.1±1.76	34.5±1.86	82.5±2.92	44.8±2.14	62.1±2.50	t = -15.36; P < 0.0001; d.f. = 9
F2	41.8±2.54	34.5±2.55	41.4±2.42	59.4±3.00	58.6±2.20	62.1±2.40	t = -10.00; P < 0.0001; d.f. = 9
F3	45.50±2.50	31.0±2.30	41.4±3.40	60.1±3.05	55.2±2.75	69.0±2.75	t = -8.27; P < 0.0001; d.f. = 9
F4	34.5±2.43	31.0±1.45	38.0±1.15	41.1±2.28	62.0±2.80	62.0±2.90	t = -4.63; P < 0.0001; d.f. = 9
F5	31.0±2.16	31.0±1.50	38.0±2.20	55.4±2.05	48.3±2.15	58.6±2.20	t = -18.27; P < 0.0001; d.f. = 9
F6	37.2±2.54	31.0±1.25	44.8±1.50	59.4±2.24	51.7±2.40	72.4±2.50	t = -14.70; P < 0.0001; d.f. = 9
F7	41.7±2.29	44.8±2.40	65.0±4.35	62.1±1.86	69.0±3.15	100.0±2.50	t = -10.25; P < 0.0001; d.f. = 9
F8	41.3±2.29	62.0±2.52	82.8±2.85	55.4±1.70	103.5±4.40	131.0±4.90	t = -11.01; P < 0.0001; d.f. = 9
F9	41.3±0.94	82.8±3.00	82.8±2.75	55.2±2.41	131.0±4.25	131.0±2.50	t = -11.97; P < 0.0001; d.f. = 6
Total length of antenna	523.8±4.98			730.2±22.0			t = -20.43; P < 0.0001; d.f. = 5
Flagellar Length	368.7±4.19			523.9±17.1			t = 19.77; P < 0.0001; d.f. = 5

The data are Mean ± S.D

*Only the lengths of various antennal components of adult male and female, *C. transversalis* were subjected to t-test

and female, *C. septempunctata* (Fig. 10), while a single Ca was found in the congregation of sensillae between F8-F9 junction of adult female (Fig. 12), and one on F8 flagellomere of the adult male, *C. transversalis* (Fig. 12).

5. Sensilla Coeloconicum (Co)

Both male and female antennae had a single pore-like tiny aperture-shaped sensillum coeloconicum (Co) on F8 of *C. septempunctata* (Fig. 11), and on F9 flagellomere of *C. transversalis* (Figs. 12).

6. Sensilla ampullacea (Am)

Sensilla ampullacea appeared as large apertures. A single Am (diameter 1–3 μm) was found on the terminal portion of F9 of the adult female, *C. septempunctata* (Fig. 11), while male lacks it. Two Am (diameter 1–3 μm), one each at the junction between F7-F8 and F8-F9 were present only on the antenna of adult females of *C. transversalis* (Fig. 12). However, no Am was found on the antenna of the adult male.

7. Sensilla Styloconica (St)

The antenna of the adult female, *C. transversalis* contained a few sensillae styloconica (3–6 μm) distributed between Tr and Ba at the terminal region of F9 (Fig. 12). However, the male antenna had only one St.

8. Sensilla Sporangia (Sp)

Sensilla sporangia appeared as pole-shaped with a bulbous top as in sporangium. Two Sp (1–3 μm) were present at the F8-F9 junction on the antenna of the adult female, *C. transversalis* while the adult male antenna had none (Fig. 12).

Discussion

The results revealed that mouthparts of the two ladybird species consisted of mandible, maxilla, maxillary palp, labium, labial palp and labrum. Significant sexual dimorphism was evident comparing the morphometric analysis of the mouthparts of both the species, as adult females had bigger mouth parts, viz. labrum, clypeus, maxillary palps along with their sensory fields. Generally, adult females are bigger than males in body size (Yasuda and Dixon 2002), therefore their labrum and labial palps are bigger, which may ease foraging, prey-holding and capturing. The females need abundant aphids to meet out energy demands for reproduction. We found a dense aggregation of sensilla chaetica particularly on the dorsal side of labrum and clypeus of female *C. septempunctata*. Chaetica are primarily mechanoreceptors, which enable prey-recognition in insects, particularly ladybirds (Broeckling and Salom 2003), which suggests that adult females are more voracious than males. This is probably due to greater food demand for egg production and oviposition. Both the ladybird species

had bifid tipped mandibles with two teeth at the distal incisor region (Samways et al. 1997).

Significant main effects of “palp” and its “distribution” in both the species on the body length revealed that both maxillary and labial palps differed in size and distribution. Maxillary palps had a major role in holding the prey than the labial ones. They were significantly greater in length than the labial palps making the latter to be secondary or accessory palps. The distal region of the maxillary palps was more than twice in length than proximal and middle regions in both species. This enlargement of the distal region of the maxillary palp provides a strong grip to hold the prey. The distal region of labial palp, though much shorter than that of the maxillary palp, was significantly greater in length than the middle and the proximal regions of the labial palp. This distal region of the labial palp provides initial support to hold the prey, while consuming it. The prey was further gripped by the distal regions of maxillary palps before it is properly consumed. Yan et al. (1987) reported 1500 sensilla basiconica on the inner lateral surface of the distal segment of maxillary palp, and about half the number on the labial palps of *C. septempunctata*. Basiconica seemed to be gustatory in function and helped in food detection when adult ladybirds encounter aphids or any artificial diet (Yan et al. 1987). However, the sensilla of both maxillary- and labial-palps behave differently, as during feeding maxillary palps are lifted aloft in the air, whereas labial palps directly contact the food. Thus, maxillary palps seem to detect food, while labial palps regulate the food intake during feeding. The significant main effect of “sex” on the body length of *C. transversalis* revealed that females were bigger than males. The female had much larger maxillary and labial palps making her more equipped to hold and consume prey. This makes her a highly formidable aphid-predator and an attacker of other heterospecific predators in intraguild combat. We found more variety of sensillae, including basiconica, on the distal ends of maxillary palps of the adult males of both species. This indicates that either adult males may better perceive the prey quality or these sensillae aid them in mate-recognition and courtship during mating.

The distal region of maxillary palps in both ladybird species possessed an abundance of trichoidea followed by chaetica. Their sensillae are largely involved in thigmo-reception, which provides basic identification of the prey-types. Strong aggregation of various sensillae in the form of a chemosensory field was found on the terminal end of the distal region of both maxillary and labial fields, which seems highly sensitive to different prey-types. This is similar to the chemosensory field of F9 flagellomere of the antenna. Trichoidea seems to be more sensitive in perceiving the fine details of the prey. A dense aggregation on the distal segment of maxillary palp indicates that a predator, particularly an adult

female further recognizes its prey while touching and holding it. This may enhance its foraging efficiency and probably help in prey specialization. Brožek and Chlond (2010) proposed the mechano-sensory function of trichoidea. Congregation of *Harmonia axyridis* (Pallas) is perhaps linked with trichoidea mediated-pheromone reception (Chi et al. 2009). Six common types of sensillae, viz. Sc, Co, Ca, Pl, Ba and St, were found on labial palps of both the ladybird species making these palps highly sensory for the final intake of prey. These sensillae further assist in identifying food. Sensillae styloconica at the terminal ends of labial palps are associated with the olfactory and gustatory function (Lopes et al. 2002). This quantitative and qualitative sensillae diversity on the mouthparts enhances the predatory capabilities of adult females, and perhaps polyphagy, as *C. septempunctata* has a wide prey-range including a variety of aphids, scale-insects, and mealybugs (Omkar and Pervez 2004). Wang et al. (2020) also suggested that morphological disparity of the mouthparts and sensillae in insects is directly associated with the evolution of polyphagy and feeding specialization.

We found sexual dimorphism in terms of the length of the antenna and its components, which were shorter in length in male ladybirds than those on adult females. This agrees with the previous findings on *C. septempunctata* (Srivastava and Omkar 2003). However, the female antenna of *Hippodamia variegata* (Goeze) was slightly shorter in length than that of males (Hao et al. 2020). We found that both the scape and pedicel of male ladybirds of *C. septempunctata* were greater in length than those of females. This seemingly contradicts previous findings on *C. septempunctata* (Srivastava and Omkar 2003) and other ladybird species (Omkar and Pervez 2008; Chi et al. 2009), where male antennal segments were shorter in size. The antennal morphology of the two ladybird species resembles that of other coccinellid species in terms of nine flagellomeres (Jourdan et al. 1995; Chi et al. 2009; Ping et al. 2013; Hao et al. 2020), except for *Cryptolaemus montrouzieri* Mulsant (8 flagellomeres) (Liu et al. 2013) and *Pseudoscymnus tsugae* Sasaji and McClure (7 flagellomeres) (Broeckling and Salom 2003).

We identified six and eight types of antennal sensillae in *C. septempunctata* and *C. transversalis*, respectively. Five different sensillae had been reported in *Semiadalia undecimnotata* Schn. (Jourdan et al. 1995), followed by seven in *H. axyridis* (Chi et al. 2009) and *C. montrouzieri* (Ping et al. 2013), and eight in *C. septempunctata* (Srivastava and Omkar 2003). The antennal sensillae, viz. Sc, Tr and Ba were greater in lengths on female antenna exhibiting sensilla-dependent sexual dimorphism in *C. septempunctata*. Chaetica was the longest antennal sensilla of *C. septempunctata*, which was greater in length towards the lateral side of flagellomere than towards centre and have mechanoreceptive function, which is perhaps mate-recognition. It was found

that adult male *P. dissecta* (Omkar and Pervez 2005) and *H. axyridis* (Obata 1987) examined their mates by touching their body and antenna with their antennae. However, it is also chemoreceptive in the case of cabbage stem flea beetle, *Psylliodes chrysocephala* (L.) (Isidoro et al. 1998). It is sometimes mistaken with sensilla trichoidea due to similar morphology (Zhu et al. 2019). Trichoidea are the second-largest sensilla in terms of length and is commonly found in most ladybirds on the F9 flagellomere of the antenna (Hamilton et al. 1999; Omkar and Pervez 2008; Chi et al. 2009). Young males examine the female partners by touching them with F9 (Obata 1987; Omkar and Pervez 2005). The mechano-sensory function of Tr had been earlier proposed (Brožek and Chlond 2010). Aggregative behaviour of *H. axyridis* seems to be linked with Tr mediated-pheromone reception (Chi et al. 2009). The ladybird, *Hippodamia convergens* Guérin-Méneville failed to respond to odours after the removal of sensilla trichoidea, which suggests their potential role in long-distance olfactory reception. However, they are perhaps responsible for mass aggregation in *H. axyridis* (Chi et al. 2009).

Basiconica is conspicuous and the third-most abundant sensilla on the antennae of adults of the two species, as also reported in other ladybird species (Jourdan et al. 1995; Srivastava and Omkar 2003; Chi et al. 2009; Ping et al. 2013). Ba is associated with chemoreception of female sex-pheromones, thereby enabling long-distance mate search and mate-recognition. Jourdan et al. (1995) found a greater number of Ba on the antenna of male *S. undecimnotata*. A high number of Ba on the antenna of male, *Leptura arcuata* Panzer and *Leptura aethiops* Poda (Coleoptera: Cerambycidae) further supports its role in sex-pheromones reception during mate-search (Zhang et al. 2011). Ba was also surmised to have thermo- and hygro-sensory-receptive functions (Bartlet et al. 1999; Steinbrecht 1989). Rondoni et al. (2021) raised the possibility of Ba associated with CO₂ perception, and to enable ladybirds to locate both prey and mate, as also by mosquitoes who are attracted towards breathing mammals. Jourdan et al. (1995) found 40 Böhm sensillae on scape and pedicel of *S. undecimnotata*, which they assumed to be for proprioception. Similar observations were also noted on *H. axyridis* (Chi et al. 2009). However, we didn't find Böhm sensilla on the antennae of the two *Coccinella* species. These appear to be like miniaturized chaetica, which are hair-like and are found opposite to the intersegmental membrane and are often confused with chaetica, trichoidea and basiconica. Ping et al. (2013) reported perforated-cavity like sensilla auriciliica on the scape of a ladybird, *Cryptolaemus montrouzieri* Mulsant. However, Srivastava and Omkar (2003) found sensilla scolopalialia on F9 of *C. septempunctata*, which is similar to basiconica in size but tapered from the base.

A single coeloconicum on male and female antennae of the two ladybird species is known for hygro- and thermo-reception (Ruchty et al. 2009). Sensilla coeloconica may also perceive water vapours, carbon-dioxide and temperature changes (Hao et al. 2020). A single sensillum campaniformia was found on F8 of antenna of males and females of *transversalis*. Ca is responsible for proprio-reception (Meng and Qin 2017) and a probable gustatory function (Ochieng et al. 2000). The terminal portion of F9 had a single sensillum ampullacea on the female antenna of both the species, which seemingly is associated with the detection of CO₂ concentration (Kleineidam et al. 2000). Sensilla sporangium was found only on female F9 flagellomere, thereby showing sexual dimorphism, as it was not found on the male antenna of *transversalis*.

The evolutionary significance of the diversity of sensillae on ladybirds' mouthparts and antennae, despite their critical roles, has been poorly understood. However, it is likely that larger body-parts including antennae may support greater number and diversity of sensillae. Hence, adult females of both *Coccinella* species, due to larger body-size, were better predators in terms of perceiving the odours and locating prey-habitats. This explains why sensilla sporangium was found only on female antenna and were lacking in males' antennae. Furthermore, greater number of styloconica were identified on female antenna than that of male. The differences in antennal sensillae of the two ladybird species may possibly be due to the cosmopolitan nature of *C. septempunctata* and localized distribution of *C. transversalis* in the Oriental region. This is supported by the fact that *C. septempunctata* is a dominant species in agroecosystems with a much wider prey-range than *C. transversalis* (Omkar and Pervez 2004).

It is concluded that (i) sexual dimorphism was evident, as female ladybirds had bigger mouth parts, viz. labrum, clypeus, maxillary and labial palps along with their larger sensory field, (ii) mandibles were present with a bifid tip, (iii) females had larger maxillary and labial palps for better gripping and consuming prey, (iv.) maxillary palps were the main organs to hold the prey, (v) distal region of maxillary palps provides a template for holding prey, (vi.) there is a strong aggregation of various sensillae in the form of a chemosensory field at the terminal end of the distal region of both maxillary and labial fields, (vii) male antennae of the two species had shorter antennal and flagellar length than those of adult females, (viii) six and eight types of sensillae were identified on the antennae of *C. septempunctata* and *C. transversalis*, which are largely involved in chemo-, thermo-, proprio-, mechano- and thigmo-reception. However, more morphological investigations are needed, to conclusively address the question of the precise role of the sensillae present on the mouthparts and antennae of the two ladybird species.

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Declarations

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