Ann. soc. entomol. Fr. (n.s.), 2011, 47 (1–2) : 119-127 ARTICLE

Sensilla on antennae, ovipositor and tarsi of the larval parasitoids, *Cotesia sesamiae* (Cameron 1906) and *Cotesia flavipes* Cameron 1891 (Hymenoptera: Braconidae): a comparative scanning electron microscopy study

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Abstract. Two braconid parasitoids of cereal stemborers in eastern Africa, *Cotesia sesamiae* and *Cotesia flavipes*, have been shown to display a similar hierarchy of behavioural events during host recognition and acceptance. In order to understand the mechanisms underlying host recognition and acceptance, the morphology of antennal sensilla on the last antennomeres, on the ovipositor, and on the fifth tarsomere and pretarsus of the prothoracic legs tarsi were studied using scanning electron microscopy followed by selective silver nitrate staining. It appeared that female *C. sesamiae* and *C. flavipes* shared the same types and distribution of sensory receptors, which enable them to detect volatiles and contact chemical stimuli from their hosts. In both parasitoids, four types of sensilla were identified on the three terminal antennomeres: (i) non-porous sensilla trichodea likely to be involved in mechanoreception, (ii) uniporous sensilla chaetica with porous tips that have gustatory functions, (iii) multiporous sensilla placodea, which are likely to have olfactory function, and (iv) sensilla coeloconica known to have thermo-hygroreceptive function. The tarsi of both parasitoids possessed a few uniporous sensilla chaetica with porous tips, which may have gustatory functions. The distal end of the ovipositor bore numerous dome-shaped sensilla. However, there were no sensilla coeloconica or styloconica, known to have gustatory function in other parasitoid species, on the ovipositors of the two braconid wasps.

Résumé. Sensilles des antennes, de l'ovipositeur et des pattes de deux espèces de parasitoïde larvaire, *Cotesia sesamiae* (Cameron 1906) and *Cotesia flavipes* Cameron 1891 (Hymenoptera : Braconidae) : une étude comparative en microscopie électronique à balayage. Deux espèces proches de guêpes parasitoïdes, *Cotesia sesamiae* et *Cotesia flavipes,* présentent une similarité dans la hiérarchie des étapes comportementales associées à la reconnaissance et à l'acceptation de l'hôte. Afin de développer des bases solides de recherche sur les mécanismes impliqués dans la reconnaissance et l'acceptation de l'hôte par ces deux espèces de parasitoïde, nous avons décrit la morphologie des sensilles situées sur les antennes (les derniers segments), l'ovipositeur et les tarses (le cinquième tarsomère et le prétarse des pattes antérieures). Des observations en microscopie électronique à balayage ont été menées et complétées par une coloration sélective au nitrate d'argent. Les femelles de *C. sesamiae* et *C. flavipes* présentent les mêmes types de sensilles ayant les mêmes distributions leur permettant de détecter les volatils et les composés chimiques de contact provenant de leurs hôtes potentiels. Chez les deux espèces de parasitoïde, quatre types de sensilles sur les trois derniers segments antennaires ont été identifiés : (i) des sensilles trichoïdes non poreuses probablement impliquées dans la méchanoréception, (ii) des sensilles uniporeuses chaétiques (avec un pore terminal) potentiellement impliquées dans des fonctions gustatives, (iii) des sensilles multiporeuses placoïdes présentant vraisemblablement des fonctions olfactives et (iv) des sensilles coeloconiques connues pour avoir des fonctions plutôt thermo-hygroréceptives. Les pattes possèdent un petit nombre de sensilles chaétiques uniporeuses (avec un pore terminal) qui peuvent jouer un rôle dans la gustation. La partie terminale de l'ovipositeur possède de nombreuses sensilles en forme de dôme. Cependant, aucune sensille coeloconique ou styloconique, ayant une fonction gustative chez d'autres espèces de parasitoïdes, n'y a été observée.

Keywords: External morphology, antennae, ovipositor, tarsi, chemosensilla, host acceptance.

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Accepté le 11 février 2010

Lepidopteran stemborers are a major constraint to maize production in sub-Saharan Africa (Kfir *et al.* 2002). In eastern Africa, the braconid larval endoparasitoid, *Cotesia flavipes* Cameron 1891 (Hymenoptera: Braconidae) was introduced from Asia for control of the invasive stemborer *Chilo partellus* (Swinhoe 1885) (Lepidoptera: Crambidae) to complement the action of the closely related indigenous *Cotesia sesamiae* (Cameron 1906: Overholt *et al.* 1994a, b; Overholt *et al.* 1997).

The efficiency of a natural enemy largely depends on its ability to locate, accept, and successfully parasitize hosts (Vinson 1976; 1985; 1998; Godfray 1994). An earlier study described each event of the behavioural sequence of host recognition and acceptance by *C. sesamiae* and *C. flavipes* (Obonyo 2009). During host recognition and acceptance, the females of the two parasitoids were shown to display a similar hierarchy of behavioural events. While the antennae and particularly the distal antennomeres appeared to be used for host recognition, both antennae and the tarsi were involved in host acceptance and oviposition. By contrast, there was no evidence that the ovipositor played a role in these processes. In order to understand the mechanisms underlying host recognition and acceptance by the two wasp species, the numbers and morphology of antennal

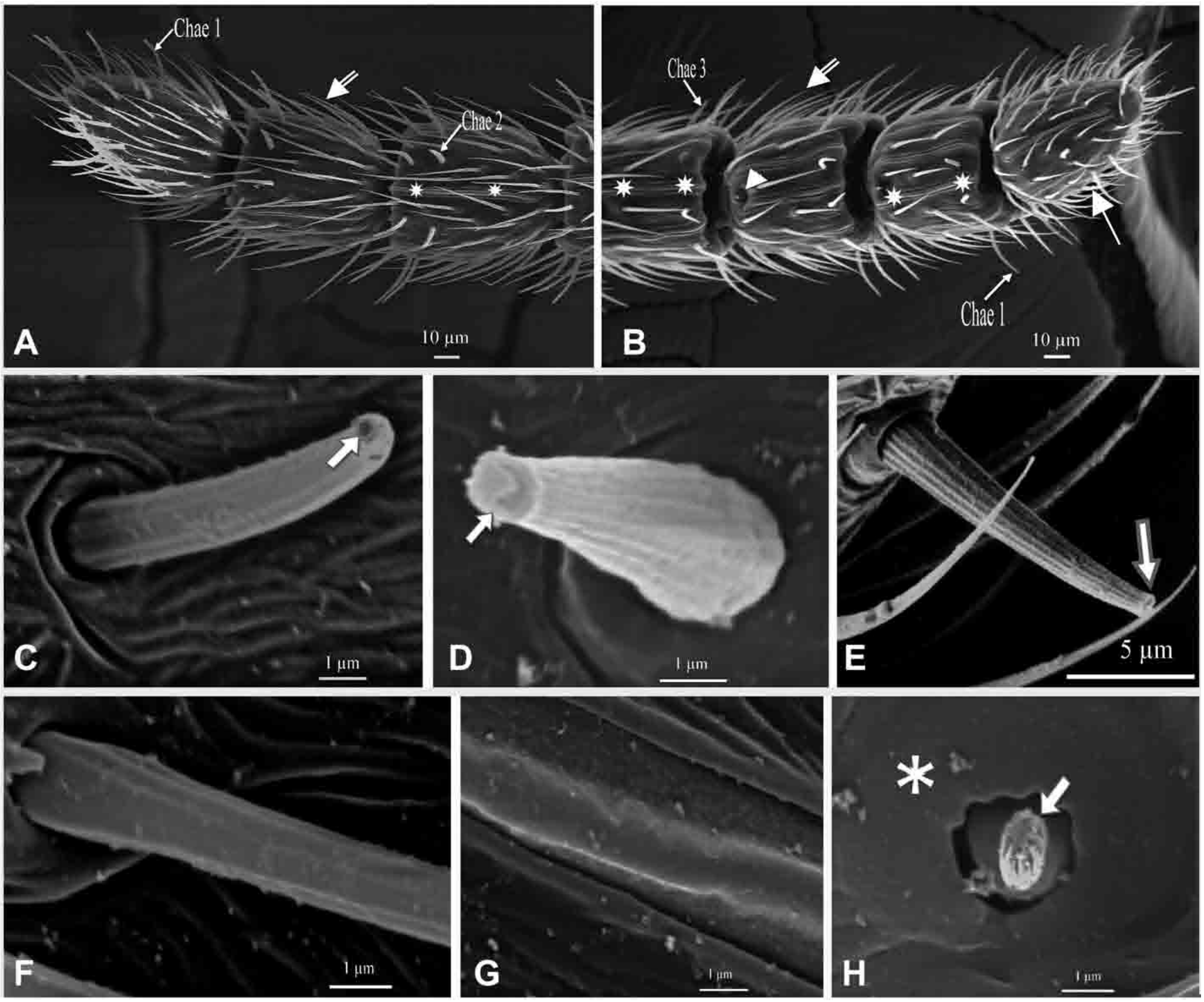

Figure 1
Distal antennomeres of adult females of Cotesia sesamiae (**A**, dorsal view and **B**, ventral view) observed by scanning electron microscopy, showing distributions of sensilla chaetica (arrows indicating sensilla chaetica type 1, 2 and 3 denoted Chae 1, 2 and 3, respectively), sensilla trichoidea (double-stemmed arrow), sensilla placodea (asterisks) and sensilla coeloconica (arrowhead). **C**, Sensillum chaeticum type 1 with a single pore on the tip (arrow). Sensilla chaetica type 2 and 3 which each tip forming a flap with a slit (arrows) (**D** and **E**). **F**, The basis of a sensillum trichoideum with a grooved cuticular surface and the absence pores. **G**, Portion of a placodeum sensillum with a sponge-like surface. **H**, Sensillum coeloconicum with a bulb-like terminal (arrow) surrounded by a doughnut-shaped ring (asterisk).

sensilla on the last antennomeres, the fifth tarsomere and pretarsus of the prothoracic legs tarsi, and on the ovipositor were studied.

Materials and methods

Insects

The adults of *C. sesamiae* and *C. flavipes* were obtained from laboratory-reared colonies established at the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya. The *C. sesamiae* colony was initiated with materials obtained from *Busseola fusca* (Fuller 1901) (Lepidoptera: Noctuidae) collected from maize fields in Kitale, Western Kenya, in 2006, while *C. flavipes* was obtained from *C. partellus* from coastal Kenya in 2005. Twice a year, field collected parasitoids were added to rejuvenate the colonies. *Cotesia sesamiae* and *C. flavipes* were reared on larvae of their suitable host *B. fusca* and *C. partellus*, respectively, according to the method described by Overholt *et al.* (1994a). The parasitoid cocoons were kept singly in glass vials (7.5 × 2.5 cm) until adult emergence.

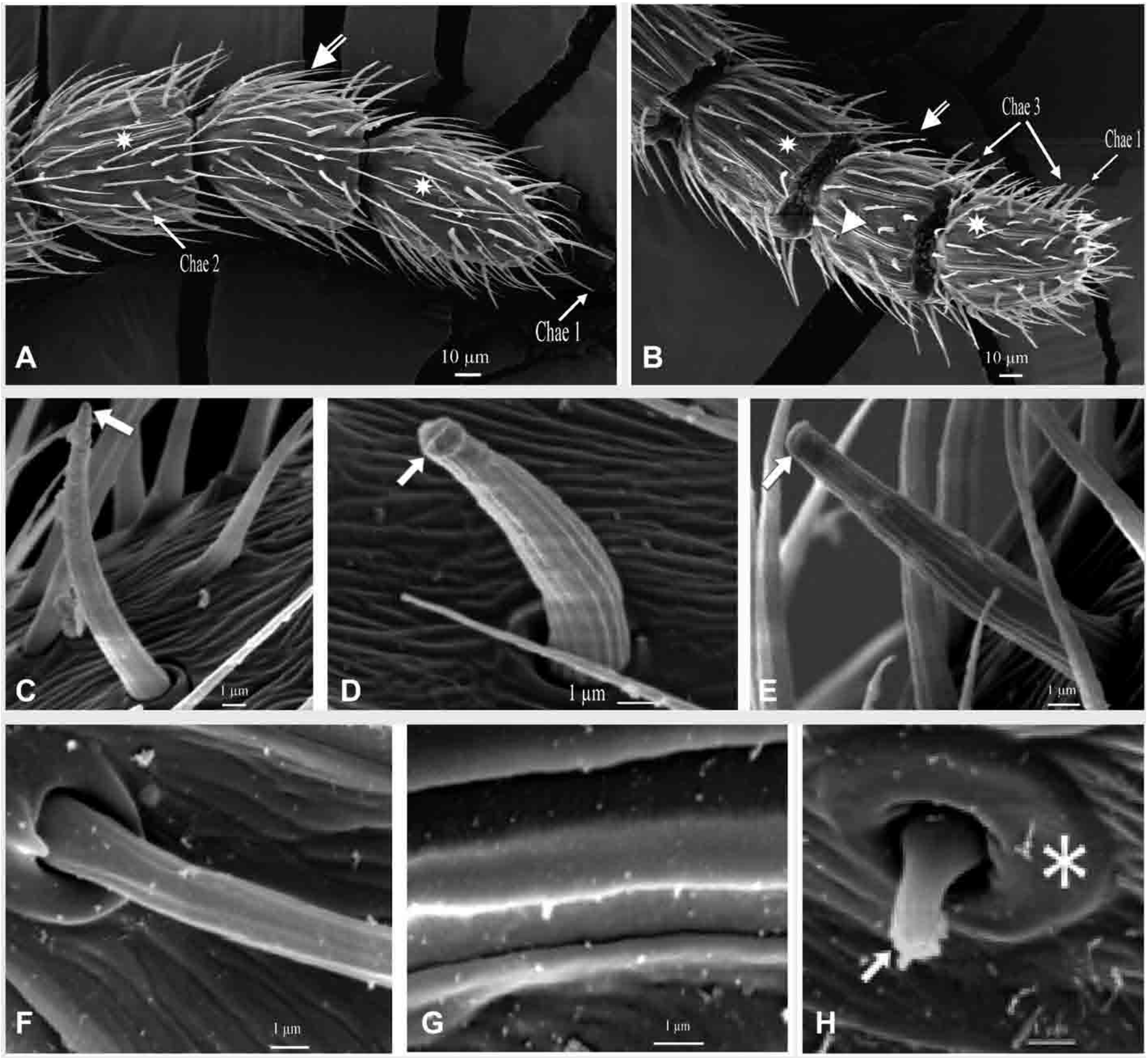

Figure 2
Distal antennomeres of adult females of *Cotesia flavipes* (**A,** dorsal view and **B,** ventral view) observed by scanning electron microscopy, showing distributions of sensilla chaetica (arrows indicating sensilla chaetica type 1, 2 and 3 denoted Chae 1, 2 and 3, respectively), sensilla trichoidea (double-stemmed arrow), sensilla placodea (asterisks) and sensilla coeloconica (arrowhead). **C**, Sensillum chaeticum type 1 with a single pore on the tip (arrow). Sensilla chaetica type 2 and 3 which each tip forming a flap with a slit (arrows) (**D** and **E**). **F,** The basis of a sensillum trichoideum with a grooved cuticular surface and the absence of pore. **G,** Portion of a placodeum sensillum with a sponge-like surface. **H,** Sensillum coeloconicum with a bulb-like terminal (arrow) surrounded by a doughnut-shaped ring (asterisk).

Organ length measurements

For each parasitoid species, the length of the antennae, ovipositor, fifth tarsomere and pretarsus of the prothoracic legs were determined under a binocular Leica EZ4D system (magnification at 35×) including a standard software (Leica Application Suite, version 1.4.0). Five females of each parasitoid species were dissected and their organs measured.

Scanning electron microscopy

For each parasitoid species, ten live female adults were used for scanning electron microscopy. The female wasps were first placed in a 2.5% (vol/vol) glutaraldehyde, 0.1 M phosphate buffer (pH 7.4) solution and left overnight for fixation. The specimens were then dehydrated in a graded series of ethanol (70, 90 and 100%) and finally critical point dried. The head, abdomen and forelegs of each wasp were separated and mounted on stubs with conductive double-side adhesive tape, sputter-coated with gold and examined with a JEOL JSM-T330A scanning electron microscope (JEOL, Tokyo, Japan) at either 10 or 15 kV.

Silver nitrate staining

Silver nitrate staining was carried out to determine the presence of porous sensilla in the antenna, ovipositor and fifth tarsomere and pretarsus. Intact wasps were stained according to the method described by Nayak & Singh (1983) but with some modifications. The wasps were first immersed in 70% ethanol containing 1 M silver nitrate for 1 hr then dehydrated in two concentrations of ethanol (90 and 100%). Afterwards, their heads, abdomens and forelegs were detached from the body and cleaned separately in xylene overnight. The specimens were mounted in Mountex (Histolab) for light microscope observations. A total of 10 females were examined for each parasitoid species.

Data analysis

Statistical tests were performed with StatView software (Abacus Concept, version 5.0, USA). Mann-Whitney U-test was used to compare the length of the antennae, ovipositor, the fifth tarsomere and the pretarsus between *C. sesamiae* and *C. flavipes*.

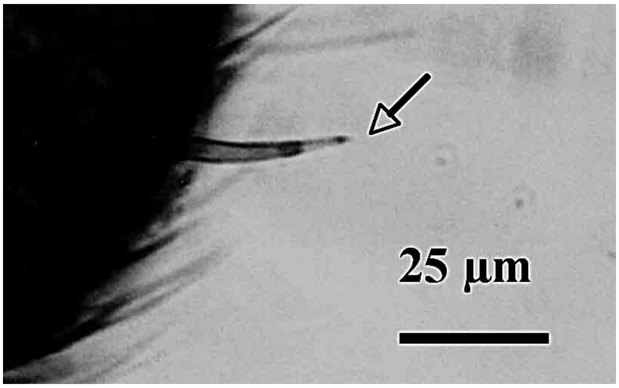

Figure 3
Example of the silver nitrate penetrating into a sensillum chaeticum type 1 located on the last antennomere of *Cotesia flavipes via* the single pore at the tip (arrow).

Results

Antennae

The antennae of *C. sesamiae* and *C. flavipes* females were 1195.9 ± 25.5 and 1116.9 ± 35.2 µm (means ± SE) long respectively (p = 0.1745, Mann-Whitney U-test). Each species had 16 antennomeres on the flagellum. In both species, scanning electron micrographs of the distal antennomeres revealed the existence of four different types of sensilla: trichodea, chaetica, placodea and coeloconica (figs. 1 and 2).

All the antennal segments of either parasitoid species were abundantly covered by sensilla trichodea which were ~24 µm long (figs. 1a, b and 2a, b). These sharply pointed structures were inclined toward the apex of the segment. The sensillar cuticle was non-porous since there was no evidence of silver nitrate staining (data not shown) and as no pores were observed (figs. 1f and 2f). The bases of these sensilla were inserted in a flexible socket (figs. 1f and 2f).

There were three types of sensilla chaetica on the distal antennomeres, which were classified as sensilla chaetica type 1, 2 and 3. Sensilla chaetica type 1 were present on both species and they were mostly located on the distal portion of each terminal segment and on the terminal antennomere. Some of these were long (~20–25 µm) and curved and more abundant, while others were short (~5–7 µm), curved but there were only about 1–2 on the ventral and dorsal surfaces of each terminal segment (figs. 1a, b and 2a, b). All of these sensilla appeared clearly argyrophilic, i.e., they stained in silver nitrate indicating their porous characteristic. An example of silver staining of such a sensillum is given in fig. 3. A single pore on the tip of these sensilla was observed (figs. 1c and 2c). The bases of these sensilla were inserted in a flexible socket (figs. 1c and 2c). Two short and curved sensilla chaetica type 2 (length ~10 µm) were found only on the dorsal surface of distal antennomeres of *C. sesamiae* and on both the ventral and dorsal surface of distal antennomeres of *C. flavipes* (figs. 1a, b and 2a, b). These were clearly visible on the adjacent antennomeres but not on the last antennomeres of either species. They appeared argyrophilic (data not shown) and the tips of the sensilla formed a flap with slits (figs. 1d and 2d). The base of these sensilla was inserted in a flexible socket (figs. 1d and 2d). One sensillum chaetica type 3 (length ~15 µm), which was longer than sensilla chaetica type 2, was located laterally on each terminal antennomere of *C. sesamiae* and *C. flavipes* (figs. 1a, b and 2a, b). It appeared argyrophilic (data not shown) and the tips of the sensilla formed a flap with slits (figs.

1e and 2e). The base of these sensilla was inserted in a flexible socket (figs. 1e and 2e).

About 2–3 sensilla placodea were found on both surfaces of all antennomeres of *C. sesamiae* and *C. flavipes* (figs. 1a, b and 2a, b). These sensilla were slightly elevated above the antennal surface and occurred along the longitudinal axis of the antennomere. The dimensions of these sensilla were about 40 to 50 µm long and 2 to 4 µm wide. The tips of the sensilla appeared porous (see the sponge-like surface on figs. 1g and 2g) but they did not clearly stain in silver nitrate solution (data not shown).

Sensilla coeloconica were observed on the ventral surface of each adjacent antennomere but not on the terminal antennomere of either species (figs. 1a, b and 2a, b). There was only one per segment and it was located in sunken grooves surrounded by a doughnut-shaped ring (figs. 1h and 2h). They terminated in a bulb-like tip. These sensilla did not stain in silver nitrate solution.

Ovipositor

The lengths of the ovipositors of *C. sesamiae* and *C. flavipes* females were 369.6 ± 9.2 and 371.3 ± 16.9 µm (means ± SE), respectively (p = 0.7540, Mann-Whitney U-test). On the paired valves of the ovipositors no sensilla were observed, whereas the unpaired dorsal valve had numerous dome-shaped sensilla of different sizes concentrated on the tip (figs. 4a and 5a). The dome-shaped sensilla were not clearly stained by silver nitrate solution (data not shown). Their tips (the domes) appeared to be a single continuum of the cuticle without pores (figs. 4b and 5b). The dome seemed to protect big holes or deep invaginations of the cuticle.

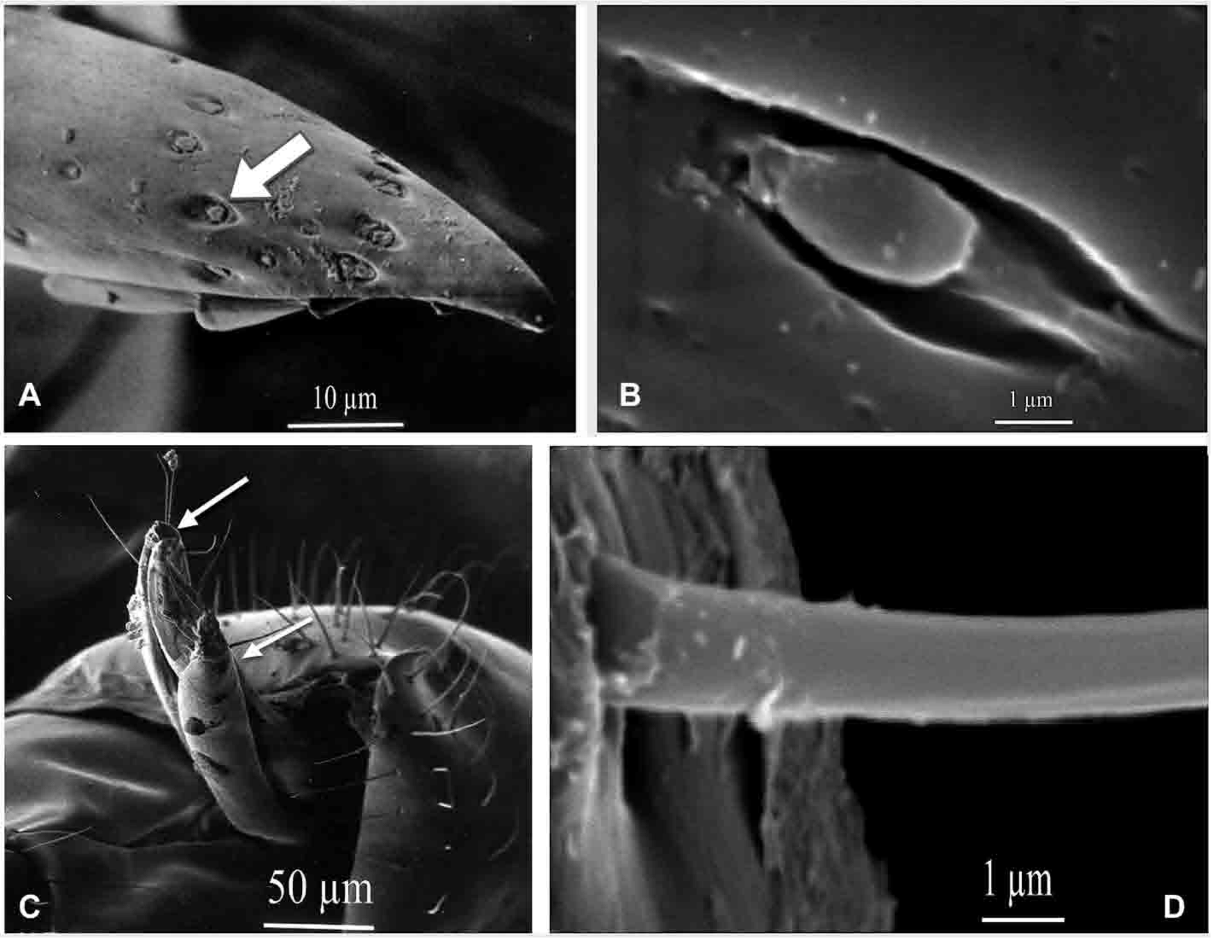

Figure 4
A, Dorsal view of the distal portion of the ovipositor of *Cotesia sesamiae* by scanning electron microscopy, showing the dome-shaped sensilla (arrow) near the apical part of the ovipositor. **B,** View of a dome-shaped sensillum and **C,** of the ovipositor enclosed by valvulae (arrows) covered by long non-porous sensilla trichoidea. **D,** The basis of a sensillum trichoideum with absence of pores.

For both parasitoids, the ovipositor was enclosed by a valvulae whose tips were covered by long sensilla trichodea (length ~30–45 µm) (figs. 4c and 5c). These sensilla appeared non-porous since they did not stain in the silver nitrate solution (data not shown) and as no pore was observed on the cuticular surface (figs. 4d and 5d).

Pretarsus and fifth tarsomere of the prothoracic legs

The total length of the fifth tarsomere and pretarsus of *C. sesamiae* and *C. flavipes* was 158.6 ± 12.6 and 133.1 ± 7.1 µm (means ± SE), respectively ($p = 0.0758$, Mann-Whitney U-test). For either parasitoid, a single sensillum chaeticum (length ~20 µm) was observed on the medium dorsal side of each claw while two were located on the ventral surface and two on each terminal part of the fifth tarsomere (figs. 6a and c). All these sensilla were found to be argyrophilic (data not shown). A single pore was observed on each sensillum chaeticum. Examples of sensilla chaetica from the tarsi with a tip pore are given in figs. 6b and d.

Discussion

The distal antennomere, the ovipositor, the fifth tarsomere, and the pretarsus of the prothoracic legs of both *C. sesamiae* and *C. flavipes* females had the same types and distribution of sensilla. Obonyo (2009) hypothesised that for both parasitoids the distal antennomeres were the most important structures involved in host recognition and acceptance. The distal antennomeres of the congeneric parasitoids possess uniporous sensilla chaetica which according to sensillar classification by Zacharuk (1980) are involved in taste

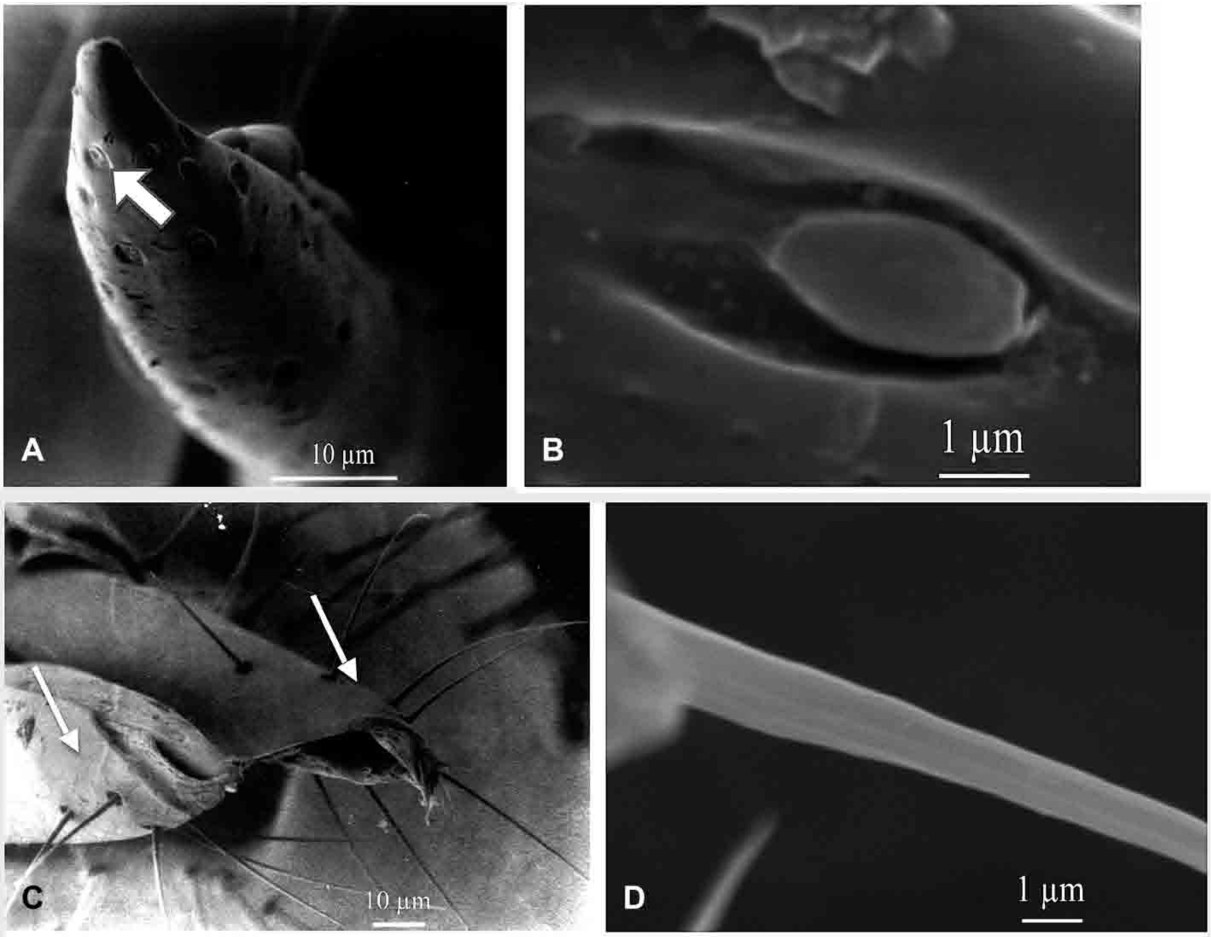

Figure 5
A, Dorsal view of the distal portion of the ovipositor of *Cotesia flavipes* by scanning electron microscopy, showing the dome-shaped sensilla (arrow) near the apical part of the ovipositor. **B,** View of a dome-shaped sensillum and **C,** of the ovipositor enclosed by valvulae (arrows) covered by long non-porous sensilla trichoidea. **D,** The portion of a sensillum trichoideum with absence of pores.

perception; the involvement of the distal antennomeres in host recognition has been well demonstrated by ablation experiments for other parasitic Hymenoptera (Weseloh 1972; Borden *et al.* 1973; Barlin *et al.* 1981; Bin 1981). It is suggested that during host examination the distal antennomeres of *C. sesamiae* and *C. flavipes* are involved in the perception of chemical cues on the cuticle of larvae.

Females of *C. sesamiae* and *C. flavipes* antennate the larval body before stinging. During this process the apical parts of their antennae are curved to allow for maximum contact with the substrate (i.e., frass or larva) (Obonyo 2009). Thereby the sensilla chaetica of the distal antennomeres are exposed to the chemical stimuli on the substrate. These findings corroborate those of Isidoro *et al.* (1996) working with other parasitic Hymenoptera. They referred to the antennomeres bearing substrate-contacting sensilla as the "touch and taste areas" as they were associated with gustatory sensilla, which must "touch" active compounds in order to "taste" the proper chemical stimuli on the substrate during host recognition. In addition, such uniporous sensilla chaetica, which bear socket-like insertions in the antennal cuticle, are also mechanoreceptors (Zacharuk 1980). This dual gustatory and mechanoreceptory function of the sensilla chaetica has also been reported for *Trissolcus basalis* (Wollaston 1858) (Hymenoptera: Platygastridae) (Isidoro *et al.* 1996) as well as *Microplitis croceipes* (Cresson 1872) (Hymenoptera: Braconidae) (Ochieng' *et al.* 2000).

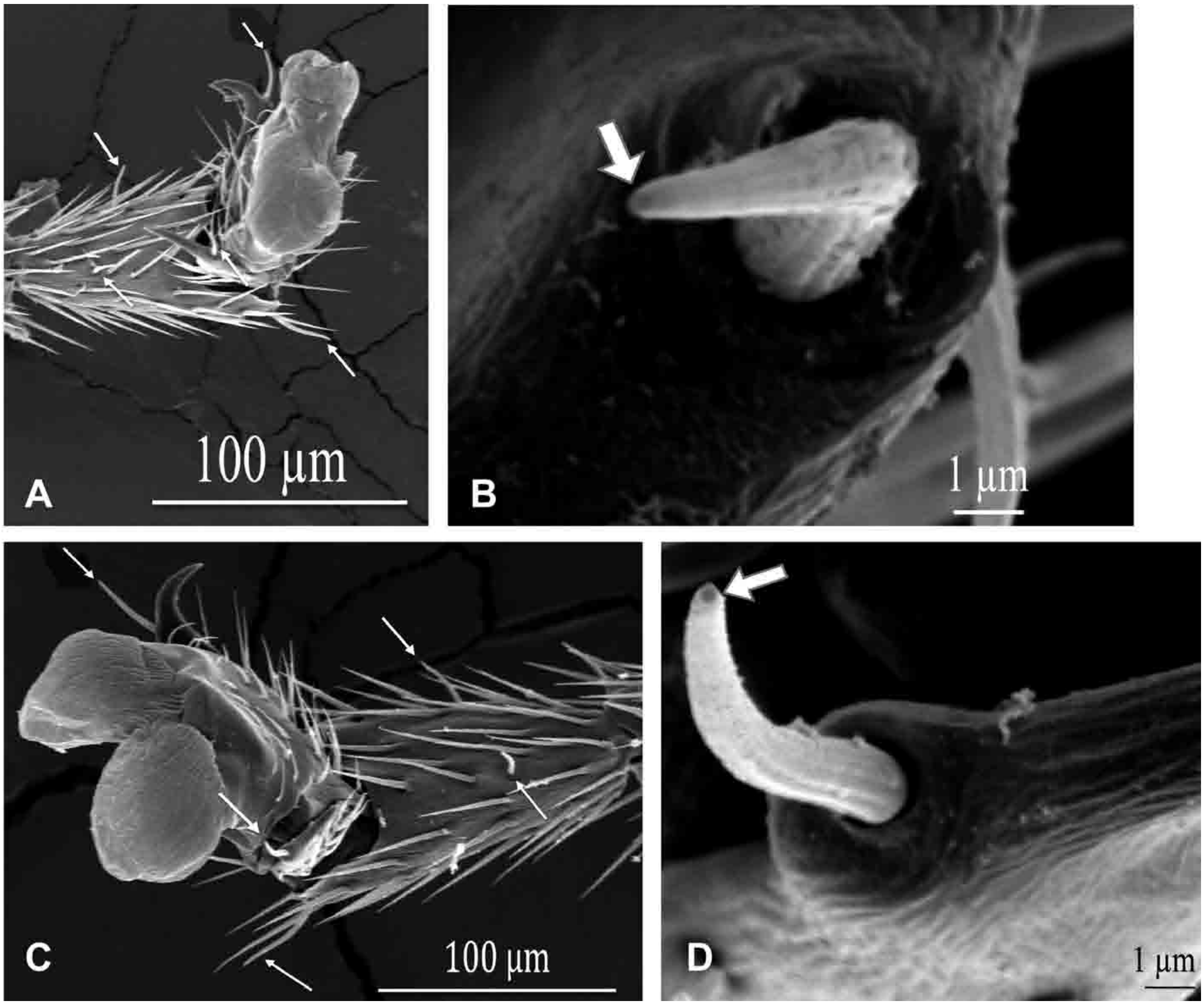

Figure 6
Ventral views of the pretarsi and last tarsomeres of **A,** *Cotesia sesamiae* and **C,** *Cotesia flavipes* observed by scanning electron microscopy, showing the uniporous sensilla chaetica (arrows). Sensillum chaeticum with a single pore on the tip (arrow) located on the claw of **B,** *Cotesia sesamiae* and **D,** *Cotesia flavipes*.

In both *C. sesamiae* and *C. flavipes*, the uniporous sensilla chaetica were surrounded by numerous non-porous sensilla trichodea. This is in contrast to Bleeker *et al.* (2004) who reported numerous multiporous sensilla trichoidea, described as olfactoreceptors, on the antennae of *Cotesia glomerata* (Linnaeus 1758) and *Cotesia rubecula* (Marshall 1885) (Hymenoptera: Braconidae). In *C. sesamiae* and *C. flavipes*, these sensilla trichodea appeared non-olfactory as also reported in other parasitic Hymenoptera (Norton & Vinson 1974; Isidoro *et al.* 1996; Ochieng' *et al.* 2000; Gao *et al.* 2007) and they are very likely involved in mechanoreception only.

Electron microscopy did not reveal the nature of the sensilla placodea but their sponge-like surface characteristics indicate that they are porous. Among other parasitoids, the sensilla placodea have been described as multiporous functioning as olfactoreceptors (Barlin & Vinson 1981a,b; Steinbrecht 1984; Ochieng' *et al.* 2000; Bleeker *et al.* 2004; Gao *et al.* 2007). This could explain their abundance on the antennae of braconids and other parasitoid families (Barlin & Vinson 1981b). Thus, it is suggested that for *C. sesamiae* and *C. flavipes* the sensilla placodea have olfactory receptors, which may play a role in remote host location, whereas gustatory receptors on sensilla chaetica on the distal antennomere detect non-volatile cues on the host cuticle upon contact.

In other *Cotesia* species, two types of sensilla coeloconica have been described (Bleeker *et al.* 2004; Roux *et al.* 2005). *Cotesia sesamiae* and *C. flavipes* possessed only one type as also observed in *Microplitis* species (Ochieng *et al.* 2000; Gao *et al.* 2007). For several parasitoid species, these sensilla have been shown to have olfactory (Ochieng *et al.* 2000; Roux *et al.* 2005) or thermo-hygroreceptive (Altner *et al.* 1983) functions.

Obonyo (2009) observed that during larval examination the wasp often walked on the larva while moving the tarsi indicating that it took up cues from the larval body. This is corroborated by the presence of uniporous sensilla chaetica on the fifth tarsomere and pretarsus of either parasitoid. Sensilla chaetica are believed to have taste functions (Zacharuk 1980). As also shown by Canale & Raspi (2000) for *Opius concolor* (Szèpligeti 1910) (Hymenoptera, Braconidae), mechanoreceptors in the tarsi of *C. sesamiae* and *C. flavipes* might perceive vibrational signals upon contact with the larvae.

Once the parasitoid had mounted the larva, mobile larvae were attacked faster than sessile ones (Obonyo 2009). Thus, very likely the tarsi contribute to mechanical sensation. Thereby, the mechanoreceptory sensilla on the arolium may be used in the perception of vibrational signals as also reported for *Sympiesis sericeicornis* (Nees 1834) (Hymenoptera: Eulophidae) (Meyhofer *et al.* 1997).

For some parasitoids, host internal markers perceived by the sensilla on the ovipositor determine acceptance or rejection of a host (Godfray 1994; Le Ralec *et al.* 1996). Chemoreceptors that are uniporous and are believed to be gustatory organs are concentrated around the ovipositor tips. These chemoreceptors have been referred to as sensilla coeloconica or styloconica (Quicke *et al.* 1999). Recently, van Lenteren *et al.* (2007) recorded action potentials from a sensillum coeloconicum at the tip of the ovipositor of *Leptopilina heterotoma* (Thompson 1862) (Hymenoptera: Eucoilidae), which confirmed the taste function of the ovipositor in parasitic Hymenoptera. However, in the ovipositor of *C. sesamiae* and *C. flavipes*, no sensilla coeloconica or styloconica were observed except for the numerous porous dome-shaped sensilla at the tips of the dorsal valves that were also described from various parasitoid species (Quicke *et al.* 1999). It is suggested that the pores on these sensilla allow for host haemolymph uptake by capillary action (Larocca *et al.* 2007), thus these sensilla could be osmoreceptors.

In conclusion, the females of *C. sesamiae* and *C. flavipes* share the same type and distribution of sensilla enabling them to detect volatiles and contact chemical stimuli from potential hosts. The olfactory receptors are restricted on the antennae while taste receptors are present on the antennae and tarsi.

Acknowledgements. The authors are grateful to Peter Owuor and Julius Obonyo for parasitoid colony rearing and the staff of *icipe*'s mass rearing unit for stemborer colony maintenance. Appreciation is also given to Fabian Haas for his help in the organ lengths evaluation, to Laure Kaiser-Arnauld and Peter G. Njagi for critical revision of earlier versions of this manuscript and to Alain Couté for facilitating the use of the electron microscopy facilities of the National Museum (Paris, France). This work was funded by IRD, France and the German academic exchange DAAD for which the authors are very grateful.

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