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# Ultrastructural comparison and distribution of sensilla on male and female antennae of the sand fly *Phlebotomus papatasi* (Diptera: Psychodidae): the vector of cutaneous leishmaniasis in Egypt

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## Abstract

**Background:** Since sand flies are insects of medical importance and most of its sensilla were found on the antennae, the present investigation was designed to characterize the ultrastructure of the antennae of males and females and the sensilla distribution using scanning electron microscopy (SEM).

**Results:** The filiform antenna of males and females consisted of a scape, pedicel, and flagellum. Male antennae appeared longer than those of females and exhibited obvious sexual dimorphism. In addition to the microtrichiae, six cuticular sensillary types, namely trichoid, coeloconic (subtype the common grooved coeloconic), chaetic, campaniform, squamiform, and the basiconic, were identified. The trichoid sensilla occurred in five subtypes, namely long blunt-tipped trichoid, short sharp-tipped trichoid, short blunt-tipped trichoid, medium pointed-tipped trichoid, and apical trichoid. Little changes in the number and distribution pattern of same sensillar types between males and females were revealed. Trichoid sensilla were the most abundant of all sensillar types. The short sharp-tipped trichoid sensilla were observed on the pedicel of males, while in females they were found on both scape and pedicel. The position of the apical trichoid sensilla on the last flagellomere differs in males than in females.

**Conclusions:** The current study is the first to describe differences in the last three flagellomeres between males and females. Our results could provide a foundation for further research on sensory organs and approaches for the control of sand flies and enable for the use of new taxonomic characters to differentiate among species.

**Keywords:** Sand flies, Sensilla, Antennae, Leishmaniasis, Scanning electron microscopy

## Background

*Phlebotomus papatasi* (Scopoli, 1786) (Diptera: Psychodidae) is the sand fly vector of *Leishmania major* (Yakimoff and Schokhor, 1914) (Kinetoplastida: Trypanosomatidae), the etiological agent of zoonotic

cutaneous leishmaniasis in the Old World, a human disease that spreads in rural areas (WHO, 2018). Old World sand fly species exhibited variations of important taxonomic characters. The measurements of the antennal segments are important in systematic descriptions. The number and disposition of the ascoids (chaetic sensilla) on the antennae are important taxonomic characteristics of Phlebotominae (Kirk & Lewis, 1951). Sand fly antennae are very fragile and could be easily lost or damaged during handling for any routine microscopic

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investigation. Scanning electron microscopy (SEM) enabled the characterization of morphological criteria of sensilla such as distribution, presence, and number. Antennae of phlebotomine sand flies are small in size and densely covered with pilosities and bristles which renders measuring the odor response difficult (Fernandes et al., 2008). Observations on the antennal sensilla using SEM were considered necessary before carrying out electrophysiological studies because they enable precise introduction of electrode to detect olfactory stimuli in insects (Fernandes et al., 2020). Olfaction in insects is important for survival, reproduction, and communication with conspecifics. Odor detection is perceived by sensilla mainly located on the antennae (Cassau & Krieger, 2021).

Sand flies are insects of medical importance, and most of its sensilla were found on the antennae (Chapman, 1991; Hallberg & Hansson, 1999). Hematophagous insects including sand flies use sensory organs (sensilla) to locate vertebrate host for blood meal acquisition as well as detecting variations both internally and externally (Fernandes et al., 2008). Only female sand flies feed on blood which can be obtained from various vertebrate hosts including humans. However, males in nature feed entirely on plant juices and honeydew secretions of aphids. More importantly, female sand flies need sugary substances for the development of *Leishmania* parasites in their guts and egg maturation (Kassem, 1998; Souza et al., 1995).

Accordingly, the present investigation was designed to characterize the ultrastructure of the antennae of males and females and the sensilla distribution using scanning electron microscopy (SEM). This study presented a detailed description of antennal sensilla of male and female *P. papatasi*, based on current nomenclature used for sand flies which could provide foundation for further investigations on the antennae of Phlebotominae.

## Methods

### Sand fly

Specimens of *Phlebotomus papatasi* flies used in this study were obtained from a perpetuating colony originally caught from Sad El Rawafaa in Northern Sinai, Egypt. The sand fly colony was maintained in a walk-in insectary environmentally controlled and regulated to  $27 \pm 2^\circ\text{C}$ , 60–70% relative humidity, and 12:12 light/dark photoperiod (L:D) at Faculty of Graduate Studies and Environmental Research, Ain Shams University. The sand fly colony has never been exposed to insecticides. Colonization and rearing procedures for sand flies were similar to those of Modi and Tesh (1983).

### Identification of male and female sand flies

Males and females *P. papatasi* were differentiated by their general shape and external genitalia according to the keys of Kirk and Lewis (1951) and Lane (1986). Specimens were segregated under a dissecting microscope. The styles of male terminalia bear well distinguished spines, while the abdomen of females appears almost rounded and has no styles or spines.

### Specimen preparation and scanning electron microscopy (SEM) examination

Specimens of males and females were selected, and the heads were dissected, together with part of the thorax, washed in phosphate-buffered saline (PBS), and immediately fixed in 70% ethyl alcohol. They were mounted on aluminum stubs with double-sided sellotape and sputter-coated on Eduardo S150 Sputter coater with a thin layer of gold. Specimens were photographed using JEOL-JSM-5500LV (SEM) with high vacuum mode at the Regional Center of Mycology and Biotechnology (RCMB), Al-Azhar University, Cairo, Egypt.

### Ultrastructural analysis of antennae

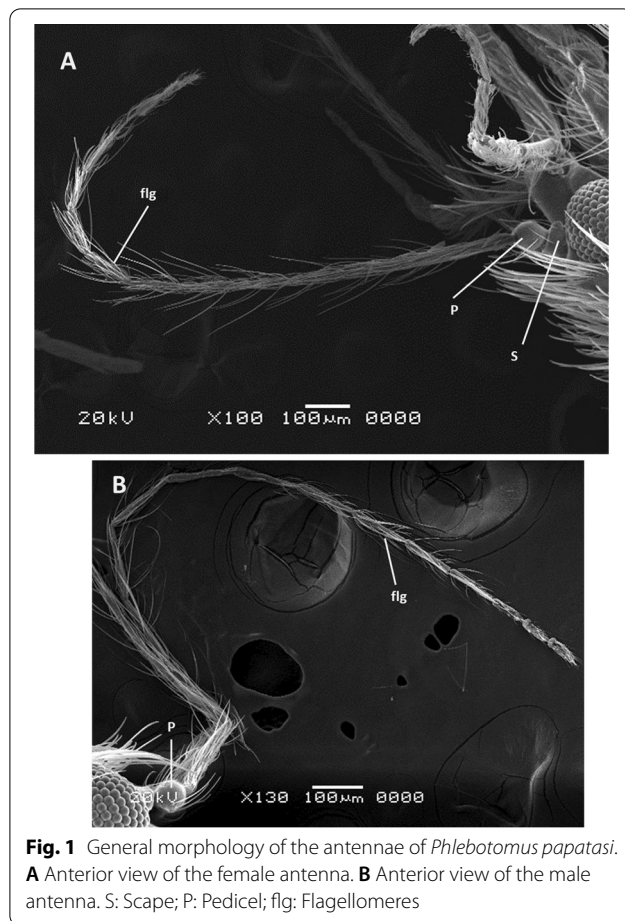
The sensillary classification were performed according to the descriptions of morphological types illustrated in specialized literature. To classify sensillary types, we adopted the nomenclature originally developed by researchers in insect sense organs (e.g., McIver, 1982; Zacharuk, 1985; Hallberg & Hansson, 1999) and updated for the sensory subtypes by Fernandes et al. (2020). The general aspects of the antennal segments of *P. papatasi* as well as the typology and distribution of antennal sensilla have been documented by SEM and discussed with the previous studies carried out on *P. papatasi* (Jobling, 1987; Quate, 1964; Zayed et al., 2002a) and other sand fly species (Ilango, 2000; Zayed et al., 2002a, 2002b; Fernandes et al., 2008; Fernandes et al., 2020; Bahia et al., 2021).

## Results

### Morphological characteristics of *Phlebotomus papatasi* antennae

*Phlebotomus papatasi* male and female antennae were filiform, composed of a short scape with irregular shape (first antennal segment), a dome-like pedicel (second antennal segment) and a flagellum consisting of 14 flagellomeres (Fig. 1A, B). The length of the male antennae appeared longer than female antennae.

Flagellomere I was the longest of all flagellomeres (Fig. 1A, B). The flagellomeres II–XI were morphologically similar to distinct filiform shape. However, the flagellomeres from XII–XIV were slightly different



being shorter and globular in females (Figs. 1A and 3D), while in males they look abraded with a distinct fault in the last flagellomere (Figs. 1B and 3F).

### Typology of sensilla

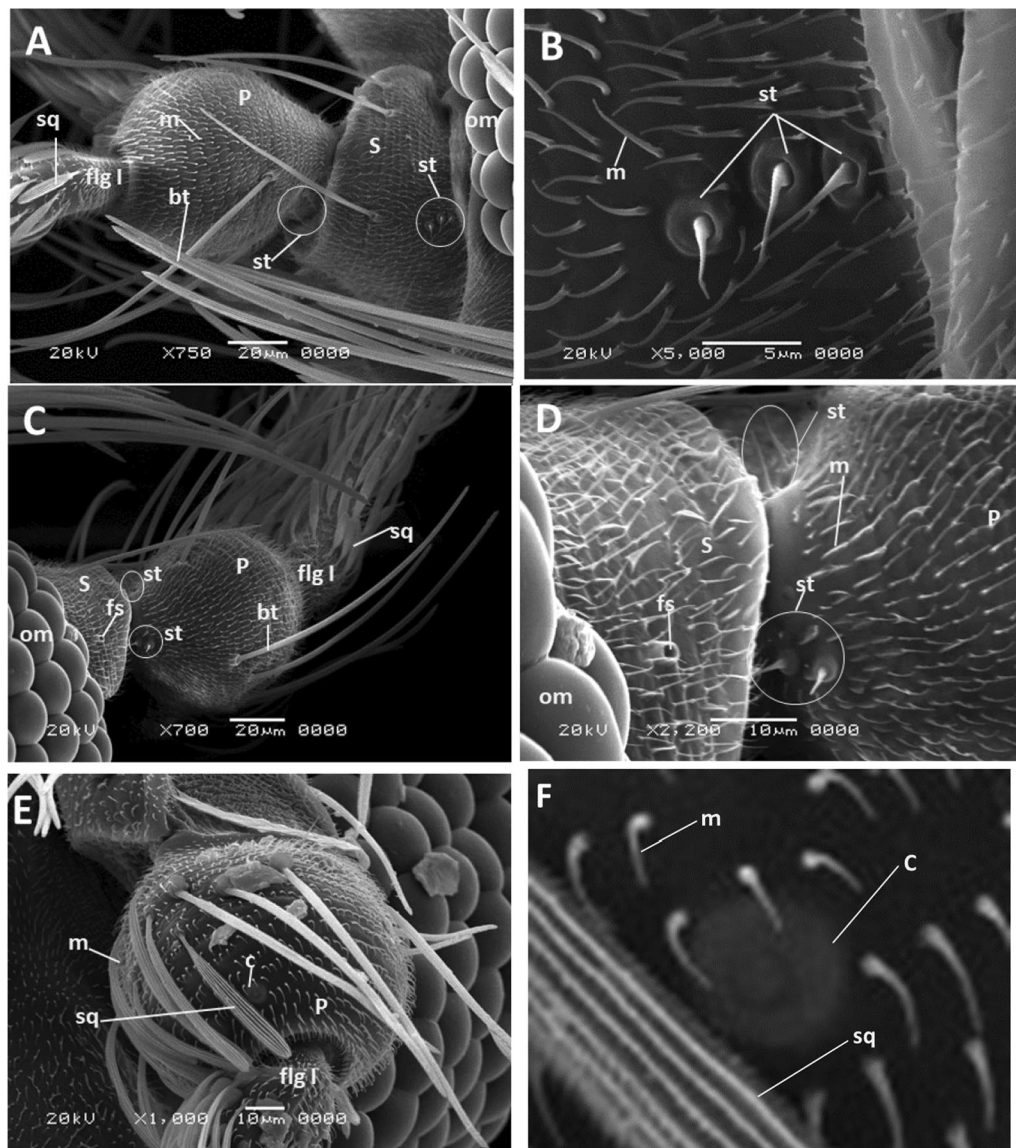
In case of similar sensillar types, electromicrographs of either males or females were provided to avoid redundancy. We observed six cuticular sensillar types, namely trichoid, common grooved coeloconic, chaetic, campaniform, squamiform, and the basiconic. The trichoid sensilla occurred in five subtypes, namely long blunt-tipped trichoid, short sharp-tipped trichoid, short blunt-tipped trichoid, medium pointed-tipped trichoid, and apical trichoid sensillum. In addition to these sensillar types and subtypes, numerous smaller spinules called microtrichiae were observed on both male and female antennae, being more abundant on the proximal antennal segments.

1. Trichoid sensilla: differentiated into well-defined subtypes

- a. Long blunt-tipped trichoid sensilla, cylindrical-shaped bristles of varying thickness and size, long in many antennal segments (Fig. 2A) but may also be of medium size, presenting a blunt tip and flexible insertion base (Fig. 2C). These sensilla appeared serrated due to the presence of parallel rows of spines covering its surface (Fig. 2A).
- b. Short sharp-tipped trichoid sensilla, small hairs with a prominent implantation base and thin tip. They were found in a group of three on scape and two on pedicel in females (Fig. 2A, B). In males, the short-tipped trichoid sensilla were present only on pedicel as a set of three in addition to a set of two at the neck between the scape and pedicel (Fig. 2C, D).
- c. Short blunt-tipped trichoid sensilla, small hairs with slightly blunt tip with a cuticular collar surrounding its implantation base; smaller than the short sharp-tipped trichoid sensilla (Fig. 3B).
- d. Medium pointed-tipped trichoid sensilla, medium size pointed hairs with no cuticular collar, found on flagellomeres XII and XIII (Fig. 3D, F).
- e. Apical trichoid sensillum, a single small hair, only found at the apex of the terminal flagellomere of male antenna (Fig. 3F) while observed on the base of the extension of the last flagellomere of females (Fig. 3D, E).

2. Common grooved coeloconic sensilla: were characterized by small size and a shallow pit surrounded by protective covering and appeared like fingers of a hand. They could be seen on the proximal part of flagellomeres I and XIII in females (Fig. 3C), and in larger numbers on the flagellomere XIII of males (Fig. 3F).
3. Chaetic sensilla: long robust hairs found in pairs on both sides of flagellomeres I–XIII (Fig. 3C).
4. Campaniform sensilla: circumvallate papilla occurred only on the pedicel (Fig. 2E, F), embedded in the cuticle within a marginally circular collar.
5. Squamiform sensilla: hair with an implantation base similar to the long blunt-tipped trichoid sensilla; however, its dorsal surface was covered by brush-like pilosities (Fig. 3A, B).
6. Basiconic sensilla: found on the base of the first flagellomere in a set of three near the distal margin (Fig. 3A). They appeared as small cone-like spines with their base directly implanted into the cuticle.





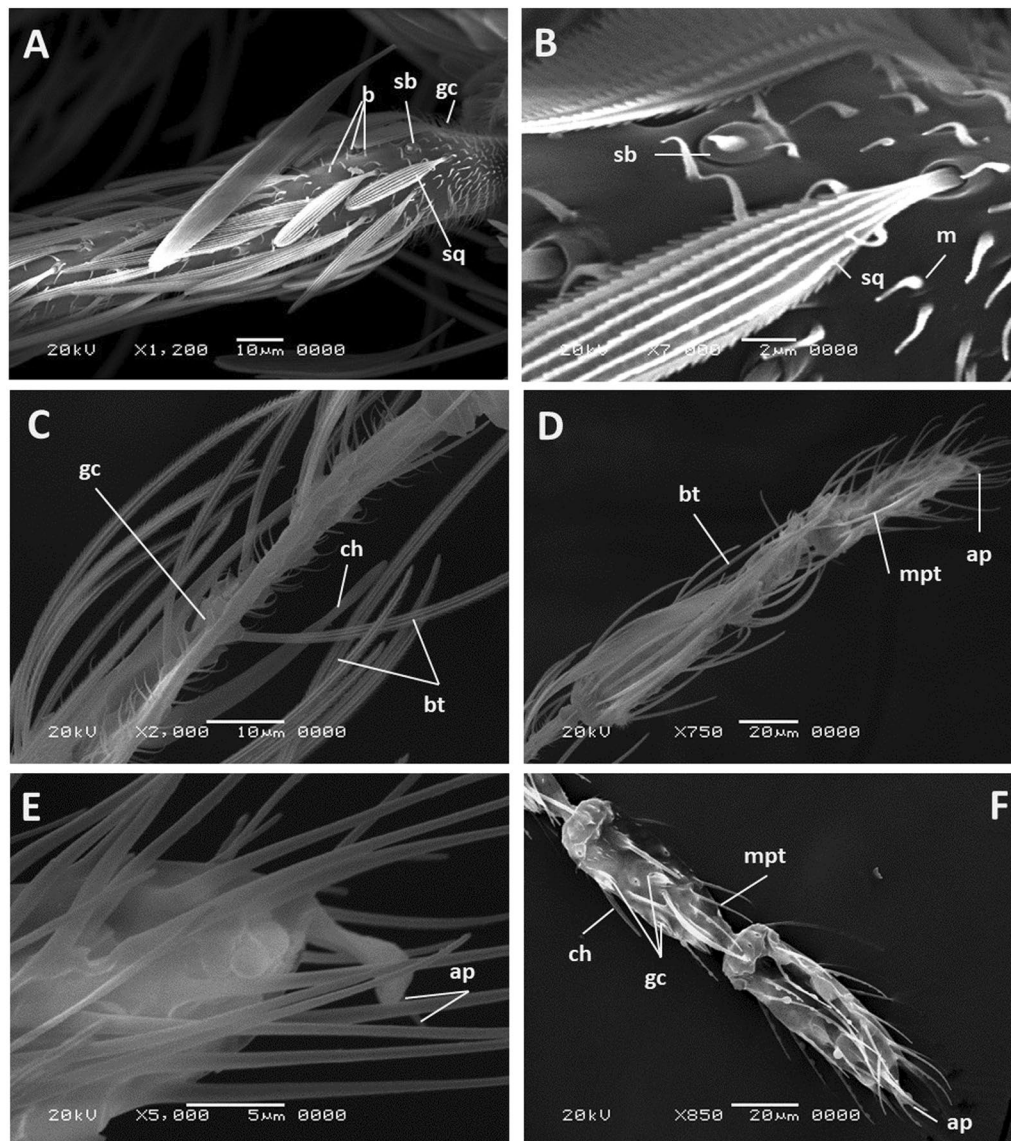
**Fig. 2** SEM micrographs of the antennae of female and male *Phlebotomus papatasi*. **A** Lateral view of the female first two segments and first flagellomere showing, scape (S) and pedicel (P); with short-tipped trichoid (st); arranged in a set of three on the scape and a set of two on the pedicel; long blunt-tipped trichoid (bt) sensilla; next to some ommatidia (om); and squamiform (sq) sensillum on the first flagellomere (flg I); and microtrichiae (m) covering the surface of these antennal segments. **B** Three short sharp-tipped trichoid (st) sensilla observed in higher magnification on scape (encircled area) in female. **C** Male antenna showing, pedicel (P) with set of three short sharp-tipped trichoid (st); two short sharp-tipped trichoid (encircled area); a fallen sensillum insertion site (fs). **D** Higher magnification of short sharp-tipped trichoid (st) observed in a set of two and three on pedicel of male (encircled) area. **E** Campaniform (c) sensillum; surrounded by microtrichiae (m) on the pedicel of female. **F** Higher magnification of campaniform (c) sensillum; long blunt-tipped sensillum (bt); microtrichia (m) on the pedicel of female

## Discussion

### Antennal morphology

In the present study, the shape and number of the antennal segments of the males and females *P. papatasi* coincide with the previously described in the New World sand flies: males and females of *Lutzomyia longipalpis* (Fernandes et al., 2008); the females of

*Nyssomyia intermedia* (Fernandes et al., 2020) and Old World sand flies: Ilango (2000) in female *P. argentipes*; and Bahia et al. (2021) in females *P. duboscqi*. Few studies were available in literature on the antennae of male sand flies. Most studies focused on females because they are most targeted in control campaigns and they solely feed on blood and thus could be easily located



**Fig. 3** SEM micrographs of *Phlebotomus papatasi* flagellomeres. **A** Flagellomere I of female showing, squamiform sensilla (sq); basiconic (b); short blunt-tipped trichoid (sb); and common grooved coeloconic sensilla (gc). **B** Higher magnification of female flagellomere I showing, squamiform (sq); short blunt-tipped (sb) sensilla, besides microtrichia (m). **C** Flagellomere XI of female showing, long blunt-tipped trichoid (bt); common grooved coeloconic (gc); chaetic (ch) sensillum. **D** Last three flagellomeres of females showing, long blunt-tipped trichoid (bt); medium pointed-tipped trichoid (mpt); chaetic (ch) sensillum; and last antennal flagellomere XIV showing, apical trichoid (ap) sensillum. **E** The apex of the last flagellomere in higher magnification in the female showing, the apical trichoid sensillum. **F** Last two flagellomeres in male showing, apical trichoid (ap) sensillum; common grooved coeloconic sensilla (gc); chaetic (ch) sensillum; and medium pointed-tipped trichoid (mpt) sensilla

near its vertebrate hosts (Bahia et al., 2021). The antennae of male *P. papatasi* were longer than in females, which could provide more sensorial zone of pheromone and allelochemical perception (Romero-López et al., 2010). Similar results have been reported previously in Lepidoptera especially those that use sex pheromones (Wee et al., 2016; Yan et al., 2017) and Diptera (Zhang et al., 2021). Morphological difference between male

and female *P. papatasi* antennae was more distinctive in the last three flagellomeres, being shorter and globular in females, while in males they appeared truncated with a clear well-defined fault in the last flagellomere. To our knowledge, such difference has not been previously recorded in the available literature and could provide a new taxonomic character among others to differentiate between males and females.

### Typology of sensilla

All sensillar types described in this study were found in both male and female *P. papatasi*. The chaetic sensillum (previously known as ascoids) was observed on the flagellomeres of *P. papatasi* in both sexes. The morphology of the chaetic sensilla provided a useful characteristic for taxonomic separation between important vectors by light microscopy (e.g., El Sawaf et al., 1985; Jobling, 1987; Kirk & Lewis, 1951). Chaetic sensilla were found to be responsible for olfactory stimuli in *Lu. longipalpis* (Dougherty et al., 1995, 1999; Fernandes et al., 2008). The olfactory function of chaetic sensillum on *Lu. longipalpis* antennae was confirmed by Fernandes et al. (2008). Although no measurements were made for the chaetic sensilla in the present work, it appeared shorter in males than females. This observation corroborated the findings of Quate (1964).

The morphology of the common grooved coeloconic sensilla (commonly known as papillae) provided a useful characteristic for taxonomic identification of sand flies (Galati, 2003). In the present work, the number and distribution of the common grooved coeloconic sensilla on the flagellomeres of *P. papatasi* differ in males than in females being greater in males. The number of sensory cells of the common grooved sensilla was around five in *P. papatasi*. Sensilla of this type (appearing as fingers of a hand) were classified as a subtype among other grooved coeloconic sensilla and were observed on the last flagellomere of *Lu. longipalpis* (Fernandes et al., 2008).

Here, the campaniform sensilla observed on the antennae (and the cervical sclerites and tergites; photographs not provided) of *P. papatasi* were much similar to those found on *Lu. longipalpis* (Fernandes et al., 2008). In other insect species, this type of sensilla was responsible for monitoring the stress caused by mechanical distortion of the cuticle (proprioception) (Chapman, 1991).

The squamiform sensilla on *P. papatasi* antennae appeared morphologically similar to the long blunt-tipped trichoid sensilla observed in *Lu. longipalpis* (Fernandes et al., 2008) and similar to the mechanoreceptors sensilla described in other insect species (Fernandes & Linardi, 2002; Spiegel et al., 2005). Scales similar to squamiform sensilla were implicated to concentrate sex pheromones closer to the olfactory sensilla in moth species (Wang et al., 2018). However, the role of squamiform sensilla in sand flies needs to be demonstrated.

The basiconic sensilla were observed on *P. papatasi* as small sensilla, with their base directly inserted into the cuticle and occurred in sets of three spine-like sensilla. The basiconic sensilla were observed as small little fingers in female *P. duboscqi* (Bahia et al., 2021) a closely related species to *P. papatasi*. The morphological functional

classification of these sensilla was considered olfactory (Fernandes et al., 2020).

The trichoid sensilla were the most common type found on the antennae of *P. papatasi*. Five subtypes of trichoid sensilla were observed, namely long blunt-tipped, short sharp-tipped, short blunt-tipped, medium pointed-tipped, and apical. Bahia et al. (2007) observed the trichoid sensilla in the larvae of *Ny. whitmani* and *Ny. intermedia*, and they considered it as the most common sensory organ in mature and immature stages of insects.

In female *P. papatasi*, the short sharp-tipped trichoid sensilla were observed as a set of three sensilla on the scape in addition to a set of two on the pedicel. In males, however, they were observed only on the pedicel as a set of three and a set of two at the neck between the scape and pedicel. The short sharp-tipped trichoid sensilla as well as the campaniform sensilla have been described as olfactory and mechanoreceptors in *Lu. longipalpis* and *Ny. intermedia* sand flies (Fernandes et al., 2008, 2020). Similarly, they were also found on the scape and pedicel of mosquitoes and other insects (Zacharuk, 1985). It is possible that they have the same function in *P. papatasi*.

The long blunt-tipped trichoid sensilla and squamiform sensilla of *P. papatasi* are morphologically similar and were described in some other sand fly species (Bahia et al., 2021; Fernandes et al., 2008, 2020). However, they can be easily distinguished from each other by the serrations found on the long blunt-tipped trichoid, while the squamiform sensilla were characterized by brush-like pilosities covering its dorsal surface.

In male *P. papatasi*, the apical trichoid sensillum was seen at the apex of the last flagellomere. In females, however, it was found on the base of the extension of the last antennal segment. Such difference in the strategic position of the apical trichoid sensillum could be attributed to morphological differences observed in the last three flagellomeres of both sexes. The position of the apical trichoid sensilla on the tip of the antennae of insects was considered very important in detection of sex pheromones and other harmful substances (Fernandes et al., 2020). The short, medium pointed trichoid sensilla and the apical sensilla found on the antenna of *P. papatasi* were very similar to the chemoreceptor sensilla described in *Lu. longipalpis* (Fernandes et al., 2008).

Previous studies on external morphology of sand fly antennal sensilla using SEM varied among species regarding their types, number, and distribution on the antennal segments. Ilango (2000) described trichoidea (two subtypes), coeloconica, chaetica, basiconica, and auricillia on *P. argentipes* antennae. Fernandes et al. (2008) described 11 subtypes of sensilla in *Lu. longipalpis*, including five subtypes of trichoidea sensilla. Two coeloconic sensilla (grooved and praying hands subtypes) and campaniform,



chaetica, basiconica, and squamiformia sensilla. More recently, Fernandes et al. (2020) identified 14 well-differentiated sensilla in *Ny. intermedia* among six cuticular types: trichoidea, campaniformia, squamiformia, basiconica, chaetica, and coeloconica. Bahia et al. (2021) identified 13 well-differentiated sensilla among six types (trichoid, squamiform, campaniform, basiconic, coeloconic, and chaetic) on the antennae of female *P. duboscqi*. Zayed et al. (2002a) observed trichoidea (three subtypes), chaetica, basiconica, campaniformia, squamiformia, Böhm, and falcate sensilla on *P. bergeroti* antennae and observed trichoidea (three subtypes), chaetica, basiconica, campaniformia, squamiformia, Böhm on *P. papatasi* antennae. In the present work, 11 well-differentiated sensilla among six cuticular types were identified: trichoid sensilla (five subtypes), campaniform, squamiform, basiconic, chaetic, and common grooved coeloconic. All the previously mentioned sensillar types were evidenced in the present work in males and females *P. papatasi* except the Böhm, falcate, auricillia, and the praying hand coeloconic sensilla. Zayed et al. (2002a) described Böhm's sensilla and three subtypes of trichoidea in *P. papatasi*. However, in the present work Böhm's sensilla could not be identified. Additionally, coeloconic sensilla and five subtypes of trichoidea were identified herein. This might be attributed to differences in nomenclature systems used. However, Böhm's bristles/sensilla were identified on the scape and pedicel of *Plutella xylostella* (Lepidoptera: Plutellidae) (Yan et al., 2017) and in moth flies (Diptera: Psychodidae) (Faucheux & Gibernau, 2011).

In this study, we described and updated the nomenclature of sensillary types found on the antennae of *P. papatasi*. In addition, comparison of the number, distribution, and morphology of sensillar types on male and female antennae was defined. Previous studies on sand flies have described sensory organs on different parts of the body (Mohamed et al., 1999; Ilango, 2000; Zayed et al., 2002a, 2002b). Although sexual differences in the antennal morphology of *P. papatasi* were observed, further investigations are needed to investigate sexual antennal dimorphism in other sand fly species. Such information could be of taxonomic and biological importance. Electrophysiological studies are needed to identify the role of sensilla found on the antennae of *P. papatasi*. Such information may assist in discovering new insect attractants and/or repellents to control sand flies thus suppressing leishmaniasis transmission.

## Conclusions

Sexual dimorphism in the morphology of male and female *P. papatasi* antennae was observed. Male antennae were longer than female antenna. In addition, the last three flagellomeres appeared shorter and globular

in females, while a distinct fault was seen in the last three flagellomeres of males. The antennae were identified as filiform. In addition to the microtrichiae, six types of sensilla were observed, including five subtypes of trichoid sensilla (long blunt-tipped, short sharp-tipped, short blunt-tipped, medium pointed-tipped, and apical), the common grooved coeloconic, campaniform, chaetic, basiconic, and squamiform. Trichoid sensilla were categorized into five subtypes widely distributed over antennal surface, including the scape and pedicel, and flagellum. These results not only improve our understanding of insect biology, host location mechanisms, but also provide important information for future electrophysiological and behavioral analysis of the chemical ecology between sexes.

## Abbreviations

ap: Apical trichoid sensillum; b: Basiconic sensillum; bt: Long blunt-tipped trichoid sensilla; c: Campaniform sensillum; ch: Chaetic sensillum; flg: Flagellomeres; fs: Fallen sensillum insertion site; gc: Common grooved coeloconic sensilla; (L:D): Light/dark; m: Microtrichiae; mpt: Medium pointed-tipped trichoid sensillum; om: Ommatidia; P: Pedicel; S: Scape; sb: Short blunt-tipped trichoid sensilla; sq: Squamiform sensilla; st: Short-tipped trichoid sensilla; SEM: Scanning electron microscopy.

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## Author contributions

BS contributed to conceptualization, supervision, and writing—original draft; MA conducted the research and was involved in investigation; AF and JG contributed to supervision; and HK was involved in supervision, provided study material, and contributed to writing, review, and editing. All authors read and approved the final manuscript.

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## Availability of data and materials

All data generated or analyzed during this study are included in this published article [and its supplementary information files].

## Declarations

### Ethics approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

### Competing interests

The authors declare that they have no competing interests.

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