



Sensory structures on the maxillary palp of the termite species *Hospitalitermes jepsoni* Snyder (Termitidae: Isoptera)

Khirod Sankar Das, Joycy Mary Kharthangmaw, K Chanreila L Nonglait, Cynthia Bansara Marwein, Sudipta Choudhury*

Department of Zoology, Entomology laboratory and North Eastern Hill University, Shillong, Meghalaya, India

Abstract

The maxillary palp of the soldier and worker of the termite species *H. jepsoni* were examined by scanning electron microscopy to elucidate the sensory structures present on the palpal segments. We observed six different types of sensilla viz., sensillum chaetica (subtypes- SC-I, II, III, IV and V), sensillum trichodea (ST), sensillum trichodea curvata (STC), sensillum campaniformia (SCa), glandular pores (GP), basiconic capitate peg sensilla (BCPS) along with nano scale pores on the surface of the palpal segments. Morphological features of these palpal sensilla indicate that they may putatively function as gustatory, mechanosensory, olfactory, thermosensitive and proprioceptive mechanosensory.

Keywords: termites, maxillary palp, sensilla, scanning electron microscope

Introduction

Insects possess various sensory structures called sensilla that perceive taste, smell, vibration, touch, vision, proprioception, thermoreception and hygroreception (Shields, 2011) ^[1]. These sensilla are located on different body parts of insects such as antennae, mouth parts, wings, legs, ovipositors etc. According to Zacharuk and Shields (1991) ^[2], different body parts of insects contains various chemosensory sensilla, of which the olfactory sensilla are mostly present on the antennae whereas the gustatory sensilla are mostly present on mouth parts, legs, and ovipositor. Existence of olfactory sensilla is also known in the maxillary palp (Zhang *et al.*, 2011) ^[3]. Among all the body parts of insects, the antennae and maxillary palps are the major sensory organs that contain various types of sensilla for detecting chemical and mechanical stimuli from the surrounding environment (Keil, 1997) ^[4]. Antennae and maxillary palps are involved in various behaviors of adult insects and the sensilla present on these organs play an important role in their adaptation according to their habitat (Chapman, 1982) ^[5]. Maxillary palps are generally involved in the feeding behavior of insects. Maxillary palp of the mosquito species *Culex quinquefasciatus* has a proposed biological and ecological role in the detection of the plant and nectar based sources (Sayed and Leal, 2007) ^[6]. Sensory system in maxillary palp is complementary to the antennal sensory system of insects. They can detect odors in concentrated form primarily over short ranges whereas the antennal sensory system that works over longer ranges (Wasserman and Itagaki, 2003; Dweck *et al.*, 2016) ^[7, 8]. In many species of Dipteran flies, presence of several olfactory sensilla has been found on their maxillary palps (Isberg *et al.*, 2013; Zhang *et al.*, 2013; Bohbot *et al.*, 2014; Omondi *et al.*, 2015; Pezzi *et al.*, 2016) ^[9, 10, 11, 12, 13]. Olfactory sensilla in flies develop distinct features according to different ecological niches (Zhang *et al.* 2012) ^[14]. The German Cockroach, *Blattella germanica* perform their courtship behavior following the pheromones which they detect by the sensory structures present on the antennae, labial palp and maxillary palp (Ramaswamy and Gupta, 1981) ^[15].

In case of eusocial insects, communication is the basis for all the social activities and behaviors. In termites too, all their behaviors are based on the complex network of chemical signals which are complemented by vibration-based signals as the role of visual cues is negligible because of the dark environments where they live and the blind members of their colonies (Costa-Leonardo and Haifig 2014; Bagnères and Hanus 2015) ^[16,17]. To understand their complex communication system, several studies have been done and they were primarily on the antennal sensory systems of termites (Prestage *et al.*, 1963; Tarumingkeng *et al.*, 1976; Deng *et al.*, 2006; Ishikawa *et al.*, 2007; Yanagawa *et al.*, 2009; Yanagawa *et al.*, 2010; Huang *et al.*, 2012; Fu *et al.*, 2020) ^[18, 19, 20, 21, 22, 23, 24, 25]. But, information on the sensory system of maxillary palp of termites is rare. Therefore, in this study, we aimed to elucidate in details the external morphology of the sensory structures present on the maxillary palp of the termite species *Hospitalitermes jepsoni*.

Materials and Methods

The termite species, *Hospitalitermes jepsoni* were collected from the Nongkhylllem reserve forest, Lailad, Ribhoi, Meghalaya, India and brought to the laboratory for further processing for Scanning electron microscopy (SEM). We collected and processed both soldier (n=5) and worker (n=5) individuals of *H. jepsoni*. Samples were

cleaned with distilled water first and then dissected the head of both soldier and worker along with the maxillary palp. For scanning electron microscopy we followed the method of Dey *et al.*, (1989) [26]. Samples were fixed in 2.5% Glutaraldehyde for 24 hours prepared in 0.1 M Sodium Cacodylate at 4° C. Then the samples were dehydrated in ascending grades of acetone (30%, 50%, 70%, 80%, 90%, 95% and 100%), keeping in each grades twice for 15 minutes which were performed twice in each grade. After dehydration, samples were dried in Tetra methyle saline for 5-10 minutes twice. Then the gold coated specimens were viewed under SEM (Jeol- JSM 6390). Classification of sensilla were done based on their external morphology following Schneider (1964) [27], Zacharuk (1985) [28], Yanagawa *et al.*, (2009) [23] and Fu *et al.*, (2020) [25].

Results

The maxillary palp (Fig 1) of *H. jepsoni* is five segmented in both the soldier and worker. It is approximately $1117.16 \pm 84 \mu\text{m}$ and $1210.17 \pm 99 \mu\text{m}$ in length respectively in soldiers (n=5) and workers (n=5). The longest and widest segment is segment-V which is $351.48 \pm 3 \mu\text{m}$ and $372.47 \pm 0.9 \mu\text{m}$ in length $89.55 \pm 16 \mu\text{m}$ and $90.04 \pm 23 \mu\text{m}$ in width respectively in soldier and worker. In soldier, the shortest segment is segment-I which is $92.48 \pm 1.1 \mu\text{m}$ in length and the narrowest is segment-II which is $79.7 \pm 14 \mu\text{m}$ in width. In worker, it is segment-I which is $94.38 \pm 0.8 \mu\text{m}$ in length and $77.21 \pm 7 \mu\text{m}$ in width.

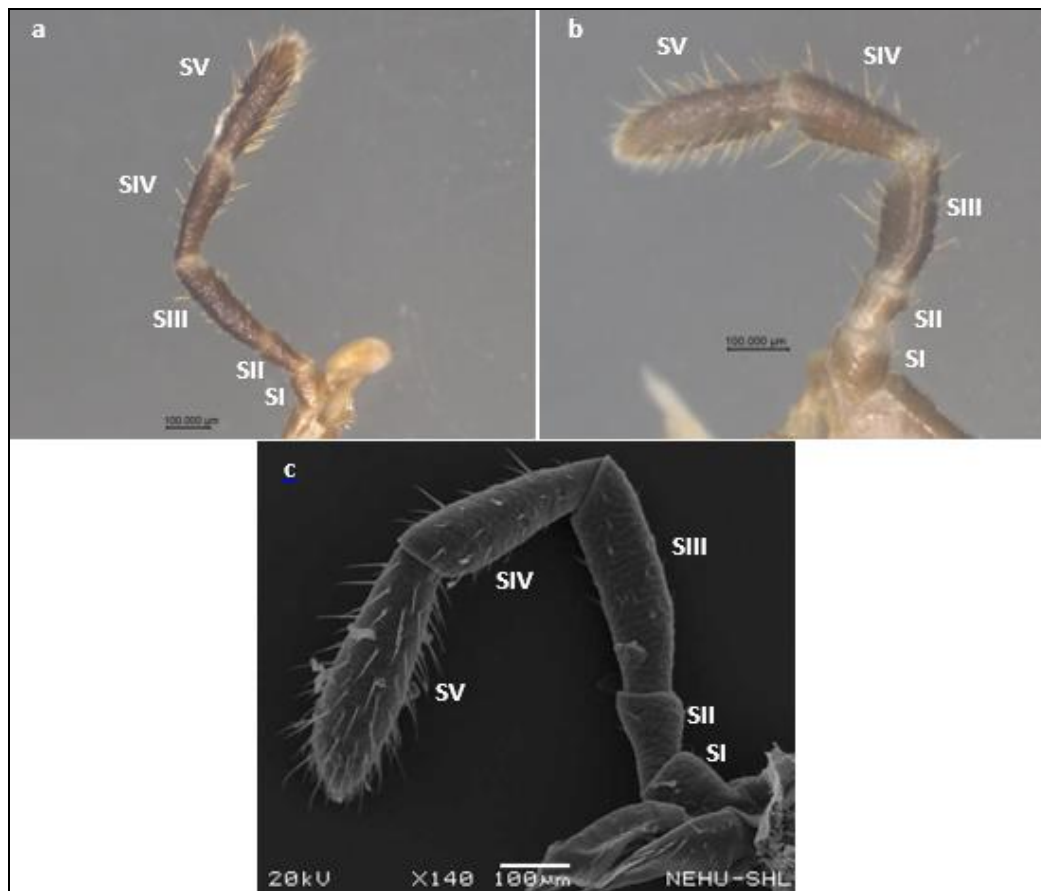


Fig 1: Maxillary palp of *Hospitalitermes jepsoni*. (a) Soldier caste (b) Worker caste (c) Worker caste (SEM) SI= Segment I, SII= Segment II, SIII= Segment III, SIV=Segment IV, SV=Segment V.

Palpal segments contain five different subtypes of sensillum chaetica (SC) viz., SC-I, SC-II, SC-III, SC-IV and SC-V (Fig 2). SC-I is $55.27-83.95 \mu\text{m}$ in length, $3.10-4.26 \mu\text{m}$ in basal diameter and $0.40-1.04 \mu\text{m}$ in distal diameter. In appearance, it is straight with a slight curve near the tip towards the antennal surface. It has a flexible socket, longitudinal grooves on the wall and a terminal pore. SC-II also shares the same characteristics with SC-I except SC-II become gradually slender and there is no curve near the tip. SC-II I is $51.63-80.30 \mu\text{m}$ in length, $3.24-4.11 \mu\text{m}$ in basal diameter and $0.22-0.42 \mu\text{m}$ in distal diameter. SC-III is shorter than SC-I and II. Its length is $35.46-36.71 \mu\text{m}$, basal diameter is $3.53 \mu\text{m}$ and distal diameter is $0.43-0.50 \mu\text{m}$. It has a flexible socket, longitudinal grooves on the wall and a blunt tip. SC-III sharply bends towards the antennal surface from the distal one third of its length. SC-IV has similarity in its length with SC-III. The length is $29.14-35.52 \mu\text{m}$, basal diameter is $2.58-3.22 \mu\text{m}$ and distal diameter is $0.20-0.50 \mu\text{m}$. The sensilla arise from a flexible socket and gradually become tapered towards the distal end with a pointed tip. Longitudinal grooves are present on its wall. SC-V is the shortest among all the subtypes of SC. It is $9.62-18.37 \mu\text{m}$ in length, $1.70-2.42 \mu\text{m}$ in basal diameter and $0.21-0.33 \mu\text{m}$ in distal diameter. It arises from a comparatively wider flexible socket with longitudinal grooves on the side walls. Tip is blunt and without any pore. All the subtypes of SC are distributed on all the palpal segments of both worker and soldier of *H. jepsoni*.

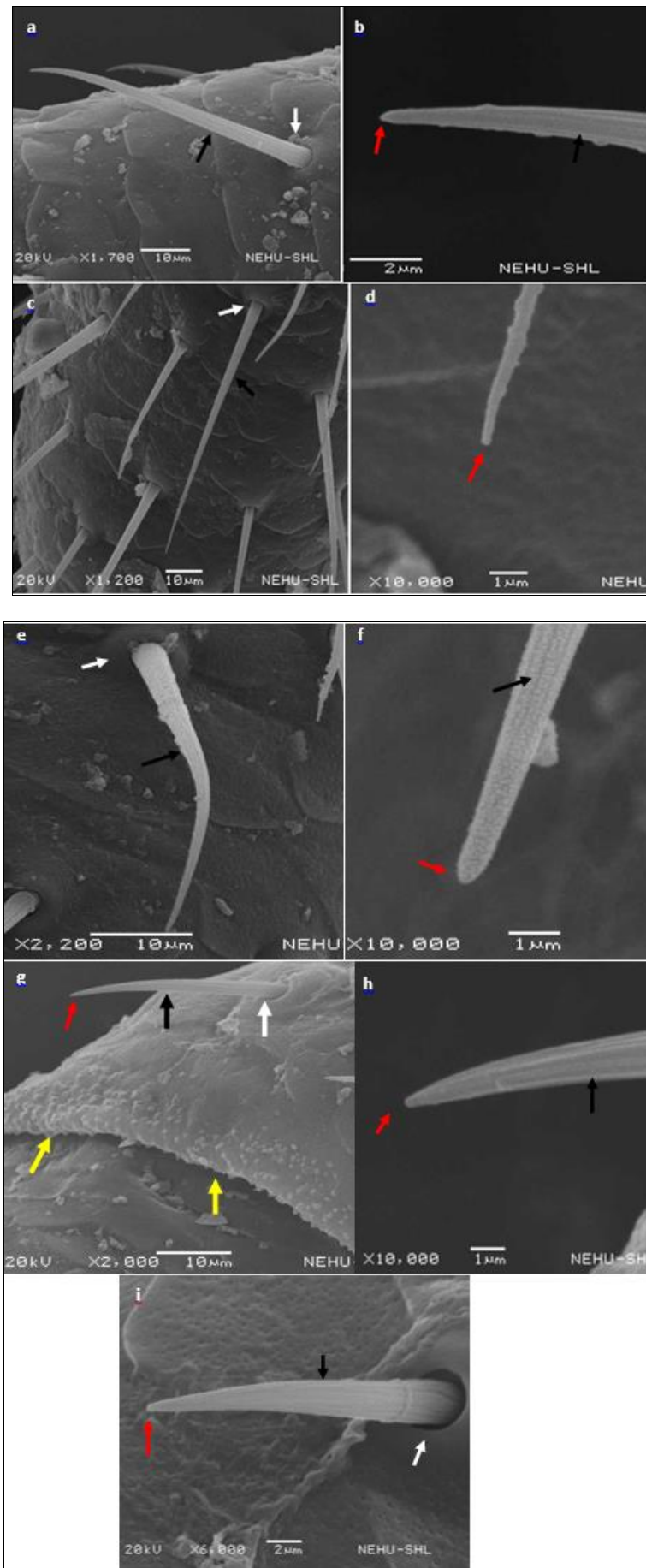


Fig 2: Shows sensilla chaetica (SC) and Basiconic capitate peg sensilla (BCPS) (a) Complete SC-I (b) Tip of SC-I (c) Complete SC-II (d) Tip of SC-II (e) Complete SC-III (f) Tip of SC-III (g) Showing SC-IV (red, black and white arrowed) and BCPS (yellow arrowed) (h) Tip of SC-IV (i) Complete SC-V. Red arrow shows tip, black arrow shows longitudinal lines on the side wall and white arrow shows socket.

Sensillum trichodea (ST), on the palpal segments of *H. jepsoni*, observed as straight sensilla in appearance with a protuberant base, shallow longitudinal lines on the side wall and a terminal pore (Fig 3 a-b). It is 17.50-24.48 μm in length, 1.80-2.26 μm in basal diameter and 0.44 μm in distal diameter. On the other hand, sensillum trichodea curvata (STC) is 10.31-11.44 μm in length, 1.81-1.97 μm in basal diameter and 0.25-0.51 μm in distal diameter (Fig 3c-d). STC curves towards the antennal surface and has a circular protuberant base and a terminal pore. Side wall has shallow longitudinal lines which arise from the proximal one third of its length. Both the ST and STC were observed predominantly on the tip area of the terminal palpal segment of both the soldier and worker castes.

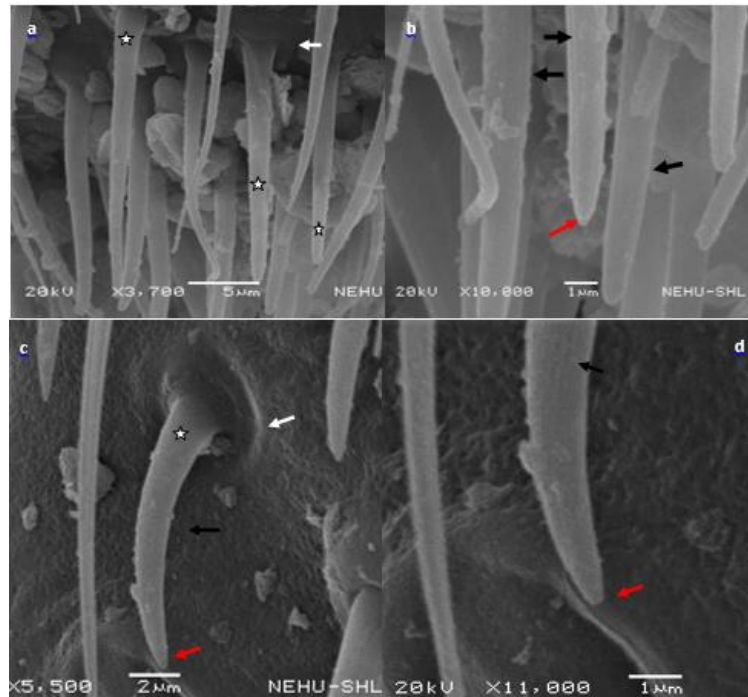


Fig 3: Shows sensilla trichodea (ST) and sensilla trichodea curvata (STC). (a) Complete ST (white asterisk) (b) Shows side wall and tip of ST (c) Complete STC (white asterisk) (d) shows side wall and tip pore of STC. Red arrows shows tip, black arrow shows side wall and white arrow shows socket.

Sensillum Campaniformia (SCa) (Fig 4a) is a shallow dome shaped sensilla surrounded with a discoid collar which is oval in shape in parallel to the longitudinal axis of the antenna. It is 6.24-7.90 μm in diameter. SCa is distributed on the distal end of the palpal segments including the tip of the first palpal segment. Glandular pores (Fig 4b) is small, circular openings mostly present on the shallow cavities formed bordering the markings on the antennal surface. It is 0.33-0.55 μm in diameter. They present on all the palpal segments of workers and soldiers. Basiconic capitate peg sensilla (Fig 2g; 4a; 5a) are small structures that occur specifically on the segmental junctions of all the palp in circular manner. It has a broad protuberant base that gives raise a short finger like peg with a blunt tip. All the palpal segments also possess numerous porous structures (Fig 5B) on the scale surface which are approximately 0.09-0.36 in diameter.

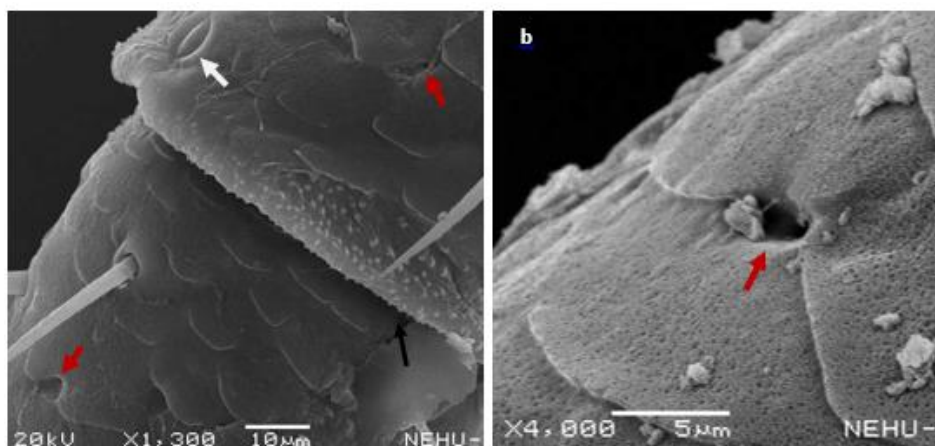


Fig 4: (a) White arrow shows sensilla Campaniformia (SCa), Red arrow shows sensilla ampullaceal (SA), black arrow shows BCPS (b) Red arrow shows SA.

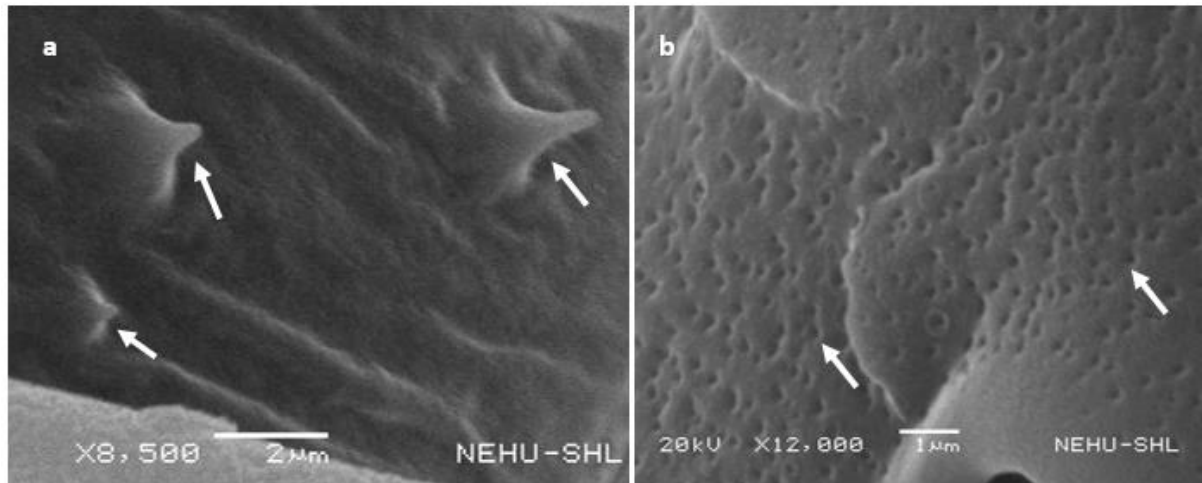


Fig 5: (a) Arrows show basiconicum capitates peg sensilla (BCPS) (b) Arrows show nanoscale porous structures on the surface of palpal segments

Discussion

In termites, intra and inter specific communications are very complex and depend on their various sensory systems for its accomplishment. Most of the earlier studies were focused primarily on the antenna of termites in order to understand the function of their sensory systems (Prestage *et al.*, 1963; Tarumingkeng *et al.*, 1976; Deng *et al.*, 2006; Ishikawa *et al.*, 2007; Yanagawa *et al.*, 2009; Yanagawa *et al.*, 2010; Huang *et al.*, 2012; Fu *et al.*, 2020) [18, 19, 20, 21, 22, 23, 24, 25]. Like the antenna of termites, maxillary palp also contains sensory structures on its palpal segments and can act as an important sensory organ perceiving a range on external cues. In external morphology, maxillary palps of soldiers and workers of *H. jepsoni* are similar except in their length which is slightly more in workers than the soldiers.

The maxillary palp of soldiers and workers of *H. jepsoni* were found to possess six different types of sensilla viz., SC (SC-I, II, III, IV & V), ST, STC, SCa, GP and BCPS. Numerous tiny pores were also observed on the surface of the palpal segments. In case of SC, five different subtypes were observed. SC-I & II were very similar in morphological features except their profile. Both the sensilla have a terminal pore and longitudinal ridges on their wall with a flexible socket. Sensilla with these kinds of features were considered as gustatory sensilla or contact chemosensilla (Altner and Prillinger, 1980; Ozaki and Tominaga, 1999) [29, 30]. Earlier studies on the antennae of termites were also reported single pore sensilla chaetica with gustatory function (Tarumingkeng *et al.*, 1976; Yanagawa *et al.*, 2009; Fu *et al.*, 2020) [19, 22, 25]. On the other hand, SC-III, IV & V found to be non-porous with longitudinal grooves on the wall and wide flexible socket and sensilla with these kind of features were reported as mechanosensory sensilla (McIver, 1975; Yanagawa *et al.*, 2009; Fu *et al.*, 2020) [31, 22, 25]. In termite colonies, vibrational cues are important and can provide information of conspecific alarm signals or arrival of predators (Kirchner *et al.*, 2010; Oberst *et al.*, 2017) [32, 33], which they perceive with the help mechanoreceptors. In *H. jepsoni* too, SC-I and II may function as gustatory and SC-III, IV and V may function as mechanosensory sensilla. The ST on the palpal segments of *H. jepsoni*, possesses a single terminal pore with shallow lines on the side wall. Similar kinds of STs were also observed in *C. formosanus* antenna (Yanagawa *et al.*, 2009) [22]. STC observed in our study has similarity with STC of *C. formosanus* which was considered as olfactory and thermosensitive in function (Fu *et al.*, 2020) [25]. In leaf cutting ant, *Atta volenweideri*, these kinds of sensilla were also reported as thermosensitive and olfactory (Ruchty *et al.*, 2005) [34]. The *H. jepsoni* is an open air column procession termite species which exhibit similar foraging behavior like ants. Thus, we supposed that both ST and STC may probably function as olfactory and thermosensitive in *H. jepsoni*. In case of SCa, we observed only one type of SCa unlike the three types described by Fu *et al.*, (2020) [25] on the antenna of *C. formosanus*. On the palpal segments, SCa were observed primarily on the distal ends including the tip of the terminal segment (segment-V). In termites, SCa were reported previously as proprioceptive mechanosensory sensilla (Leonardo and Soares, 1997; Yanagawa *et al.*, 2009; Fu *et al.*, 2020) [35, 22, 25] and in the maxilla of *H. jepsoni* too, we expect that SCa should function as mechanosensory proprioceptor and perceive the cuticular deformations of the palpal segments. GPs found on the palpal segments of *H. jepsoni* are circular openings and similar structures were also reported on other insects such as- the honey bee, *Apis mellifica*, ant, *Atta sexdens*, mosquito, *Culex quinquefasciatus* (Lacher, 1964; Kleineidam *et al.*, 2000; Syed and Leal, 2007) [36, 37, 6] and considered as CO₂ sensitive. In the termite species *C. formosanus* too, similar structures were observed and considered as sensilla ampullacea and proposed to have putative function as CO₂ receptor (Fu *et al.*, 2020). Das *et al.*, (2021) [38] also observed similar structures on the antenna of the termite species *O. parvidens*. In case of the termite species, *H. jepsoni*, we consider these small surface pores as GP function of which can be confirmed only after details functional studied of these pores. The BCPS observed on the junction of the palpal segments are small sensory peg. Similar sensory structures were also reported earlier on the antenna of *Reticulitermes chinensis* (Huang *et al.*, 2012) [24]. Since the BCPS are located only on the junctional areas of the palpal segments, thus they may probably function as proprioceptive perceiving the position of the palpal segment of *H.*

jepsoni. The nanoscale pores that observed on the surface of all palpal segments of *H. jepsoni* were also observed by Fu *et al.*, (2020) [25] on the antennal surface of *C. formosanus*. The function of these nanoscale pores is still unknown which can only be confirmed with further detailed SEM and TEM studies on these pores.

In *H. jepsoni*, the maxillary palp possesses variety of sensilla with putative function of gustatory, mechanosensory, olfactory, proprioceptive and thermosensitive. Mechanosensory (SC-III, IV, V) and proprioceptive (SCa and BCPS) were distributed on all the palpal segments, gustatory (SC-I, II) sensilla were distributed on segment-V & IV, whereas the olfactory (ST and STC) and thermosensitive (STC) sensilla were primarily distributed on the tip portion of the segment-V. Segment wise, segment-V is the most diverse palpal segment with the presence of all the five types of sensilla. The 5th palpal segment of *S. longipalpa* too, was reported as the most diverse segment with the presence of all types of sensilla and actively participates in foraging (Prakash *et al.*, 1995) [39]. On the other hand, segment-I and II are the least diverse segments with least sensilla types, mostly mechanosensory sensilla (SC-IV and V).

Conclusion

Based on the present study, we found that the maxillary palp of *H. jepsoni* bears six different types of sensilla viz., sensillum chaetica (subtypes- SC-I, II, III, IV and V), sensillum trichodea (ST), sensillum trichodea curvata (STC), sensillum campaniformia (SCa), glandular pores (GP), basiconic capitate peg sensilla (BCPS). Tiny nano scale pores were also observed on the surface of the palpal segments. These sensillar types with putative function as gustatory, mechanosensory, olfactory, thermosensitive and proprioceptive complements the sensory systems of the primary sensory organs such as antenna of the species *H. jepsoni*. This study is the first of its kind that describes the sensory structures present on the maxillary palp of the termites and this preliminary information on the external morphology of maxillary palp sensilla would serve to take up more related studies to understand the sensory structures of maxillary palp and their functional role and involvement in different behavioral responses of termites.

Acknowledgements

We would like to thank the head, department of Zoology, NEHU, Shillong for providing us all necessary facilities to do the work. We are thankful to UGC for Rajib Gandhi National Fellowship to K.S. Das. We also express our gratitude to SAIF, NEHU, for providing the scanning electron microscopy images.

References

1. Shields V. Ultrastructure of the uniporous sensilla on the galea of larval *Mamestra configurata* (Walker) (Lepidoptera: Noctuidae). *Canadian Journal of Zoology*, 2011;72:2016-2031.
2. Zacharuk RY, Shields VD. Sensilla of immature insects. *Annual Review of Entomology*, 1991;36:331-354.
3. Zhang GN, Hull-Sanders H, Hu F, Dou W, Niu J-Z, Wang J-J. Morphological characterization and distribution of sensilla on maxillary palpi of Six *Bactrocera* fruit flies (Diptera: Tephritidae). *Florida Entomology*, 2011;94:379-388.
4. Keil TA. Functional morphology of insect mechanoreceptors. *Microscopy Research and Technique*, 1997;39:506-531.
5. Chapman RF. Chemoreception: the significance of receptor numbers. *Advances in Insect Physiology*, 1982;16:247-356.
6. Syed Z, Leal WS. Maxillary palps are broad spectrum odorant detectors in *Culex quinquefasciatus*. *Chemical Senses*, 2007;32:727-738.
7. Wasserman SL, Itagaki H. The olfactory responses of the antenna and maxillary palp of the fleshfly, *Neobellieria bullata* (Diptera: Sarcophagidae), and their sensitivity to blockage of nitric oxide synthase. *Journal of Insect Physiology*, 2003;49:271-280.
8. Dweck, HKM, Ebrahim SAM, Khallaf MA. Olfactory channels associated with the *Drosophila* maxillary palp mediate short-and long-range attraction. *elife*, 2016;5:e14925.
9. Isberg E, Hillbur Y, Ignell R. Comparative study of antennal and maxillary palp olfactory sensilla of female biting midges (Diptera: Ceratopogonidae: Culicoides) in the context of host preference and phylogeny. *Journal of Medical Entomology*, 2013;5:485-492.
10. Zhang D, Wang QK, Liu X, Li K. Sensilla on antenna and maxillary palp of predaceous fly, *Lispe neimongola* Tian et Ma (Diptera: Muscidae). *Micron*, 2013;49:33-39.
11. Bohbot JD, Sparks JT, Dickens JC. The maxillary palp of *Aedes aegypti*, a model of multisensory integration. *Insect Biochemistry and Molecular Biology*, 2014;48:29-39.
12. Omondi B A, Majeed S, Ignell R. Functional development of carbon dioxide detection in the maxillary palp of *Anopheles gambiae*. *Journal of Experimental Biology*, 2015;218:2482
13. Pezzi M, Whitmore D, Chicca M, Semeraro B, Brighi F, Leis M. Ultrastructural morphology of the antenna and maxillary palp of *Sarcophaga tibialis* (Diptera: Sarcophagidae). *Journal of Medical Entomology*, 2016;53:807-814.
14. Zhang D, Wang QK, Hu DF, Li K. Cuticular structures on antennae of the bot fly, *Portschinskia magnifica* (Diptera: Oestridae). *Parasitology Research*, 2012;111:1651-1659.

15. Ramaswamy SB, Gupta AP. Sensilla of the Antennae and the Labial and Maxillary Palps of *Blattella germanica* (L.) (Dictyoptera: Blattellidae): Their Classification and Distribution. *Journal of Morphology*,1981;168:269-279.
16. Costa-Leonardo AM, Hafig I. Termite communication during different behavioral activities. In: Witzani G (ed) *Biocommunication of Animals*. Springer Science+Business Media, Dordrecht, 2014, 161-190.
17. Bagnères AG, Hanus R. Communication and social regulation in termites. In: Aquiloni L, Tricarico E (eds) *Social Recognition in Invertebrates*. Springer International Publishing, Switzerland, 2015, 193-248.
18. Prestage JJ, Slifer EH, Stephens LB. Thin-walled sensory pegs on the antenna of the termite worker, *Reticulitermes flavipes*. *Annals of Entomological Society of America*,1963;56:874-878.
19. Tarumingkeng RC, Coppel HC, Matsumura F. Morphology and ultrastructure of the antennal chemoreceptors and mechanoreceptors of worker *Coptotermes formosanus* Shiraki. *Cell and Tissue Research*,1976;173:173-178.
20. Deng TF, Mo JC, He HY, Pan CY, Cheng JA. Differences of morphology of antennae between soldiers and workers in *Coptotermes formosanus* (Isoptera: Rhinotermitidae). *Sociobiology*,2006;48:1-12.
21. Ishikawa Y, Koshikawa S, Miura T. Differences in mechanosensory hairs among castes of the damp-wood termite *Hodotermopsis sjostedti* (Isoptera: Termopsidae). *Sociobiology*,2007;50:895-907.
22. Yanagawa A, Shimizu S, Noma K, Nishikawa M, Kazumasa O, Yokohari F. Classification and distribution of antennal sensilla of the termite *Coptotermes formosanus* (Isoptera: Rhinotermitidae). *Sociobiology*,2009;54:327-349.
23. Yanagawa A, Yoshimura T, Yanagawa T, Yokohari F. Detection of a humidity difference by antennae in the termite *Coptotermes formosanus* (Isoptera: Rhinotermitidae). *Sociobiology*,2010;56:255-269.
24. Huang QY, Guan CS, Shen Q, Hu CQ, Zhu BB. Aggressive behavior and the role of antennal sensillae in the termite *Reticulitermes chinensis* (Isoptera: Rhinotermitidae). *Sociobiology*,2012;59:1239-1252.
25. Fu BX, Rong NH, Hong J, Zhu ZR, Mo JC, Zhang D. Comparative study with scanning electron microscopy on the antennal sensilla of two main castes of *Coptotermes formosanus* Shiraki (Blattaria: Rhinotermitidae). *Micron*, 2020, 102777.
26. Dey S, Baul TSB, Roy B, Dey D. A new rapid method of air-drying for scanning electron microscopy using tetramethylsilane. *Journal of Microscopy*,1989;156(2):259-261. <https://doi.org/10.1111/j.1365-2818.1989.tb02925.x>
27. Schneider, D. Insect antennae. *Annual Review of Entomology*,1964;9:103-122.
28. Zacharuk RY. Antennae and sensilla. In: Kerkut GA, Gilbert LI (ed.) *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, Vol. 6. Pergamon Press, Oxford, 1985, 1-69.
29. Altner H, Prillinger L. Ultrastructure of invertebrate chemo-, thermo- and hydroreceptors and its functional significance. *International Review of Cytology*,1980;67:69-139.
30. Ozaki M, Tominaga. IV contact chemoreceptors. In: Eguchi E, Tominaga Y (eds) *Atlas of Arthropod Sensory Receptors*. Springer-verlag, Tokyo, Hongkong, 1999, 143-154.
31. McIver SB. Structure of cuticular mechanoreceptors of arthropods. *Annual Review of Entomology*,1975;20:381-397.
32. Kirchner WH, Broecker I, Tautz J. Vibrational alarm communication in the damp-wood termite *Zootermopsis nevadensis*. *Physiological Entomology*,2010;19(3):187-190.
33. Oberst S, Bann G, Lai JC, Evans TA. Cryptic termites avoid predatory ants by eavesdropping on vibrational cues from their footsteps. *Ecology Letters*,2017;20:212-221.
34. Ruchty M, Romani R, Kuebler LS, Ruschioni S, Roces F, Isidoro N *et al*. The thermo-sensitive sensilla coeloconica of leaf-cutting ants (*Atta vollenweideri*). *Arthropod Structure and Development*,2009;38:195-205.
35. Lacher V. Electrophysiologische untersuchungen an einzelnen rezeptoren für den geruch, kohlendioxid, luftfeuchtigkeit und temperatur auf den antennen der arbeitsbiene und der drohne (*Apis mellifica* L.). *Zeitschrift für vergleichende Physiologie*,1964;54:75-84.
36. Kleineidam C, Romani R, Tautz J, Isidoro N. Ultrastructure and physiology of the CO₂ sensitive sensillum ampullaceum in the leaf-cutting ant *Atta sexdens*. *Arthropod Structure and Development*,2000;29:43-55.
37. Das KS, Marwein CB, Nonglait KCL, Choudhury S. Sensory structures on the antenna of soldier and worker castes of the termite species *Odontotermes parvidens* (Termitidae: Isoptera: Blattaria). *Microscopy Research and Technique*, 2021, 1-15. <https://doi.org/10.1002/jemt.23965>
38. Prakash S, Mendki MJ, Rao KM, Singh K, Singh RN. Sensilla on the maxillary and labial palps of the Cockroach *Supella longipalpa* Fabricius (Dictyoptera: Blattellidae). *International Journal of Insect Morphology and Embryology*,1995;24:13-34.