Original Article

Morphology and distribution of maxillary sensilla in the larvae of *Oryctes rhinoceros* (Coleoptera: Scarabaeidae)

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Abstract

Oryctes rhinoceros larvae are voracious, nonspecific detritivores and utilise the same medium for feeding and breeding. This report describes the mouthparts of *Oryctes rhinoceros* larvae and the different types of sensilla present on the maxillae. The larvae possess mouthparts specialised for biting and chewing, commonly referred to as the mandibulate type. These comprise five principal parts arranged from dorsal to ventral side *viz*., the upper lip or labrum, a pair of sclerotised and toothed mandibles, a pair of maxillae, the lower lip or labium, and the hypopharynx; all of which operate together to cut, grind, and manipulate solid food. Insects rely on their sensory systems to detect environmental cues and assess food quality, both of which are critical for feeding, growth, and reproduction. Feeding is regulated by sensory structures located on mouth parts, known as sensilla, which detect phagostimulants, deterrents, and the physical characteristics of the food. Among the mouth parts, the maxillae serve as the most important sensory structures and were, therefore, subjected to detailed examination using scanning electron microscopy (SEM). SEM analysis revealed a diverse array of sensilla, including trichoid sensilla, sensilla chaetica, basiconic sensilla, coeloconic sensilla, campaniform sensilla, and placoid sensilla, among others. This report provides a description of the morphology and the probable functions of the different types of sensilla present on the maxillae in larvae of *Oryctes rhinoceros.*

Keywords: Basiconic sensilla, coeloconic sensilla, maxilla, mouthparts, *Oryctes rhinoceros*, sensilla chaetica, trichoid sensilla.

Introduction

Insects rely on their sensory systems to detect environmental cues and monitor the quality of food they eat. These systems are critical for behaviours like food selection, which is vital for the growth and development of immature stages (larvae), metamorphosis, and reproductive development in adults.[1] *Oryctes rhinoceros* larvae are voracious, nonspecific feeders of detritus.[2] The regulation of feeding in insects involves a complex interplay of neural and endocrine signals in response to both internal and external stimuli.[1,3] Internal stimuli are mediated by singly distributed gut endocrine cells, neurosecretory cells located in the brain and ganglia of the stomatogastric nervous system, and nerve endings associated with the gut musculature. External stimuli, on the other hand, are detected by specialized sensory structures known as sensilla present on the mouth parts.

As far as external stimuli are concerned, the taste and smell (chemosensory or olfactory) receptors guide insects to food.[4] The feeding will continue till they attain a degree of satiation. External stimuli that significantly influence the decision to feed are primarily perceived by the maxilla, the principal gustatory organ in most insects. The maxilla contains specialized structures called sensilla, which are integumentary processes rich in nerve endings. Most of the sensilla act as chemoreceptors, detecting chemical cues such as phagostimulants (substances that stimulate feeding) and deterrents (substances that discourage feeding).[4] The mouthparts are also equipped with various types of mechanosensory sensilla that may detect the physical characteristics of the environment and food. The number and structure of sensilla on mouthparts and antennae may vary depending on the complexity of the insect's chemical environment, such as food availability or host plant chemicals. This adaptability is known as plasticity.[1] This report describes the morphology of the maxilla and various sensilla associated with it in the final instar larvae of *Oryctes rhinoceros.*

Materials and Methods

Actively feeding third instar larvae of the *Oryctes rhinoceros* were used for the study. The larvae were collected from the Kariavattom campus at Thiruvananthapuram and nearby areas.

Dissection of mouthparts

The mouthparts of the third-instar larvae of *Oryctes rhinoceros* were dissected as described below. The larvae were anesthetized by placing them inside a closed jar containing a cotton swab soaked in diethyl ether for approximately 10 min until they were immobilized. The larvae were then surface sterilized by wiping with a cotton dipped in 70% ethanol before dissection to remove debris and potential ectoparasites from the surface. Next, the etherized larvae were firmly secured, ventral side up, on a wax-bottomed Petri dish, placed under a dissection microscope. The mouthparts were removed sequentially using a pair of fine-tipped forceps and microscissors. This proceeded in the anatomical order in which they were arranged: isolating first the labium, then the maxillae followed by the mandibles and hypopharynx, and finally the labrum. Each isolated mouthpart was dipped in insect saline to prevent desiccation and maintain tissue turgor. The cleaned mouthparts were carefully arranged on a glass microscopic slide in their correct anatomical sequence. The specimen was then documented photographically for detailed morphological examination.

Scanning electron microscopic examination of the maxilla

The maxillary morphology was studied by Scanning Electron Micrography (SEM) following the method of Rekha and Sreekumar (2004).[5] The maxillae were dissected out carefully and subsequently washed in double-distilled water and in 0.1 M phosphate buffer. They were fixed in 2% glutaraldehyde and kept at 4^0C overnight. The specimens were then rinsed in phosphate buffer and dehydrated by being kept in two changes of 30%, 50%, 70%, 90%, and absolute acetone, each for 30 min. For critical point drying, the specimens were placed in a critical point dryer (HCP-2 Hitachi) for 30 min. They were mounted on a SEM specimen stub with double-sided adhesive tape and sputter-coated with gold palladium using an E101 ion sputtering unit (Hitachi). The processed specimens were viewed under the SEM at magnifications of 40X and 1000X, and images of maxillary sensilla were taken. Counting and measurements of sensilla were done using the software 'Image J'.

Observations and Results

The mouthparts of *Oryctes rhinoceros* larvae consist of the following structures: labrum, a pair of mandibles, a pair of maxillae, and labium (Figure 1).

Figure 1: Mouth parts of *Oryctes rhinoceros*

The labrum or upper lip, is a single flap located on the dorsal side. Just below it lies a pair of mandibles, which are heavily sclerotized (hardened) and toothed. These function as jaws for grasping, cutting, and crushing food. Situated beneath the mandibles is a pair of maxillae, which assist in manipulating food. On the ventral side is the labium, or lower lip, which is a median flap. The labium plays a role in both food manipulation and sensory perception. The hypopharynx is a tongue-like structure situated between the labrum and the labium.

Structure of the maxilla

The detailed structure of the maxilla (plural maxillae) is shown in Figures 2A and 2B. Insects have paired maxillae, located behind the mandibles. The maxilla has two basal segments, namely the proximal cardo (plural cardines), and the distal stipes (plural stipites). The cardo is comparatively a small structure located basally. The stipes is the most conspicuous proximal part, and it bears the maxillary palp, galea, and lacinia (plurals galeae and laciniae). Diagrammatic sketches of the maxilla from dorsal and ventral views are given in Figures 2A and 2B.

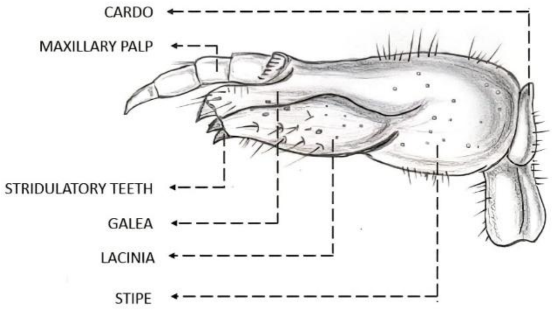


Figure 2A: Ventral view of the Maxilla

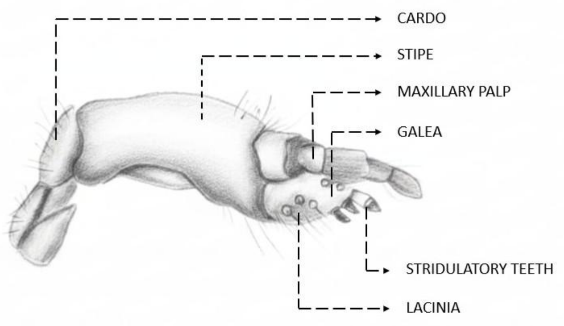
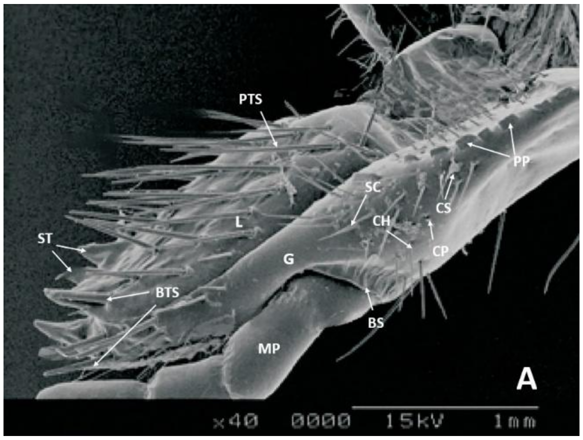


Figure 2B: Dorsal view of the Maxilla

The lacinia and galea remain partially fused and can be identified separately only from the underside. Of the two structures, the galea can be identified as the outer lobe located between the maxillary palp and lacinia. Lacinia is the larger lobe placed inside and has stridulatory teeth that are truncated (Figure 3). The maxillary palps are five segmented appendage-like structures held by stipes. The palps are sensory structures that help in food selection.



G=Galea; L=Lacinia, MP=Maxillary Palp, BS=Böhm sensilla, BTS=Blunt-tipped Trichoid Sensilla, PTS=Pointed-tipped Trichoid Sensilla, CH=Cuticular Hairs, CP=Cuticular Pores, CS=Campaniform Sensilla, PP=Pore Plate, SC=Sensilla Chaetica, ST=Stridulatory Teeth

Figure 3: Scanning Electron Micrography image of Maxilla (40X)

Sensory structures of the maxilla

The scanning electron micrographs of the maxilla revealed that, in the larvae of *Oryctes rhinoceros*, all four parts of the maxilla, i.e., lacinia, galea, stipes, and maxillary palp, were densely covered with different types of sensilla. The sensilla were observed to be primarily of the trichoid and basiconic types (Figure 3).

Sensilla trichoidea (Trichoid sensilla)

Under SEM, the trichoid sensilla were categorized into two main types. The first type consisted of blunt-tipped sensilla, which were thick and long with a rounded apical end. The second type comprised pointed-tipped sensilla, which were thin and elongated with tapering tips (Figures 3, 4A and 4B). The trichoid sensilla could also be categorised into different types based on length (Table 1). They remain anchored within the sockets formed from the integument.

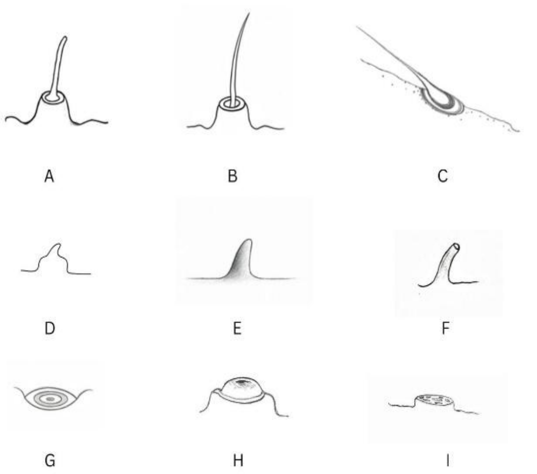
The pointed-tipped sensilla were located mostly on the basal part of the lacinia, with a few occurring on the basal region of the galea and on the stipes. They exhibited an attachment angle of 0.83 ± 0.04° and a length of 4.53 ± 1.82 µm.

The blunt-tipped trichoid sensilla were predominantly distributed on the apical region of the lacinia, numbering approximately 20–30 sensilla. They were also present in large numbers on the apical part of the galea. These blunt-tipped sensilla had an attachment angle of 11.08 ± 5.61° and a length of 0.54 ± 0.06 µm.

Table 1: Structure and distribution of Trichoid Sensilla and Sensilla Chaetica in *Oryctes rhinoceros*

Type of sensilla	Appearance of the setae	Length (µm)	Angle of attachment (degrees)	Distribution in the maxilla	Number observed	Functions
Trichoid sensilla (Blunt tipped)	Thick, Long, Tip blunt	0.540 ±0.06*	11.08 ±5.61*	Apex of Lacinia	≈ 20-30	Olfactory, Thermo-reception
Trichoid sensilla (Pointed tipped)	Thin, Long, Tip tapering	0.832 ±0.04*	4.53 ±1.82*	Apex of Galea	≈ 70-80	Olfactory, Chemo-Mechanosensory
Chaetica Sensilla	Thin, long, Tip pointed	0.271 ±0.02*	23.3 ±6.22*	Galea, apex of Lacinia	Numerous	Chemosensory, Gustatory

*Each number represents Mean ± Standard Deviation of 10 observations



A=Trichoid Sensilla (blunt), B=Trichoid Sensilla (pointed), C=Sensilla Chaetica, D=Basiconic Sensilla (pointed), E= Basiconic Sensilla (cylindrical), F= Coeloconic Sensilla (cylindrical), G=Coeloconic Sensilla (saucer-shaped), H=Campaniform Sensilla, I=Placoid Sensilla (pore plate)

Figure 4: Diagrammatic sketches of maxillary sensilla in *Oryctes rhinoceros*

Sensilla chaetica (Chaetica sensilla)

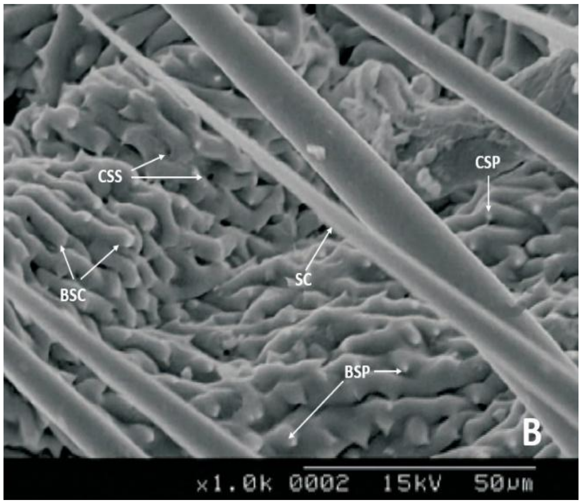
These were long, hair-like bristles with a tapering tip, like trichoid sensilla (Figures 3, 4C and 5). However, they were sturdy and had a thick-walled cuticle, typically set in a socket, occasionally found very deep. The angle of attachment was 23.30±6.22° and measured 0.27±0.02 μm in length. They were found to be densely distributed on the galea, particularly towards the apex and the basal region. They were also present on the apical parts of the lacinia and maxillary palps. Although they occur on both the upper and lower surfaces, most of them are oriented towards the interior, *i.e.,* the food-facing side.

Basiconic sensilla

These structures possessed a prominent anchoring region and resembled a peg. Some were pointed, with a broad base and a tapering tip, while others were short and cylindrical. Both, pointed and cylindrical types were abundantly present on the galea, often occurring in clusters (Figures 4D, 4E and 5).

Coeloconic sensilla

Some of these appeared very much like basiconic cylindrical type sensilla and were distinguishable due to the presence of an apical pore leading to a cavity inside. The coeloconic sensilla vary in length. A few of them were saucer shaped (Figures 4F, 4G and 5). The coeloconic sensilla were fewer in number and were found primarily on the galeae and on the lower surface of the apical regions of the palps.



BSC=Basiconic Sensilla (Cylindrical), BSP=Basiconic Sensilla (Pointed), CSP=Coeloconic sensilla (Peg-like), CSS=Coeloconic Sensilla (saucer-shaped), SC=Sensilla Chaetica

Figure 5: Distribution of sensilla on galea (1000X)

Companiform sensilla

These were large dome-shaped sensilla, surrounded by a circular ridge. They were identified on galea (Figures 3 and 4H).

Placoid sensilla (Pore plates)

Placoid sensilla or pore plates were found to be plate-like projecting structures with several pits. These were found on the basal part of the galea and stipes (Figures 3 and 4I). In addition to the pore plates, minute singly distributed cuticular pits were also found distributed over several regions of the maxilla, particularly on the basal parts of the galea.

Böhm sensilla (Bristles)

These were minute bristle-like structures present at the rim of the stipes of the maxilla. An array of Böhm sensilla may appear like a bush border (Figure 3).

Cuticular hairs

Fine cuticular hairs were observed on the basal part of the galea, and a few were also present near its apex (Figure 3).

Discussion

The present study reveals that the mouthparts of *Oryctes rhinoceros* belong to the mandibulate type, which are used for gathering, masticating, and ingesting solid food. The mouth parts consist of a labrum, a pair of mandibles, a pair of maxillae, a hypopharynx, and a labium.[6] The labrum is a broad lobe in front of the mouth and forms the upper lip. It is a single, fused plate, possessing on its surface several sensory setae.[1] On its inner side, it is membranous and may be produced into a median lobe, the epipharynx. Beneath the labrum, a pair of jaw-like mandibles, which serve as pincers, can be seen. They are heavily sclerotized structures having cutting edges that move transversely to grasp or cut food.[7] In the entognathous groups and the Archaeognatha, the mandibles are relatively long and slender, and they have only a single point of articulation with the head capsule.[1] Maxillae are a pair of appendages that is divisible into the cardo, which articulates with the head; the stipes, which bears a sensory maxillary palp; and the galea and lacinia. The maxillae serve to manipulate food. The labium, or lower lip, is a median flap located on the ventral side. Unlike many other insects, the labial components in *Oryctes rhinoceros* larvae, including the labial palps, remain fused and cannot be individually distinguished. The labium plays a role in both food manipulation and sensory perception.[1] The labrum and hypopharynx do not represent true appendages due to their non-metameric origin; however, they are also considered buccal appendages due to their important role in feeding.[8]

In *Oryctes rhinoceros* larvae, the maxillae exhibit typical anatomical features. They are paired structures located behind the mandibles and consist of a basal segment, the cardo, followed by the stipes, which bears the lacinia, galea, and maxillary palp. The lacinia, the larger inner lobe, is equipped with short stridulatory teeth. Both the lacinia and galea function together to grasp and crumble food. The maxillary palps are five-segmented, appendage-like sensory structures that play a crucial role in food selection by assessing the edibility of potential food through tasting and tactile evaluation. Overall, the maxillae work in coordination with the mandibles to manipulate food, holding it in place so that it can be chewed or sliced by the mandibles.[1]

The maxilla, being the most important sensory structure among the mouthparts, possesses various types of sensilla. The most prominent sensilla present on the maxilla are the trichoid types. They are slender structures remaining anchored within the sockets of integument, permitting free movement.[4] Among the different trichoid sensilla found on the maxilla, the pointed types are supposed to have olfactory and chemo-mechanosensory function, whereas the blunt-tipped types are found to play only a chemosensory role.[9] It was observed in this study that in *Oryctes rhinoceros* larvae, the blunt-tipped trichoid sensilla were predominantly distributed on the apical regions of the lacinia and galea, whereas the pointed-tipped ones were found on the basal part. The blunt-tipped trichoid sensilla present on maxilla of *Oryctes rhinoceros* exhibit an attachment angle of $11.07 \pm 5.61^{\circ}$, as observed under SEM. The mean length is measured to be $0.54 \pm 0.06 \mu m$. The pointed-tipped sensilla are found mostly on the basal part of the lacinia. They are also sparsely distributed on the basal part of the galea. They are 0.83 ±0.04µm long with an attachment angle of 4.52 ±1.82°. In *Polistes dorsalis,* the blunt-tipped trichoid sensilla are found to be nearly straight or slightly curved with a smooth cuticular surface, measuring 16–35 µm in length. The hair bases are oriented at an angle of 60–90° relative to the antennal surface.[10] In *Bembidion properans*, the trichoid sensilla are characterized by their long, hair-like morphology, firmly anchored within distinct sockets, indicating a non-flexible and stable attachment, suggestive of a mechanosensory or protective function.[11] In male moths, trichoid sensilla exhibit specific responsiveness to female sex pheromones, functioning as primary olfactory receptors involved in pheromone detection and mate recognition.[4,12] No significant sexual dimorphism was observed in the number of immovable blunt-tipped trichoid sensilla in the ground beetles *Bembidion lampros*, *Bembidion properans*, and *Polistes dorsalis*, suggesting that these sensilla are probably involved in detecting aggregation pheromones produced by conspecific individuals.[13]

Sensilla chaetica are specialized cuticular structures that function primarily as mechanoreceptors.[4] The present study reveals that in *Oryctes rhinoceros* larvae, sensilla chaetica are prominently distributed on the galea, lacinia, and to some extent on the maxillary palps. They occur on both the upper and lower surfaces; however, a denser concentration is found on the inner, food-facing side, particularly near the apical part. Their positioning reflects functional adaptation to feeding, facilitating food assessment. The sensilla chaetica are typically about 0.271 µm in length on average and show an attachment angle of approximately 23.3°. Sensilla chaetica appear as sturdy and bristle-like structures. In the maxillary palp of *Poecilus cupreus*, their sockets are flexible, and the shafts are smooth, ranging from 6–12 µm in length.[14] They have a grooved architecture that likely reinforces mechanical strength while simultaneously increasing the effective surface area, which may enhance the reception of tactile or chemical stimuli. In *Microvelia douglasi* and *Neoalardus typicus* these are described as stiff hair-like structures that are long and straight and thicker than sensilla trichoidea. [15] These sensilla terminate in sharply pointed tips and are anchored within deep, broad sockets. They are straight or slightly curved and are oriented either perpendicular to the antennal surface or angled slightly so that they point toward the antennal apex.[16] The three subtypes of sensilla chaetica—long, distal, and stout, are described in cerambycids by Dyer and Seabrook (1975).[17] These are likely common across all subfamilies, including Cerambycinae, Lamiinae, Lepturinae, and Spondylidinae.

Basiconic sensilla observed in the present study appears to have a folded basal membrane with a prominent anchoring region and a peg-like apical part.[18] In *Oryctes rhinoceros* larvae, the basiconic sensilla are of two types: some are short and cylindrical in shape, while others possess a short, broad base with a tapered apex. The basiconic sensilla are associated with chemosensory and gustatory reception.[19] A rather good correlation between morphology and function has been demonstrated in insect sensilla.[20] Veena *et al*. (2011) have observed degenerative changes in the morphology of trichoid and basiconic sensilla in frontal ganglionectomised larvae, which may cause weakened chemosensory input from the maxillary sensory system because of decreased intake of food. [21]

The coeloconic sensillum is a thermo- and hygroreceptor organ.[22,23] Although the shape of thermo- and hygroreceptor sensilla may vary among insects, they appear very much like basiconic sensilla and are distinguishable due to the presence of an apical pore leading to a cavity inside.[24] In *Oryctes rhinoceros* larvae, the coeloconic sensilla vary in length and are also differently shaped; some appear like pegs, and a few of them are saucer shaped. They are less numerous and are located mostly on the galeae and lower surface of the apical parts of the palps. In *Hylamorpha elegans*, sensilla coeloconica are significantly more numerous in males than in females.[25] In *Bombyx mori*, the neurons of the coeloconic sensilla respond to a range of green leaf volatiles (C_3–C_{10}), as well as to certain aromatic compounds and monoterpenes.[26]

The present study suggests that in *Oryctes rhinoceros*, the coeloconic sensilla can be recognised into two types. Type I coeloconic sensilla appear as small, peg-like structures set within cuticular pits and are typically associated with chemosensory and thermo-hygrosensory functions.[27] In *Lithobius forficatus* and *Scutigera coleoptrata*, type 1 sensilla are described as thick, predominantly conical structures.[28] In *Oryctes rhinoceros* larvae, the saucer-shaped depressions, often with a slightly protruding area bearing a pore, represent the type II coeloconic sensilla. Their functional role may be more specialized, being strongly associated with chemoreception, particularly the detection of specific volatile cues related to decaying organic matter. In *Holotrichia parallela*, a type II coeloconic sensilla is described, possessing multiple finger-like cuticular projections emerging from the distal portion of the shaft. Such specialized surface ornamentations are associated with sensory function.[29] According to Meinecke (1975), coeloconic sensilla are characterized by a short morphology with a rounded apex.[27] In *Asanada socotrana* and *Craterostigmus tasmanianus*, type II sensilla are described as slender structures with rounded tips.[28]

Böhm's bristles are tiny, specialized hair-like mechanosensory structures found on the antennae and function as proprioceptors.[29] The present study shows that in *Oryctes rhinoceros* larvae, these are located at the outer rim of the stipes of the maxilla. They are observed to be present at the base between the scape and the pedicel of antennae in *Eucryptorrhynchus chinensis* and *Eucryptorrhynchus brandti*.[29] In *Paussus favieri* they are observed as thorn-like bristles, sharp or blunt-tipped, straight or slightly curved, set in a wide socket.[15] In *Phyllotreta striolata,* Böhm bristles are surrounded by a deep cuticular socket, and the slender conical shaft is smooth and probably movable.[30] The concentration of Böhm sensilla at the intersegmental joints, between the scape and the head, as well as between the scape and the pedicel, in *Bembidion properans* suggests that these sensilla probably perceive the antennal position and movements. It is proposed that these intersegmental sensilla, in combination with the antennal shaft, may perceive both wind direction and strength in anemotactic reactions.[11] An array of Böhm sensilla may appear like a bush border as observed in this study. They are tactile and detect the movement of the maxillary palp.

A campaniform sensillum (CFS) is an elementary mechanosensory organ that functions in sensing mechanical strain and deformation in an insect's exoskeleton.[31] These sensilla in *Oryctes rhinoceros* appear as large dome-shaped structures surrounded by a circular ridge. Merivee *et al.* (2000) have noticed campaniform sensilla at the base of the antenna.[32] In *Paussus favieri* the campaniform sensilla are represented by cuticular caps, emerging from large sockets. The cap is cylindrical and sub-truncate at the apex, with a small pore in the middle. Cross sections show a peg-in-pit appearance occupying a round cavity. The cuticular walls of the sensillum are thick and without pores in *Paussus favieri.*[33] These sensilla in carabid beetle larvae are regularly distributed on the labial palp surface, and additionally, they form a ring around the apex. The external body is dome-shaped, and a flexible socket gives the cuticular insertion. On the maxillary palps of *Calathus mollis,* their distribution and size are similar; however, two rings are usually evident.[14]

Placoid sensilla or pore plates are chemoreceptors, primarily involved in olfaction. [34] The present study shows that in *Oryctes rhinoceros*, these projecting plate-like sensilla with multiple pores are distributed across various regions of the maxilla, particularly on the basal part of the galea. On the antennae, these are typically visible as flat, circular, or oval plates embedded in the cuticle and they have a porous surface.[34] The pore plates help in detecting airborne chemical signals such as pheromones for mating and plant odours for locating food sources and egg laying.[35] The placoid sensilla appear as a convex and rugged plate whose infoldings form a circle of irregular cavities in *Melolontha melolontha.*[36] In *Popillia japonica*, placoid sensilla are more numerous in males than in females, suggesting their role in the detection of female pheromones during mating.[37] They consist of thin oval cuticular plates, with no difference in size between sexes. In *Hylamorpha elegans*, the plates of the placoid sensilla containing pores are seen bulging outwards.[25]

Our study reveals that the maxilla of *Oryctes rhinoceros* bears a complex array of morphologically and functionally distinct sensilla, including trichoid sensilla, sensilla chaetica, basiconic sensilla, coeloconic sensilla, placoid sensilla, and Böhm sensilla, in addition to a small number of singly distributed cuticular pores and hairs. All these structures are associated with feeding and are specialized for detecting various physical and chemical stimuli. Among the mouthparts, the maxillae are regarded as the most important sensory structures; nevertheless, they are not the only ones that bear sensilla. A comprehensive investigation of feeding-related sensilla should therefore include other mouthparts and associated structures such as the labrum and labium, and antennae.

Conclusion

The present study reveals that the mouthparts of *Oryctes rhinoceros* larvae are structurally adapted for consuming solid food. The maxillae play a crucial role in feeding, facilitating food selection and rejection, processes that are aided by the diverse sensilla distributed on them. This adaptation is particularly important since the larvae are non-selective feeders and rely entirely on the feeding medium itself for their development and metamorphosis.

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