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RESEARCH ARTICLE

Light and scanning electron microscopy study of the olfactory organ of Milkfish, *Chanos chanos*

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Abstract. This study investigates the ultrastructural and histological organization of the olfactory organ in milkfish (*Chanos chanos*). The olfactory rosette is fan-shaped and consists of 26-28 lamellae radiating from a central raphe located on the floor of the nasal chamber. Each lamella contains a connective tissue core covered by a two-layered epithelium composed of sensory and non-sensory regions. The sensory epithelium, located on the dorsal lamellar processes and the apical regions of the lamellae, contains three types of olfactory receptor neurons: ciliated, microvillous, and rod cells. The non-sensory epithelium, distributed along the basal, median, and outer regions of the lamellae, comprises mucous, chloride-like, lymphatic, basal, and supporting cells (both ciliated and non-ciliated). The stratified epithelial cells of the central raphe are densely packed and exhibit prominent microridges. The structural organization of the olfactory mucosa indicates a high degree of functional specialization associated with chemoreception in aquatic environments.

Keywords: Olfactory system, structural organization, microanatomy, chemosensation, Milkfishes

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Introduction

In fish, chemical senses are categorized into three distinct modalities: olfaction, solitary chemosensory cells, and the taste system. Among these, olfaction is a biologically essential component of chemoreception, playing important roles in homing, kin recognition, predator avoidance, feeding, mate selection, and other behaviors (Wilson 2004). Olfactory cues are detected by sensory receptor cells in the olfactory organ, eliciting corresponding behavioral responses in the organism. Dissolved substances reach and interact with olfactory cells as water flows into the olfactory chamber through the anterior inlet and exits via the posterior outlet (Fishelson 1995). Extensive studies have been conducted to describe the structure of the olfactory epithelium across diverse teleost species (Hansen and Zielinski 2005, Kuciel et al. 2011, Ghosh and Chakrabarti 2016, Pintos et al. 2020, Aicardi et al. 2022, Ghosh 2024, Klimenkov et al. 2025, Al-Zahaby et al. 2025). Different species exhibit significant variation in the number, shape, degree of development, and arrangement of olfactory lamellae across taxonomic levels and ecological contexts. The floor of the nasal chamber is lined with mucosa, which is organized into lamellae comprising a mosaic of numerous receptor cells interspersed with non-receptor cells; this

arrangement varies among fishes depending on their feeding niches. Fish classified as microsmatic have few lamellae in their olfactory rosette, whereas macrosmatic fish have many lamellae. Mediosmatic refers to an intermediate condition between microsmatic and macrosmatic states (Atta 2013). Yamamoto (1982) classified fish olfactory organs into eight morphological types based on the arrangement of lamellae around the central axis: Type B: single longitudinal; Type C: single transversal; Type D: numerous longitudinal; Type E: fan-shaped; Type F: radiative; Type G: fish bone-like, and Type H: double-sided comb-like with a raphe.

However, detailed studies on the cellular organization and topological architecture of the olfactory organ in Gonorynchiformes species are lacking. *Chanos chanos* (Gonorynchiformes: Chanidae) is an omnivorous species that feeds on a wide variety of food items, including diatoms, zooplankton, various types of algae, benthic invertebrates, small fishes, detritus, and even trace amounts of sand particles (Vasava et al. 2018). In aquatic ecosystems that are often characterized by low light but are rich in dissolved chemical compounds, the olfactory sense plays a crucial role in the survival and successful adaptation of fish to their surroundings. Consequently, it is important to investigate in detail the functional characteristics of the different cell types that comprise the olfactory organ of this species. The present study aims to elucidate the tissue organization and surface ultrastructure of various cell types in the olfactory epithelium of milkfish, *Chanos chanos*, using light and scanning electron microscopy.

Materials and Methods

Obtaining specimens and collecting tissues

Twelve sexually mature specimens of *C. chanos* (mean total length, 48 ± 6.27 cm) were obtained from brackish water bheries in South 24 Parganas, West Bengal, India. The fish were anesthetized using an overdose of 2-phenoxyethanol and euthanized. The olfactory tissues were then carefully dissected from the nasal cavities and immediately processed for histological and scanning electron microscopy investigations.

Preparation for histology

The olfactory tissues were fixed in aqueous Bouin's solution for 18-24 h. After fixation, picric acid was removed by repeatedly washing the tissues in 70% ethanol. The samples were then dehydrated through a graded ethanol series and cleared with benzene. The tissues were infiltrated with paraffin wax (56-58°C) for 1.5 h in a thermostat-controlled vacuum paraffin embedding bath and subsequently embedded in paraffin blocks. Sections of 4 μm thickness were cut from the paraffin blocks using a rotary microtome (Weswox MT-1090A). The sections were mounted on Mayer's albumin-coated glass slides, deparaffinized, and stained with Mallory's Triple (MT) stain (Mallory 1936) and Azan Trichrome (AT) stain (Heidenhain 1915). The stained sections were examined under a Zeiss Primo Star compound microscope equipped with a Tucsen 5.0 MP camera, and images were captured at different magnifications.

Preparation for scanning electron microscopy

Following dissection, 2.5% glutaraldehyde buffered with 0.1 M phosphate buffer (pH 7.4) was perfused into the olfactory rosettes of the nasal cavity for 10–15 min. After dissecting the entire olfactory rosettes, their surfaces were carefully cleaned of mucus and debris using a 1% Tween 40 (polyoxyethylene sorbitan monopalmitate) solution. The samples were washed in the same solution, fixed overnight at 4°C in 2.5% glutaraldehyde, and then post-fixed for 2 h at room temperature in 1% osmium tetroxide (OsO_4) buffered with 0.1 M phosphate buffer (pH 7.4). Following dehydration through an ascending acetone series, the samples were immersed in isopentyl acetate and dried using the critical point drying

technique (Cohen et al. 1968) with liquid carbon dioxide. The dried tissues were mounted on metal stubs, coated with a 15 nm layer of platinum using a sputter coater (BT-150 Coater, Hind High Vacuum Co. Pvt. Ltd.), and examined using a ZEISS EVO 18 scanning electron microscope.

Results

In *C. chanos*, a well-developed ovoid olfactory rosette is formed by the mucosa lining the floor of the nasal cavity, which extends upward into a series of lamellae (Fig. 1A). The olfactory rosette, composed of 26-28 leaflets of varying diameters radiating from the central axis, is fan-shaped and nearly occupies the nasal chamber. The lamellae are attached to the raphe at their proximal ends and are secured to the nasal chamber wall by their convex inner edges. The raphe, formed by an infolding of the ventral wall of the nasal cavity, creates a broad horizontal platform that supports and anchors the olfactory rosette. A small amount of fibrous connective tissue secures the olfactory organ within the nasal cavity. The structural organization of the olfactory organ is further characterized by the presence of dorsal lamellar processes (Figs. 1A and 1B). The olfactosensory epithelium appears as discrete islets on the dorsal lamellar processes and the apical portion of the lamella, whereas the non-sensory epithelium is distributed along the basal, median, and outer regions of the lamella.

Three morphologically distinct types of olfactory receptor cells—ciliated, microvillous, and rod-shaped—were identified in the sensory islets (Fig. 1C). The Type-I ciliated receptor cell possesses an apical process that terminates at the free epithelial surface. The compact mass of cilia gives the sensory islet a hair-like appearance. Type-II microvillous receptor cells, characterized by numerous microvilli at the superficial end of their apical processes, exhibit a distinct surface morphology and are interspersed among the ciliated receptor cells. Type-III rod receptor cells are distinguished by a single slender cytoplasmic rod protruding from the free surface and are devoid of both cilia and microvilli. Numerous mucin droplets and occasional blood cells are present on the surface of the olfactory mucosa.

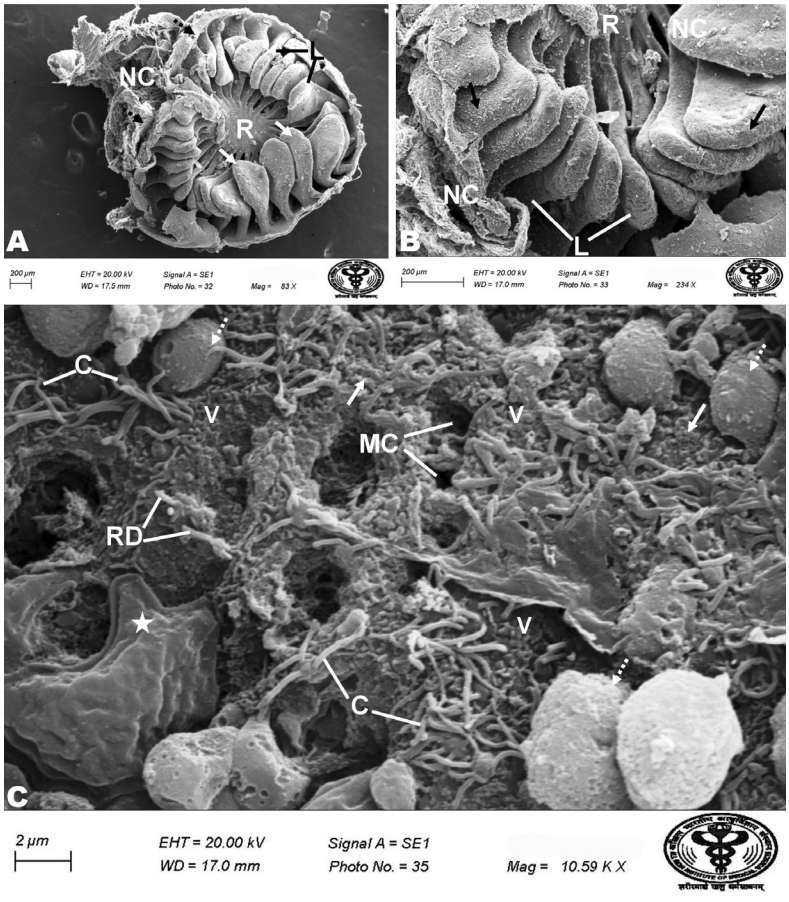

Figure 1. Scanning electron micrographs show the morphology of the olfactory apparatus in *Chanos chanos*. (A) Shows a dorsal view of the olfactory rosette situated within the nasal cavity (NC), comprising multiple lamellae (L) arranged radially around the central raphe (R). Arrows highlight the presence of distinct dorsal processes on the lamellae. (B) The lamellae (L) are anchored to the central raphe (R) by their proximal ends and affixed to the nasal cavity (NC) along their inner margins. Arrows indicate the presence of sensory islets distributed on the lamellar surface. (C) The olfactosensory epithelium displays ciliated neuronal cells (C), microvillous neurons (arrowheads), and rod neurons (RD). Notably, blood cells (asterisk) and secreted mucin (broken arrows) from mucous cells (MC) are present, while solid arrows indicate chloride-like cells.

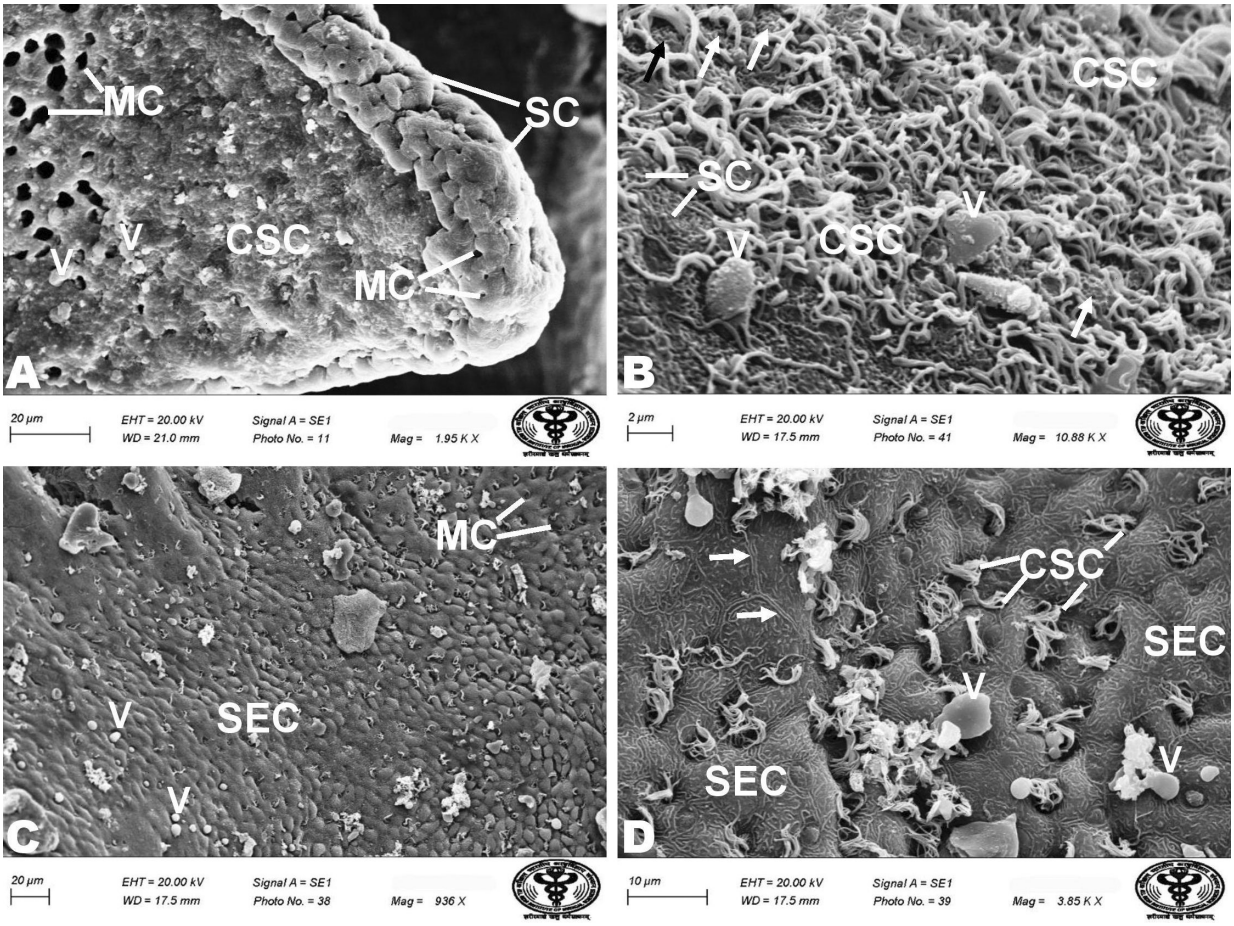

Figure 2. Scanning electron micrographs of the olfactory organ in *C. chanos*. (A) The lateral surface of the lamellae exhibits a non-sensory epithelium, comprising numerous mucous cells (MC), ciliated supporting cells (CSC), and non-ciliated supporting cells (SC). Arrowheads mark the presence of mucin masses. (B) A portion of the non-sensory epithelium showing chloride-like cells (solid arrows), along with tufts of CSC and SC. Mucin masses are indicated by arrowheads. (C) The raphe contains stratified epithelial cells (SEC) and mucous cells (MC). Arrowheads depict mucin droplets overlying the SEC. (D) A surface view of the raphe shows compactly arranged SEC characterized by prominent microridges, interspersed with CSC. Solid arrows indicate the distinctive double-ridge structures of the SEC, while arrowheads mark the presence of mucin plugs.

The non-sensory epithelium comprises clusters of ciliated non-sensory cells interspersed with supporting cells bearing prominent microridges (Fig. 2A). The extensive layer of non-sensory cilia imparts a spongy appearance to the epithelial surface. Irregularly sized openings of mucous cells are distributed throughout the non-sensory epithelium, with a substantial accumulation of mucus observed within these openings and overlying the supporting cells. Chloride-like cells are present in both sensory and non-sensory regions of the olfactory mucosa (Figs. 1C and 2B). Their outer surfaces exhibit a distinctive morphology, characterized by microvilli-like projections and a well-defined cellular profile. These cells frequently display small apical invaginations or pits, and in some cases, convex protrusions are also observed.

The raphe is composed of oval to spherical stratified epithelial cells with intricate microridges on their apical surfaces, interspersed with mucous cells (Fig. 2C). These epithelial cells form a characteristic double-ridged structure due to their close attachment to neighbouring cells (Fig. 2D). A tuft of ciliated supporting cells surrounds the opening of each mucous cell.

Histologically, the lamella (or lamina) of the olfactory apparatus comprises a central core (submucosa) lined on both sides by a well-organized

epithelial layer. A distinct basement membrane separates the mucosa from the underlying submucosa (Figs. 3A and 3B). The central core contains dense connective tissue bundles with nerve fibers, blood vessels, and pigment cells, providing structural support to the lamellae (Figs. 3C and 3F). The mucosa varies in thickness and exhibits folding in certain regions. Its cellular components include receptor cells, supporting cells, chloride-like cells, lymphatic cells, mucous cells, and basal cells.

The ciliated receptor cells possess prominent cell bodies with spherical nuclei and extend cylindrical dendrites to the epithelial surface, where the distal end expands into an olfactory vesicle within the interlamellar space (Fig. 3E). In some regions, the proximal portion of the ciliated receptor cell gives rise to an axonal process extending into the submucosa and contributing to nerve fascicles (Fig. 3D). Microvillous receptor cells are fewer in number and are located more superficially within the mucosa. Rod receptor cells exhibit slender cell bodies with scant cytoplasm surrounding elongated nuclei.

Supporting (sustentacular) cells are differentiated into non-ciliated and ciliated types. Non-ciliated supporting cells are interspersed among receptor cells and possess prominent basophilic oval nuclei with relatively short cell bodies (Fig. 3F). In contrast, ciliated supporting cells are columnar, oriented perpendicularly to the basement membrane, and extend apical processes bearing numerous elongated cilia to the epithelial surface (Fig. 3C). Their nuclei are positioned at varying levels, contributing to the stratified appearance of the epithelium.

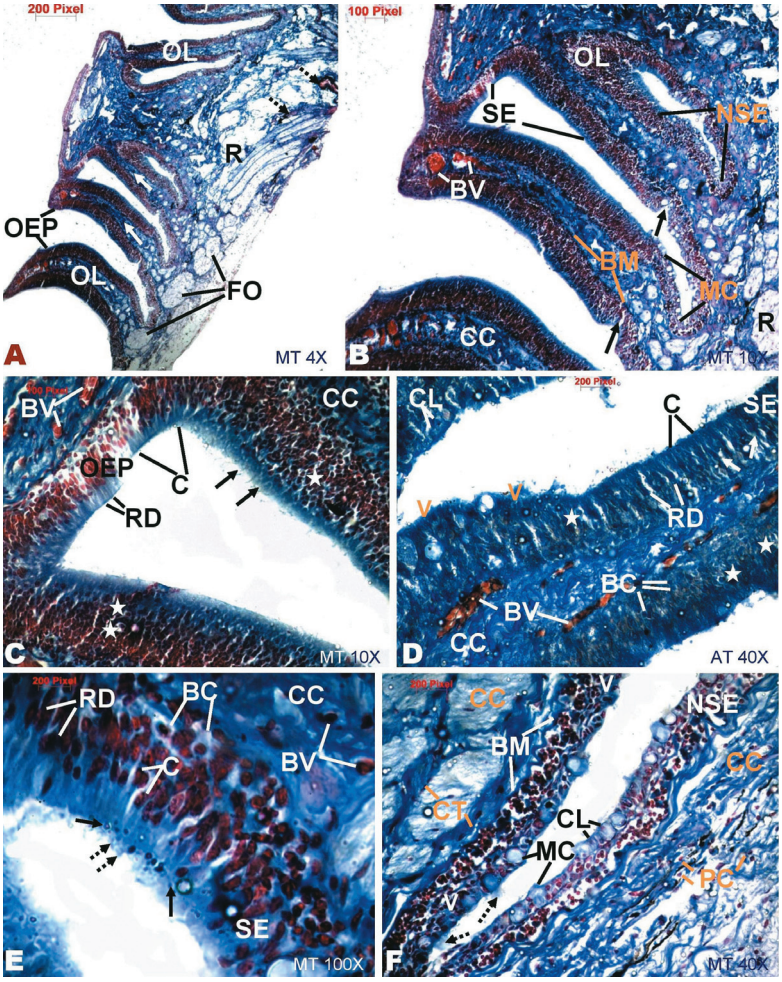

Figure 3. Histological sections of the olfactory rosette in *C. chanos*, stained with Mallory's Triple (MT) and Azan Trichrome (AT) stains. (A) Olfactory lamellae (OL), radiating from the raphe (R), display the olfactory epithelium (OEP) and central core (solid arrows). Broken arrows indicate the presence of blood capillaries, while fila olfactoria (FO) are observed within the raphe. (B) OL, supported by R, exhibit both sensory epithelium (SE) and non-sensory epithelium (NSE), containing numerous mucous cells (MC). Note the presence of the basement membrane (BM), separating the olfactory epithelium from the central core (CC). BV denotes blood vessels, and arrows indicate folding of the mucosa. (C) Fragments of the OEP show ciliated receptor cells (C), rod receptor cells (RD), and ciliated supporting cells (arrows), along with lymphatic cells (asterisks). Note the presence of BV within CC. (D) The sensory epithelium (SE) is characterized by the presence of ciliated (C), microvillous (arrowheads), and rod receptor cells (RD). Chloride-like cells (CL), lymphatic cells (asterisks), and basal cells (BC) are scattered throughout the mucosa. Note that the axonal processes (solid arrows) of C extend toward CC, which contains BV. (E) A magnified view of the SE shows various types of receptor cells, including microvillous cells (solid arrows), rod cells (RD), and ciliated cells with protruding dendrites (C) adorned with olfactory vesicles (broken arrows). Note the presence of BC in the deeper zone of the epithelium and BV within CC. (F) The non-sensory epithelium (NSE) contains MC with secreted mucin (broken arrows), non-ciliated supporting cells (arrowheads), and CL. CC, comprising pigment cells (PC) and bundles of connective tissue (CT), is separated from the mucosa by BM.

Chloride-like cells are spherical or pear-shaped and located near the mucosal lining. They are characterized by lightly stained globose nuclei and granular cytoplasm (Figs. 3D and 3F). Lymphatic cells are cuboidal or ovoid, with conspicuous nuclei, and are distributed in the middle region of the mucosa (Figs. 3C and 3D). The superficial layer of the mucosa, particularly near the base of the lamellae, is rich in mucous cells (Fig. 3B), which exhibit muciferous activity and variable morphology. Basal cells are located in the deepest layer above the basement membrane and display darkly stained nuclei with distinct chromatin. Their occasional migration toward upper layers suggests a role in epithelial renewal.

The raphe contains thick, non-ciliated supporting cells and a well-developed submucosa rich in collagen fibers, histiocytes, fibroblasts, and fila olfactoria. It is also well vascularized, with capillary branches extending into the olfactory lamellae (Figs. 3A and 3B).

Discussion

The structure of the olfactory organ and its degree of specialization in teleosts are significantly influenced by the ecological niche they occupy. The present study demonstrates that the fan-shaped, multilamellar olfactory rosette of *C. chanos* comprises approximately 26-28 lamellae arranged around a central axis. This species, which belongs to the macrosmatic group of fishes, exhibits pronounced behavioral responses to olfactory stimulation. Based on the arrangement of lamellae around the central axis, the olfactory rosette of *C. chanos* is classified as Type-G (fan-shaped), according to Yamamoto (1982). The lamellae are arranged on either side of a median raphe and correspond to Bateson's (1889) rosette type-III or Burne's (1909) rosette column-I. Furthermore, according to Teichmann (1954), this oval-shaped olfactory organ falls under the category of eye-nose fishes, indicating that this group possesses equally well-developed optic and olfactory senses. Effective transmission of chemical cues along the olfactory lining requires adequate ventilation of the nasal chamber (Belanger et al. 2003).

The olfactory epithelium of *C. chanos* is a complex system comprising both sensory and non-sensory regions. The distribution of sensory and non-sensory epithelium on the lamellae is discontinuous and corresponds to Type-II, as described by Yamamoto (1982). The sensory epithelium is restricted to the dorsal lamellar processes and the apical portion of each lamella. This arrangement is likely adaptive, as the chemosensory cells within the sensory islets are oriented toward the incoming water current, thereby facilitating the detection of multiple olfactory cues. Furthermore, the folding of the lamellae markedly increases the olfactory surface area, enhancing the efficiency of odorant detection (Zeiske et al. 1976).

The sensory epithelium comprises three morphologically distinct types of olfactory receptor neurons: ciliated, microvillous, and rod-shaped cells. Although these neuron types coexist within the epithelium, their relative proportions vary among different species (Zeiske et al. 2003). According to Yamamoto and Ueda (1978), ciliated receptor cells correspond to Type I cells. Microvillous receptor cells are associated with Type-II cells, as described by Müller and Marc (1984), whereas rod receptor cells correspond to Type IV cells identified by Ichikawa and Ueda (1977). According to Hamdani and Dřving (2007), each of these neuron types transmits distinct chemical signals that elicit specific behavioral responses to olfactory cues, which are critical for various life processes in fish. The distal end of ciliated receptor cells bears an apical swelling, known as the olfactory knob, which has been identified as the primary locus of odorant receptor sites (Hansen et al. 2004). These neurons are responsible for the early recognition of odors and the transduction of odorant molecules (Simpson 2018). Kuciel et al. (2011) reported that the apical region of ciliated receptor cells, which bears cilia, is involved in specific ligand–receptor interactions. Microvillous receptor cells, characterized by surface microvilli, play a role in detecting pheromones and a wide range of chemical

substances in the aquatic environment (Mokhtar and Abd-Elhafeez 2014). According to Hernádi (1993), the presence of rod receptor cells may reflect adaptation to a novel physiological environment, whereas Yamamoto (1982) suggested that they may also arise as a result of the aging of ciliated receptor cells. These morphologically distinct receptor cell types are therefore likely to mediate responses to specific classes of odorants (Meredith et al. 2012).

Supporting cells in the olfactory epithelium have been reported to possess functional significance beyond mere structural support, including the secretion of products onto the epithelial surface (Hara 1994). According to Yamamoto and Ueda (1977), the presence of directed water flow over the lamellae is indicated by the uniform bending of supporting cell cilia in one direction across large areas of the mucosa. Simpson (2018) reported that ciliary clusters lack chemosensory function but may contribute to mechanical support. Tufts of ciliated non-sensory cells surround the openings of mucous cells, which are strategically positioned within the non-sensory epithelium. This arrangement likely facilitates mucus transport and dispersion across the epithelial surface. Microridges on the apical surface of stratified epithelial cells help maintain the mucus layer across the mucosa and protect sensory cells from mechanical damage (Mandal et al. 2005). Secreted mucin likely assists in trapping fine detritus and maintaining sensory neurons in a responsive state (Bandyopadhyay and Datta 1996). Banerjee (1993) proposed that the mucus layer also acts as an ion trap, delaying the penetration of heavy metals into the underlying cells. Chloride cells in the olfactory organ likely contribute to establishing a specific ionic environment on the surface of the olfactory mucosa and are considered an electrogenic mechanism that secretes potassium into the receptor medium (Ruzhinskaya et al. 2001). Additionally, lymphatic cells in the olfactory mucosa play a role in supporting cellular immunity (Lieschke and Trede 2009, Kim et al. 2019). Basal cells appear to function as stem cells, becoming active during cell turnover and regeneration of the olfactory epithelium (Farbman 1994). Undifferentiated basal stem cells give rise to new olfactory receptor neurons (Fitzgerald et al. 2012).

Further experimental studies using transmission electron microscopy and immunohistochemistry are warranted to better understand the chemosensory processes related to the ecological and feeding habits of this species.

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