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Original Article

The histology and surface morphology of the olfactory organ in Silond catfish, *Silonia silondia* (Hamilton, 1822)

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Abstract: Histological and scanning electron microscopy techniques were employed to study the olfactory organ of *Silonia silondia* (Siluriformes: Schilbeidae). The thorough examination revealed a well-developed olfactory organ characterized by a series of intricately arranged lamellae that were elegantly inserted into a narrow midline raphe, forming an elongated rosette structure. It comprised the olfactory lamellae, adorned with olfactory epithelium and a distinct median raphe. On each lamella, sensory and nonsensory epithelium were distinctly segregated. The dorsal lamellar processes housed the sensory area, while the nonsensory area enveloped the remainder of the olfactory lamellae. Histologically, each lamella exhibited a central lamellar space, enveloped on either side by olfactory epithelium characterized by receptor cells, supporting cells, lymphatic cells, mast cells, mucous cells, and basal cells. The sensory epithelium contained three morphologically distinct receptor cells: ciliated, microvillous, and rod types. The cellular organization of the olfactory lining was explored in conjunction with the chemosensory system of the fish under investigation.

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Introduction

Olfaction plays an important role for fishes, intricately guiding their fundamental behavioral patterns. The olfactory sense is pivotal in various aspects of a fish's life, including food foraging, predator evasion, kin identification, nest localization, reproductive rituals, maternal-offspring bonding, homing instincts, and many other vital activities (Farbman, 1994). In the aquatic ecosystem, where light may be scarce but dissolved compounds abound, the olfactory system of fishes shows remarkable adaptations tailored to their specific ecological niches and lifestyles, distinguishing them from higher vertebrates (Bone and Moore, 2008). The olfactory organ of fish serves as a distance range chemical sensor and exhibits remarkable development in certain nocturnal species and those inhabiting dark or turbid aquatic environments. Numerous researchers have previously documented the structure and function of olfactory organs in fishes (Lazzari et al., 2007; Yoshihara, 2014; Smith and Bhatnagar, 2019; Pintos et al., 2020; Triana-Garcia et al., 2021; Ghosh, 2022; Klimenkov et al., 2023; Dieris et al., 2024).

The sense of olfaction is primarily achieved through olfactory receptor cells located on the epithelial surface within the nasal cavity. These receptor cells detect odour molecules in the aquatic environment and transmit signals directly to the central nervous system via the olfactory tract. Among teleosts, there is considerable variation in the olfactory organ's gross morphology, topology, and cellular structure. The ecological niche inhabited by fish species significantly influences their olfactory structure and degree of specialization (Hara, 1994). However, there remains a scarcity of understanding regarding the structural organization and functional importance of various cells lining the olfactory mucosa of schilbid catfishes, particularly concerning their ecological specificity and lifestyle adaptations.

Silonia silondia is a carnivorous riverine catfish that occurs in shoals and feeds on copepods, prawns, crabs, insects, nauplii, molluscs, and other young fishes (Gupta, 2015). This investigation's objective is to delineate the cellular attributes of the olfactory

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lining and their particular relevance in the olfaction process of the Silond catfish, *S. silondia* (Hamilton, 1822), using light and scanning electron microscopy techniques.

Materials and Methods

Source of materials: The investigation was conducted on ten adult specimens of *S. silondia* (with a mean total length of 52±16.07 cm) captured from the Bhagirathi-Hooghly River at Kalyani and surrounding areas in West Bengal using traditional fishing gear. The specimens were anaesthetized with an overdose of 2-phenoxyethanol and then euthanized. Subsequently, the olfactory rosettes were surgically removed from the nasal cavity of the specimens and immediately processed for histological and scanning electron microscopy studies.

Histological method: The olfactory rosettes were fixed in aqueous Bouin's fluid for approximately 18-24 h. Following fixation, the tissues were thoroughly washed in 70% ethanol, dehydrated through a graded ethanol series, and cleared with xylene. Subsequently, the tissues were infiltrated with paraffin wax (56-58˚C) using a thermostat vacuum paraffin-embedding bath for 1 h and 30 min and then embedded in paraffin blocks. Transverse sections of tissue blocks, with a thickness of 4 μm, were obtained using a rotary microtome (Weswox MT-1090A), and the tissue sections were stretched onto Mayer's albuminized glass slides. The dewaxed tissue sections were then stained using Mallory's Triple (MT) stain (Mallory, 1936) and Azan Trichome (AT) stain (Heidenhain, 1915). Finally, the staining slides were examined and photographed using a light microscope (Zeiss Primo Star) equipped with a Tucsen 5.0 MP camera at various magnifications.

Scanning electron microscopy method: After dissection, the olfactory rosettes within the nasal cavity were perfused with 2.5% glutaraldehyde buffered with 0.1 M phosphate buffer (pH 7.4) for 10-15 min. The entire olfactory rosettes were dissected and thoroughly washed with a 1% Tween 40 (Polyoxyethylene sorbitan monopalmitate) solution to remove mucus and debris from the surface. The samples were rinsed in the same buffer, followed by fixation in 2.5% glutaraldehyde (primary fixative) for 24 h at 4°C and subsequently fixed in 1% osmium tetroxide buffered with 0.1 M phosphate buffer (pH 7.4) for an additional 2 h at room temperature. The samples were then dehydrated using an ascending series of acetone, immersed in isoamyl acetate, dried in liquid CO_2 at the critical point (Cohen et al., 1968), and mounted with glue on aluminum stubs. After sputter-coating with platinum, the samples were observed using a ZEISS EVO 18 scanning electron microscope.

Results

The olfactory organ of *S. silondia* is elongated, nearly entirely occupying the nasal chamber (Fig. 1A). It comprises a series of approximately 46±8 olfactory lamellae arranged parallel to one another within a vertical plane. A lengthy and slender median raphe runs through the center of the rosette, extending from its anterior to the posterior end. The olfactory lamellae remain affixed to the wall of the nasal chamber by their ventral margins and are connected to the raphe by their proximal ends. The number of lamellae in the rosette expands with the length of the fish, with new lamellae being added at both the anterior and posterior ends. The dorsal lamellar process gracefully extends from the distal free margin of each lamella, adding to the structural elegance of the olfactory organ. The lining membrane of the nasal chamber remains smooth beyond the area covered by the olfactory rosette, indicating a distinct demarcation in anatomical structure. Sensory and nonsensory areas are distinctly situated on each lamella. Typically, the dorsal olfactory processes house the sensory region, while the nonsensory area covers the remaining part of the olfactory lamellae (Fig. 1B).

The sensory islets exhibit three distinct types of olfactory receptor cells: ciliated, microvillous, and rod, each characterized by unique surface specialization. These include a tuft of cilia, numerous microvilli, and a lengthened perch-like texture, respectively. Ciliated receptor cells stand out due to the presence of elongated cilia, typically arranged in

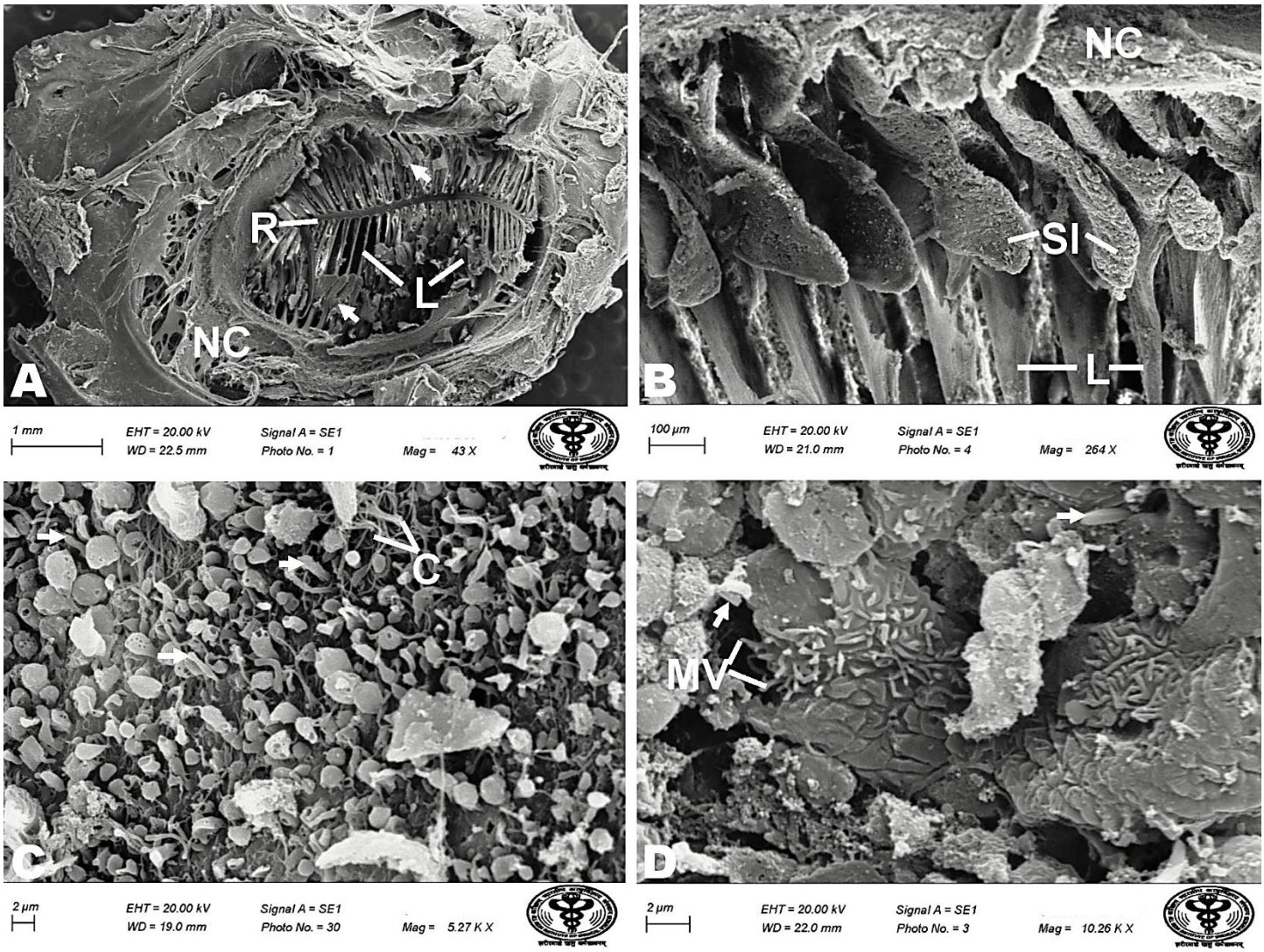

Figure 1. Photomicrographs of the olfactory structure of *Silonia silondia* by scanning electron microscopy (SEM). **(A)** Inhabiting the nasal chamber (NC), the elongated olfactory rosette shows olfactory lamellae (L) radiating from the median raphe (R). Arrows mark the dorsal processes of the lamella, **(B)** L attached with NC shows sensory islets (SI), **(C)** The apical part of the sensory epithelium shows ciliated receptor cells (C) and rod receptor cells (arrows), and **(D)** The sensory epithelium is embossed with microvillous receptor cells (MV) and rod receptor cells (arrows).

clusters (Fig. 1C). The epithelial surface showcases an array of numerous microvillous projections, imparting a sculpted appearance to the mucosal lining (Fig. 1D). Rod cells, in contrast, are characterized by rod-like projections tapering to a point from the knob-like apex. Olfactory rods are not evenly distributed across the sensory islets but are mostly clustered posterolaterally in each dorsal process (Fig. 1C).

The non-sensory epithelial surface displays non-sensory cells adorned with compound cilia alongside clusters of stratified epithelial cells featuring microfolds (Figs. 2A, B). The non-sensory epithelium's surface presents a spongy texture, attributed to a dense layer of non-sensory cilia covering it (Fig. 2C). Throughout the nonsensory epithelium and raphe, numerous perforations are evident, representing the sites of erupted mucous cells. Sparse blood cells and abundant mucin droplets are discernible atop the stratified epithelial cells. Moreover, the surface of the midline raphe comprises stratified epithelial cells with prominent microridges on their exposed surface (Fig. 2D). Notably, no cilia are observed on the raphe.

Histologically, each olfactory lamella comprises a central core or submucosa, flanked on both sides by a cellular layer of mucosa (Fig. 3A). The basement

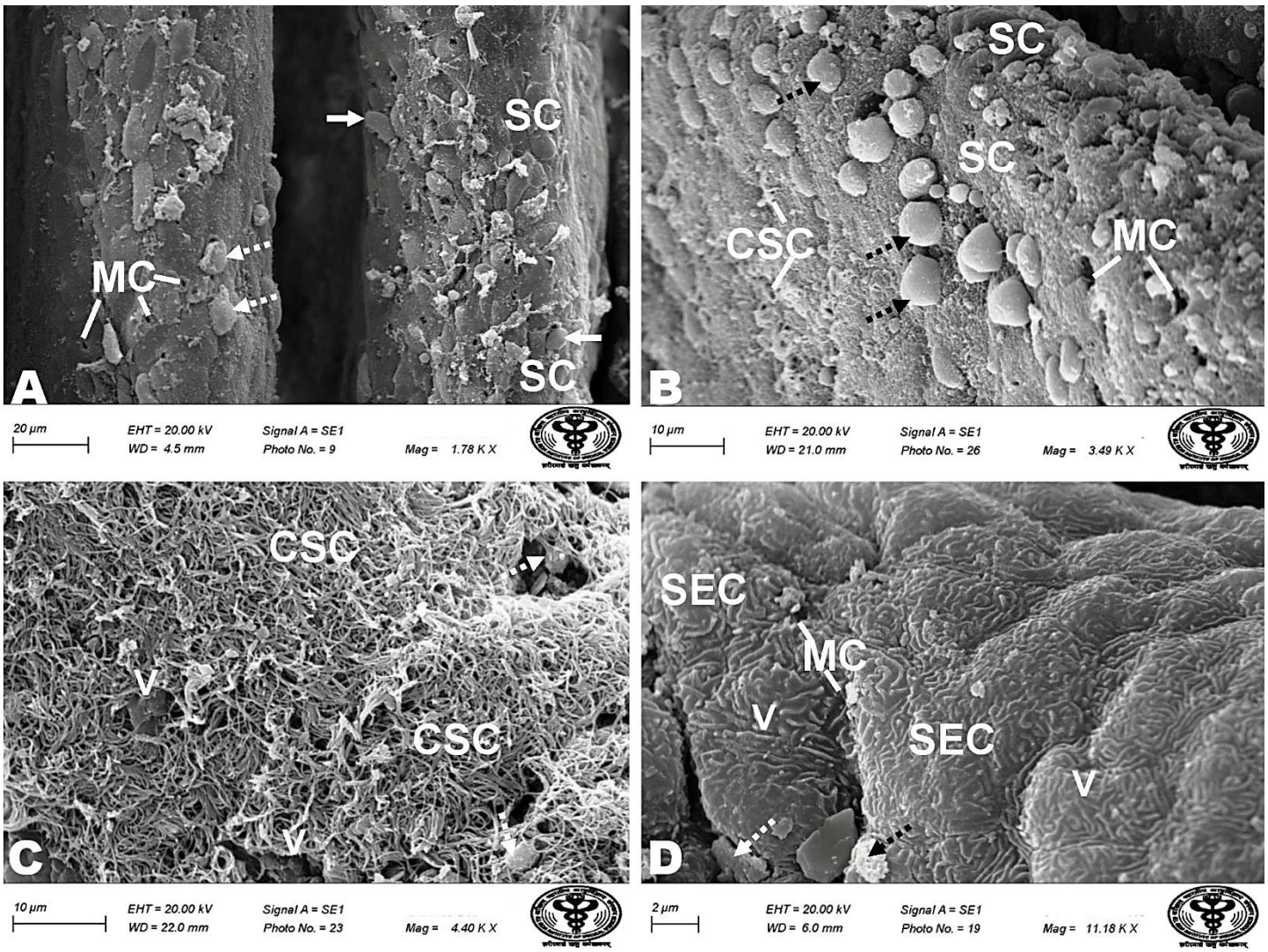

Figure 2. Scanning electron microscopy (SEM) photomicrographs of the olfactory epithelium of *Silonia silondia*. **(A)** Non-sensory epithelium (NSE) shows supporting cells (SC), blood cells (Solid arrows) and mucous cells (MC) with secreted mucin (broken arrows), **(B)** Upon magnification, NSE exhibits the opening of mucous cells (MC), as well as ciliated (CSC) and non-ciliated (SC) supporting cells. Notably, mucin balls (broken arrows) are observed atop SC, **(C)** The nonsensory epithelium appears densely packed, and ciliated non-sensory cells (CSC) and supporting cells (arrow heads) are relatively scarce. Broken arrows mark mucin balls, and **(D)** Raphe contains stratified epithelial cells (SEC) bearing microfolds (arrowheads) and MC. Note the presence of mucin masses (arrowheads) over SEC.

membrane is demarcated and stands as a partition between the central core and mucosa (Fig. 3B). The central core is densely supplied with blood vessels interwoven amidst collagen connective tissue fibres, pigment cells, fibroblasts and nerve fibres (Figs. 3A-D). The raphe consists of nonciliated supporting cells and lacks sensory cells. Blood supply is present within the raphe, with branches of blood capillaries extending to all the lamellae (Fig. 3A). The olfactory epithelium is thick and consists of sensory and nonsesory cells. The ciliated receptor cells are columnar, featuring more or less spherical nuclei and prominent cell bodies adorned with thin, elongated dendrites that form a swelling known as the olfactory knob at the mucosal surface (Fig. 3C). A thin proximal process of axon extends up to the central core, where it forms synaptic contact. In certain regions of the sensory epithelium, these receptor cells show characteristics typical of bipolar neurons (Fig. 3D). Microvillous receptor cells are dispersed throughout the sensory zone of the lamella. They are characterized by their lightly stained appearance and small size. Microvillous receptor cells are scattered over the sensory zone of the lamella. They are lightly stained, small in size, with a cell body positioned midway (Fig. 3C). The rod receptor cells are characterized by

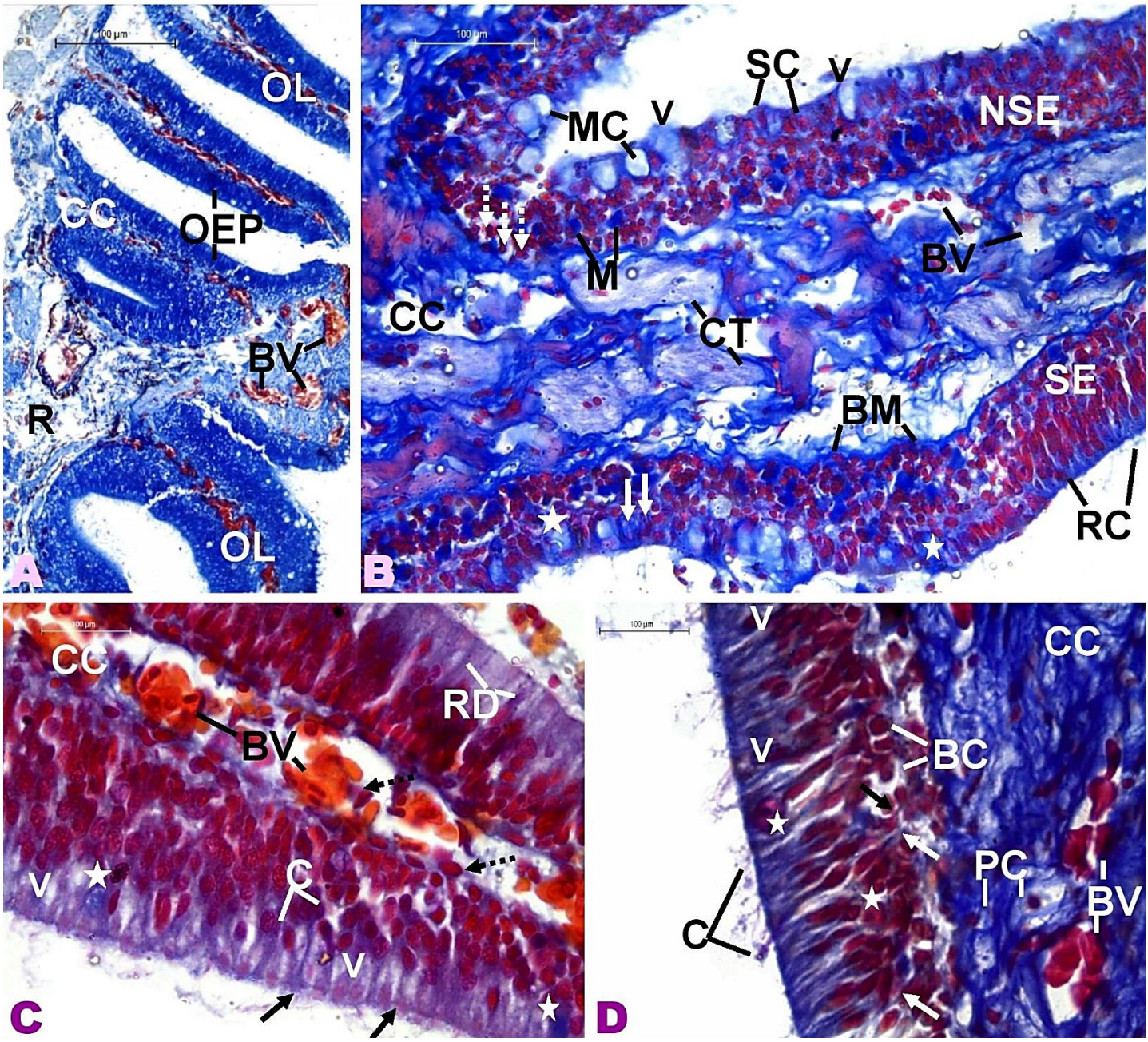

Figure 3. Photomicrographs of the histoarchitecture of olfactory lamellae of *Silonia silondia* stained with Mallory's Triple (MT) and Azan Trichome (AT) stain. **(A)** Olfactory lamellae (OL), firmly attached to the raphe (R), display the olfactory epithelium (OEP), which is separated by a central core (CC). Blood vessels (BV) are observed within the central core and the raphe (MT 5X), **(B)** The sensory epithelium (SE) is characterized by the presence of various receptor cells (RC), while the nonsensory epithelium (NSE) comprises mast cells (M), lymphatic cells (asterisks), mucous cells (MC) secreting mucins (arrowheads), ciliated supporting cells (solid arrows), and non-ciliated supporting cells (SC). The connective tissues (CT) and blood vessels (BV) within CC are differentiated from the olfactory epithelium by the presence of a basement membrane (BM) (MT 15X), **(C)** The magnified sensory epithelium reveals ciliated receptor cells (C) with knob-like structures (solid arrows) alongside rod receptor cells (RD) and microvillous receptor cells (arrowheads). Lymphatic cells are marked with asterisks, while blood vessels (BV) and pigment cells (broken arrows) are observed within the CC region (AT 100X), and **(D)** OEP exhibits ciliated receptor cells characterized by their protruding dendrites (C), lymphatic cells (asterisks), and BC. Within CC area, BV and pigment cells (PC) are present. Notably, bipolar neurons (arrow heads) and axonal processes (solid arrows) towards CC are discernible (MT 100X).

narrow, protruding dendrites and a slender body with scanty cytoplasm surrounding deeply stained nuclei (Fig. 3C). The supporting cells are categorized into ciliated supporting cells and non-ciliated supporting cells (Fig. 3B). The ciliated supporting cells are located on the peripheral surface of the lamella. They

are tall and abundantly ciliated, featuring spherical or oval nuclei with clear chromatin material. In contrast, the non-ciliated supporting cells are shorter and possess darkly stained oval nuclei with faintly visible chromatin material. Their cytoplasm exhibits a granular appearance. Ovoid lymphatic cells are dispersed throughout the mucosa, characterized by intensely stained nuclei and fuchsinophilic cytoplasm. The nuclei occupy most of the cell's volume (Figs. 3B-D). Mast cells are indeed small in size, round-shaped, with relatively little cytoplasm and polymorphous nuclei. The mucous cells are confined in the surface zone of the epithelium, intermingled with supporting cells (Fig. 3B). They are globular in shape, showing muciferous activity (Fig. 3B). Basal cells are uniformly distributed in the basal zone of the epithelium above the basement membrane. They are oval-shaped and contain clearly visible rounded nuclei (Figs. 3B-C).

Discussions

The olfactory epithelium, comprised of sensory and nonsensory cells, is commonly situated along the floor of the nasal chamber, where it frequently forms folded structures known as olfactory lamellae. In certain species, modifications to the olfactory structure may manifest as adaptations to suit particular environmental conditions (Zeiske et al., 1992). *Silonia silondia* features elongated olfactory rosettes housing approximately 46±8 lamellae, placing it within Teichmann's (1954) third category known as nose fishes, where olfaction supersedes sight in importance. This type of olfactory organ aligns with Pol Gerard's (1954) third category, denoted as macrosmic, indicating a well-developed sense of smell primarily for locating food. Classified according to lamellar distribution by Yamamoto (1982), it falls under Type-H, characterized by a double-sided comb-like appearance along the midline raphe. The distribution of sensory and non-sensory areas within the olfactory lamella varies among fish species, influenced by their ecological niche and feeding behaviors. The findings of this study demonstrate that the olfactosensory epithelium is arranged in the shape of islets situated within the dorsal processes of the lamella, whereas the broader sections of the lamellae are composed of non-sensory epithelium. This arrangement likely arises because the sensory islets are positioned to face the flow of incoming water current, resulting in a greater number of cellular layers and a richer population of chemosensory cells compared to the epithelium on the opposite side.

In the present study concerning *S. silondia*, the sensory epithelium exhibits three morphologically distinct types of receptor cells: ciliated, microvillous, and rod cells. Among these, the ciliated receptor cells are particularly noteworthy as they play a crucial role in the olfactory transduction mechanism, responding to odorous substances and facilitating the detection of food. These ciliated receptor cells correspond to type I cells as classified by Yamamoto and Ueda (1978), while the microvillous receptor cells align with type II cells identified by Muller and Marc (1984), and the rod receptor cells resemble type IV cells described by Ichikawa and Ueda (1977). Each receptor cell carries specific chemical stimuli that elicit distinctive behaviours in response to olfactory cues, which are integral to vital life processes in fish (Hamdani and Døving, 2007). The dendritic processes of ciliated receptor cells harbor receptor sites for olfactory stimuli, enabling fish to detect food and explore their environment (Hansen et al., 2004). Additionally, the bipolar neurons of receptor cells are of particular interest as they play a role in the olfactory transduction mechanism and respond to odorous substances. It is widely recognized that receptor cells within the olfactory epithelium can sense chemical changes in the surrounding environment (Data and Das, 1980). Zippel et al. (1997) noted that ciliated receptor cells respond to amino acids while microvillous receptor cells react to pheromones. The olfactory knob adorned with sensory hairs and microvilli of receptor cells suggests various useful functions and abilities for recognizing chemical cues (Mokhtar and Abd-Elhafeez, 2014). Bhute and Baile (2007) also argued that microvillous receptor neurons perceive and process pheromone signals, which are crucial for breeding behaviors in species like *Labeo rohita*.

Muller and Marc (1984) documented the presence of rod receptor cells displaying receptive properties in goldfish and catfish. Hernadi (1993) noted that the presence of rod cells is associated with the habitat and physiological climate of the organism. The existence of rod receptor cells indicates the aging of ciliated receptor cells as described by Yamamoto (1982).

The non-sensory epithelium, characterized by diffuse non-sensory cilia, lacks sensory function but likely aids in mechanical dissociation processes. The movement of these cilia plays a role in propelling the mucin mass secreted by mucous cells, as described by Bandyopadhyay and Datta (1998). Additionally, the ciliary movement drives streams of incoming water containing dissolved chemicals between the olfactory lamellae and across the sensory islets. The nonsensory epithelium and raphe, comprised of stratified epithelial cells adorned with microridges on their apical surface, are crucial in anchoring a protective mucus film over the epithelial membrane. This film acts as a barrier, shielding the epithelium from various harmful substances. The mucin secreted by mucous cells likely plays a vital role as a medium through which odorants diffuse (Waryani et al., 2013). Furthermore, the mucin produced by the mucous cells in the raphe aids in facilitating the smooth flow of water within the olfactory chamber by binding and trapping microscopic debris, which is subsequently expelled through the posterior nostril (Bandyopadhyay and Datta, 1996). Mast cells within the olfactory mucosa are thought to significantly influence the reproductive processes of *Labeo rohita* (Bhute and Baile, 2007) and Baltic trout (Bertmer, 1982). These cells can modulate the metabolic activity of receptor cells, consequently impacting the sensitivity of the olfactory epithelium. The presence of lymphatic cells within the epithelial layer contributes to cellular immunity, as noted by Lieschke and Trede (2009) and Kim et al. (2019). The basal cells reside within the deeper layers of the mucosa and are believed to serve as progenitors for both receptor and supporting cells, as suggested by Zeiske et al. (1992) and Frabman (1994). Additionally, Moller et al. (1989) proposed that basal cells may function as stem cells responsible for regenerating lost or damaged ciliated non-sensory and mucous cells.

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