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Anatomy and Histology of the Olfactory Organ of Asian Swamp Eel *Monopterus albus*

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ABSTRACT **The anatomy and histology of the olfactory organ of *Monopterus albus* was investigated using stereo microscopy, light microscopy, and scanning electron microscopy. The external structure of the olfactory organ exhibited closed anterior and posterior nostrils parallel to the skin surface. The interior structure consisted of a pipe-like chamber, and lower and upper accessory nasal sacs. The olfactory chamber was composed of the sensory and non-sensory epithelium, and an unidentified organ. The sensory epithelium of the pseudostratified epithelial layer was composed of olfactory receptor neurons, supporting cells, basal cells, and lymphatic cells; and the non-sensory epithelium of the stratified squamous layer contained stratified epithelial cells and mucous cells with acidic mucopolysaccharides. The presence of intraepithelial blood capillaries and abundant dermal vascularization in the sensory epithelium of the olfactory chamber may provide strong histological evidence that respiration occurs through the olfactory epithelium.**

Key words: Olfactory organ, pipe-like chamber, intraepithelial blood capillary, dermal vascularization, respiratory function

INTRODUCTION

Fully aquatic teleost fishes typically respire through their gills, but there are exceptional cases where they can supplement deficient oxygen through the gastrointestinal surface (Grosell *et al*., 2010), swim bladder (Fernandes *et al*., 2012), branchial chamber (Sundin *et al*., 1999), labyrinthine organ (Zaccone *et al*., 2019), and skin (Glover *et al*., 2013). Among these types of respiration, the skin can provide 5~30% of the necessary oxygen within a fish's body, and amphibious fishes can obtain more than 50% supplementary oxygen through the skin (Graham, 1997, 2011). Regarding cutaneous respiration, the skin as a type of epithelial tissue has revealed the following histological evidence: 1) intraepidermal blood capillaries, 2) rich vascularization within the dermis, 3) the presence of large cells, such as mucous cells, club cells, and swollen cells, and 4) reduced or absent scales (Glover *et al*., 2013).

The olfaction in teleost fishes plays a crucial role in triggering ecological habits and behavioral responses related to searching for food, feeding, social communication, mating, predator detection, and contamination detection in their habitat (Bone and Moore, 2008). For chemoreception, the olfactory organ has adapted to the physical environment of its habitat and unique ecological characteristics, resulting in a variety of positions, structures, and distributional patterns in the nostril, olfactory chamber, and accessory nasal sac, as well as the olfactory epithelium and olfactory receptor neurons by species (Kasumyan, 2004). Among these, the olfactory epithelium is typically a pseudostratified epithelial layer, including olfactory receptor neurons, supporting cells, basal cells, and mucous cells, without blood capillaries (Kasumyan, 2004). However, during histological studies on muddy fishes, intraepithelial vessels and vascularization were found in the olfactory epithelium of *Monopterus albus* that were indicative of aerial respiration.

The Asian swamp eel *M. albus* is widely distributed in East Asia including rivers in India, Indonesia, China, Japan, and South Korea flowing into the Western and Southern seas (Chae *et al*., 2019). *M. albus* prefers shallow water, such as muddy riverbeds, ponds, and rice fields, and has a high

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tolerance for drastic temperature changes and exposure to poor oxygen conditions during the dry season (Lefevre *et al*., 2016). This eel also has a respiratory behavior of exposing its snout above the water's surface to intake air into its mouth (Liem, 1967). It has been reported that *M. albus* obtains supplementary oxygen from such behavior through the skin and buccal cavity (Liem, 1967; Damsgaard *et al*., 2014), and the amount of oxygen obtained is approximately three times more than it acquires underwater (Liem, 1967). The olfactory organ of *M. albus* also was assumed to have an additional respiratory function based on epithelial modification with intraepithelial blood capillaries (Beon *et al*., 2013; Glover *et al*., 2013). Therefore, we aimed to describe the new type of olfactory respiratory organ in *M. albus* based on histological findings of intraepithelial blood capillaries and dermal rich vascularization.

MATERIALS AND METHODS

1. Specimen preparation

For morphological and histological analysis, 10 adult *M. albus* (Fig. 2A) were caught in a rice field between May and June 2023 (35°53′27″N, 127°07′01″E, Jeonmi-dong, Jeonju-si, Jeonllabuk-do, South Korea, Fig. 1; Fig. 2C) using a scoop net (4×4 mm mesh size). The captured specimens were immediately anesthetized with 0.1% m-aminobenzoic acid ethyl ester methanesulfonate solution (MS222, Sigma-Aldrich, St Louis, MO, USA) in the field, and then six specimens were fixed in 10% neutral buffered formalin solution (pH 7.4) and the rest were fixed in 2.5% neutral glutaraldehyde solution (pH 7.4; EMS, USA). The collection was primarily conducted at night after observing the swamp eel exposing its snout above the water surface (Kim and Park, 2002; Fig. 2B). The experimental procedure for this study strictly followed the rules of the "Institutional Animal Care and Use Committee of Jeonbuk National University" (License Number: CBNU-2023-00060).

2. Microscopic investigation

To determine the anatomy of the olfactory organ, the external morphology was observed under a stereo microscope (Stemi DV4, Carl Zeiss, Germany). Skin tissue was dissected using surgical blades (stainless No. 10 and 11, Japan) to expose the internal structure, and filmed with a digital camera (TG-3, Olympus, Japan). To confirm the cytological characteristics and structure of the olfactory epithelium, the tissue sections were fixed for 24 hours and were dehydrated in ascending concentrations of alcohol (50%, 60%, 70%, 80%, 90%, 100%) for 1 hour each. Then, the sections were cleared in xylene for 1 hour. The paraffin blocks (Paraplast, Oxford) were five micrometer-sectioned using a microtome (Leica RM 2255, Leica, Germany), and stained

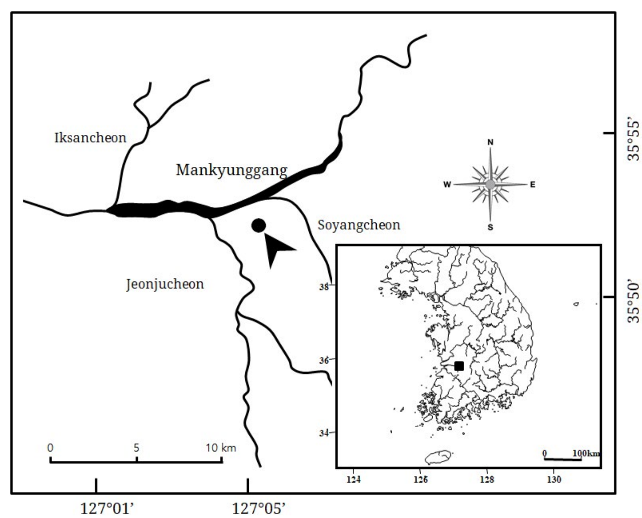

Fig. 1. The collection site (arrowhead) of *Monopterus albus* in Jeonmi-dong, Jeonju-si, Jeollabuk-do, South Korea.

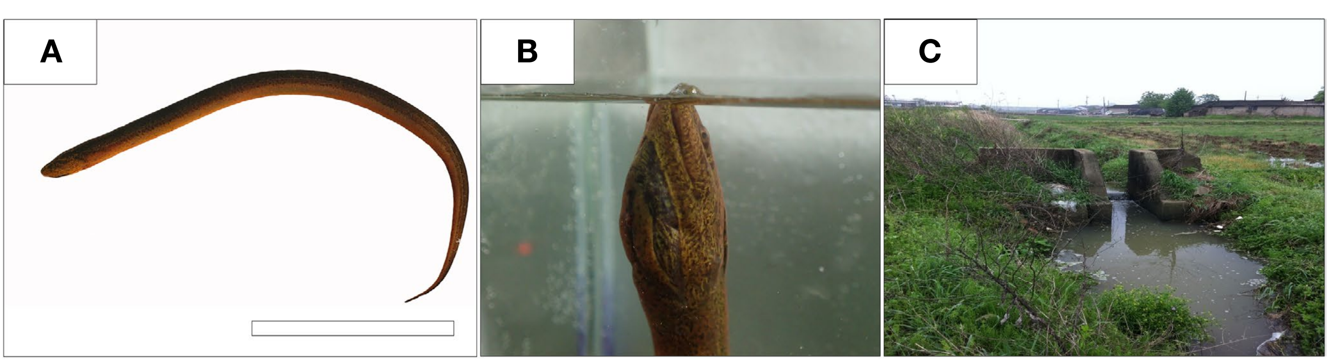

Fig. 2. The photograph of *Monopterus albus* (A), its breathing behavior with the aerial exposure of snout (B), and its habitat (C). The bar indicates 10 cm.

with Harri's hematoxylin-eosin (H&E) for general structure and with Masson's trichrome (Masson, 1929) to differentiate the epithelium and connective tissue. Additional special staining was performed using nuclear fast red-Alcian blue pH 1.0 and 2.5 solutions (Yamabayashi, 1987) to highlight the mucous cells' specificity. In order to examine the surface features of the olfactory epithelium in the olfactory chamber, the tissues were pre-fixed in 2.5% glutaraldehyde solution, post-fixed in 1% osmium tetroxide solution with phosphate buffer (pH 7.4), dehydrated in ascending alcohol series (60%, 70%, 80%, 90%, 95%, 100%, tert-butanol), and frozen at 4°C for 24 hours. The tissues were dried using a t-BuOH freeze dryer (VFD-21S, Vacuum Device Co. Ltd., Ibaragi, Japan), coated with osmium tetroxide using a plasma coater (HPC-1SW, Vaccum Device Inc., Tokyo, Japan), and finally photographed with a scanning electron microscope (SUPRA40VP, Carl Zeiss, Germany).

RESULTS

1. Anatomy

The paired olfactory organ of *M. albus* on each dorsal side of the snout externally displayed two openings (anterior nostril at the anterior tip of the snout and posterior nostril above the eyes) (Fig. 3). Both nostrils were non-protruding openings parallel to the skin surface and the distance between them was 5.57~7.10 mm on average. The interior structure consisted of a pipe-like chamber and two sacs (lower and upper accessory nasal sacs) at the posterior end of the chamber (Fig. 3). No rosette structure was found within the olfactory chamber.

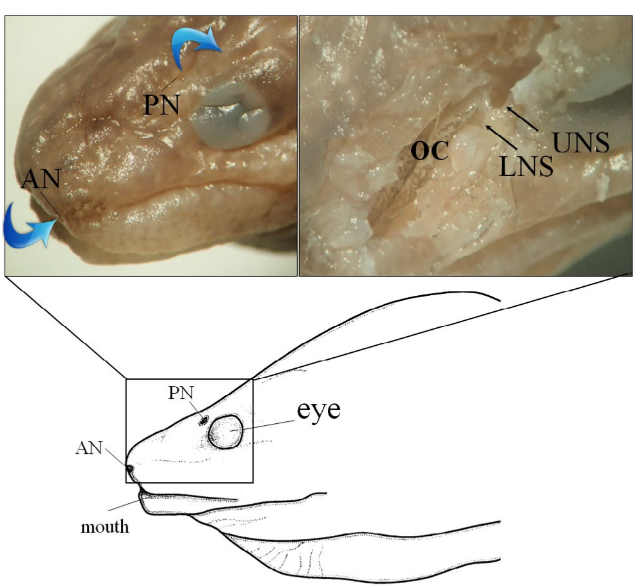

Fig. 3. Anatomical structure (left photograph, external view; right, internal view) of the olfactory organ of *Monopterus albus*. AN, anterior nostril; LNS, lower accessory nasal sac; OC, olfactory chamber; PN, posterior nostril; UNS, upper accessory nasal sac.

2. Histology

The epithelium of the olfactory chamber was classified into the sensory epithelium of the pseudostratified layer and the non-sensory epithelium of the stratified squamous epithelium (Fig. 4A and B). In addition, there was an unidentified organ that developed from the epithelial side toward the inner lumen (Fig. 4A and B).

The sensory epithelium at the ventral wall of the olfactory chamber consisted of olfactory receptor neurons (ORNs), supporting cells (SCs), basal cells (BCs), lymphatic cells (LCs), and blood capillaries (Fig. 4C and D). The ORNs were bipolar cells composed of dendrites that extended to the surface, axons connecting to the basement membrane, and a long oval-shaped nucleus. The nucleus appeared as a dark purple color in the H&E and Masson's trichrome stainings. The SCs had more round-shaped nuclei than those of the ORNs and they were lighter purple in the H&E and Masson's trichrome stainings. They were situated among the ORNs in the sensory epithelium. The BCs were distributed in the bottom of the sensory epithelium and had the lightest purple nuclei and pale pink cytoplasm in the H&E and Masson's trichrome stainings. The LCs were circular cells distributed in the middle and lower layers of the sensory epithelium. They were the smallest in size compared to the other epithelial cells and showed the darkest purple color in the H&E staining. The intraepithelial blood capillaries were scattered in the middle and lower layers of the sensory epithelium and contained one to three blood cells (Fig. 4C and D). More abundant dermal vascularization was observed in the connective tissue just below the bottom of the sensory epithelium and among the pigment cells and dermal collagen fibers than in intraepithelial vessels (Fig. 4C and D).

The non-sensory epithelium at the dorsal wall of the olfactory chamber consisted of stratified epithelial cells (SEC) and mucous cells (MC) (Fig. 4E and F). The SECs were polygonal cells exhibiting nuclei with a purple color in the Masson's trichrome and a weak pink color in the nuclear fast red staining, and they contained wide cytoplasm. The MCs had nuclei located at the cell bottom and the cytoplasm stained in a blue color with nuclear fast red-Alcian blue with a pH of 2.5. However, they did not exhibit reactivity in Masson's trichrome staining.

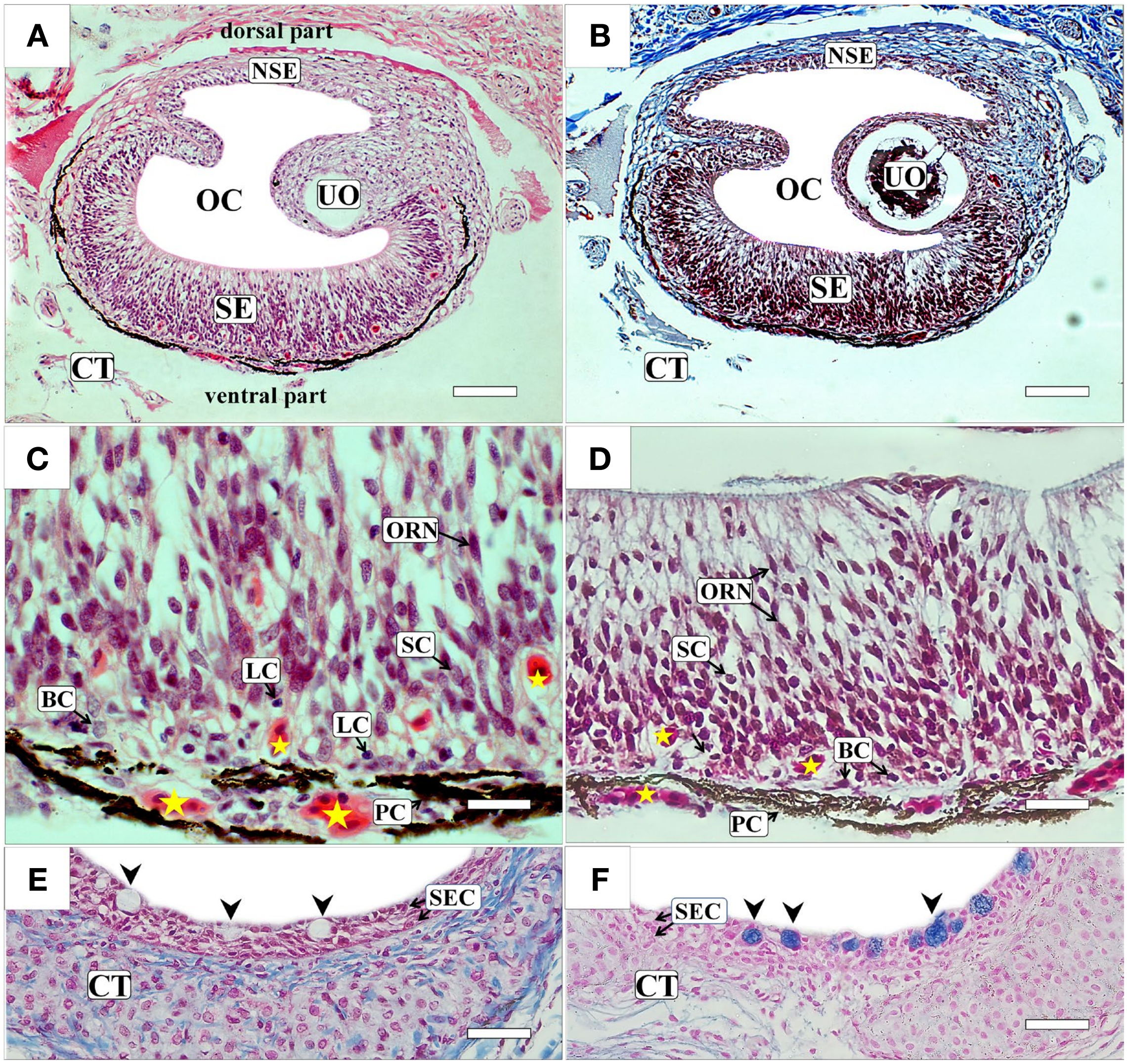

Fig. 4. Histological characteristics of the olfactory canal (OC) of *Monopterus albus*, stained with Harri's hematoxylin and eosin (A, C), Masson's trichrome (B, D, E), and nuclear fast red-alcian blue pH 2.5 solution (F). A and B, the olfactory epithelium consisting of three large parts, sensory epithelium (SE), non-sensory epithelium (NSE), and unidentified organ (UO) and surrounded by the connective tissue (CT); C and D, the SE having olfactory receptor neurons (ORN), supporting cells (SC), basal cells (BC), lymphatic cells (LC), pigment cells (PC), and interepithelial blood capillary (yellow asterisk); E and F, the NSE consisting of stratified epithelial cells (SEC) and mucous cells (arrowhead). Bars indicate 20 µm in C, 50 µm in D~F, 200 µm in A, B, respiectively.

Under scanning electron microscopy, the surface of the sensory epithelium indicated numerous cilia from ORNs, SCs, and mucous mass (Fig. 5A), and a fingerprint-like pattern was observed on the surface of the non-sensory epithelium (Fig. 5B).

DISCUSSION

In teleost fishes, the anatomy and histology of the olfactory organ is known to be closely related to their ecological habits and the physical conditions in their habitat. Most underwater teleost fishes have an oval olfactory chamber with a rosette structure but no accessory sac (Zeiske *et al*., 1992). However, the olfactory organs of amphibious fishes that inhabit mudflats, paddy fields, ponds, and similar environments with frequent exposure to air possess only one lacrymal accessory nasal sac, such as in *Periophthalmus modestus* (Kim *et al*., 2019) and *P. barbarus* (Kuciel, 2013), or the two ethmoidal and lacrymal accessory nasal sacs, such as in *Boleophthalmus pectinirostris* (Kim and Park, 2020), *Odontamblyopus lacepedii* (Kim *et al*., 2018), *Scartelaos histophorus* (Kuciel *et al*., 2013), and *Parapocryptes rictuosus* (Kuciel *et al*., 2013). In addition, they are

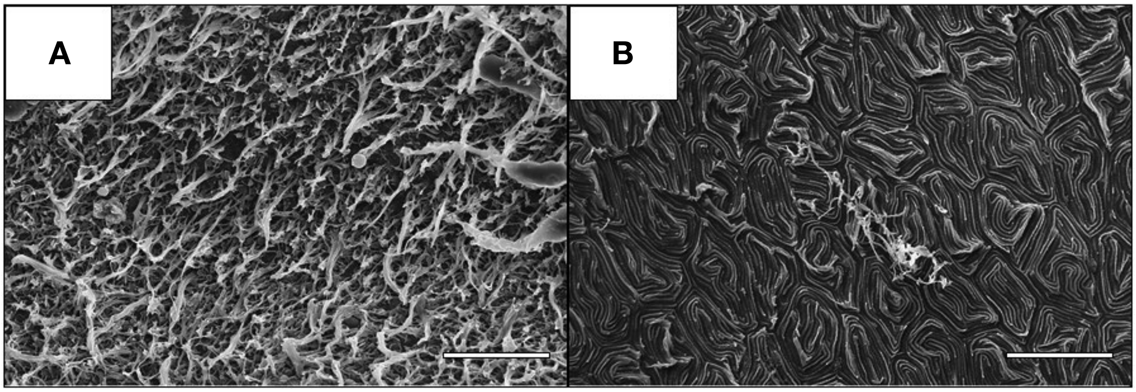

Fig. 5. Scanning electron micrographs showing the surface structure of the sensory (A) and non-sensory epithelium (B) of the olfactory organ of *Monopterus albus*. Bars indicate 5 μm, respectively.

characterized by tubular anterior nostrils, olfactory chambers with a pipe-like form, and the absence of a rosette structure. In this study, *M. albus* also displayed pipe-like olfactory chambers lacking a rosette structure and two sacs (lower and upper accessory nasal sacs). In general, the olfactory activity of amphibious fishes in stagnant or shallow water conditions tends to be highly dependent on the structure of the olfactory chambers and the nasal sacs' pumping mechanisms (Kuciel, 2013). Kim *et al.* (2019) opined that *P. modestus* on wet mudflats with extremely shallow water move their heads' skeletons and straw-like olfactory chambers to facilitate the inflow of water into the internal olfactory organ and such olfactory activity is relevant to the "sniffing" of the mudskipper. Therefore, the pipe-like olfactory chamber and two accessory nasal sacs of *M. albus* could be considered structural adaptations that play an important role in allowing external water to be drawn into the olfactory cavity, particularly in stagnant water environment, such as rice fields, ponds, swamps, and rivers. Moreover, although *M. albus* and most amphibious species share similar habitat environments with stagnant water, the nostril morphology of *M. albus* differs from these species (a closed hole parallel to the skin surface vs. an open hole with ascending tubular form) (Belanger *et al.*, 2003; Ma and Wang, 2010; Kim and Park, 2016). This seems to be a morphological adaptation to different ecological habits rather than the habitat differences of *M. albus*. Meanwhile, the unidentified organ inside the olfactory chamber is considered to be a unique structure not previously reported in other fish taxa. Therefore, it was suggested that further anatomical and histological analysis is needed to confirm its detailed function.

The olfactory epithelium of teleost fishes has multiple cells that play diverse functions, such as chemical reception of olfactory neurons, cilia possession of supporting cells for mucus spreading, progenitors of olfactory neurons in basal cells, and mucus secretion for olfactory cell protection against infective pathogens or harmful substances (Hara, 1994). However, the respiratory function in the olfactory epithelium has not been reported in fish thus far, including all evolutionary stages of fish groups beyond the Agnatha (jawless fish) (Fernandes, 2016). Therefore, the development of blood capillaries within the sensory epithelium and the rich dermal vascularization of the *M. albus* olfactory organ was considered to be a meaningful modification in this study. It also could be considered strong histological evidence supporting its respiratory function (Beon *et al.*, 2013). In the view of skin histology, the presence of intraepidermal blood capillaries and abundant dermal vascularization have been described as significant modifications that prove cutaneous respiration in fishes, such as *P. modestus* (Park *et al.*, 2000), *P. magnuspinnatus* (Park *et al.*, 2006), *Rhinogobius brunneus* (Kim *et al.*, 2022), *P. cantonensis* (Yokoya and Tamura, 1992), *Pseudobagrus brevicorpus* (Park and Kim, 2007), *Liobagrus mediadiposalis* (Park *et al.*, 2003), and *Tridentiger obscurus* (Suzuki and Hiraki, 1991), that can survive in adverse environments with extremely low oxygen levels or limited water, and occasionally prolonged exposure to air. Based on such histological references, the olfactory organ of *M. albus* is suggested to have an additional respiratory function along with the buccal cavity, which it uses by protruding its snout above the water's surface when submerged.

Furthermore, we confirmed that the sensory epithelium of the olfactory organ of *M. albus* contained ORNs, SCs, BCs, and LCs, which are fundamentally essential to the cellular composition found in the sensory epithelium of teleost fishes for detecting chemical odorants in the surrounding environment (Hara, 1994). In addition, the components of the mucous cells in the non-sensory epithelium were characterized by negativity on nuclear fast red-Alcian blue staining at a pH of 1.0, but positivity at a pH of 2.5. These results imply that acidic mucopolysaccharides containing carboxyl groups are the major constituents within the cytoplasm (Lev and Spicer, 1964).

ACKNOWLEDGMENTS

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드렁허리 *Monopterus albus* 후각기관의 해부 및 조직학적 특성 연구

김현태

전주교육대학교 과학교육과

요 약 : 본 연구에서는 드렁허리 *Monopterus albus* 후각기관의 형태 및 조직학적 특성을 실체, 광학 및 주사전자현미경하 관찰을 통하여 조사하였다. 후각기관의 외부 형태는 피부와 평행한 폐쇄형 전비공과 후비공을 나타냈다. 내부 구조는 파이프형 비강과 뒤쪽의 위아래의 두 개 비낭으로 구성되었다. 비강의 내벽은 위중층상피층의 감각상피와 중층편평상피층의 비감각상피, 미확인기관으로 이루어졌다. 감각상피는 후감각뉴런, 지지세포, 기저세포, 림프구로 구성되며, 비감각상피는 중층상피세포와 산성의 점액다당류를 보유하는 점액세포를 보유했다. 특히, 감각상피층 내 모세혈관과 풍부한 진피에서의 혈관화는 논, 농수로, 연못, 늪과 같은 진흙 하상의 정체된 수환경에 적응된 후각기관 내 부가적인 호흡기능의 증거이며 이는 이전에 원구류 이상의 어류 분류군에서 확인되지 않은 새로운 결과로 확인된다.

찾아보기 낱말 : 후각기관, 파이프형 비강, 상피 내 모세혈관, 진피 내 혈관화, 호흡 기능