Fine structure of the vomeronasal organ in the grass lizard, *Takydromus tachydromoides*

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**A B S T R A C T**

The squamates are composed of many taxa, among which there is morphological variation in the vomeronasal organ (VNO). To elucidate the evolution of chemoreception in squamate reptiles, morphological data from the VNO from a variety of squamate species is required. In this study, the morphology of the VNO of the grass lizard *Takydromus tachydromoides* was examined using light and electron microscopy. The VNO consists of a pair of dome-shaped structures, which communicate with the oral cavity. There are no associated glandular structures. Microvilli are present on the apical surfaces of receptor cells in its sensory epithelium, as well as on supporting cells, and there are centrioles and ciliary precursor bodies on the dendrites. In addition to ciliated cells and basal cells in the non-sensory epithelium, there is a novel type of non-ciliated cell in *T. tachydromoides*. They have constricted apical cytoplasm and microvilli instead of cilia, and are sparsely distributed in the epithelium. Based on these results, the variation in the morphology of the VNO in scincomorpha, a representative squamate taxon, is discussed.

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**1. Introduction**

Vertebrate species possess two types of olfactory sensory epithelia, the olfactory epithelium (OE) and the vomeronasal sensory epithelium (VSE) (Parsons, 1967; Eisthen, 1992; Shipley et al., 1995). The OE is present in all vertebrate species, but the VSE is not present in fish, first appearing in amphibians (Bertmar, 1981; Eisthen, 1992, 1997). The vomeronasal organ (VNO), containing the VSE, is observed as a separate region or diverticulum of the nasal cavity in amphibians (Seydel, 1895; Parsons, 1967; Franceschini et al., 1991; Eisthen, 2000; Saito et al., 2003), but the VNO is an independent organ in some reptile species. Reptiles living in the water, such as crocodilians and sea turtles, lack a VNO (Parsons, 1970; Bertmar, 1981; Eisthen, 1992). In contrast, squamates such as lizards and snakes possess a well-developed VNO, and are thought to be vomeronasal specialists based on the well-developed VSE and the accessory olfactory bulb, which is the primary center of the VSE located in the dorsomedial region of the olfactory bulb (Franceschini et al., 2000, 2001). The VNO also plays a significant role in the behavior of these animals (Halpern, 1987, 1992). A study of the squamate VNO may lead to an understanding of its evolutionary changes, as well as the physiological function of the VNO in vertebrates.

Squamates are divided into several subfamilies, including Iguania, Gekkota, Anguimorpha, Serpentes, Scincomorpha, and Amphisbaenia (Estes et al., 1988; Schwenk, 1993). Generally, the squamate VNO is in the form of a pair of dome-shaped structures because of the eminence of a mushroom body covered by nonsensory epithelia (Parsons, 1967). The VSE lines the opposite wall of the mushroom body, and consists of receptor cells, supporting cells, and basal cells with no glandular structures in the lamina propria (Parsons, 1967; Kratzing, 1975; Wang and Halpern, 1980). The VNO communicates only with the oral cavity, not the nasal cavity (Parsons, 1967; Bertmar, 1981), and the source of luminal fluid in the VNO is likely the Harderian gland (Rehorek, 1997; Rehorek et al., 2000a).

There is a considerable degree of variation in the morphology of the squamate VNO. For example, the burrowing lizard *Anguis fragilis* (Bannister, 1968) and the scincomorph *Lacerta sicula* (Altnier et al., 1970) appear to lack a certain number of centrioles in the dendrites of the microvillious receptor cells, although these structures have been reported for most vertebrate species, including other scincomorph species (Kratzing, 1975; Ciges et al., 1977). Squamates consist of many taxa, and a detailed structural examination of a variety of squamate species is thought to be required to elucidate the evolution of chemoreception in squamate reptiles, as suggested...
by Schwenk (1993). Therefore, we examined the ultrastructure of the VNO of a scincomorph, T. tachydromoides. We report a novel type of cell found in the mushroom body, as well as fine structural variation in the VNO.

2. Materials and methods

2.1. Animals

Three male and three female adult grass lizards T. tachydromoides, weighing 2.5–4.1 g, were obtained from the Japan Snake Institute (Gunma, Japan). One male and one female were used for light microscopic examination, and two lizards of each sex were used for electron microscopic examination, as no morphological differences based on sex were observed. After anesthetizing the animals with ice, 5.0 × 10^{-3} ml/g body weight sodium pentobarbital was injected intraperitoneally (Abbott, North Chicago, USA), and they were processed (as described below) for light or electron microscopic examination. All animals were dissected in the summer of 2005. All procedures in this experiment were in accordance with the Guide for the Care and Use of Animal Experimentation at Iwate University and Gifu University, Japan.

2.2. Light microscopy

After anesthesia, the animals were euthanized by cardiac perfusion with physiological saline and Bouin’s solution without acetic acid. The premaxilla, including the whole nasal cavity, was excised, immersed in the same fixative for 24 h, and decalcified in a mixture of 10% formalin and 10% formic acid for 7 days. We did not slice the nasal cavity in half for use of one-half in electron microscopy, because we wanted to obtain intact VNOs. After decalcification, the specimens were routinely embedded in paraffin. Serial paraffin sections were cut coronally at 5 μm and stained with hematoxylin–eosin.

2.3. Electron microscopy

After anesthesia, the animals were euthanized by cardiac perfusion with physiological saline followed by modified Karnofsky's solution (2.0% glutaraldehyde, 2.5% paraformaldehyde in 0.2 M cacodylate buffer, pH 7.4). The VNO was removed and immersed in the same fixative for 2 h at 4 °C, post-fixed in 1% osmium tetraoxide solution, and dehydrated and embedded in Quetol-812. Ultrathin sections with a silver/gray interference color were obtained using an ultramicrotome (ULTRACUTS, Nissei Sangyo Co., Ltd., Japan) stained with uranyl acetate and lead citrate, and examined in a Hitachi H-7100 Transmission Electron Microscope. Semi-thin sections adjacent to the ultrathin sections were cut at 2 μm and stained with 0.5% toluidine blue for light microscopy.

3. Results

3.1. Light microscopy

The VNO of T. tachydromoides consisted of a pair of dome-shaped structures, about 1 mm in diameter, and was located under the rostral floor of the nasal cavity (Fig. 1). Cartilaginous
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