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VOMERONASAL ORGAN IN DOMESTIC ANIMALS
(A SHORT SURVEY)

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In 1809, the Danish anatomist Ludwig Jacobson (1783–1843) reported about an organ, situated in the nasal cavity of mammals, that was not known until then (Jacobson, 1809). On the basis of thorough observations, the author described the glands, the double innervation and the blood supply at this locus (Jacobson, 1813).

The vomeronasal organ (VNO) is an anatomical formation, with unique structure and function. It is located below the nasal mucous coat, ventrolaterally to the nasal septum. Since 1813 and by now, it has been the subject of numerous investigations, but still, the information about it is not enough. In human medicine, some authors disagree with its functioning, because in men, it is rudimentary. It is accepted that in animals, VNO participates in the social and sexual communication as a chemosensory organ. The importance of these facts for animal behaviour as well as for animal reproduction was the reason to perform a short description of its topographical location, structure and species-related features in various domestic animals and man with regard to future, more detailed breed-associated studies within the frame of certain animals species.

MORPHOGENESIS

VNO or Jacobson's organ, is a paired formation (complex) representing an "epithelial pocket" that lies on both sides of the base of the nasal septum. Its peak development occurs during the foetal period and at a considerably lesser extent after birth (Powers & Winans, 1975; Powers, 1977; Johns *et al.*, 1978; Aron, 1979; Wysocki, 1979; Meredith *et al.*, 1980). The complex could be divided into rostral, intermediate and caudal parts, each one with a specific pattern of vascularization (Soler & Suburo, 1998).

VNO derives from the origin of the nasal septum and is developed just after the middle of the embryonal period in mammals. The "Anlage" stage consists of the cellular germ, that grows dorsally, caudally and medially. During the next embryonal phase, the organ is a band-like cluster of cells. The growth of the nasal septum results in sinking and formation of a sulcus, bilaterally to the developing nasal septum (Barone, 1997, Dellman & Eurell, 1998). The process continues with formation of two tube-like structures representing the future vomeronasal organ. The next stage – early morphogenesis, includes closure of the vomeronasal sulcus in order to form a paired parasagittal blindly ending tube in the nasal septum, that opens in the nasal and/or oral cavity. Its lumen acquires a crescent-like shape and simultaneously the differentiation of the epithelium is further progressing. This occurs initially on the concave side and then, gradually, on the convex side. The lateral non-sensory epithelium (NSE) has a kidney-like shape on a VNO cross-

section (Winans & Powers, 1977; Dellmann & Eurell, 1998).

The next stage, or late morphogenesis, consists in different height of both type epithelium. The number of microvilli increases. The capillaries penetrate through the most basal part of the neuroepithelium and vomeronasal glands, that are few and underdeveloped. It is assumed that the function of VNO as responsible for the chemical bond among individuals (Meredith, 2001) determines its tubular shape and the length of about 2 to 20 cm depending on the size of mammals (Takigami *et al.*, 2000). The caudal part of tubes ends blindly whereas the rostral end opens in both incisive canals, that connect nasal and oral cavities through the rostral end of the palate (Barone, 1997). Its lumen is lined with sensory (SE) and non-sensory epithelium (NSE). SE is composed of sensory, supporting and basal cells that develop prior to birth. For NSE, composed only of supporting and basal cells, the development ends in the age of puberty (Fig. 1). (Garrosa *et al.*, 1998).

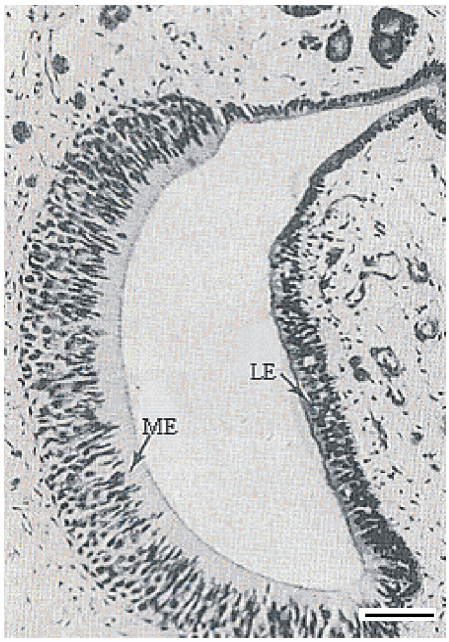

Fig. 1. Cross-section of VNO in a dog. LE – epithelium on the lateral side, containing ciliary and non-ciliary cells; ME – medial epithelium containing neuroepithelial cells; bar= 100 μm.

PHYSIOLOGICAL TRAITS

VNO or the second olfactory organ in animals receives pheromones and thus, plays a role in the sexual, parental and social behaviours (Hofer *et al.*, 2000; Gulimova, 2002). Some authors (Smith *et al.*, 2001) determined VNO as a chemosensory organ that is involved in the sociosexual relationships in mammals. It is thaught that it has a important role for the detection of female individuals and the sexual behaviour in sheep (Kratzing, 1971).

According to Keverne (1999), vomeronasal neurons have two distinct types of receptors that are different and are from the big family of odorant receptors. They are closely related to the hypothalamus and participate in its activation that occurs via an accessory olfactory bulb and the Amygdala. It is known that the hypothalamic region regulates the reproductive, defensive and feeding behaviour. It plays an essential role in the initiation of the sexual behaviour. There are neurosecretory neurons, forming the so-called sexual centre. The neuronal path including the regulation of the sexual behaviour, is predominantly located in the anterior part of the hypothalamus. By feedback, the sexual centre receives and processes the systemic signals related to the endocrine status. It is also responsible for the sexual behaviour via secretion of releasing factors (GnRH from RH factors) for gonadotropic pituitary hormones, participaing in the sexual cycle regulation in mammals (Reeves,

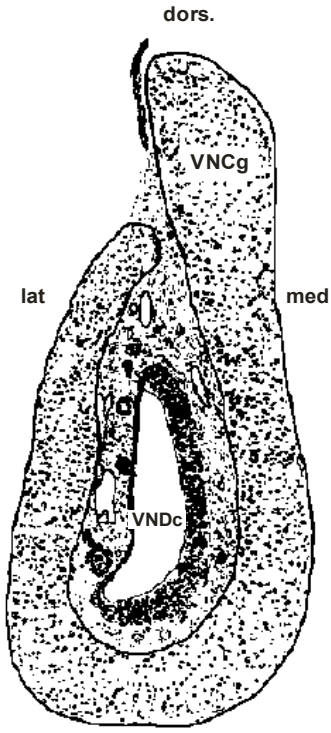

Fig. 2. Schematic presentation of VNO. VNDc – vomeronasal duct; VNCg – vomeronasal cartilage.

1986) (Fig. 2). The relationship between VNO and the aforementioned regulatory functions of hypothalamus are to be studied in detail.

SPECIES-RELATED TRAITS

In *horses*, the rostral end of the incisive canal is closed, unlike swine and cows. There is no communication betwenn VNO and the oral cavity. The rostral part of the canal is characterized with layered columnar epithelium (Dellman & Eurell, 1998). At the same time, the bigger caudal part is built of simple columnar epithelium (Barone, 1997; Salazar *et al.*, 1997).

In *cattle*, the caudal part of VNO ends at the level of the first or second premolars (Kumar *et al.*, 1981). The lumen of the ventral part of VNO is not covered with the cartilage that constitutes the organ.

The VNO in *sheep* is composed by a pair of tubules closed caudally and opened rostrally in the nasopalatinal canal. The caudal part ends at the level of the first (P1) or second (P2) premolars (May, 1964; Kratzing, 1071). The sensory epithelium is located on the medial surface and the nonsensory and the ciliary – laterally. Receptor cells possess a big cellular body of a neurogenic type with proximal and distal ends (Kratzing, 1971). The vertical diameter of the VNO lumen has a width of 1 cm in its central part (May, 1964).

In *goats*, the caudal end of VNO ends at the level of the third premolar (Besoluk *et al.*, 2001). Its lumen is lined with the cartilage that builds the organ and, in this species, it is observed ventrally as well (Besoluk *et al.*, 2001). The vertical diameter in its central part is 5 mm (Takigami *et al.*, 2000).

In *swine*, the VNO length is up to 4 cm. Caudally, it ends blindly and reaches the P2 level (Salazar *et al.*, 1997).

In *dogs*, the VNO complex is structurally well developed. The big blood vessels are deeply situated in both the lateral, "non-receptor" and the medial, epithelial tissue. The venous plexuses are well-developed and located on lateral and medial part of the organ (Adams & Wiekamp, 1984; Dennis *et al.*, 2003).

In *cats*, Frewein & Falmerhaus (2003) describe the VNO as a very short and straight canal with a blind caudal end. Anteriorly, it reached the P2 level. The lumen is full with a serous fluid. The subepithelial layer is richly vascularized. Among the ciliary receptor cells on the medial surface, supporting cells could be encountered (Soler & Suburo, 1998).

In *rabbits*, VNO is a well-developed organ, lying on both sides of the base of the nasal septum. It is lined with neuroepithelial tissue, connected with the accessory olfactory system. The experimental removal of VNO reduced reproduction rates and increase aggressiveness in rabbits (Aron, 1979; Gaafar *et al.*, 1998).

In *birds* and *fish*, VNO is lacking. It is neither present in the *crocodile* and the *chameleon*. It is however well developed in *snakes*, its lumen opening in the oral cavity (Kjell & Trotier, 1998).

In *men*, the research on VNO function was tightly related to another question, namely whether a pheromone relationship did exist among men.

Gulimova (2002) established that at an ultrastructural level, the sensory cells appeared as bipolar neurons with marked microvilli on their free surface. The vomeronasal glands are represented by tubulo-acinous glands with serous acinar cells. The lumens of canals of these glands reach the dorsolateral region between NSE and SE. The vascular part of glands is composed by fenestrated and nonfenestrated capillaries.

In available literature, there are no data about the possible differences between wild and domesticated representatives. Also, some questions regarding the breed-related differences in the topographic location in a given species – large and small ruminants, horses, swine, cats, as well as the boundaries of location of the SE and NSE in animals, remain unclear.

In conclusion, the vomerosanal organ is an attractive anatomical object. It is involved in the reception of pheromones, as intraspecific chemical messengers, released from individuals in oestrus. The further study of problems related to species-specific and breed-specific morphological traits of VNO could contribute to extending the knowledge about the anatomo-physiological basis of reproduction in animals.

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