Nervi Terminalis, Vomeronasalis and Olfactorius of *Uromastyx aegyptius* (Squamata – Lacertilia - Agamidae)

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Abstract: The present work was aimed to study the anterior cranial nerves which innervate the olfactory apparatus of *Uromastyx aegyptius*. The olfactory apparatus of *Uromastyx aegyptius* includes the main olfactory organ and the vomeronasal organ or organ of Jacobson. The main olfactory organ is innervated by the olfactory nerve which arises from the sensory olfactory epithelium and leaves the capsular cavity through a separate foramen, i.e., there is no foramen olfactorium advehens. The vomeronasal organ is innervated by two nerves: the terminal and the vomeronasal nerves. They arise from the sensory epithelium in combination. The terminal nerve carries a terminal ganglion. The nervi terminalis and vomeronasalis combined together as one separate nerve which leaves the cavity of the nasal capsule together with few bundles of the olfactory nerves through a special foramen. The nervi terminalis, vomeronasalis and olfactorius enter the cranial cavity through a large foramen olfactorium evehens and they connect separately the anterior part of the brain. The vomeronasal nerve enters the accessory olfactory bulb (vomeronasal formation) of the fore brain. The nervus olfactorius enters the main olfactory bulb whereas the terminal nerve connects the anterior end of the olfactory lobe. The olfactory bulb has a long olfactory peduncle. The three nerves carry pure special somatic sensory fibres.
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1. Introduction

Agamid lizards constitute a relatively large family of suborder Lacertilia of the order Squamata.

Many studies were carried out on the skeletal system of the agamid lizards (Ramaswami, 1946; Malan, 1946; Barry, 1953; Eyal-Giladi, 1964). However, little works were obtained on their cranial nerves such as Soliman *et al*. (1984 & 1990) on *Agama pallid* and Shamakh (2009) on *Laudakia stellio*. Concerning the cranial nerves in reptiles, in general, many studies were reported in Lacertilia and Ophidia such as Soliman and Hegazy (1969) on *Chalcidis ocellatus*, Soliman and Mostafa (1984) on *Tarentola mauritanica*, Dakrory (1994) on the amphisbaenian *Diplometopon zarudnyi*, Abdel-Kader (2006) on the cat snake *Telescopus dhara* and Abdel-Kader *et al*. (2007) on *Mabuya quinquetaeniata*.

Uromastyx aegyptius is chosen for this study. It is known as spiny-tailed lizard or dabb lizard. This species is adapted to the arid habitat. The anatomy and morphology of the cranial nerves of member of the family Agamidae is poor and scarce. Hence, it was convenient to study the anterior cranial nerves which innervate the olfactory apparatus of the animal to elucidate their neural characters and to analyze the fibre components of these nerves. This may help in understanding the phylogeny, taxonomy and behavior of this primitive lacertilian family.

2. Materials and Methods

The fertilized eggs of *Uromastyx aegyptius* are collected from Gabal Al-Maghara, South of El-Arish City, Northern Sinai, Egypt, during August 2004, at the last days of the incubation period. After careful removing of the embryos from the shells, they were fixed immediately in an aqueous Bouin's fluid for 24 hours, and then washed with 70% ethyl alcohol for several days to remove the excess of fixative. Thereafter, the heads were decalcified using EDTA solution for about 3-4 weeks, changing the solution every 4 days. The heads were then dehydrated, cleared, mounted and embedded in paraffin wax and serially sectioned transversely at 10 µm thick. The serial sections were stained with Mallory's Triple Stain.

The transverse sections were drawn with the help of a projector microscope. In order to show the relations of the nerves to the different parts of the head, several sections were also photomicrographed.

3. Results

Nervus Terminalis (N. 0)

In the agamid lizard *Uromastyx aegyptius*, the fibres of the nervus terminalis arise from the sensory epithelium of the vomeronasal organ along its entire length in combination with the fibres of the vomeronasal nerve. The nerve fibres are originated from the medial, dorsal and lateral aspects of the sensory epithelium at the anterior blind end of the organ, and collect into three branches. These branches are located, dorsomedial, dorsal and dorso lateral to the organ epithelium (Fig. 1, N.0). Shortly posterior, and opposite to the anterior end of the organ cavity, the nerve fibres originating from the sensory epithelium collect into four small nerve branches (Fig. 2, N.0). Thereafter, fine branches are formed from the nerve fibres arising from the medial, dorsal and dorso lateral sides of the organ epithelium lining the anterior half of the organ. These branches extend posteriorly passing dorsomedial, dorsal and dorsolateral to the organ epithelium, where they gradually approach each other and fuse forming four small nerve bundles (Fig. 3, N.0). These nerve bundles gradually fuse together near the posterior aspect of the organ forming one large bundle that run posteriorly. It runs posteriorly passing dorsomedial to the organ epithelium and lateral to the internasal septum.

The nerve fibres originating from the epithelium of the middle part of the organ aggregate together into three small nerve branches. These branches run posteromedially passing dorsal to the organ epithelium and ventral to both the organ cartilaginous roof and the septomaxillary bone (Fig. 4). Shortly backwards, another five branches are formed; one from the medial epithelium and four from the lateral and dorsolateral epithelium of the organ, opposite to the organ duct (Fig.3, N.0). These branches extend posteromedially passing dorsal to the organ epithelium and ventral to the septomaxillary bone. They gradually fuse together forming a second large bundle. The two bundles extend posterodorsally passing lateral to the internasal septum and medial to the septomaxilly bone till they leave the organ capsule and enter the nasal capsule.

The sensory nerve fibres arising from the caudal end of the organ collect together forming numerous branches. These branches extend posterodorsally to leave the organ capsule and enter the olfactory capsule (Fig. 4, N.0). At this point, some of these branches are added to the previously formed bundles and the remainder fuse together forming third nerve bundle (Fig. 6, N.0).

Shortly posterior, within the olfactory capsule, the first large bundle carries few scattered ganglionic cells. These cells represent the ganglion terminale (Fig. 5, G.T). The three large nerve bundles continue running posterodorsally within the olfactory capsule passing medial to the olfactory eptithelium, dorsal to both the paraseptal cartilage and the prevomer bone and lateral to the internasal septum, where the second bundle receives fine branches from the olfactory nerve. More backwards, the three bundles gradually approach and fuse together forming the nervus terminalis carrying the vemeronasal fibres. In the posterior part of the olfactory capsule, the internasal septum degenerates and the two nervi terminale extend side by side till they leave the cavity of the nasal capsule through their own common foramen; terminal foramen (Figs. 10&11, F.NT).

The terminal foramen is located at the most medial aspect of the posterodorsal edge of the olfactory capsule. Extracapsullary, this nerve enters directly the cranial cavity through the foramen olfactorium evehens (Figs. 7, 10&11, F.OE). Within the cranial cavity, the nervus terminalis carrying the vomeronasal fibres extends posteriorly passing ventromedial to the main olfactory bulb. After a posterior distance, it separates from the vomeronasal nerve fibres. The later nerve enters the accessory olfactory bulb (Fig. 12, AOLB); whereas the terminale nerve connects the anterior end of the fore brain.

Nervus Olfactorius (N.I)

In *Uromastyx aegyptius*, the fibres of the nervus olfactorius arising from the sensory olfactory epithelium aggregate forming several branches. These branches run posterodorsally around the walls of the olfactory chamber at the middle and the posterior regions of the nasal cavity. They extend in a place bounded dorsally and laterally by the parietotectal cartilage and medially by the internasal septum.

During their backward course these branches gradually approach and unite together into separate bundles, constituting the ordinary nervus olfactorius (Figs. 7, 8 &11, N.I). The nerve branches formed from the most ventral and middle parts of the medial olfactory epithelium extend posterodorsally passing lateral to the paraseptal cartilage and medial to the the olfactory epithelium and ventrolateral to the nervus terminalis. After a short distance, these reach and fuse with latter nerve (Figs. 6&8, N.I).

The olfactory nerve branches formed from the sensory epithelium of the dorsal part of the medial epithelium, at its anterior end extend posterodorsally to leave the nasal capsule through the posteromedial corner of the largest olfactory foramen (Fig. 8, N.I). An olfactory nerve branch is formed from the aggregation of the sensory nerve fibres arising from the most posterior part of the medial olfactory epithelium. This branch extends posterodorsally to leave the nasal capsule together with the nervus terminalis through the terminal foramen (Figs. 10&11).

The olfactory nerve branches formed from the dorsal sensory epithelium run posterodorsally passing medial and ventral to the parietotectal cartilage. These branches leave the capsular cavity through a somewhat large foramen as two or three large bundles (Fig. 7, F.OL). This foramen is bundled anteriorly by parietotectal cartilage medially by the internasal septum, anteriolaterally the sphane inmaidal commissure and posteriorly by the lamina orbitonasalis (Planum antoribitale). From the posterior region of the sensory olfactory epithelium several fine olfactory nerve branches (about seven branches) are formed and leave the capsular cavity separately, each through its own foramen in the lamina orbitonasalis (Figs. 7,8,10&11, F.OL).

Extracapsular, the olfactory nerve branches run posterodorsally to enter the cranial cavity through a large foramen olfactorium evehns (Figs. 9,10&11, F.OE). Within the latter cavity, these branches join the main olfactory bulb from its ventral, ventromedial and ventrolateral sides (Figs. 8&11, N.I). This bulb has a posteromedial part which is termed accessory olfactory bulb (Fig. 12, AOLB) or vomeronasal formation that receives the vomeronasal nerve.

Both the main and the accessory olfactory bulbs are connected with the anterior part of the fore brain (olfactory lobe) by a somewhat elongated olfactory peduncle or tract (stalk).

It is obvious from the above description that, the olfactory apparatus of *Uromastyx aegyptius* is innervated by three nerves: terminale, vomeronasal and the main olfactory. Both the nervi terminalis and vomeronasalis originate from the sensory epithelium of Jacobson's organ (an accessory olfactory organ), whereas, the nervus olfactorius arises from the epithelium of the main olfactory organ. These nerves carries special somatic sensory fibres. There is no foramen olfactorium advehens, but instead, there are many olfactory foramina and one foramen for the combined nervi terminalis, vomeronasalis and few branches of the olfactory nerve.

The olfactory bulb is pedunculated, i.e., there is an olfactory peduncle "tract or stalk" connecting it with the olfactory lobe.

Fig. (1): Photomicrograph of a part of transverse section of the olfactory region of *Uromastyx aegyptius* showing the issue of the nerve fibres from the anterior wall of the sensory epithelium of Jacobson's organ(x 40).

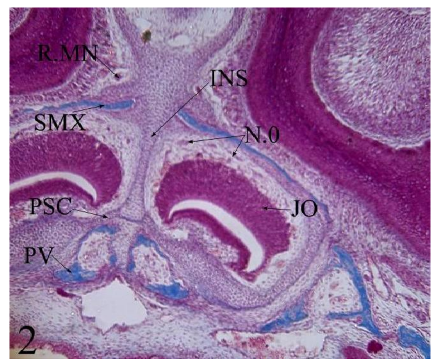

Fig. (2): Photomicrograph of a part of transverse section of the olfactory region of *Uromastyx aegyptius* showing the issue of the nerve fibres from the dorsal side of the sensory epithelium of Jacobson's organ. (x 40).

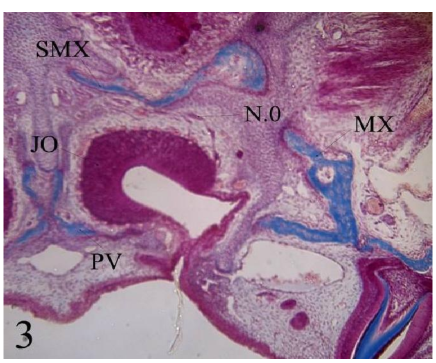

Fig. (3): Photomicrograph of a part of transverse section of the olfactory region of *Uromastyx aegyptius* showing the issue of the nerve fibres from the sensory epithelium of Jacobson's organ opposite to the organ duct(x 40).

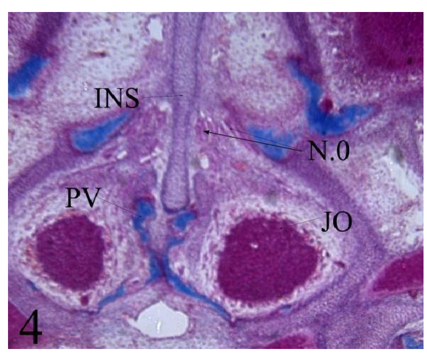

Fig. (4): Photomicrograph of a part of transverse section of the olfactory region of *Uromastyx aegyptius* showing the issue of the nerve fibres from the posterior wall of the sensory epithelium of Jacobson's organ (x 40).

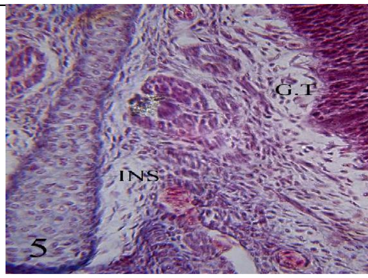

Fig. (5): Photomicrograph of a part of transverse section of the olfactory region of *Uromastyx aegyptius* illustrating the terminal ganglion (x 100).

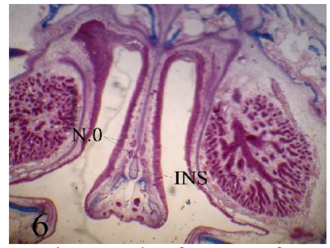

Fig. (6): Photomicrograph of a part of transverse section of the olfactory region of *Uromastyx aegyptius* showing the bundles of the terminal nerve passing within the olfactory capsule (x 40).

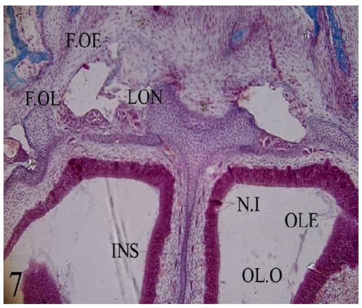

Fig. (7): Photomicrograph of a part of transverse section of the olfactory region of *Uromastyx aegyptius* demonstrating the origin of the olfactory nerve, the olfactory foramen and the foramen olfactorium evehens (x 40).

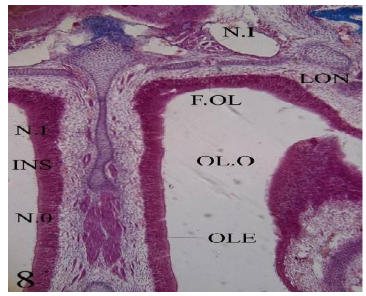

Fig. (8): Photomicrograph of a part of transverse section of the olfactory region s of *Uromastyx aegyptius* howing the bundles of the terminal nerve passing within the olfactory capsule, the origin of the olfactory nerve and the foramen olfactorium evehens (x 40).

Fig. (9): Photomicrograph of a part of transverse section of the olfactory region of *Uromastyx aegyptius* illustrating the foramen olfactorium evehens, olfactory bulb and the passage of the terminal nerve within the olfactory capsule (x 40).

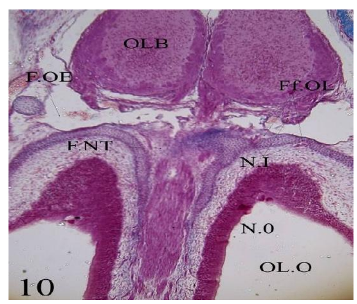

Fig. (10): Photomicrograph of a part of the transverse section of the olfactory region of *Uromastyx aegyptius* showing the foramina of the olfactory nerve, the foramen olfactorium evehens and the foramen of the terminal nerve (x 60).

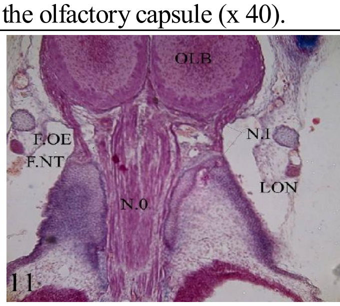

Fig. (11): Photomicrograph of a part of transverse section of the olfactory region of *Uromastyx aegyptius* illustrating the passage of the terminal nerve through its own foramen and the olfactory foramina in the lamina orbitonasalis (x 60).

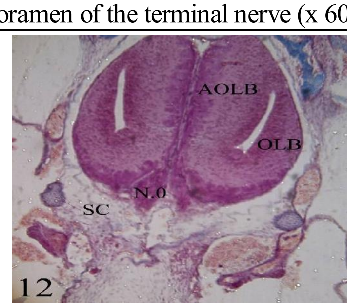

Fig. (12): Photomicrograph of a part of transverse section of the olfactory region of *Uromastyx aegyptius* illustrating the main olfactory bulb, the accessory olfactory bulb and terminal nerve (x 60).

4. Discussion

The microscopic examination of the innervation of the olfactory apparatus in *Uromastyx aegyptius* succeeds in demonstrating three groups of nerve fibres which arise from the sensory cells of this apparatus and connect separately to the anterior portion of the forebrain. These fibres constitute the nervus terminalis, the ordinary olfactory nerve and the vomeronasal nerve. The fibres of the nervus terminalis differ essentially from those of the latter two nerves.

The nervus terminalis was identified nearly in all the vertebrate classes except cyclostomes and birds, as has been reported by Watanabe and Yasuda (1968), Romer and Parsons (1985), Soliman *et al.* (1986) and Shamakh (2009). On the other hand, Von Bartheld *et al.* (1987) and Northcutt and Puzdrowski (1988) stated that a terminal nerve is found in lampreys, follows the application of horseradish peroxidase to the olfactory mucosa.

Some anatomists suggested that this nerve is possibly a ganglionated remenant of an anterior branchial nerve which primitively innervated the mouth region (Weichert, 1958; Kent, 1978; Goodrich, 1986).

Concerning the structural components of the nervus terminalis, it was reported that this nerve contains elements of a sympathetic nature. According to Haller von Hallerstein (1934) the nervus terminalis carries somatic sensory fibres in addition to some sympathetic ones. Jollie (1968), however, mentioned that this nerve is presumed a sensory nerve (general cutaneous), but it may be a part of the autonomic system.

Eventually, there is a conflict of opinion about the exact function of the nervus terminalis. Haller von Hallerstein (1934) suggested that this nerve acts as a Jacobson's organ nerve in terrestrial vertebrates, while in aquatic forms it performs a special function. However, Weichert (1958), Kent (1978), Romer and Parsons (1985) and Goodrich (1986) are of the opinion that the function of the nervus terminalis is not clear. It has been reported that although this nerve is apparently sensory, yet it is unrelated to olfaction.

In the present study, the nervus terminalis arise from Jacobson′s organ in combination with the vomeronasal nerve. The fibres of the two nerves are also closely associated throughout their nasal course as well as their intracranial distribution. A similar condition was described in lizards *Diplometopon zarudayi* (Dakrory, 1994), *Acanthodactylus boskianus* (El-Ghareeb, 1997) and in the serpents *Naja haje haje* (Abdel-Kader *et al.*, 2000) and in *Natrix tessellate* (El-Ghareeb *et al.*, 2004). On the other hand, the result of the present study is totally different from what was described by Hegazy (1976) in serpents *Psammophis sibilans, Eryx jaculus* and *Cerastes vipera* and by Mostafa (1990a) in *Psammophis schokari, Coluber elegantissimus* and *Spalerosophis diadema*. In such snakes the nervus terminalis was found to arise from Jacobson's organ in a separate manner that is apart from the vomeronasal nerve.

In *Uromastyx aegyptius*, a number of ganglion cells are found associated with some of the nerve bundles forming the terminal and vomeronasal nerve. These ganglionic cells evidently represent the ganglion terminale as mentioned by Arey (1966), Bhatnagar and Kallen (1974), Hegazy (1990), Dakrory (1994), El-Ghareeb (1997), Abdel-Kader *et al.*(2000), El-Ghareeb *et al.* (2004) and Shamakh (2009).

The configuration of the terminal ganglion, met with in the present study, differs entirely from what was described by Hegazy (1976) and Mostafa (1990a) in Ophidia. These authors recorded that the terminal nerve arises apart from the vomeronasal nerve of Jacobson's organ and it carries the ganglion intracranially near its termination in the forebrain.

According to Haller von Hallerstein (1934), Weichert (1958), Grüneberg (1973), Goodrich (1986) and Dakrory (1994) the nervus terminalis of fishes, amphibians, reptiles and mammals bears during its course one or two ganglia terminale.

In the present study, the olfactory bulb lies at a considerable distance anterior to the cerebral hemisphere of the brain, to which it is joined by an olfactory peduncle. This was generally found in Lacertilia and Ophidia by Haller von Hallerstein (1934). The presence of an olfactory peduncle has been described by many authors in the majority of Lacertilia and Ophidia, and consequently it seems a common character in Squamata. It was described by in the lizards *Lacerta viridis* (Goldby, 1934), *Anguis fragilis* (Pratt, 1948), *Chalcides ocellatus* (Hegazy, 1969), *Tarentola mauritanica* (Mostafa, 1970), *Agama pallida* and *Ptyodactylus hasselquistii* (Abdel-Kader, 1990), *Uromastyx aegyptius* (Mostafa, 1990b). An olfactory peduncle was also described by Hegazy (1976) in *Psammophis sibilans, Eryx jaculus* and *Cerastes vipera* by Mostafa (1990a) in *Psammophis schokari, Coluber elegantissimus* and *Spalerosophis diadema* by Abdel-Kader *et al*. (2000) in *Naja haje haje* and by El-Ghareeb *et al*. (2004) in *Natrix tessellate*. In Chelonia, on the other hand, Soliman (1964) found that the olfactory peduncles are absent and the olfactory bulbs join the cerebral hemispheres directly.

The connection of the vomeronasal nerve with the organ of Jacobson from one side and the vomeronasal formation (accessory olfactory bulb) from the other side, met with in the present study, is the case found in the lizards by Pratt (1948), Dakrory (1994& 2011), El-Ghareeb(1997) and by Shamakh(2009)and also in the snakes described by Abdel-Kader *et al*. (2000) and Mahgoub (2004). According to Bellairs (1950) and Jollie (1968), this condition seems to be a common character in *Sphenodon* and squamates.

The vomeronasal nerve, Jacobson's organ, and consequently the accessory olfactory bulbs, are not represented in chelonians and crocodilians among reptiles, and in all birds (Jollie, 1968; Romer and Parsons, 1985; Soliman *et al.,* 1986). Among mammals, the structures in question, are lacking in many bats, various aquatic forms as whales, in some carnivorous and in man and the other higher primates as maquque (Jawlowski, 1955; Mann, 1961; Bhatnagar and Kallen, 1974; Romer and Parsons, 1985). Evidently, these findings affirm satisfactorily the concept which has been accepted among morphologists that the accessory olfactory bulb is apparently restricted to animals having a vomeronasal organ.

In *Uromastyx aegyptius* studied, the nervus terminalis, being associated with the vomeronasal nerve carrying few olfactory bundles, exits from the cavity of the nasal capsule through special foramen. Also, the nervus olfactorius leaves the capsular cavity as separate bundles through separate foramina (found in the olfactory capsule; one for each bundle). Among agamids, a typical condition was found in *Agama stellio* (Eyal-Giladi, 1964) and in *Laudakia stellio* (Shamakh, 2009). Also, Malan (1946) recorded a number of foramina for the emersion of these nerves from the capsular cavity in *Sceloporus undulates* and *Iguana iguana*. It appears that the exit of these nerves from the olfactory capsule in agamides is modified completely from that found in other lacertilians, where there is a single foramen olfactorium advehens for their exit. Such modifications are due to the backward movement of the dorsal part of the nasal capsule relative to its ventral part. Malan (1946) reported that the nervus vomeronasalis leaves the capsular cavity through a separate foramen which is situated so low down on the posterior face of the capsule as to be located almost ventral in position. This condition is very similar to that found in *Laudakia stellio* (Shamakh, 2009).

On the other hand, a closed foramen olfactorium advehens is found in most of the lizards so far described. It is mentioned by Rice (1920) in *Eumeces* and by Ramaswami (1946) in *Calotes*. This appears to be due to the fusion between the planum antorbitale and the nasal septum. However, the foramen olfactorium advehens of amphisbaenian *Diplometopon zarudnyi* (Dakrory, 1994) is in the form of a wide incisura and not a closed foramen. This is due to the lack of connection between the planum antorbitale and the nasal septum.

Among Ophidia, a closed foramen olfactorium advehens was recorded in *Vipera resselii* (Srinivasachar, 1955), *Cerastes vipera* (Hegazy, 1976), *Spalerosophis diadema* (Mostafa, 1990a) and in *Naja haje haje* (Abdel-Kader *et al*., 2000). On the other hand, such foramen is in the form of a wide incissure and not a complete foramen in the snakes *Typhlops delalandii* (Smit, 1949), *Malpolon monospessulana* (El-Toubi *et al*., 1973), *Psammophis sibilans* and *Eryx jaculus* (Hegazy, 1976) and in both *Psammophis schokari* and *Coluber elegantissinus* (Mostafa, 1990a).

Among birds, the presence of a defined fenestra olfactorium advehens appears to be common (Soliman *et al*., 1986). However, the nervus olfactorius leaves the capsular cavity through fissura orbitonasalis in *Sternus vulgaris* (De Kock, 1955) and by means of a bony canal in *Colius indicus* (Schoonees, 1963).

In Mammalia, the fenestra olfactoria advehens, or fenestra cribrosa, is subdivided into numerous pores of the cribriform plate. The subdivision of the fenestra olfactoria advehens was described in *Galago senegalensis* (Kanagasuntheram and Kanan, 1964) and *Manis javanica* (Jollie, 1968). The subdivision of the fenestra olfactoria advehens seems to be a typical mammalian character, except in monotremes. In such case, nervus terminalis, being combined with the vomeronasal nerve, and the ordinay nervus olfactorius leaves the nasal cavity through two separate foramina of the cribriform plate (Hegazy, 1990) in the hedgehog. Earlier, Huber and Guild (1913) and McCotter (1915) dealing with the rabbit and man, respectively, mentioned that the nervus terminalis passes through the cribriform plate anterior to the exit of the vomeronasal nerve.

In the present study, the nervi terminalis, vomeronasalis and olfactorius enter the cranial cavity through the foramen olfactorium evehens. This result agrees with the result of Ramaswami (1946) in *Calotes versicolor*, Hegazy (1969) in *Chalcides ocellatus,* Mostafa (1970) in *Tarentola mauritanica* and Shamakh (2009) in *Laudakia stellio*. On the other hand, due to the absence of a foramen olfactorium evehens, the nervi terminalis, vomeronasalis and olfactorius enter the cranial cavity through the membranous cranial wall as recorded in the amphisbaenian *Diplometopon zarudnyi* (Dakrory, 1994).

In Ophidia, the lack of the foramen olfactorium evehens seems to be a common pattern (Pringle, 1954; Hammouda, 1963; El-Toubi *et al*., 1973; Mostafa, 1990a; Abdel-Kader *et al*., 2000). These authors concluded that the lacking of the foramen olfactorium evehens is due to the complete lack of the sphenethmoid commissure.

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