Innervation of the Olfactory Apparatus of Varanus Niloticus (Squamata– Lacertilia-Varanidae)

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Abstract: The olfactory apparatus of *Varanus niloticus niloticus* includes the main olfactory organ and the vomeronasal organ or organ of Jacobson. The vomeronasal organ is innervated by two associated 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 combine together as one separate nerve which leaves the cavity of the nasal capsule together with three bundles of the olfactory nerve through the fenestra olfactoria advehens. The main olfactory organ is innervated by the olfactory nerve which arises from the sensory olfactory epithelium and leaves the capsular cavity through the fenestra olfactoria advehens as separate bundles. The three nerves enter the cranial cavity through a large fenestra olfactoria evehens. They connect separately the anterior part of the brain. The nervi terminalis and vomeronasalis enter the accessory olfactory bulb whereas, the nervus olfactorius enters the main olfactory bulb. The olfactory bulb has a long olfactory peduncle. The three nerves carry pure special sensory fibres.

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1. Introduction

The varanids are generally large lizards, with small heads, elongated necks and long robust bodies. The tails are muscular, long to very long and lacks caudal autotomy. This family "Varanidae" comprises about 51 species belonging to two subfamilies, subfamily Lanthanotidae with one genus and one species and subfamily Varaninae with one genus and about 50 species (Zug et al., 2001). They are active predators having strong jaws and sharp, conically recurved teeth. They catch live prey but also are scavengers (Lenz, 1995&2004 and Campbell, 2003). Most species are terrestrial to semiarboreal, although a few species are strongly arboreal. The Australian bulliwallah; Varanus mertensi is seldom more than a meter from water and commonly feeds and escapes into the water (Lenz, 1995& 2004 and Bennett, 1998). All varanids are oviparous, and do not show evidence of parental care. Eggs are typically buried and have a moderately long incubation, seldom less than 100 days to nearly one year (Bennett, 1998 and Branch, 1998).

Varanus niloticus niloticus is semi-aquatic and adaptable lizard, i.e., it is not habitat- specific and can be found in almost any habitat where permanent bodies of water exist (Lenz, 1995& 2004 and Bennett, 1998). It is omni-carnivorous, eating invertebrates, human feceas, young crocodiles, eggs of birds, turtles, frogs, rats and snakes (Lenz, 1995&2004 and Campbell, 2003). The females are highly fecund; they lay and bury eggs in the termite mounds; the female lays from 7-35 soft-shelled eggs (Bennett, 1998 and Branch, 1998). The incubation period lasts from 8-10 weeks. Varanus niloticus niloticus is a diurnal lizard lives more than 10-15 years (Campbell, 2003 and Lenz, 2004). It is much exploited for its meat and skin (Spawls et al., 2002 and Baha El-din, 2006). It has elongated, snake-like head, sharp claws and long compressed tail. The skin is rough and beady, with dark olive colour and containing yellow spots arranged in distinctive bands (Steel, 1996; Branch, 1998 and Lenz, 2004).

The varanid lizards are characterized by possessing a highly developed olfactory (chemosensory) apparatus comprising the main olfactory organ and the vomeronasal (Jacobson's) organ. Generally, the previous studies are concerned only with the structural, functional, behavioral and reproductive aspects in squamates (Halpern, 1987& 1992; Schwenk, 1993 and Eisthen, 1997), with little attention being given to the innervations of the olfactory system (Kratzing, 1975; Wang and Halpern, 1980 and Halpern, 1992).

Although many studies have carried on the varanids concerning their biology (King and Green, 1993), ecology (Auffenberg, 1981 and Pianka, 1994) and evolution (Greer, 1989 and Pianka, 1995), yet the works on the anatomy especially those on the cranial nerves and the sensory systems were scarce. There were few studies on the cranial nerves of varanids, these include the primitive and classical study on *Varanus bengnlensis* (Fischer, 1852) and on *Varanus bivittatus* (Watkinson, 1906). Moreover, Bellairs (1949) described the structure and morphology of the nasal region, but the nerves of special sense were neglected in his study reporting that the nervus terminalis could not be identified in varanids.

From the above mentioned review, it obvious that the study of the cranial nerves and the innervations of the chemosensory system in varanids are poor or totally neglected. Thus, the study of the innervations of this system in *Varanus niloticus niloticus* is very important both anatomically and phylogenically. Moreover, it is necessary to examine and analyze the fibres arising from the vomeronasal organ (Jacobson's organ) on an attempt to ensure the presence or absence of the terminal nerve in *Varanus niloticus niloticus*.

2. Materials and Methods

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Six specimens of the juvenile Varanus niloticus niloticus ranges from 30- 31.5 cm total body length were caught from Abu-Semble at Aswan Governorate during August 2008. These specimens were carried out and anthetized in the lab. The heads were taken and fixed in aqueous Bouin's solution for 24-48 hours. After that, the fixed heads were treated with EDTA solution for about 60 days with changing the solution every 4 days for decalcification. At the end of this process, the heads were washed with 70% ethyl alcohol several times. This was followed by embedding of the heads in paraffin wax and then sectioned transversely at 15 µm thickness. The serial sections were stained with Mallory's Triple Stain (Pantin, 1946). The transverse sections were drawn with the help of a projector microscope. In order to illustrate the relations of the nerves to other different parts of the head, several sections were photomicrographed.

3. Results

The microscopic investigation of the serial sections of the young *Varanus niloticus niloticus* has succeeded in demonstrating the presence of a nervus termialis in this species arising from the sensory epithelium of the vomeronasal organ of Jacobson together with those of the nervus vomeronasalis.

Nervi Terminalis and Vomeronasalis

The nerve fibres arise from the medial, dorsomedial and dorsal side of the epithelium lining the anterior half of the organ and run posteriorly in the dorsomedial direction. These fibres gradually approach each other forming numerous fine nerve fascicles (Figs. 1&2). Anterior to the opening of the organ duct into the mouth roof, these fascicles extend dorsal, medial, dorsomedial to the sensory epithelium, lateral to the internasal septum and ventral to the septomaxillary bone (Fig. 1, Nn.TV). Just at the level of the opening and backwards, the sensory epithelium appears covered by a fasculated layer of the nerve fibres dorsomedially (Figs. 1& 2,).

The terminal fibres arise from the vomeronasal sensory epithelium of the posterior part collect into small fascicles. These fascicles gradually approach the previously formed ones and fuse together forming large bundles. These bundles extend posteriorly passing lateral to the internasal septum, ventral to the septomaxilla and dorsomedial to the sensory epithelium. More backwards these bundles continue passing lateral to the internasal septum, ventral to the medial edge of septomaxilla and dorsal to the paraseptal cartilage (Fig. 3).

The sensory fibres issue from the caudal end of the organ and collect into numerous fascicles. These fascicles run posteriorly extending ventral to the paraseptal cartilage and dorsal to the prevomer bone (Fig. 3). More backwards, they fuse into large bundles, which gradually approach those of the anterior part.

Posterior to the organ of Jacobson, the nervus terminalis carrying the vomeronasal nerve fibres appears in the serial transverse sections as six nerve bundles, which run posteriorly in a space surrounded by both the internasal septum and the prevomer bone medially, the latter bone ventrally and ventrolaterally and the septomaxilla laterally and dorsally. Here, few ganglionic cells are found among fibres of some of the nerve bundles. These cells represent the ganglion terminale (Fig. 4). The nerve bundles continue posterodorsally passing lateral to the internasal septum and medial to both the septomaxilla and the olfactory canal. Thereafter, they leave the organ capsule and enter the nasal capsule. Within the latter, the nerve bundles constituting the nervi terminalis-vomeronasalis continue their posterodorsal course running lateral to the internasal septum, ventral to the ramus medialis nasi and medial to the olfactory canal. During the latter course, the nerve bundles approach gradually till they join together forming large bundle (Fig. 5).

At the end of their intracapsular course, the common nervi terminalis- vomeronasalis leave the nasal capsule through the fenestra olfactoria advehens (Fig. 6, FOA). After a short extracapsular course, they enter the cerebral cavity through the fenestra olfactoria evehens (Fig. 6). Intracranially, the nervi terminalis-vomeronasal extend posteriorly passing ventromedial to the olfactory bulb (Figs. 6-8). Thereafter, they shift posterodorsally passing medial to the main olfactory bulb till they enter the accessory olfactory bulbs (vomeronasal formation) from its ventromedial side (Fig. 8). The latter structure is located posteromedial to the main olfactory bulb.

Nervus Olfactorius

In *Varanus niloticus niloticus*, the olfactory nerve originates from the sensory olfactory epithelium of the main nasal chamber. This epithelium has a relatively small area compared to the main olfactory chamber. It is located in the most posterodorsal part of the chamber, just medial to both the lateral nasal gland and nasal concha. Its anterior end lies posterior to the anterior limit of the internal naris or choana, i.e., the sensory epithelium lies opposite to the posterior part of choana.

The nerve fibres arise from the sensory olfactory cells and collect gradually into numerous nerve fascicles. These fascicles extend posteriorly along the lateral, dorsal and medial sides of the nasal chamber. The nerve fibres arise from the lateral olfactory epithelium extend backwords in the dorsal direction passing lateral to the olfactory epithelium and medial to the parietotectal cartilage (Fig. 5). The fibres originate from the medial olfactory epithelium run posterodorsally extending medial to the sensory olfactory epithelium and lateral to both the nervi terminalisvomeronasal and the internasal septum. The fibres issue from the dorsal olfactory epithelium pass posteromedially ventral to the parietotectal cartilage and dorsal to the olfactory epithelium (Fig. 5).

The fascicles of the medial side gradually approach and fuse together forming three bundles. Also, the fascicles of the lateral epithelium together with those of the dorsal olfactory epithelium form another large bundle. Again, the fibres originate from the dorsal olfactory epithelium at its posterior end collected into a few fascicles, which gradually approach forming a third large nerve bundle. These bundles leave the cavity of the capsule through the fenestra olfactoria advehens (Fig. 6). Shortly posterior, these nerve bundles enter cranial cavity through the fenestra olfactoria evehens (Fig. 6, FOE). Within cranial cavity, they join the anterior extremity of the main olfactory bulb (Fig. 6). The fibres arise from the medial part of the sensory olfactory epithelium collect together into three fascicles. These run posterodorsally lateral to the terminalvomeronasal nerves. These fascicles continue till they leave the capsule, along with the vomeronasal nerve through the fenestra olfactoria advehens. Extracapsular, they remain

passing lateral to the terminal-vomeronasal nerves till they enter the cranial cavity together through the fenestra olfactoria evenes. Intracranially, one of the three olfactory nerve fascicles enters the olfactory bulb from its ventromedial corner. The other two fascicles enter the bulb from its medial side (Fig. 6).



Fig. (1) :Photomicrograph of a part of transverse section passing through the anterior olfactory region of Varanus niloticus niloticus showing the position of the vomeronasal organ, vomeronasal concha and the most anterior fascicles of the terminal-vomeronasal nerves. SMX, Septomaxilla; V, Vestibule; PSCA, Paraseptal cartilage; PV, Prevomer; INS, Internasal septum; CO.VN, Vomeronasal concha; O.VN, Vomeronasal organ; Nn.TV, Terminal-vomeronasal nerves.



Fig. (2): Photomicrograph of a part of transverse section passing through the anterior olfactory region (at the posterior end of Jacobson's concha) of Varanus niloticus niloticus showing the septomaxilla forming roof of the vomeronasal organ, the prevomer forming its floor and the bundles of the terminal-vomeronasal nerves. SMX, Septomaxilla; PSCA, Paraseptal cartilage; PV, Prevomer; INS, Internasal septum; O.VN, Vomeronasal organ; Nn.TV, Terminal-vomeronasal nerves.



Fig. (3): Photomicrograph of a part of transverse section passing through the anterior olfactory region (at the caudal end of the vomeronasal organ) of Varanus niloticus niloticus showing the fragmented paraseptal cartilage and terminal-vomeronasal nerves passing dorsomedial and through the fragmented paraseptal cartilage. SMX, Septomaxilla; PSCA, Paraseptal cartilage; PV, Prevomer; INS, Internasal septum; Nn.TV, Terminal-vomeronasal nerves; PPMX, Palatal process of premaxilla; R.MN, Ramus medialis nasi.

http://www.americanscience.org

120



Fig. (4): Photomicrograph of a part of transverse section passing through the anterior olfactory region of Varanus niloticus niloticus (at the caudal end of the vomeronasal organ) showing ganglion terminale and the terminal-vomeronasal nerves entering the olfactory capsule as sixth or seventh nerve bundles. SMX, Septomaxilla; PV, Prevomer; INS, Internasal septum; Nn.TV, Terminal-vomeronasal nerves; G.T, Ganglion terminale.



Fig. (5): Photomicrograph of a part of transverse section passing through the anterior olfactory region of Varanus niloticus niloticus showing the passage of terminal-vomeronasal nerves inside the olfactory capsule and illustrates the bundles of the olfactory nerve. PV, Prevomer; INS, Internasal septum; Nn.TV, Terminal-vomeronasal nerves; R.MN, Ramus medialis nasi; OC, Olfactory chamber; ON, Olfactory nerve; PCA, Parietotectal cartilage



Fig. (6): Photomicrograph of a part of transverse section passing through the posterior olfactory region of Varanus niloticus niloticus showing the exit of the terminal-vomeronasal nerves from the olfactory capsule through the fenestra olfactoria advehens and its entrance the cranial cavity through the fenstra olfactoria evehens and also illustrates the bundles of the olfactory nerve. Nn.TV, Terminal-vomeronasal nerves; OC, Olfactory chamber; ON, Olfactory nerve; PCA, Parietotectal cartilage; FR, Frontal; FOE, Fenestra olfactoria evehens; FOA, Fenestra olfactoria advehens; OB, Olfactory bulb.



Fig. (7): Photomicrograph of a part of transverse section passing through the most posterior olfactory region of Varanus niloticus niloticus showing the passage of the terminal-vomeronasal nerves between the two main olfactory bulbs. Nn.TV, Terminal-vomeronasal nerves; FR, Frontal; OB, Olfactory bulb; INS, Internasal septum; PAOR, Planum anteorbitale; SECO, Sphenethmoidal commissure.



Fig. (8): Photomicrograph of a part of transverse section passing through the most posterior olfactory region of Varanus niloticus niloticus showing the entrance of the terminal-vomeronasal nerves into the accessory olfactory bulbs and the posterolateral parts of the main olfactory bulbs. Nn.TV, Terminal-vomeronasal nerves; FR, Frontal; OB, Olfactory bulb; INS, Internasal septum; SECO, Sphenethmoidal commissure; AOB, Accessory olfactory bulb.

4. Discussion

The description of the innervation of the olfactory apparatus in *Varanus niloticus niloticus* succeeds in demonstrating three types of nerve fibres, which arise from the sensory cells of this apparatus and connect separately the anterior portion of the forebrain. These 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 first described by Pinkus (1894) in the dipnoan Protopterus annectens. Thereafter, it was identified nearly in all the vertebrate classes except cyclostomes and birds, as has been reported by Haller von Hallerstein (1934), 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 remnant of an anterior branchial nerve which primitively innervated the mouth region (Romer and Parsons, 1985; Goodrich, 1986). As to the structural components of the nervus terminalis, it was stated that this nerve contains elements of a sympathetic nature. According to De Beer (1924) and 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 to be a sensory nerve (general cutaneous), but it may be a part of the autonomic system.

Eventually, there is a conflict of opinion between authors about the exact function of the nervus terminalis. Plate (1922) and 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. 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 the olfactory sense.

In the present study, the nervus terminalis exits from the organ of Jacobson 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 the lizards *Diplometopon zarudayi* (Dakrory, 1994), in *Laudakia stellio* (Shamakh, 2009), in the serpents Naja haje haje (Abdel-Kader *et al.*, 2000) and in *Natrix tessellate* (El-Ghareeb *et al.*, 2004). The same result was also encountered in mammals. It was found in the hedgehog (Hegazy, 1990). On the other hand, this condition 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 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. From the above discussion, it can suggest that the association of these two nerves in *Varanus niloticus niloticus* is a primitive lacertilian character.

In *Varanus niloticus niloticus*, number of ganglion cells is found associated with some of the nerve bundles forming the terminal and vomeronasal nerves. These ganglionic cells evidently represent the ganglion terminale as named by Döllken (1909). This is the view mentioned by Hegazy (1990), Dakrory (1994), 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), Goodrich (1986) and Dakrory (1994) the nervus terminalis of fishes, amphibians, reptiles and mammals bears during its course one or two ganglia terminale. However, such ganglion is lacking in Mustelus (McKibben, 1914), rarely found in Urodela (Haller von Hallerstein, 1934) and is not represented in some mammals (Gruneberg, 1973).

In the present study, the olfactory bulb lies a considerable distance anterior to the cerebral hemisphere of the brain, to which it is joined by an olfactory peduncle. This is generally found to be present in Lacertilia and Ophidia by Haller von Hallerstein (1934). The presence of an olfactory peduncle has been generally described by many authors in the majority of Lacertilia and Ophidia, and consequently it seems to be a common character in Squamata. It was described in the lizards Lacerta viridis (Goldby, 1934), Anguis fragilis (Pratt, 1948), Uromastyx aegyptius (Mostafa, 1990b), Diplometopan zarudnyi (Dakrory, 1994), and Laudakia stellio (Shamakh, 2009). In serpents, 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 studied by Pratt (1948), Dakrory (1994), and Shamakh (2009) and also in the snakes described by Hegazy (1976), Mostafa (1990a), 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). Also, it is absent in birds (Watanabe and Yasuda, 1968 and 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 (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 Varanus niloticus niloticus studied, the nervi vomeronasalis- terminalis, together with few olfactory bundles, exit from the cavity of the nasal capsule through a fenestra olfactoria advehens. A closed fenestra olfactoria advehens is found in most of the lizards so far described. It is mentioned by Rice (1920) in Eumeces, De Beer (1937) in Lacerta, and by Ramaswami (1946) in Calotes. This appears to be due to the fusion between the planum antorbitale and the nasal septum.

The fenestra olfactoria advehens in the amphisbaenian *Diplometopon zarudnyi* (Dakrory, 1994), however, it 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 fenestra olfactoria advehens was recorded in Vipera aspis (Peyer, 1912), 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 fenestra is in the form of a wide incissure and not a complete foramen in the snakes Tropidonotes natrix (De Beer, 1937), 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).

On the other hand, these nerves together with the olfactory nerve leave the capsular cavity as separate bundles through separate foramina (found in the olfactory capsule; one for each bundle) in agamid lizards. It was found in *Agama atra* (Malan, 1946), *Agama hispida* (Barry, 1953), *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*.

Among birds, the presence of a defined fenestra olfactoria advehens appears to be common (Soliman *et al.*, 1986). However, the nervus olfactorius leaves the capsular cavity through an undelimited fenestra in *Anas boschas* (De Beer, 1937), 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 (De Beer, 1937; Jollie, 1968; Hegazy, 1990).

In the present study, the nervi terminalis, vomeronasalis and olfactorius enter the cranial cavity through the fenestra olfactoria evehens. This result agrees with the results of De Beer (1937) in *Lacerta agilis*, Ramaswami (1946) in *Calotes versicolor*, and Shamakh (2009) in *Laudakia stellio*. This was also the case described for the chelonian *Emys lutaria* (De Beer, 1937). On the other hand, the absence of a fenestra olfactoria evehens and so the nervi terminalis, vomeronasalis and olfactorius enter the cranial cavity through the membranous cranial wall. This condition was recorded in the amphisbaenian *Diplometopon zarudnyi* (Dakrory, 1994).

In Ophidian, the lack of the fenestra olfactoria eveness seems probable to be a common pattern (De Beer, 1937; Mostafa, 1990a and Abdel-Kader *et al.*, 2000). These authors concluded that the lacking of the fenestra olfactoria eveness is due to the complete lacking of the sphenethmoid commissure.

Conclusions

There are three groups of nerve fibres originate from the olfactory apparatus. They organized into three nerves; terminalis, vomeronasalis from the vomeronasal organ and the nervus olfactorius from the main olfactory organ. The nervus terminalis has scattered ganglionic cells which form the ganglion terminale.

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125