

# THE COMPLEX VOMERONASAL STRUCTURE OF *DIPSOCHELYS* GIANT TORTOISES AND ITS IDENTIFICATION AS A TRUE JACOBSON'S ORGAN

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The nasal structure of the western Indian Ocean *Dipsochelys* giant tortoises is described. These tortoises are known to possess structures facilitating 'nasal drinking'. Additional unique nasal features include the processus dorsalis vomerinus supporting an enlarged medial nasal gland and a 'tuberculum palatinum'. The medial nasal gland can be considered homologous to the vomeronasal organ (Jacobson's organ) and is connected directly to the tuberculum palatinum in the buccal cavity through the foramina praepalatina. An homologous vomeronasal organ with a direct buccal connection is also identified in existing literature accounts of the leatherback turtle *Dermochelys coriacea* and may have been overlooked in other Chelonia.

*Key words:* Chelonia, olfaction, tortoise, palatine gland, pheromones

## INTRODUCTION

The nasal region is of great significance in individual interactions in many tetrapod groups because of the role of the vomeronasal organ (sometimes referred to as Jacobson's organ) in pheromone detection. This structure is well developed in many reptile groups, most notably the lizards and snakes, but its presence in the Chelonia has been disputed over many years (Parsons, 1970). Tissue layers in the nasal region of several turtles have been associated with the vomeronasal organ although no discrete structure comparable to the complex Jacobson's organ of many mammals and squamate reptiles is apparent in most species examined. The view that chelonian nasal structures are highly conservative compared to other classes of tetrapods (Parsons, 1970) is not supported by some recent studies (Saito *et al.*, 2000; Murphy *et al.*, 2001). Discussion of the apparent vomeronasal structures in chelonians date from 1895 when Seydel concluded that a Jacobson's organ was present on the grounds that the vomeronasal epithelium develops ventrally and medially (as opposed to the dorsal olfactory epithelium), with innervation of the vomeronasal nerve from the accessory olfactory bulb and no Bowman's glands. This contrasts with more recent studies that have not accepted the chelonian structure as a true Jacobson's organ on the basis of not forming a distinct evaginated structure (Parsons, 1959). The presence of vomeronasal epithelium in pockets of the nasal cavity in some chelonians has obscured such classification (Parsons, 1970) and the vomeronasal epithelium is now generally referred to as a vomeronasal organ despite the absence of discrete physical structures (Murphy *et al.*, 2001).

Some of the most complex chelonian nasal structures have been described from the western Indian Ocean giant tortoise genus *Dipsochelys* (Bour, 1982; Arnold,

1979; Gerlach & Canning, 1998). The raised nasal opening and the structures within the nasal chamber have been interpreted as adaptations to facilitate drawing water up through the nasal passages during drinking through the nose (Arnold, 1979). This behaviour has been reported in wild *D. dussumieri* (also referred to as *Geochelone gigantea* or *D. elephantina*) on Aldabra (Arnold, 1979). Further discussion of the structures of the *Dipsochelys* nasal region has considered the possibility of this genus having an enhanced olfactory capability, a suggestion following from the description of a bony support for a 'vomeronasal organ' (Gerlach & Canning, 1998). The palate has also been noted as being unusual in possessing a tuberculum palatinum as described by Fritsch (1870):

"In *Testudo elephantina* [= *Dipsochelys dussumieri*] an oval whitish body 3 mm long is located ventral to the hard palate in the anterior of the upper jaw, its precise outline is obscured by the enclosing membrane. Under closer examination this body appears as only an apparent swelling in the membrane covering the partition that separates the choanae from one another, as the section is not distinguished in coloration or structure, which would allow the so called Tuberculum palatinum to be recognised as a separate organ."

The published interpretations of the nasal structures have relied on comparative osteology and dissection. These provide structural information but there have been no published accounts of the detailed morphology of the 'flap-like ridge' (Arnold, 1979) or the 'vomeronasal organ' (Gerlach & Canning, 1998) to support functional interpretations. In order to investigate these structures in more detail available dissections and microscopic preparations were examined to provide morphological and histological data on the unique features of *Dipsochelys*. The availability of freshly preserved material allowed new dissections to be prepared. The results are described below, identifying the structure as a true vomeronasal organ with a level of complexity comparable to the Jacobson's organ of mammals or squamates.

## MATERIAL AND METHODS

During a taxonomic revision a detailed osteological study was made on 118 specimens of all species of the genus (Gerlach & Canning, 1998). During this study, careful attention was paid to the ridges and bony processes within the nasal chamber following observation that there were differences in these structures between *D. dussumieri* and *D. grandidieri*. A dissection of an adult female head of a *Dipsochelys dussumieri* from Aldabra (preserved in 70% ethanol since 1971) has previously been figured and described (Arnold, 1979); the preserved dissection (BM(NH) R1978.772) was re-examined. Recent material of one adult *D. dussumieri* on Aldabra atoll was examined. Previously undescribed material was available in the form of serial transverse sections of a *D. dussumieri* late embryo. The 10 µ sections stained with Masson's trichrome had been prepared by A. d'A. Bellairs and are stored in the British Museum (Natural History). In 2003 five full-term embryos of *D. hololissa* were preserved and stored by the Nature Protection Trust of Seychelles. These were preserved in 4% paraformaldehyde enabling new dissections and microscope preparations to be made. All sectioned material was prepared by cutting 5 µ paraffin embedded sections followed by staining with cresyl violet.

Comparison was made with '*Geochelone*' (*Stigmochelys*) *pardalis*, which may be the closest living relative of *Dipsochelys* (Gerlach, 2001; Palkovaks *et al.*, 2002) and with published accounts of the nasal anatomy of *Testudo* (Parsons, 1970) and other turtles (Bellairs & Kamal, 1981; Nick, 1912).

Due to the large size of these tortoises it is possible to observe structures in the palate when the mouth is open. One adult female *Dipsochelys hololissa* and one adult female *D. arnoldi* in the captive groups of the Nature Protection Trust of Seychelles on Silhouette island, Seychelles responded to scratching of the neck by standing upright and stretching the neck and head upwards. In this pose the lower jaw would open and could be gently levered open further to expose the palate.

## RESULTS

### OSTEOLOGY

The soft-tissue structure suggested to be a vomeronasal organ is supported by the processus vomerinus dorsalis, positioned on the dorsum of the vomer between the foramina praepalatina, anterior to the sulcus vomerinus (Figs. 1, 2). This bony process is a unique feature of *Dipsochelys* (Gerlach & Canning, 1998), no trace of any similar structure has been found in any other tortoise genus. The processus vomerinus dorsalis is a slightly elevated piece of bone on the dorsum of the premaxillae. In adult tortoises (straight carapace length over 45cm) it measures 2-6 mm diameter and is raised 0.5-6 mm. The height of the processus vomerinus dorsalis varies with different species, being low (0.5 mm) in *D. hololissa*, moderately elevated in *D. dussumieri* (0.5-2 mm) and *D. arnoldi* (1-2 mm) and high (6 mm) in the

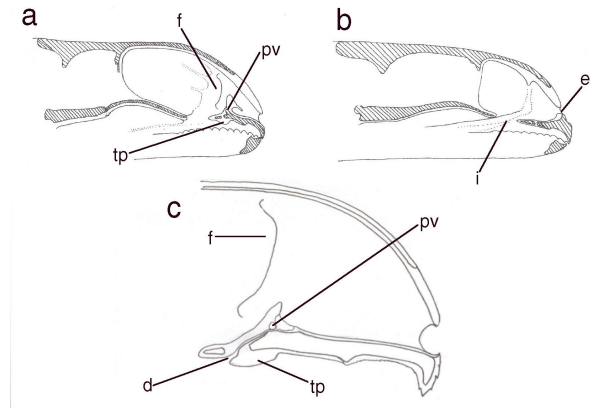


FIG 1. Nasal structures of *Dipsochelys dussumieri* and '*Geochelone*' *pardalis*; (a) medial view of right nasal passage and nasal chamber of *D. dussumieri*; (b) medial view of right nasal passage and nasal chamber of '*G.*' *pardalis*; (c). Detail of the vomeronasal structures of *D. dussumieri* in medial view; d – duct from the tuberculum palatinum; e – external naris; i – internal naris; f – nasal flap; pv – processus vomerinus dorsalis; tp – tuberculum palatinum

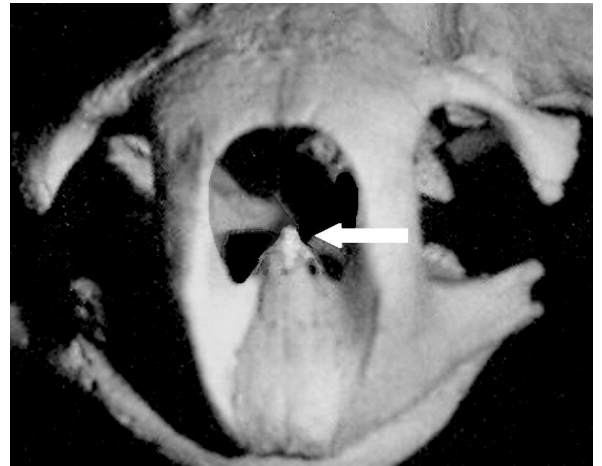


FIG. 2. Anterior view of skull of *Dipsochelys grandidieri* showing the exceptionally large processus vomerinus dorsalis (marked by arrow).

extinct Malagasy species *D. grandidieri*. In *D. grandidieri* the exceptionally large process bears two 1.5 mm diameter pits in the anterior surface (Fig. 2).

### SOFT-TISSUE ANATOMY

The nasal passage in *Dipsochelys* is exceptional in tortoises in rising steeply above a vertical cartilaginous process on the floor of the nasal passage supported by the processus vomerinus dorsalis. This elongate process contains a deep pocket directed posteriorly (Fig. 1a). No distinctive features are apparent within the pocket except for a very narrow duct passing into the foramen praepalatina. The tissues lining the processus vomerinus dorsalis are innervated by both the olfactory nerve and the accessory olfactory bulb: the nervus septimarius and the vomeronasal nerve respectively.

The nasal passage descends vertically behind the cartilaginous process before dividing into the postero-ventral nasopharyngeal duct and the postero-dorsal cavum nasi proprium. The opening to the latter is par-

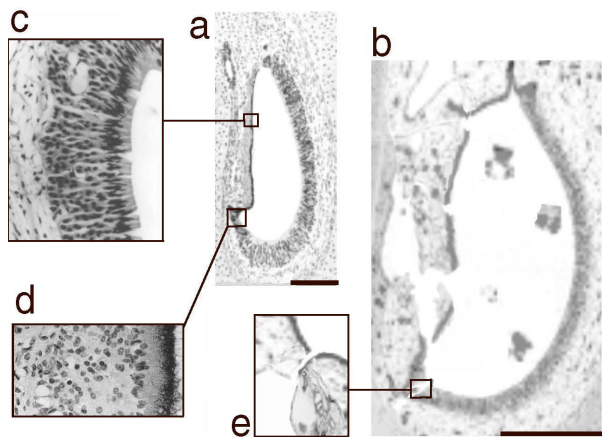


FIG. 3. Photomicrographs of the cavi nasum proprium of *Dipsochelys* embryos (Scale bar 500  $\mu$ ); (a) sectioned at point b on Fig. 4; (b) section posterior to point b on Fig. 4; (c) respiratory epithelium of the intermediate region, showing the absence of ciliated cells; (d) vomeronasal epithelium of the medial nasal gland showing columnar cells with cilia and thickened basal connective tissue; (e) tuberculum palatinum.

tially covered by a flap of soft tissue projecting from the septum. No muscular areas are apparent in association with the flap. Two low ridges lie along the nasopharyngeal duct, one is on the medial and one on the ventro-medial wall.

On the ventral surface of the palate; situated between the foramina praepalatina is a hemispherical structure projecting into the buccal cavity; this has previously been referred to as the 'tuberculum palatinum' (Bojanus, 1819-21; Fritsch, 1870). This structure is oval, 3 mm wide and 4 mm long in the adult tortoise, 1  $\times$  2 mm in the full-term embryo. In live and in preserved material it is detectable as a pale bulge in the anterior of the palate (its exact extent is indistinct in the older preserved, bleached material). It is partially enclosed by the cartilage around the foramina praepalatina and the outline is indistinct.

The nasal branches of the palatine arteries pass through the foramina praepalatina and lie on either side of the tuberculum palatinum. Capillaries from the nasal arteries pass through the foramina praepalatina and enter the tuberculum palatinum, no major nerves enter the tuberculum. On either side of the tuberculum palatinum there is a duct passing from the buccal cavity into the processus vomerinus dorsalis.

#### HISTOLOGY

The available microscope preparations are of embryonic tortoises and the palatal region has been extensively fragmented during preparation of most sections. Consequently the description below and accompanying figures (Fig. 4-5) are based on a composite of the slides (Fig. 3).

Throughout the anterior sections the nasal passages (cavi nasi) are clearly visible as dense ovals, being closed anteriorly by the hypertrophied epithelial lining. A short distance from the external nares the nasal passages are open and the anterior portion of the cartilaginous septum is visible. At the position of the processus vomerinus dorsalis the nasal passages are dorso-ventrally elongate, broadened dorsally and with a medial fold, forming a ventro-medial pocket. Below the nasal passages the tuberculum palatinum is visible, composed of large, open cells.

The nasal passages themselves form two distinct regions; the anterior (vestibular) part and the cavum nasi proprium. The vestibulum is lined with darkly stained cuboid epithelial cells with large nuclei; a darker basal layer is also apparent. The cavum nasi proprium is lined with distinctive columnar epithelial cells above the basal layer. The medial wall is heavily stained in most sections. No elastic fibres could be detected in the basal layer.

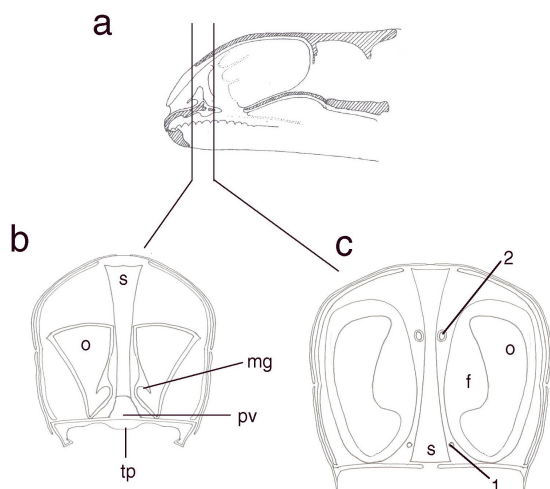


FIG. 4. Transverse sections through the nasal passages of *Dipsochelys*; (a) medial view of the skull showing the location of the sections; (b) section through the processus vomerinus; (c) section through the nasal flap; f - nasal flap; mg - medial nasal gland; o - olfactory chamber; pv - processus vomerinus dorsalis; s - septum; tp - tuberculum palatinum; 1 - nervus septi narium; 2 - vomeronasal nerve.

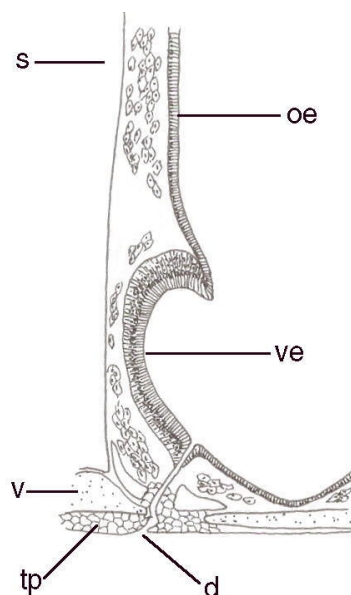


FIG. 5. Transverse section through the vomeronasal organ of *Dipsochelys*, section taken between lines b and c in Fig. 4; d - duct from the tuberculum palatinum to the vomeronasal organ; oe - olfactory epithelium; s - septum; tp - tuberculum palatinum; v - vomer; ve - vomeronasal epithelium.

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Within the cavum nasi proprium the broad dorsal olfactory region and the more compressed intermediate region are distinctive. The olfactory region is characterised by the presence of olfactory epithelium with Bowman's glands. The olfactory epithelium is distinctive in its high columnar shape and the presence of long cilia projecting into the lumen. The intermediate region is covered with respiratory epithelium (lacking the cilia of the sensory olfactory cells), with the exception of the medial pocket (the medial nasal gland) that is lined by sensory epithelium. Bowman's glands were not detected (and are absent from this region in other vertebrates). The nervous evaginations of the basal layer reported for *Testudo* (Parsons, 1970) were not observed.

The sections show a large area of thickened basal connective tissue on the medial wall of the nasal chamber. The cells present are typical basal cells with a conical form and could be interpreted as an area of erectile connective tissue as conjectured by Arnold (1979). In conjunction with this a dense network of capillaries are present between the connective tissue and the septum but the connective tissue does not surround venous spaces or contain detectable elastic tissue as would be expected in an erectile tissue. In the central and posterior sections the connective tissue is generally reduced and the medial fold absent, as is the medial pocket. The posterior portion of the nasal chamber is an elongate, dorsally broadened lumen, lined by a narrow border of sensory epithelium, with only a very narrow basal layer.

#### PALATE OBSERVATIONS

When the mouths of the tortoises are opened the tuberculum palatinum is visible as an oval yellowish area of the palate (Fig. 6).

#### DISCUSSION

The present study confirms earlier reports (Arnold, 1979; Gerlach & Canning, 1998) of the complexity of

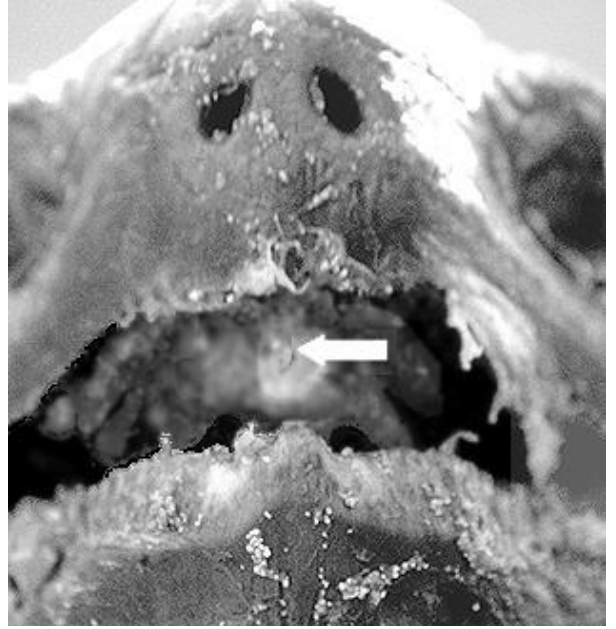


FIG. 6. Anterior view of palate of *Dipsochelys hololissa* showing the location of the tuberculum palatinum (marked by arrow).

the nasal passages of *Dipsochelys*. The largest structure in the nasal region is the flap of soft tissue projecting from the septum across the opening to the nasal chamber. This is lined with respiratory epithelium and supported by connective tissue, suggesting that it does not have a sensory function but may serve to partially close off the nasal chamber as suggested by Arnold (1979). However, the interpretation of the thickened area of connective tissue as an erectile tissue is made doubtful by the apparent absence of venous spaces or elastic tissue and it may be a passive inhibitor to water flow, permitting 'nasal drinking' but in a less specialised form than the valve proposed by Arnold (1979).

The cartilage and soft tissue structure resting on the processus vomerinus dorsalis is lined with sensory epithelium of the chelonian vomeronasal type (non-glandular). The position of the ventro-medial pocket identifiable as the medial nasal gland where the medial sulcus would be in other testudinids and its sensory development support the suggestion that the processus vomerinus dorsalis encloses a vomeronasal organ (Gerlach & Canning, 1998). This putative vomeronasal organ is connected to the tuberculum palatinum by the open lateral ducts opening directly into the buccal cavity. In other testudinids such as *Testudo* and *Geochelone pardalis* vomeronasal-like structures are less developed, lacking extensive cartilage (the paraseptal process of the septal cartilage only partly covers the duct), are not supported by a bony process of the vomer and lack a connection to the buccal cavity. The bony support and extensive cartilaginous encapsulation in *Dipsochelys* is more reminiscent of the vomeronasal organ of mammals (Rasmussen & Hultgren, 1990).

In all testudinids examined the gland is innervated by the nervus septi narium, a branch of the ophthalmic division of the trigeminal nerve. This is the case with the



vomeranasal organ of other reptiles, supporting the identification of the intermediate region of the chelonian nose as a vomeronasal organ (Tucker, 1963; Graziadei & Tucker, 1970; Parsons, 1970). There is also innervation from the accessory olfactory bulb where this has been studied (*Dipsosaurus*, pers. obs.; Caretta, Saito *et al.*, 2000) as in a true vomeronasal organ (Døving & Trotter, 1998), contrary to Gauthier *et al.*'s (1990) analysis. The pars anterior of the vomeronasal organ (equivalent to the anterior sulcus containing the medial nasal gland) is normally described as supporting sensory epithelium without Bowman's glands (olfactory regions support olfactory epithelium and Bowman's glands; Parsons, 1970). In *Testudo* the ventral, lateral walls and ventral surfaces of the olfactory ridges are non-sensory, supporting respiratory epithelium only, without Bowman's glands. The medial nasal gland duct enters the intermediate region in *Testudo* (Parsons, 1970) through the ventral surface of the medial ridge. These features are all in accordance with the observations of *Dipsosaurus*. A distinct vomeronasal organ was described in the lateral wall of the nasal septum of *Gopherus polyphemus* (Tucker, 1963) but this was subsequently noted to be the duct of the medial nasal gland (Graziadei & Tucker, 1970) and, as with *Testudo*, the general region of the anterior sulcus can be considered a poorly defined vomeronasal organ.

It appears that *Dipsosaurus* possesses an unusually well developed vomeronasal organ for a chelonian. This has an olfactory role and is generally associated with pheromone detection. Nose touching has been observed in genera other than *Dipsosaurus*: *Gopherus agassizii* (Camp, 1916) and *Homopus areolatus* (Carpenter & Ferguson, 1977). Although it appears to be an infrequent action, it has been used to suggest that olfaction and pheromones are important in species recognition (Legler, 1960; Carpenter & Ferguson, 1977). Despite this few secretory glands have been identified in tortoises: the axillary and inguinal pores of the Rathke's glands found in many chelonians are not present in the Testudinidae (Loveridge & Williams, 1957) and mental glands (Rathke, 1848; Winokur & Legler, 1975) are only found in *Gopherus* and *Manouria*. Although it has been suggested that 'cloacal discharge of female turtles attracts or stimulates males to court during the breeding season' (Manton, 1979), only one glandular tissue has been described from this region (in *Clemmys marmoratus*; Disselhorst 1904; Whiting 1969). None of these glands has been identified in *Dipsosaurus* and the 'scent-gland' described by Owen (1866) in a '*Testudo indica* of two feet long' could not be located by dissection (Gerlach, 2004) and appears to be the mental gland of a *Gopherus* specimen and not a gland of any of the giant tortoise species frequently referred to '*T. indica*' in the 19<sup>th</sup> century.

In the case of *Dipsosaurus* the contact between the buccal region and the olfactory region provided by the ducts between the tuberculum palatinum and the medial nasal gland means that the vomeronasal organ closely resembles the Jacobson's organ of squamates and mam-

mals. The lack of previous reports of such organs in chelonians may be due to the scarcity of dissections of this region in many chelonians. A review of the literature and of skull material identifies one additional taxon with a structure resembling a Jacobson's organ; the leatherback turtle *Dermochelys coriacea* possesses a direct connection between the intermediate nasal region (lined with vomeronasal epithelium; Parsons, 1970) and buccal cavities through the foramina praepalatina, a connection figured as long ago as 1912 (Nick, 1912). This connection differs from that found in *Dipsosaurus* in that there is a single opening into the buccal cavity, this is through an opening between the premaxillae (Fig. 4), this may be due to modification from a common arrangement reflecting structural differences in the rostral region of these species. As with *Dipsosaurus* the duct into the buccal cavity lies next to an area of loose connective tissue resembling the tuberculum palatinum. The function of this tissue remains obscure, in *Dipsosaurus* it could act as a pad of tissue that would be pressed against the ducts into the medial nasal gland during chewing, effectively closing them and preventing food passing into the gland. In *Dermochelys* it appears to be positioned too far posteriorly for such a function. Similarly in *Emys* where the tuberculum palatinum was first described (Bojanus, 1819-21) no connection between the buccal and nasal cavities has been reported. The vomeronasal organ in *Dermochelys* may be associated with the location of natal nesting beaches rather than social interactions as in *Dipsosaurus*. In this case a buccal connection would facilitate sensory detection underwater without flooding the nasal cavity. Other marine turtles with similar homing behaviours may also have well developed vomeronasal organs although the possibility of buccal connections is very limited due to the extensive development of the secondary palate. These findings in *Dipsosaurus* and the identification of similar structures in *Dermochelys* demonstrates that much remains to be discovered in the sensory capabilities of chelonians. Although there have been detailed investigations of the anatomy and neurobiology of olfaction in some freshwater taxa (e.g. *Geoclemys reevesii*, Graziadei & Tucker, 1970; Taniguchi *et al.*, 1995, 1996; *Sternotherus odoratus*, Murphy *et al.*, 2001; Fadool *et al.*, 2001) the Chelononia are an ecologically diverse group and there is a need for more thorough examination of the histology and function of this region.

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