

Comparative Anatomy and Physiology of Chemical Senses in Nonavian Aquatic Reptiles

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Comparative Anatomy and Function of the Chemical Senses

Comparative Anatomy of the Nasal

Cavities: Olfactory and Vomeronasal
Systems

Turtles

Crocodylians

Squamates

Olfaction and Vomeronasal Chemoreception in Aquatic Reptiles

Turtles

Crocodylians

Squamates

Comparative Anatomy of the Oral Cavity:

Gustatory System

Turtles

Crocodylians

Squamates

Chemical Senses in Fossil Aquatic

Reptiles

Mosasauirs

Phytosauirs

Plesiosauirs

Other Aquatic Mesozoic Reptiles

Functional and Evolutionary Patterns

The nonavian reptiles are an exceptionally diverse group of tetrapods that have radiated into a variety of habitats, including marine and freshwater environments. While most aquatic reptiles retain strong ties to the land, some species are among the most fully aquatic of any tetrapod, including, for example, the marine turtles (Cheloniidae) and pelagic sea snakes (Elapidae). Indeed, some species of seasnake have forsaken their connection to the land entirely, not even returning to give birth. They thus achieve a level of adaptive commitment to the water comparable to those most aquatic of tetrapods, the Cetacea. Nonetheless, only about 8% (approximately 600 species) of living, nonavian reptiles are even partially aquatic.

Crown group (nonavian) reptiles comprise the turtles (Testudines), alligators, crocodiles and gharials (Archosauria, Crocodylia), and tuatara (Rhynchocephalia), lizards, and snakes (Squamata). Each of these major clades includes some partially or fully aquatic species (see the section by Schwenk and Thewissen in chapter 1 in this volume). Among extinct lineages

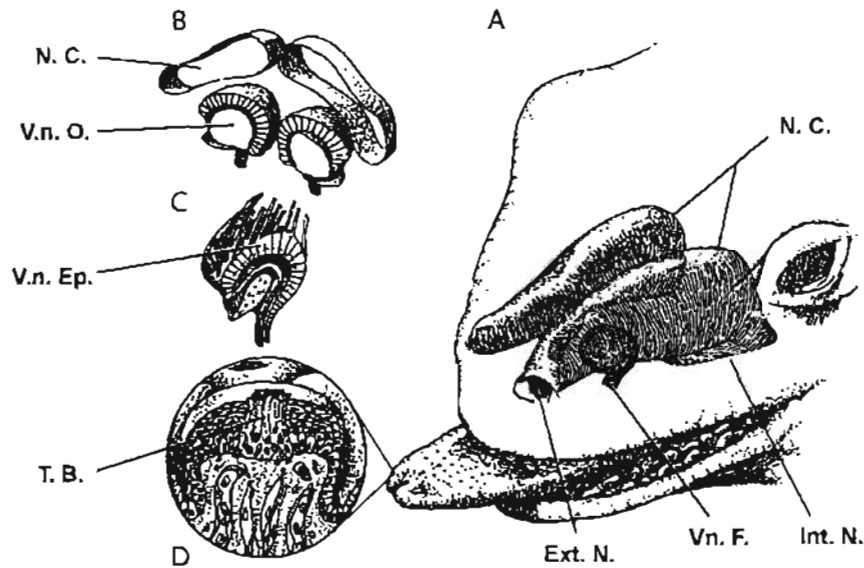


FIGURE 5.1. The three principal chemosensory systems available to reptiles as illustrated in a squamate. Gustation is mediated by taste buds in the mouth and pharynx. Olfaction is mediated by olfactory epithelium in the nasal cavities. Vomeronasal chemoreception is mediated by vomeronasal epithelium in the basal cavities (turtles) or sequestered in separate vomeronasal organs (squamates). (A) Lizard head showing location of chemosensory organs; (B) transverse section showing the spatial relationship between the nasal cavities (N. C.) and vomeronasal organs (V.n. O.); (C) sagittal section of one vomeronasal organ showing the sensory epithelium (V.n. Ep.) and sensory nerves on its convex surface; (D) magnified image of a taste bud (T. B.) within the epithelium of the tongue tip. Other abbreviations: Int. N., internal naris (choana); Ext. N., external naris; and V.n. F., vomeronasal fenestra (opening into mouth through palate). Modified from Schwenk (1995).

for which we have limited information on the chemical senses are the mosasaurs, large marine lizards, the phytosaurs, aquatic archosaurs related to crocodylians, and the plesiosaurs, a euryapsid group probably related to placodonts and ichthyosaurs.

Given the phylogenetic breadth spanned by these taxa, the extreme morphological divergence among them, and the multiple origins of their secondarily aquatic habits, one might expect pronounced diversity both in the nature of their chemical senses and in any putative aquatic adaptations they exhibit, and indeed, this is the case. In this chapter, I review briefly what is known about the structure and function of the chemical senses in aquatic reptiles and identify, to the extent possible, evolutionary patterns. Sadly, this chapter serves mostly to highlight our ignorance about the chemical senses in these groups.

COMPARATIVE ANATOMY AND FUNCTION OF THE CHEMICAL SENSES

The chemical senses potentially available to tetrapods, including reptiles, are gustation, olfaction, and vomeronasal chemoreception (Fig. 5.1) (see Wyatt, 2003; Eisthen and Schwenk, chapter 3 in this volume; Reiss and Eisthen, chapter 4 in this volume, for summaries). Gustation is mediated by taste buds located within the oral and pharyngeal cavities. Taste buds are innervated by cranial nerves VII (facial: chorda tympani and palatine branches), IX (glossopharyngeal), and X (vagus) to the floor of the mouth, anterior tongue and palate, posterior tongue and pharynx, and larynx, respectively. Olfaction and vomeronasal chemoreception constitute the nasal chemical senses associated developmentally and evolutionarily with the nasal capsule. These are often described as the “main” and “accessory”

olfactory senses, respectively, and are distinguished topologically, anatomically, neuroanatomically, and functionally. Sensory epithelia of both systems are innervated by cranial nerve I (olfactory), although the vomeronasal system is supplied by a separate branch called the vomeronasal nerve.

Below, each system is described separately. In addition to these three, widely recognized chemosensory systems, free nerve endings of cranial nerve V (trigeminal) are widely distributed in the mouth and nasal cavity of most tetrapods and are known to be generally sensitive to chemical (and mechanical) stimuli in turtles (e.g., Tucker, 1971; Scott, 1979). However, the role of the trigeminal system is poorly understood and is not considered further here.

COMPARATIVE ANATOMY OF THE NASAL CAVITIES: OLFATORY AND VOMERONASAL SYSTEMS

The morphology of the nose in reptiles has been extensively reviewed by Parsons (1959a, 1959b, 1967, 1970a). Information reported here comes from these sources unless otherwise noted. Each paired nasal cavity comprises a tube that opens to the outside through the external nares (nostrils) and to the mouth through the internal nares (choanae). Three parts of this cavity are recognized in most reptiles: an anterior vestibulum a middle cavum and a posteroventral nasopharyngeal duct. Protrusions of the wall within the cavum of lepidosaurs and crocodylians are called conchae. Olfactory epithelium is located within the cavum. The shape and relative contribution to the nasal cavity of these chambers varies among taxa. They are most clearly evident in turtles, which possess a relatively simple nasal cavity with clearly differentiated regions (Fig. 5.2). *Sphenodon* (Rhynchocephalia) and most lizards lack a well-defined nasopharyngeal duct so that the cavum opens directly into the mouth. Crocodylians and some turtles possess secondary palates that are associated with an elongated

nasopharyngeal duct (Fig. 5.3). However, some aquatic turtles lacking a secondary palate also have a relatively long nasopharyngeal duct.

TURTLES

In turtles the vestibulum is usually a short tube that leads directly into the expanded chamber of the cavum. In aquatic species with snorkel-like noses, the vestibulum is elongated (e.g., *Chelus*, *Carettochelys* and trionychids; Fig. 5.2). In sea turtles (Cheloniidae), the proximal part of the vestibulum is surrounded by vascular erectile tissue that constricts the nostrils when the turtles are resting while submerged (Walker, 1959; Parsons, 1970a). The nostrils remain open when the turtles are active, however (Walker, 1959; see below).

The cavum in turtles consists of a dorsal chamber containing the olfactory epithelium and a ventral "intermediate region." In most turtles the olfactory chamber is domed, but broadly open to the rest of the cavum below. In sea turtles, however, the olfactory region forms a partial sphere with a constricted opening at its base. The vomeronasal epithelium lies within shallow sulci on the floor of the intermediate region of most turtles, but in sea turtles it is sequestered within small dorsal and ventral diverticulae (Fig. 5.2). It has been suggested that in aquatic turtles the dorsal olfactory chamber retains an air bubble when the nasal cavity floods during submersion (Tucker, 1971). This would be most likely to occur in sea turtles given the form of the olfactory chamber. In contrast, the ventral position of the vomeronasal epithelium suggests that it is covered by water when the cavum is flooded (see below).

The turtle nasopharyngeal duct forms a tube that connects the cavum to the buccal cavity. It seems to be especially long in highly aquatic turtles (Fig. 5.2). Furthermore, the entire nasal tube (not including diverticulae) appears to be relatively straight (e.g., *Chelydra*, *Trionyx*, *Chelus*), whereas in terrestrial (*Testudo*, Testudinidae) (Fig. 1.4. in this volume) and some semi-aquatic turtles (Emydidae) it is kinked (Fig. 5.2).

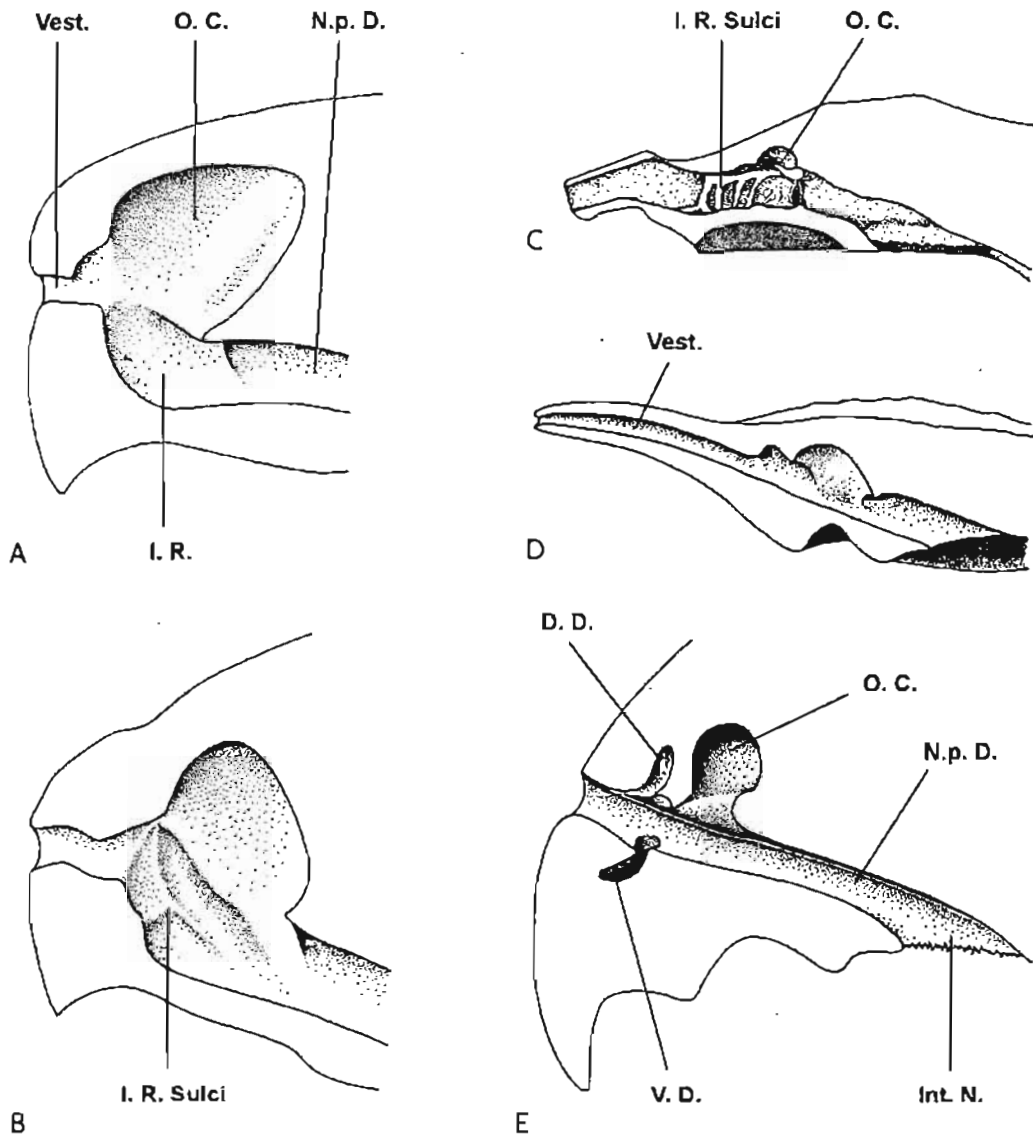


FIGURE 5.2. The nasal cavities in turtles shown in sagittal section. (A) Terrestrial *Testudo graeca* (Testudinidae); (B) semiaquatic *Emys orbicularis* (Emydidae); (C) aquatic *Apalone ferox* (Trionychidae); (D) aquatic *Chelus fimbriatus* (Chelidae); (E) marine *Chelonia mydas* (Cheloniidae). Note the relatively long, straight nasal cavities of the aquatic species. Both freshwater turtles (C and D) use the elongated snout and vestibulum (Vest.) to snorkel. In all turtles, vomeronasal epithelium is found on the floor of the cavum in the "intermediate region" (I. R.), often located in sulci (I. R. sulci) in semiaquatic and aquatic species. In sea turtles (E) the vomeronasal epithelium is sequestered within two separate pockets, the dorsal and ventral diverticulae (D. D. and V. D.). The bubblelike form of the olfactory chamber of the cavum in sea turtles might help to trap air during submersion. Other abbreviations: Int. N., internal naris (choana); N.p. D., nasopharyngeal duct; and O. C., olfactory chamber of cavum. All figures modified from Parsons (1970a).

These conformational differences might relate to the hydrodynamics of water flow through the nasal cavity and the mechanism of underwater olfaction (see below).

CROCODYLIANS

The nasal chamber of crocodylians is relatively uniform but considered to be the most complex

of reptiles (Parsons, 1970a) (Fig. 5-3). This complexity relates to the presence in archosaurs of paranasal sinuses that penetrate the surrounding bone and soft tissues (Witmer, 1995) and of several well-developed conchae within the cavum (Parsons, 1970a; Witmer, 1995). In addition, the entire nasal cavity and the nasopharyngeal duct, in particular, is elongate owing to

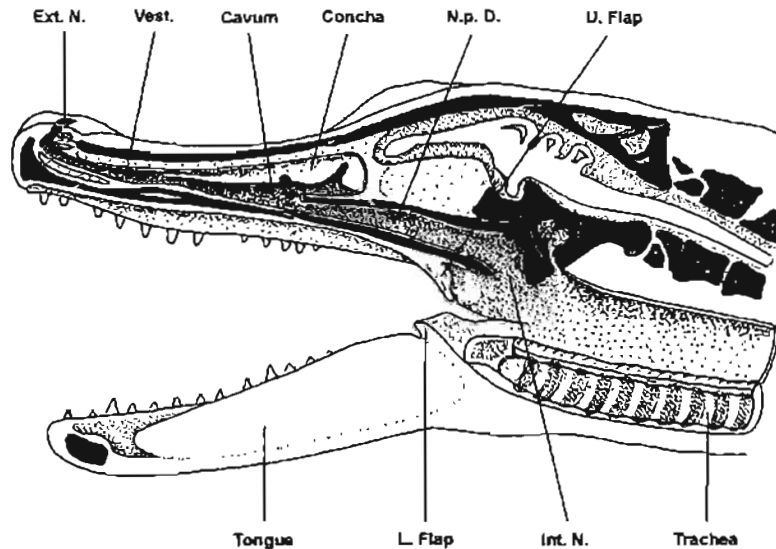


FIGURE 5.3. The head of a crocodylian (*Alligator mississippiensis*) in sagittal section, left lateral view. The nasal cavity is elongate in crocodylians owing to a long snout and a secondary palate that displaces the internal nares (Int. N.), or choanae, posteriorly into the pharynx. The cavum contains several conchae and openings into the paranasal sinuses that invade the surrounding tissues of the snout. Other abbreviations: Ext. N., external naris; L. Flap, lower flap of buccopharyngeal valve; N.p. D., nasopharyngeal duct; U. Flap, upper flap of buccopharyngeal valve; and Vest., vestibulum. Modified from Bellairs (1970).

the long snout and extensive secondary palate. The choanae lie posteriorly in the pharynx, behind a buccopharyngeal valve. This valve forms between a flap of soft tissue suspended from the back of the palate anterior to the choanae and a ventral flap extending dorsally from the floor of the pharynx just behind the tongue. The ventral flap is elevated along with the back of the tongue, thus forming a water-tight seal at the back of the buccal cavity, anterior to the choanae. This permits retention of an open airway even when the mouth is flooded. Thus crocodylians can breathe while submerged as long as the nostrils remain above the surface (Negus, 1958; Bellairs, 1970). This behavior is facilitated by the dorsal placement of the nostrils on an elevated rostrum. The nasal protuberance can become extremely large in mature male *Gavialis* (Bellairs, 1970). The crescent-shaped nostrils are closed during submersion by vascular erectile tissue and smooth muscles within the walls of the vestibulum (Bellairs and Shute, 1953; Bellairs, 1970). Olfactory epithelium covers the dorsal surfaces of the cavum but does not extend into deep sinuses

(Saint Girons, 1976). There is no vomeronasal epithelium and no functional vomeronasal system in adult crocodylians (Parsons, 1970a; Saint Girons, 1976).

SQUAMATES

Squamates are morphologically diverse, and this is reflected in their nasal anatomy (Fig. 5.1). In most species the nostrils are positioned laterally on the snouts, but in many aquatic snakes (Kathariner, 1900; Gabe and Saint Girons, 1976; Green, 1997), the aquatic lizard *Lanthanotus* (McDowell and Bogert, 1954; Parsons, 1970a; personal observations), and some aquatic varanid lizards (Bellairs, 1970) they are medial and dorsal. The length and path of the vestibulum is highly variable. It is surrounded, in part, by cavernous erectile tissue that acts to close the nostrils in aquatic snakes (Kathariner, 1900; Santos-Costa and Hofstadler-Deiques, 2002) and sand-dwelling lizards (Stebbins, 1948); however, even terrestrial lizards have some cavernous tissue in the walls of the vestibulum (Oelrich, 1956). Kathariner (1900) also observed that in some aquatic snakes the

vestibulum-cavum junction is constricted by a circular ridge. Conceivably, this constriction is also valvular, serving as an additional barrier to cavum flooding during submersion. According to Bellairs (1970), the nostrils of some aquatic monitor lizards (*Varanus*) are situated posteriorly near the eyes, and this condition is correlated with a convoluted vestibulum that might serve as an air supply during submersion. The highly aquatic homalopsine (Colubridae) snakes have slitlike, valvular nostrils and close fitting labial scale rows to seal the nose and mouth when underwater (Greene, 1997). Sea snakes (Elapidae) also have specialized structures to plug the small lingual orifice at the front of the mouth (Greene, 1997).

The squamate cavum is relatively simple, though variable. In most species there is a well-developed concha, but in some iguanians and aquatic snakes it is reduced or lost (Parsons, 1970a; Gabe and Saint Girons, 1976). The dorsal surfaces of the cavum and the concha are covered by olfactory epithelium (Gabe and Saint Girons, 1976). The olfactory region is particularly reduced in aquatic snakes (Kathariner, 1900; Gabe and Saint Girons, 1976), in contrast to the well-developed vomeronasal organ (see below). The cavum is lubricated by a large external nasal gland located at the cavum's junction with the vestibulum, but this is lost in aquatic snakes and the nasal cavity reduced to a simple, cylindrical tube (Gabe and Saint Girons, 1976). The posteroventral part of the cavum either opens directly into the mouth or is extended slightly by a short nasopharyngeal duct.

Uniquely among tetrapods, the vomeronasal epithelium in squamates is sequestered within discrete capsules lacking any connection to the nasal cavity (Fig. 5.1). However, these vomeronasal organs retain their ventral position relative to the nasal tube and open into the anterior end of the mouth via narrow ducts and tiny fenestrae. The vomeronasal organs are filled with fluid delivered from the orbital Harderian gland by the nasolacrimal duct (Bellairs and Boyd, 1950; Rehorek et al., 2000). Scent molecules are sampled from the external environment and delivered to the

vomeronasal organ by the tongue during "tongue-flicking" behavior (Halpern, 1992; Schwenk, 1995).

Tongue-flicking concentrates scent molecules in the fluid covering the tongue tips by molecular diffusion (Schwenk, 1996). Scent transfer from the tongue to the vomeronasal organs is poorly understood, but it is probably enhanced by vomeronasal suction (Broman, 1920; Young, 1993). Although there is substantial variation in the degree of vomeronasal organ development, it is always well developed in aquatic snakes, in contrast to the main olfactory system (Gabe and Saint Girons, 1976).

OLFACTION AND VOMERONASAL CHEMORECEPTION IN AQUATIC REPTILES

TURTLES

There is ample evidence that most turtles use chemical cues to direct some behaviors (Burghardt, 1970; Manton et al., 1972a, 1972b; Manton, 1979; Scott, 1979; Chelazzi and Delfino, 1986; Halpern, 1992; Quinn and Graves, 1998; Druzisky and Brainerd, 2001; Bartol and Musick, 2003; Constantino and Salmon, 2003; Muñoz, 2004). Turtles employ buccal oscillation, in which the buccal floor is rapidly depressed and elevated, as a kind of "sniffing" behavior during olfaction (McCutcheon, 1943; Root, 1949; Druzisky and Brainerd, 2001). Aquatic turtles continue buccal oscillation underwater with the nostrils open, thereby flooding the nasal cavities (Root, 1949; Walker, 1959; Manteifel et al., 1992; Druzisky and Brainerd, 2001). Therefore, aquatic olfaction is possible. Underwater nasal chemoreception is strongly implicated in general exploratory behavior (Root, 1949; Walker, 1959), food location and discrimination (Manton, 1979; Constantino and Salmon, 2003), and reproductive behavior (Manteifel et al., 1992; Muñoz, 2004). It may be a factor in long-range migratory homing in some sea turtles, which involves chemical "imprinting" of natal beaches (Koch et al., 1969; Grassman,

1993; Luschi et al., 1998). Aquatic turtles possess well-developed "musk" or Rathke's glands in axillary, inguinal, and/or inframarginal regions (Ehrenfeld and Ehrenfeld, 1973; Rostal et al., 1991). These glands appear to be an ancient chelonian characteristic (Weldon and Gaffney, 1998), but their function remains obscure (Manton, 1979). It is unknown whether underwater chemosensory behaviors are mediated by the main olfactory system or vomeronasal system, but for theoretical reasons, I suggest that the vomeronasal system is most likely (see below).

CROCODYLIANS

Crocodylians, like turtles, employ buccal oscillation (usually called "gular pumping") as an olfactory behavior (Naifeh et al., 1970; Gans and Clark, 1976; Weldon and Ferguson, 1993). Unlike turtles, however, adult crocodylians lack a vomeronasal system, therefore all olfactory behavior is attributable to the main olfactory system. Also unlike turtles, crocodylians close their nostrils and do not exhibit gular pumping when submerged, so underwater olfaction is unlikely (Bellairs and Shute, 1953; Weldon and Ferguson, 1993; Bellairs, 1971, in Weldon and Ferguson, 1993). Underwater food detection is presumably gustatory (below) and tactile (Davenport et al., 1990).

Aerial olfaction is well developed. Crocodylians locate carrion from great distances and are able to distinguish food sources without visual cues (Neill, 1971; Scott and Weldon, 1990; Weldon et al., 1990). They are also endowed with paired gular and paracloacal integumentary glands (Weldon and Sampson, 1988; Weldon and Wheeler, 2001) and, in some cases, dorsal glands (Richardson and Park, 2000). These glands are believed to function in pheromonal attraction of mates and/or nest-site marking (Weldon and Ferguson, 1993). The secretions are chemically complex, contain large volatile fractions, and exhibit taxonomic, intergland, sex, and age class differences (Whyte et al., 1999; Weldon and Wheeler, 2001; García-Rubio et al., 2002).

SQUAMATES

In general it is thought that the vomeronasal system is the predominant chemosensory system in squamates (Halpern, 1992; Ford and Burghardt, 1993; Schwenk, 1995). There is extensive literature on the squamate vomeronasal system, and this system is implicated in almost every important behavior. Only its relevance in aquatic behavior is discussed here. The role of the main olfactory system is poorly studied, but it is well developed in some species (Gabe and Saint Girons, 1976; Schwenk, 1993; Dial and Schwenk, 1996). However, highly aquatic snakes show marked regression of the main olfactory system without concomitant reduction of the vomeronasal system (Matthes, 1934; Gabe and Saint Girons, 1976). Furthermore, aquatic snakes exhibit putative adaptations to prevent flooding of the nose during submersion (see above). In contrast, aquatic snakes and lizards foraging underwater use typical tongue-flicking behavior, implicating vomeronasal system functioning (Rand, 1964; Heatwole, 1975; Hibbard, 1975; Heatwole and Cogger, 1993; Shine and Houston, 1993; Shine et al., 2003, 2004; Vincent et al., 2005). Together, these observations suggest that olfaction is unimportant to aquatic snakes and that the vomeronasal system alone functions during submersion in squamates. In seasnakes and filesnakes (Acrochordidae), underwater tongue-flicking occurs during exploratory behavior (Heatwole, 1975), foraging (Shine et al., 2003, 2004; Vincent et al., 2005) and reproductive behavior (R. Shine, pers. comm., June 2004). These behaviors are all typical of vomeronasal system function in terrestrial squamates.

COMPARATIVE ANATOMY OF THE ORAL CAVITY: GUSTATORY SYSTEM

Taste buds are small, flask-shaped organs comprising clusters of sensory and support cells embedded within an epithelium (Fig. 5.1). They are plesiomorphic for vertebrates, and therefore their wide occurrence among reptiles is

unsurprising. Many fishes have taste buds scattered across their body surface, often in high densities (e.g., Bardach and Atema, 1971); however, with the exception of some larval amphibians, taste buds are restricted to the oral and pharyngeal mucosa in tetrapods, including fully aquatic species. Also unlike fish (and some amphibians), the sensory processes of the receptor neurons are rarely exposed on the epithelial surface. Rather, they are sunken to varying degrees, accessible through a mucus-filled pore or pit. Taste receptors are regarded as sensors of proximate chemical stimuli, typically food molecules that have been released by mechanical processing within the mouth (e.g., Atema, 1987).

TURTLES

Taste buds are usually found on turtle tongues (Tuckerman, 1892; Winokur, 1973; Pevzner and Tikhonova, 1979; Korte, 1980; Uchida, 1980; Spindel et al., 1987; Iwasaki et al., 1996b; Beisser et al., 1998, 2001), but not always (Iwasaki, 1992; Iwasaki et al., 1992, 1996a, 1996c, 1996d; Beisser et al., 1995, 2004; Lemell et al., 2000). It remains possible that taste buds are present in other parts of the mouth and pharynx. Too few taxa have been examined to reveal any phylogenetic or ecological patterns in taste bud distribution among turtles. The only two sea turtles examined (hawksbill and Pacific Ridley Turtle; Cheloniidae) appear to lack tastebuds (Iwasaki et al., 1996a, 1996c), whereas in freshwater (and terrestrial) species they are variably present, even within a single family such as the semi- to highly aquatic Emydidae. Although present in modest numbers in some species (e.g., *Chrysemys scripta*) (Korte, 1980), they never achieve the densities found in many squamate reptiles (Schwenk, 1985).

Virtually no study has attempted to distinguish the role of gustation in turtles independent of nasal olfaction. One study showed that taste, alone, was insufficient for chemosensory-based operant conditioning in green sea turtles (Manton et al., 1972b). Studies of food imprinting,

however, suggest a role for gustation in turtle behavior (Burghardt and Hess, 1966; Burghardt, 1970). In any case, given the relatively large proportion of the peripheral and central nervous system devoted to the nasal chemical senses (Scott, 1979), it is likely that these are the predominant chemical senses in turtles, including aquatic species (see below).

CROCODYLIANS

Crocodylians possess modest numbers of typical taste buds on the mucosal surfaces of the tongue, mouth, palate, and pharynx (Bath, 1906; Ferguson, 1981; Shimada et al., 1990; Yoshie and Yokosuka, 2001). Small, dermal sense organs in the scales surrounding the mouth were considered possible chemoreceptors (Neill, 1971; Jackson et al., 1996), but recently they were shown to be exquisitely sensitive mechanoreceptors responsive to ripples at the water's surface (Soares, 2002). As with turtles, no studies have addressed specifically the role of gustation in crocodylian behavior, but circumstantial evidence suggests that taste may be important in underwater prey detection. American alligators exhibit increased rates of lateral head movements, mouth-opening, and snapping when food extracts are introduced into the water (Neill, 1971; Weldon et al., 1990; Banta et al., 1992). Since crocodylians do not employ olfaction underwater (see below), gustation is implicated in these behaviors. Limited evidence also suggests that taste is used to identify food and to reject unpalatable prey following contact with the mouth (Scott and Weldon, 1990; Weldon and McNease, 1991).

SQUAMATES

Taste buds are abundant in the mouth and pharynx of most lepidosaurs, reaching extremely high densities on the tongue tips of some lizards (Schwenk, 1985, 1986). Snakes lack lingual taste buds, but many, if not most, species have them in the palate (Burns, 1969; Kroll, 1973; Nishida et al., 2000; Berkhoudt et al., 2001; Atobe et al., 2004). In caenophidian snakes, including terrestrial and aquatic species

of colubrids, elapids, and viperids, the taste buds are usually elevated on small projections or papillae that also contain a variety of proprioceptive mechanoreceptors, forming a complex, compound sensory system putatively associated with the identification and manipulation of prey within the mouth (Nishida et al., 2000). As for other reptiles and tetrapods generally, gustation is implicated in the discrimination of palatable from unpalatable food once mouth or tongue contact occurs (Cooper and Pérez-Mellado, 2001; Stanger-Hall et al., 2001; Cooper et al., 2002a, 2002b); lizards and snakes are often observed to reject food items once they are held in the mouth (Burghardt, 1969; personal observations). Taste may underlie learned aversion to food following sickness (Burghardt et al., 1973; Boyden, 1976; Stanger-Hall et al., 2001; Paradis and Cabanac, 2004), although olfaction cannot be ruled out. Seasnakes are similar to other snakes in the presence of palatal taste buds (Burns, 1969; Hibbard, 1975). Drummond (1979, 1983) observed aquatic, natricine snakes (included in Colubridae) making open-mouthed searching movements in water containing prey extracts, possibly indicating gustatory behavior. Nevertheless, there is no indication that aquatic squamates, or aquatic reptiles generally, evince specializations of the gustatory system.

CHEMICAL SENSES IN FOSSIL AQUATIC REPTILES

MOSASAURS

Using phylogenetic bracketing and fossil evidence, Schulp et al. (2005) recently reconstructed tongue form in mosasaurs, ancient marine lizards related to living varanoids. They suggested that the tongue was probably deeply cleft, as in living *Gila* monsters and *Lanthanotus*, but not as deeply forked as in snakes and varanid lizards. Mosasaurs spent little, if any, time on land. It is likely that the highly protrusible tongue was used for tongue-flicking and vomeronasal chemoreception underwater (see below).

PHYTOSAURS

Phytosaur skulls exhibit impressions that have been attributed to an accessory olfactory bulb (putatively indicating a vomeronasal system), but Senter (2002) showed that the impressions resemble those left by the ophthalmic nerve in extant crocodylians. This and phylogenetic bracketing suggest that phytosaurs, like other archosaurs, lacked a vomeronasal system. Senter (2002) erred, however, in concluding that phytosaurs could not have used chemically mediated behavior or pheromonal communication. In living crocodylians, chemosensory behavior is mediated by olfaction (Weldon and Ferguson, 1993; see above), and in mammals it is well established that pheromonal communication can occur via the main olfactory system (reviewed in Baxi et al., 2006). The vomeronasal system is neither necessary for chemically mediated behavior, generally, nor pheromone reception, specifically.

PLESIOSAURS

It has been suggested that plesiosaurs used underwater olfaction (Cruickshank et al., 1991). In contrast to the usual tetrapod pattern, the internal nares are anterior to the external nares (Fig. 5.4). Grooves run in the palate from small maxillary diastemata to anteriorly directed, scooplike choanae. Aided by negative pressure generated by flow across the dorsal nostrils, water is presumed to have moved through the mouth, into the nasal cavities, and out through the external nares. Such a mechanism would permit continuous olfactory (or much more likely, vomeronasal) sampling of the water. The only modern analogue for such a system is found in some fishes that use ram-generated, continuous flow across the olfactory epithelium by means of incurrent and excurrent nares (Hara, 1997). However, in fishes there is no connection between olfactory and buccal cavities.

OTHER AQUATIC MESOZOIC REPTILES

The chemical senses of other highly aquatic, Mesozoic reptile groups remain unknown.

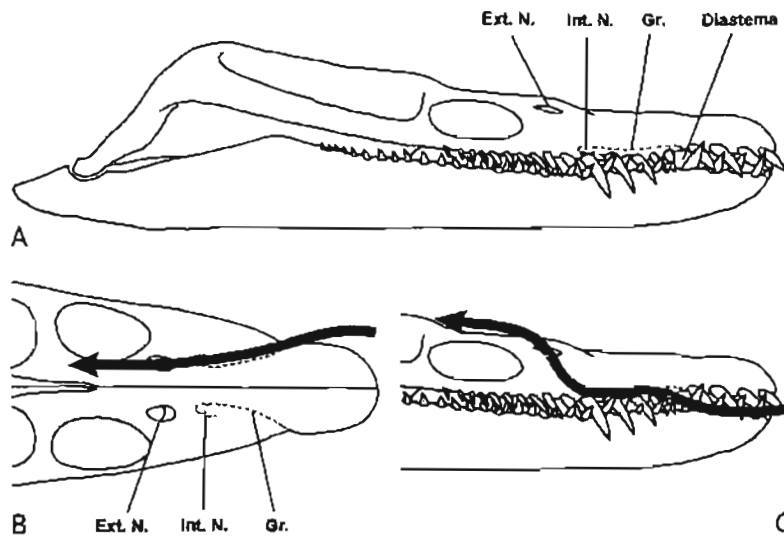


FIGURE 5.4. Reconstruction of the skull and narial anatomy in *Rhomaleosaurus*, a plesiosaur, in lateral (A, C) and dorsal (B) view. In contrast to other tetrapods, the internal nares (Int. N.) are anterior to the external nares (Ext. N.). Arrows show the putative path of water flow through the olfactory cavities as the animal swam. Water entered the mouth through a diastema between the teeth and was channeled along a groove (Gr.) in the palate (indicated with dotted lines) to scooplike internal nares. Water then passed through the nasal cavities, exiting posterodorsally through the external nares. Submersion and flushing of the nasal cavities and nasal epithelium presumably permitted underwater olfaction. Modified from Cruickshank et al. (1991).

However, the nostrils of many nothosaurs, placodonts, and ichthyosaurs are positioned posteriorly on the snout in front of the orbits, as seen in some other aquatic reptiles (see above; Carroll, 1988; McGowan, 1991).

FUNCTIONAL AND EVOLUTIONARY PATTERNS

Based on first principles, the chemosensory system most likely to adapt to secondarily aquatic habits is the vomeronasal system. The vomeronasal system has long been considered a "water sense" (the *Wassergenuchsorgan*, or water olfactory organ, of Broman [1920]) because its epithelium is virtually always flooded and because it is often responsive to high molecular weight, nonvolatile chemicals that do not stimulate the main olfactory system (Baxi et al., 2006). Indeed, association of the vomeronasal organ with fluidborne rather than airborne chemicals is so strong that homology of the vomeronasal organ to the main olfactory organ of fishes has been proposed, implying

that the tetrapod main olfactory system is neomorphic (Broman, 1920; Parsons, 1970b). Regardless, I suggest that the vomeronasal system of terrestrial reptiles is preadapted to aquatic conditions for three reasons: (1) mechanistically, it requires odorants to be in aqueous solution; (2) the set of chemicals to which it is responsive includes nonvolatile molecules; (3) the primitive mechanism for aerial acquisition of vomeronasal stimulants is compatible with aquatic acquisition. Next I evaluate the support for this hypothesis from the anatomy and function of specific aquatic reptile groups.

The strongest support comes from highly aquatic freshwater and marine snakes, which exhibit reduction of the main olfactory system while maintaining high levels of putative vomeronasal activity underwater (see above). Schwenk (1996) proposed that odorant molecules are collected on the tongue by diffusion into the fluid covering its surfaces. According to this model, tongue-flicking serves to decrease the thickness of the boundary layer at the tongue's surface, to increase the steepness of

the velocity gradient between the tongue's surface and the surrounding medium, and to increase turbulence around the tongue in order to draw more odorant molecules into contact with its surface, all of which combine to increase the rate of diffusion. At first glance, it seems unlikely that this model could work for collecting odorant molecules underwater; however, all that is required is that a boundary is maintained between the fluid on the tongue and the surrounding water during a tongue-flick. Such an interface occurs, for example, between the mucus covering a fish's body scales and the surrounding water when it swims, and the mucus covering taste buds or olfactory epithelium in fishes.

Schwenk (1994) presented evidence supporting the notion that the squamate forked tongue morphology functions as a tropotactic mechanism used to detect chemical gradients. The length of the fork reflects the scale of the gradients sensed. In the case of terrestrial snakes, this is usually a relatively discrete chemical trail. In aquatic environments; however, odor plumes tend to mix and disperse rapidly owing to turbulence (Atema, 1987). This implies that, typically, the scale of biologically relevant chemical gradients will be larger in aquatic environments than in terrestrial. It is my impression, based on very few observations, that the tines of the forked tongue in aquatic snakes are, in fact, relatively longer than in terrestrial species. This hypothesis needs to be tested quantitatively and with phylogenetic controls. If true, it would represent a distinct vomeronasal specialization of aquatic snakes.

Simultaneous consideration of crocodylians and turtles provides additional support for the vomeronasal system preadaptation hypothesis. Both taxa are mostly aquatic and were probably ancestrally so. Both taxa primitively evolved a high-impedance, positive-displacement pump (buccal or gular oscillations) to pulse air through the nasal cavities for olfaction. Only turtles, however, continue the pumping behavior underwater. It is likely that this is because crocodylians lack a vomeronasal epithelium

within the nose. The main olfactory system, adapted as it is to aerial olfaction and the sensation of land-based, volatile chemicals, is non-functional when submerged. In contrast, turtles have a well-developed vomeronasal epithelium on the floor of the cavum that even in terrestrial species, is constantly flooded by external glands (Tucker, 1971). We know that the turtle vomeronasal epithelium is responsive to chemicals in aqueous solutions, including non-volatiles (Tucker, 1971; Hatanaka and Matsuzaki, 1993; Fadool et al., 2001), and it is likely that the olfactory epithelium is protected from deluge by an air bubble (see above). Thus, putative underwater olfaction in turtles is almost certainly vomeronasal. It is conceivable that as water is pulsed through the nasal cavities, dissolved volatile chemicals escape into the air bubble surrounding the olfactory epithelium, thus providing olfactory access to waterborne chemicals, but this is purely speculative.

Speculating further, the nasal cavity of highly aquatic turtles, particular sea turtles, appears to be relatively longer, straighter, and more tubular than in other species, but this is based on the limited number of taxa figured by Parsons (1970a) and elsewhere (Fig. 5.2). Such a conformation might promote laminar flow through the nasal cavities, which would tend to reduce impedance and increase efficiency of the buccal pump. However, laminar flow creates boundary layers that limit exposure of the receptor cells to odorant molecules. Local, turbulent mixing generated by small protrusions in the mucosal surface, such as the sulcal ridges characteristic of the turtle vomeronasal region, could mitigate this problem. Receptor exposure might also be aided by the fact that fluid velocity within a pipe is slowest at the surfaces (Vogel, 1994). Finally, I note the unusual disposition of the vomeronasal epithelium in sea turtles, which is sequestered within dorsal and ventral diverticulae. The orientation of their openings suggests that the ventral diverticulum would be flooded during incurrent flow and the dorsal during excurrent flow (Fig. 5.2). Each diverticulum might then be emptied

during the opposite cycle by negative pressures generated as water moves past its aperture. The utility of a system that sequentially floods and empties the vomeronasal chambers is obvious, but the advantage of separately sampling incurrent and excurrent streams (if this really happens) is not clear. The hypothesis could be tested with physical models.

Most aquatic reptiles are amphibious, spending time both in water and on land. Adaptive commitment of any sensory system solely to water would come with negative fitness consequences. It is therefore not surprising that few aquatic reptiles evince obvious chemosensory adaptations to their aquatic environments. Rather, highly aquatic species show refinements of the existing vomeronasal system, which was preadapted to aquatic chemoreception. Loss of the vomeronasal system in ancestral archosaurs, for whatever reasons, precluded the use of underwater nasal chemoreception in crocodylians, despite their possession of an appropriate pumping mechanism.

In addition to exploring some of the speculations presented here, future work considering the nature of the chemicals sampled by the main olfactory system and vomeronasal system is worthwhile (see Baxi et al., 2006; Eisthen and Schwenk, chapter 3 in this volume). The sets of chemicals to which each system responds are overlapping, but noncongruent in all tetrapods examined. One axis along which potential odorants vary is molecular weight. Although there is no crisp distinction between the nasal chemical senses in this regard, in general the vomeronasal system is more likely to respond to high molecular weight chemicals than the main olfactory system (but see cited references above). However, larger molecules are both less volatile and less soluble than smaller ones. In contrast, molecular polarity represents a clear trade-off in the properties of solubility and volatility: polar molecules are more soluble in water than nonpolar molecules, but they have lower vapor pressures and are therefore less volatile. The polarity axis could be another factor affecting the classes of

chemicals to which each system responds and their ability to adapt to aquatic conditions (see Eisthen and Schwenk, chapter 3 in this volume, for discussion).

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