The Fish in the Turtle: On the Functionality of the Oropharynx in the Common Musk Turtle *Sternotherus odoratus* (Chelonia, Kinosternidae) Concerning Feeding and Underwater Respiration

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ABSTRACT

In tetrapods, the oropharyngeal cavity and its anatomical structures are mainly, but not exclusively, responsible for the uptake and intraoral transport of food. In this study, we provide structural evidence for a second function of the oropharynx in the North American common musk turtle, *Sternotherus odoratus*, Kinosternidae: aquatic gas exchange. Using high-speed video, we demonstrate that *S. odoratus* can grasp food on land by its jaws, but is afterward incapable of lingual based intraoral transport; food is always lost during such an attempt. Scanning electron microscopy and light microscopy reveal that the reason for this is a poorly developed tongue. Although small, the tongue bears a variety of lobe-like papillae, which might be misinterpreted as an adaptation for terrestrial food uptake. Similar papillae also cover most of the oropharynx. They are highly vascularized as shown by light microscopy and may play an important role in aquatic gas exchange. The vascularization of the oropharyngeal papillae in *S. odoratus* is then compared with that in *Emys orbicularis*, an aquatic emydid with similar ecology but lacking the ability of underwater respiration. Oropharyngeal papillae responsible for aquatic respiration are also found in soft-shelled turtles (Trionychidae), the putative sister group of the kinosternids. This trait could therefore represent a shared, ancestral character of both groups involving advantages in the aquatic environment they inhabit. Anat Rec, 293:1416–1424, 2010. © 2010 Wiley-Liss, Inc.

Key words: feeding; pharyngeal papillae; oral cavity; aquatic gas exchange; tongue

INTRODUCTION

Morphological investigations on the oropharyngeal mucosa in chelonians have demonstrated the correlation between the design of the oropharyngeal cavity and the feeding mode (Beisser et al., 1995, 1998, 2001, 2004; Iwasaki, 2002; Heiss et al., 2008; Natchev et al., 2009). Tortoises have fleshy tongues with numerous tall and slender lingual papillae (Winokur, 1988; Wochesländer et al., 1999, 2000; Beisser et al., 2004). This form of the

dorsal tongue surface promotes the interlocking effect in lingual food prehension and food transport (see Natchev et al., 2009 for overview). Aquatic turtles ingest and transport food using hydrodynamic feeding mechanisms, in which the tongue plays a subordinate role (Bramble and Wake, 1985) and the lingual papillae are moderately sized (Beisser et al., 2001) or completely absent (Beisser et al., 1995; Lemell et al., 2002, 2010).

Kinosternids are reported to be exclusively aquatic feeders (Ernst and Barbour, 1989; Rogner, 1996; Schilde, 2004), although they occasionally emerge on land. The kinosternid *Sternotherus odoratus* almost permanently lives in the water as an adult, but juveniles spend time on land, among other things searching for food. Therefore, we predict that, at least, juveniles of the musk turtle may be able to feed on land. The ability to feed on land is highly contingent on oropharyngeal morphological adaptations (Schwenk, 2000; Heiss et al., 2008; Natchev et al., 2009). However, as no detailed information is available on the morphology of the oropharyngeal mucosa in kinosternids, we explore whether and if the mucosal structure observed in kinosternids is related to feeding behavior.

The oropharyngeal morphology not only influences the feeding mode (i.e. aquatic vs terrestrial feeding), but also impacts other ecological potential, such as oropharyngeal gas exchange. Another goal of this study is therefore to search for oropharyngeal organs that are potentially responsible for aquatic gas exchange by using scanning electron microscopy (SEM) and histological methods. The capability of *S. odoratus* to remain submerged for prolonged periods has been the object of many physiological studies (see Saunders et al., 2000 for overview). According to Root (1949), Pritchard (1979), and Stone et al. (1992), common musk turtles mainly use their papillous skin for oxygen uptake, when submerged. Additionally, Root (1949) suggested that even if oropharyngeal gas exchange in *S. odoratus* happens, it may only contribute insignificantly to the ability to remain submerged. Bagatto et al. (1997), however, demonstrated that the cutaneous surface area may not be the main factor for aquatic respiration in kinosternids and that other factors must be sought. According to this, Belkin (1968) predicted, based on behavioral and physiological studies, that oropharyngeal ventilation is a respiratory response to prolonged submersion in *Sternotherus minor*. A highly vascularized oropharyngeal mucosa is known to be the key organ, responsible for aquatic gas exchange in the sistergroup of kinosternids (according to Gaffney and Meylan, 1988): the soft-shelled turtles, or Trionychidae (Gage and Gage, 1886; Dunson, 1960; Girgis, 1961; Wang et al., 1989; Yokosuka et al., 2000). We expect that a similar organ enables gas exchange in submerged *S. odoratus*. The main aim of this study is therefore to examine whether or not the oropharyngeal specializations of *S. odoratus* exhibit a dual functionality combining both feeding on land and under water and aquatic gas exchange by providing new morphological data on this species.

MATERIAL AND METHODS

S. odoratus, the stinkpot or common musk turtle, is a small-sized but abundant species ranging from southern Canada to the eastern half of the USA (Bonin et al.,

2006). This species inhabits a wide range of aquatic habitats: rivers, lakes, swamps, cattle tanks, canals, and even fast-flowing creeks with rocky bottoms (Pritchard, 1979; Rogner, 1996; Schilde, 2004; Bonin et al., 2006). *S. odoratus* are reported to be omnivorous with a strong tendency to carnivory, feeding in the wild on various plants, worms, molluscs, crayfish, insects, tadpoles, fishes, and their eggs; they can also take bites of flesh from dead animals (Ernst and Barbour, 1989; Schilde, 2004).

For this study, 5 juveniles of unknown sex, and 4 subadult, and 3 adult female *S. odoratus* ranging in size (straight carapace length) from 25.6 to 37.2 mm in juveniles, 61.5 to 69.3 mm in subadults, and 93.4 to 114 mm in adults were used. The classification in the 3 groups was based on age differences at the time studies were performed. Juveniles ranged between 2 and 6 months, subadults between 1 and 2 years, and adults were older than 3 years. The turtles were obtained commercially and kept in a 360 liter tank (40 × 150 × 60 cm) with 20% land and 80% water, and a 12 h dark/12 h light cycle. The animals were fed with earthworms, fish pieces, and turtle-food pellets from the pet trade. Animal care and treatment was in accordance with the Austrian National Protection of Animals Act (TSchG 2004).

For filming terrestrial feeding in all 12 individuals, food items were offered in front of the animals on the bottom of a glass aquarium measuring 19 × 7 × 19 cm without water. To film animals, all turtles were fed with small fish pieces, which were apparently their preferred food measuring ∼4 × 4 × 6 mm. They were filmed in lateral view with the digital high-speed camera Photron Fastcam-X 1024 PCI (Photron limited; Tokyo, JP) at 250 fr/s, with a reference grid in 1 × 1 cm as a background.

For morphological investigations, 5 juvenile and 2 subadult animals were anesthetized by intraperitoneal injection of sodium pentobarbital and, after deep narcosis, decapitated. The heads were immersed immediately in fixation solution. For SEM, 2 heads of juvenile turtles were immersed for 24 h at room temperature in modified Karnovsky solution consisting of 2.5% glutaraldehyde and 2% formaldehyde in 0.1 M cacodylate buffer (Karnovsky, 1965). After rinsing in 0.1 M cacodylate buffer, the lower jaw with all the ventral oropharyngeal structures was removed from the head to get better views from both ventral and dorsal surfaces of the oropharyngeal cavity. Then, samples were postfixed in buffered, 1% osmium tetroxide for 2 h at 37°C, washed in distilled water, and treated with 25% HCl at 40°C for 15 min to remove the mucus from the surface. After repeated washing in distilled water, the samples were dehydrated in a graded ethanol and acetone series and dried in a critical point drying machine (Polaron: Watford, UK). The dried samples were then coated with gold in an AGAR B7340 Sputtercoater (Agar Scientific, Stansted, UK) and observed in a Philips XL-20 SEM (Philips, Eindhoven, NL).

For paraffin-based histology, 2 juvenile and 2 subadult turtles were used. The heads and two biopsies of the dorsal and ventral neck were immersed in Bouin's fixative (Romeis, 1989) for 30 days, changing the solution twice a week. After complete fixation and decalcification, the upper jaw was removed from the rest of the head and the cornified rhamphothecae were cut off. Then, the samples were dehydrated in a graded ethanol-

isopropanol series and embedded in paraffin. After polymerization, 7-μm-thin serial-sections were made on a Reichert-Jung 2030 rotary microtome (Reichert-Jung, Bensheim, Germany). The sections were mounted on glass slides and, after removing the paraffin, stained with Haematoxylin–Eosin (H–E), periodic acid Schiff (PAS)–Haematoxylin and Alcian blue (AB)–Haematoxylin (after Romeis, 1989; Kiernan, 2003). The preparations were documented by digital photography under a Nikon Eclipse 800 light microscope (Nikon, Tokyo, Japan).

For semi-thin sectioning, one head of a juvenile turtle was fixed in the above–(for SEM) described modified Karnovsky solution for 48 h, washed three times in 0.1 M cacodylate buffer, postfixed for 2 h at room temperature in buffered 1% osmium tetroxide, and decalcified in EDTA (ethylenediaminetetraacetic acid) for 30 days. Afterwards, the lower jaw was removed from the rest of the head and the rhamphothecae were cut off. This procedure was followed by dehydration in a graded ethanol and acetone series and embedding in Agar 100 Resin (Agar Scientific, Stansted, UK). After polymerization at 65°C for 15 h, semi-thin (1 μm) sections were made on a Reichert Ultracut S microtome (Leica Microsystem, Wetzlar, Germany) using histo diamond knives (Diatome AG, Biel, CH). The sections were mounted on glass slides, stained with Toluidine blue (TB) and documented as described above for histological sections.

For morpho-functional comparison, sections of oropharyngeal papillae of the European pond turtle, *Emys orbicularis,* were kindly provided by Mr. Stefan Kummer, University of Vienna. *Emys orbicularis* is highly aquatic and inhabits similar environments as *S. odoratus*–but in Europe. The tissue preparation, staining, and digital imaging were the same as described above for the paraffin-based histology of *S. odoratus*.

RESULTS

Feeding Behavior

In all cases where food items were offered on the land part of the aquarium, the prey was captured by juvenile or subadult individuals and brought immediately to water for further transport, manipulation, and swallowing. Adults showed no interest in the food items presented on land. Behavioral observations, documented videographically, showed that *S. odoratus* employed hydrodynamic mechanisms to feed underwater (data not shown). Prey capture on land involved jaw prehension (Fig. 1). When access to water was hindered, none of the tested animals was able to transport the food through the oropharyngeal cavity, despite of repeated efforts (Fig. 1).

Morphology

SEM of juvenile *S. odoratus* revealed the blunt, massive, and highly keratinized rhamphothecae (Fig. 2A). The surface of the palatal mucosa was relatively flat and smooth, in contrast to the ventral side of the oral cavity, which showed a multiplicity of structures. The posterior part of the ventral rhamphotheca passed into the almost unkeratinized and triangular floor of the mouth (Fig. 2A). The floor of the mouth itself was hidden posteriorly by the tongue. The tongue of *S. odoratus* was small with a flannel-like appearance and was covered with relatively large, flattened, lobe-like lingual papillae (Figs. 2A,B). Posteriorly adjacent to the tongue lay a narrow and small groove, the glottis. The glottis itself was surrounded by oropharyngeal fold-like papillae, which closely resembled the lingual papillae (Figs. 2A–C). Posterior to the glottis, the fold-like papillae increased in number and length, often overlapped, resembling a blunt, rocky landscape (Fig. 2C). In this region, similar structures were also present in the dorsal part of the oropharyngeal cavity. The pharyngeal papillae were oriented longitudinally relative to body axis (Figs. 2A,C).

Histological sections indicated that the hypoglossum and the hyobranchial apparatus were cartilaginous, and the intrinsic musculature of the tongue was poorly developed (Figs. 3A–C). The lingual papillae, which are extensions of the lingual mucosa, were broad in transverse sections (Fig. 3A) on the anterior part of the tongue, becoming more slender posteriorly (Fig. 3B,C,4A). These slender and lobe-like papillae sometimes covered the glottal slot (Fig. 3B). On the root of the tongue and behind the tongue, the papillae became more numerous and elongated. The highest density occurred posterior to the glottis, in the pharyngeal cavity. These papillae were relatively short and simple in juvenile turtles (Fig. 3C) but tall and branched in subadults (Fig. 4A). Higher magnification showed the high degree of vascularization of the oral mucosa in *S. odoratus* (Figs. 4B,C). In the deeper lamina propria, large blood vessels ran parallel to the surface and gave rise to vessels to the superficial layer, where they formed an extensive capillary network (Figs. 4B,C). These capillary vessels ran immediately subjacent to the basement membrane and were most dense in the pharyngeal papillae (Fig. 4C).

The oropharyngeal mucosa consisted mostly—if not completely—of a nonkeratinized stratified cuboidal to columnar epithelium and an underlying connective tissue containing loosely (superiorly) to densely (in deeper regions) packed collagen fibers (Fig. 3A) and keratinization occurred exclusively on the dorsal and ventral interfaces with the rhamphothecae. The oropharyngeal epithelium consisted of 2 to 5 cell layers and the appearance of the cells varied according to their function. While the oral epithelium of the palate, floor, and tongue contained many columnar cells with mucus, these were scattered in the pharyngeal epithelium, where cuboidal cells were prevalent. The thickness of the oropharyngeal epithelial layer varied between 10 and 35 μm. No multicellular glands were found.

Compared with the oropharyngeal mucosa, the superficial layer of the dermis of the outer skin taken from the neck region contained fewer blood vessels and a well-developed capillary network was absent (compare Fig. 4C and Fig. 5A), although larger veins and arteries were present in the deeper dermis. The epithelium of the outer skin consisted of 2–3 basal cell layers plus at least 2–4 flattened superficial keratinocytes (Fig. 5A), which were eosinophilic (Fig. 5A). The whole width of the epithelium of the outer skin varied between 20 and 50 μm.

The oropharyngeal papillae in the European pond turtle *E. orbicularis*, compared with those of *S. odoratus*, were flat and rare, and capillaries were scarce (Fig. 5B).
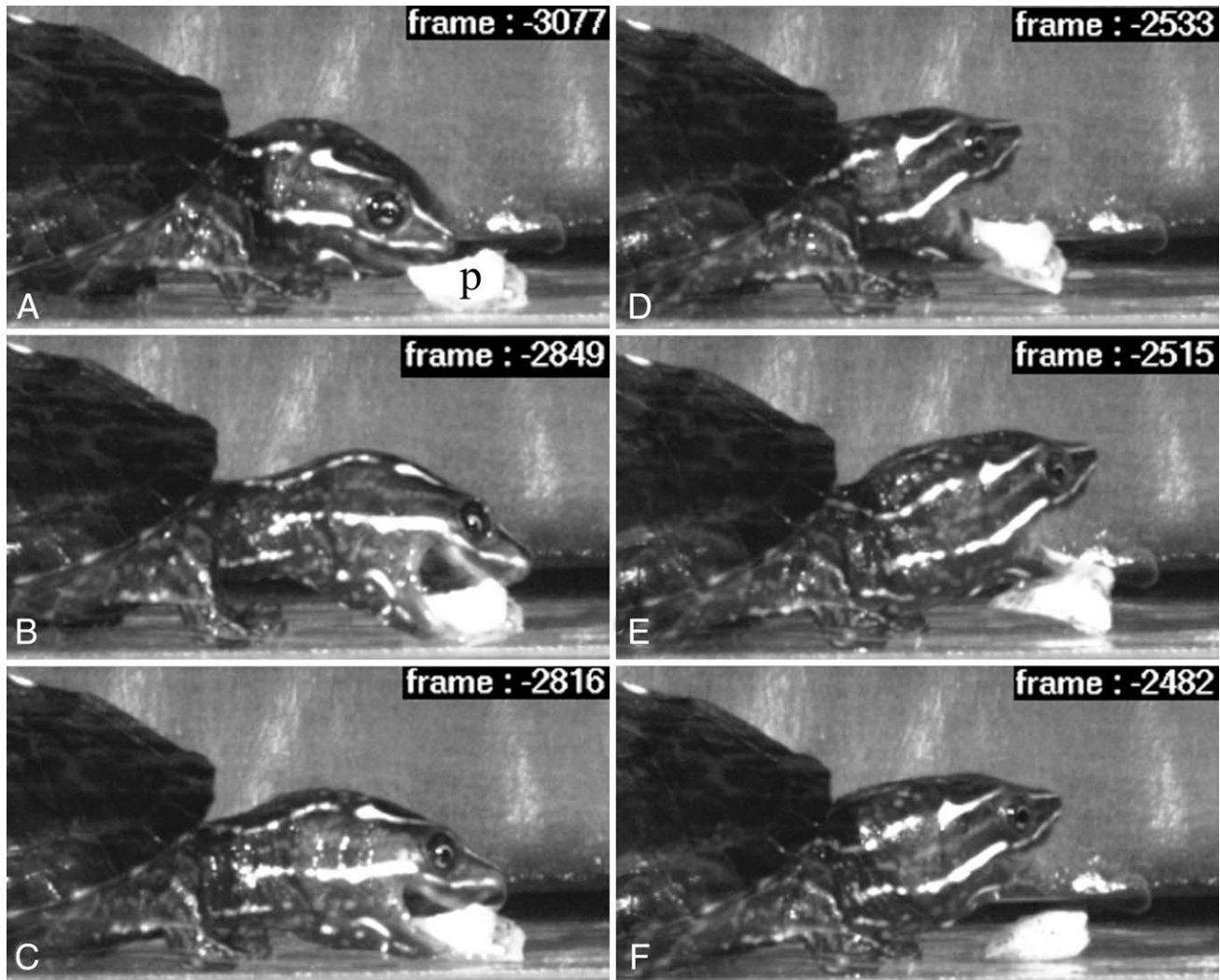
Fig. 1. Selected video frames showing a juvenile *S. odoratus* attempting to feed on land (recorded at 250 fr/s). The animal approaches (**A**) the prey item (P) grabs it with the jaws (**B, C**) but fails to transport it through the oral cavity (**D–F**).

DISCUSSION

The common musk turtle, *S. odoratus*, is highly aquatic, although occasionally found on banks of its home waters (Pritchard, 1979; Ernst and Barbour, 1989; Rogner, 1996; Schilde, 2004). Our observations of feeding behavior are consistent with this tendency to an amphibious lifestyle. When food was offered in the water, all of juvenile, subadult, and adult individuals immediately grabbed and swallowed it. Prey capture and transport occurred, as in certain other aquatic cryptodirans, via hydrodynamic mechanisms (Bramble and Wake, 1985; Lauder and Prendergast, 1992; Bels et al., 1997; Summers et al., 1998; Aerts et al., 2001; Natchev et al., 2009). As juvenile and subadult animals sometimes climbed out onto the land part of the aquarium, we tested the hypothesis that they may also be able to feed on land in contrast to adult individuals that rarely left the water. Food items offered on land were immediately grasped by juveniles and brought to the water. Sub-

adults sometimes showed a similar behavior, but adults never did. When access to water was hindered, the juvenile and subadult individuals grasped the prey successfully but failed in all cases to transport it toward the esophagus. All those turtles studied so far that feed exclusively (terrestrial) or occasionally (semiaquatic) on land use their tongue for terrestrial food transport (Weisgram et al., 1989; Wochesländer et al., 1999, 2000; Natchev et al., 2009); their tongues are fleshy and papillated with abundant mucous glands (Nalavade and Varute, 1976; Iwasaki, 1992; Iwasaki et al., 1992, 1996; Beisser et al., 2004). In contrast, exclusive aquatic feeders have a small and smooth tongue with sparse glandular tissue (Bramble and Wake, 1985; Winokur, 1988; Weisgram et al., 1989; Iwasaki, 1992; Iwasaki et al., 1992, 1996; Beisser et al., 1995, 1998, 2001; Lemell et al., 2000, 2002, 2010).

Interestingly, the common musk turtle does not fit into that dichotomy, as the morphological investigations revealed a weak and small tongue (typical for aquatic
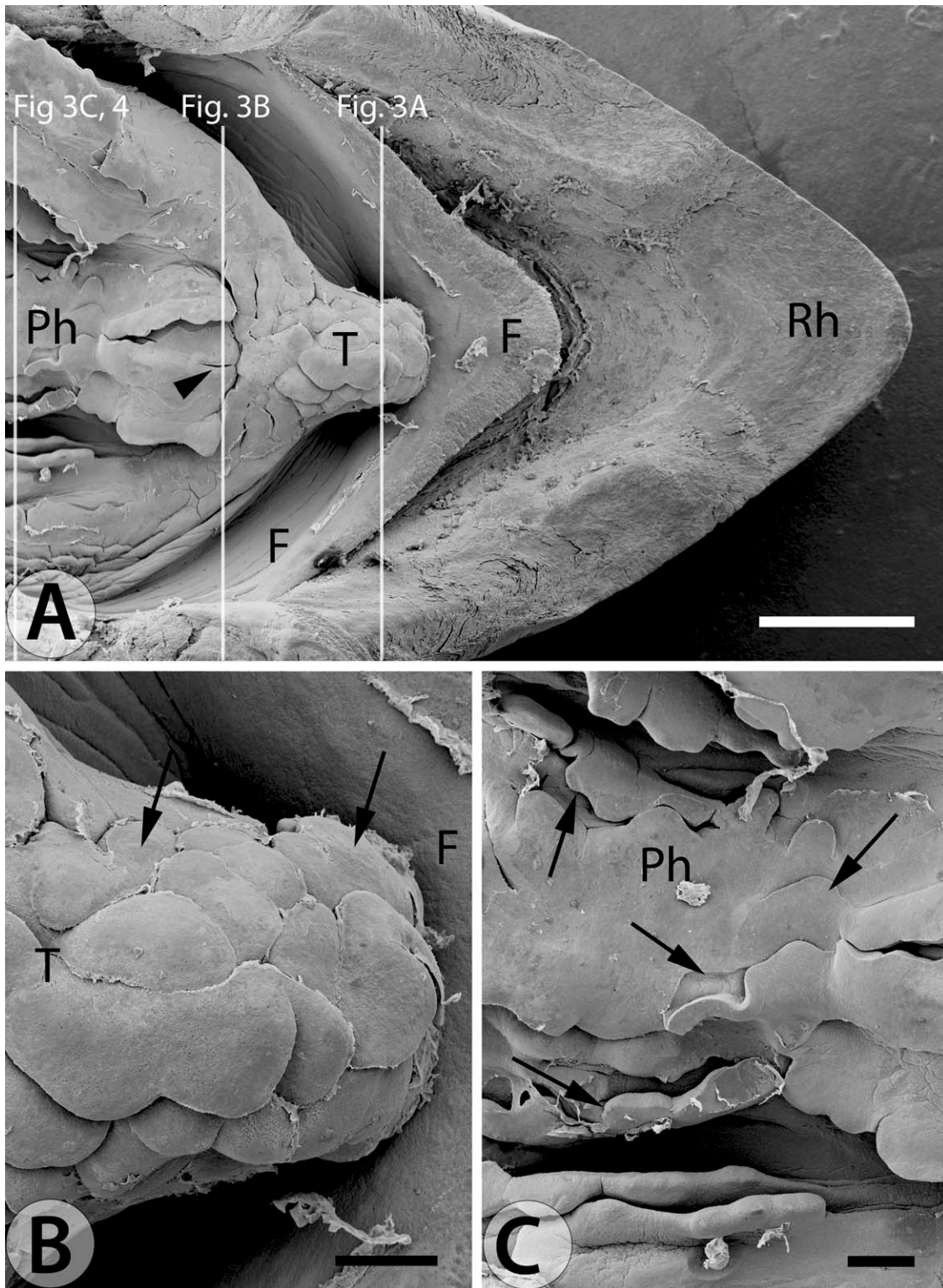
Fig. 2. Scanning electron micrographs showing the ventral surface of the mouth of a juvenile *S. odoratus*. **A** Overview, showing the massively keratinized rhamphotheca (Rh), which presents the ventral part of the "beak," the almost unkeratinized floor of the mouth (F), the small tongue (T), the glottis (indicated by arrowhead), and the pharynx (Ph). Note that the tongue (details shown in **B**) and the pharynx (details shown in **C**) are studded with flattened, floppy papillae (arrows). The white, vertical lines in micrograph A indicate where the histological sections (Figs. 3 and 4) were taken. Scale bars: A 1 mm; B and C 200 μm.
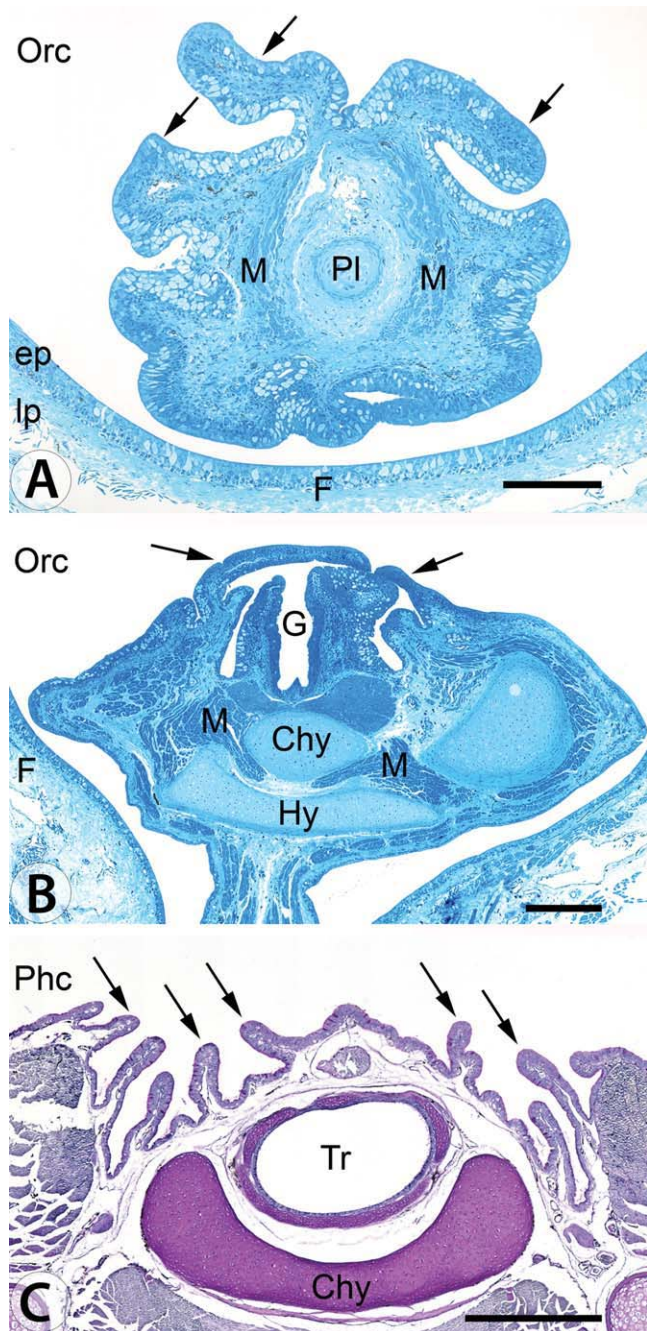
Fig. 3. Light micrographs of cross sections of the ventral oral cavity of a juvenile *S. odoratus*. For a better orientation, the white, vertical lines in the scanning electron micrograph of Figure 2A indicate where the sections were taken. **A** Anterior section showing the tongue with some flannel-like papillae (arrows) and the floor of the mouth (F). Note the thin epithelium (ep) and the scarcely developed intrinsic musculature (M). **B** Slender floppy papillae (arrows) can cover the glottal slot (G). The hyolingual skeleton is well developed and cartilaginous. **C** Floppy papillae are also abundant posterior to the glottis: in the pharynx. Chy, Corpus hyoidei; Hy, hypoglossum; lp, lamina propria; Orc, oral cavity; Phc, pharyngeal cavity; Pl, processus lingualis; Tr, trachea. Scale bars: A and B 200 μm; C 500 μm. A and B semithin sections stained with Toluidine blue; C paraffin section stained with PAS-H.

feeders) but with numerous papillae (expected for terrestrial feeders). All animals tested lost the food item when fed on land presumably because they were unable to fix the food to the palate with their tiny tongues during the first attempted transport cycle. Therefore, the presence of lingual papillae in *S. odoratus* cannot be explained as an adaptation for occasional terrestrial feeding. Furthermore, their orientation would not promote the interlocking effect between tongue and food. Finally, longer branched fold-like papillae are present posterior to the lingual root, around the glottis and throughout the pharyngeal cavity. Pharyngeal papillae in reptiles are known to have at least four different functions: First, nonkeratinized mucus secreting oral, pharyngeal, and esophageal papillae are used for protection from dangerous prey in horned lizards (*Phrynosoma*) (Sherbrooke & Schwenk, 2008). Second, keratinized pharyngeal and esophageal papillae are found in some marine turtles and are believed to provide mechanical protection from dangerous or abrasive food items (Parsons & Cameron, 1976; Meylan, 1988; Winokur, 1988). Third, nonkeratinized pharyngeal and esophageal papillae are used for food particle trapping in neustophagy found in some pleurodire turtles (Belkin & Gans, 1968; Parsons & Cameron, 1976; Vogt et al., 1998). Fourth, nonkeratinized oropharyngeal papillae are described for some softshelled turtles (Trionychidae) and were shown to function in underwater gas exchange (e.g. Gage and Gage, 1886; Dunson, 1960; Girgis, 1961; Wang et al., 1989; Yokosuka et al., 2000). While the first three possible functions of pharyngeal papillae cannot be true for *S. odoratus*, because of the ecological or structural reasons, the latter function found in trionychids seems more likely.

The Trionychidae are the putative sistergroup (according to Gaffney and Meylan, 1988) of the Kinosternidae. Trionychids practice gas exchange underwater through pharynx and skin when hibernating and diving (see Gage and Gage, 1886; Dunson, 1960; Girgis, 1961; Wang et al., 1989; Yokosuka et al., 2000). Interestingly, physiological investigations revealed that *S. odoratus* oxygenates its blood under water like soft-shelled turtles do. The common musk turtles can remain underwater at 10°C for more than 100 days (Jackson et al., 1984; Ultsch et al., 1984) and at 3°C for at least 150 days (Ultsch, 1985, 1988; Ultsch and Wasser, 1990; Ultsch and Cochran, 1994; Ultsch and Jackson, 1995) without discernible ill effects. While submerged, the turtles remain aerobic as evidenced by the relatively small increases in plasma lactate (Ultsch and Cochran, 1994; Ultsch and Jackson, 1995). Three organs are predicted to be involved in aquatic gas exchange in chelonians, namely the cloacal bursae, the skin and the oropharyngeal mucosa. Cloacal gas exchange has been demonstrated in some pleurodiran turtles (King and Heatwole, 1994; Gordos and Franklin, 2002; Clark et al., 2008). All kinosternids, however, lack cloacal bursae (Dunson, 1960; Peterson and Greenshields, 2001) and their skin is thick, strongly keratinized (especially plastron and carapace) and lacks an extensive capillary network (Fig. 5A). This excludes those two potential modes of gas exchange for *S. odoratus*. In contrast to the latter, the surface-amplifying oropharyngeal papillae are highly vascularized. Histologically, those structures are very similar to the villiform oropharyngeal papillae described for the
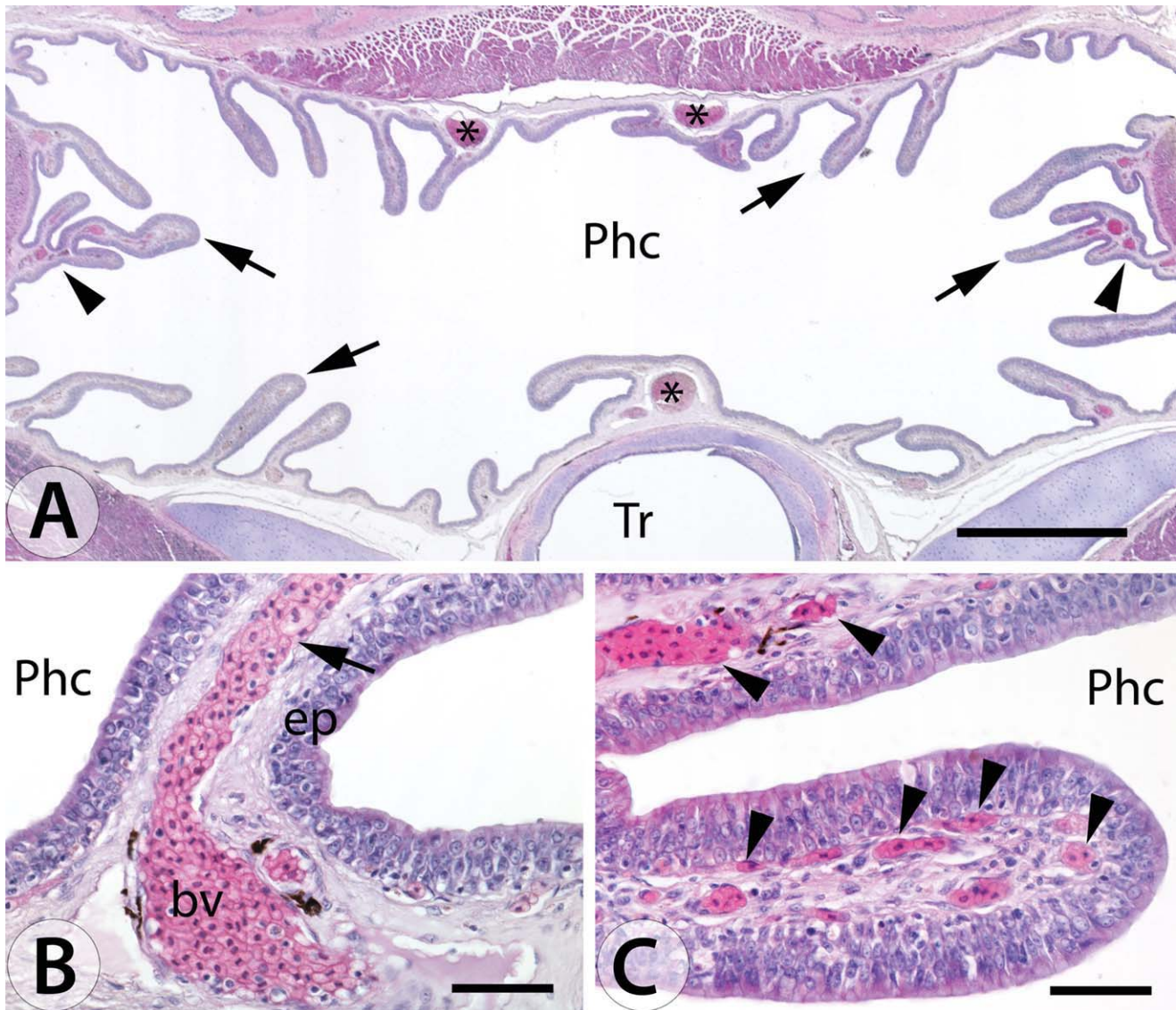
Fig. 4. Light micrographs of cross sections of the pharynx of subadult *S. odoratus*. **A** Overview showing the large and sometimes branched pharyngeal papillae (arrows). The arrowheads point to branched papillae. The asterisks mark some large blood vessels that supply the capillaries. **B** Larger blood vessel (bv, filled with erythrocytes) branches into a papilla (arrow). **C** Numerous small capillaries filled with erythrocytes, run immediately subjacent to the epithelium (arrowheads). ep, epithelium; Phc, pharyngeal cavity; Tr, trachea. Scale bars: A 1 mm; B and C 50 μm. All sections H–E stained.

soft-shelled turtle *Trionyx sinensis japonicus* in which the papillae definitely play a central role in gas exchange underwater (Yokosuka et al., 2000). The oropharyngeal papillae of *T. sinensis japonicus* are slender, tall, and branched. In contrast to this, the papillae of *S. odoratus* are lobe-like folds and oriented longitudinally relative to the body axis. A moderate to extensive capillarization, coupled with cutaneous surface amplification, is a strong indicator for cutaneous respiration in vertebrates (according to Feder and Burggren, 1985). Within tetrapods, cutaneous gas exchange contributes significantly to tissue respiration in almost all amphibians, some reptiles, and certain mammals. In *S. odoratus*, the density of capillaries just beneath the thin oropharyngeal epithelium is comparable (if not even higher) to that in the skin of lungless salamanders (Plethodontidae), which exclusively rely on cutaneous respiration (Feder and Burggren, 1985). Lungless salamanders can cover their demand for gas exchange throughout life by this way. Oropharyngeal respiration in trionychids and kinosternids can ensure survival, whereas diving at a decreased activity level (Dunson, 1960) or during hibernation (Ultsch and Jackson, 1995; Yokosuka et al., 2000). At high metabolic rates, these animals can no longer cover their oxygen demand in this manner and die if prevented from reaching the water surface to breathe (Dunson, 1960).

The high-degree of vascularization and capillarization in the oropharyngeal papillae of *S. odoratus* becomes
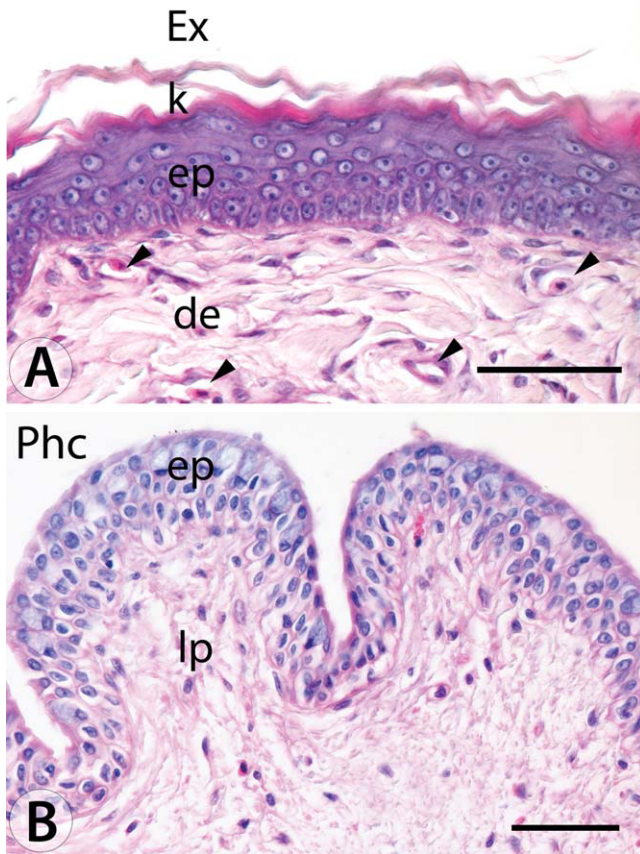
Fig. 5. Light micrographs of (**A**) longitudinal section of the skin of the neck of a subadult *S. odoratus* and (**B**) of a transverse section of two postglottal papillae of *E. orbicularis*. A Note the superficial keratin-layer (k) and the lack of a well developed capillary network in the skin of *S. odoratus*. Arrowheads point to small vessels. B Also the small and rare papillae in the pharynx of *E. orbicularis* do not show a well-developed capillary network, in contrast to those of *S. odoratus* (Fig. 4). Both integument surfaces shown here are not suitable for life-supporting cutaneous respiration. de, dermis; ep, epithelium; Ex, external space; lp, lamina propria; Phc, pharyngeal cavity. Scale bars: 50 μm. Both sections are H–E stained.

more apparent if compared with the oropharyngeal mucosa in *E. orbicularis* belonging to Emydidae. The ecology and feeding behavior of this aquatic European turtle are similar to those of the common musk turtle. *E. orbicularis* has a prolonged hibernation, but it has a far lower capacity for lengthy submergence than *S. odoratus*. *E. orbicularis* must periodically seek the water surface to breath during hibernation (Bonin et al., 2006) and *S. odoratus* need not (Ultsch and Cochran, 1994; Ultsch and Jackson, 1995). The oropharyngeal surface in *E. orbicularis* is flat with few and small papillae that contain some blood vessels but lack a well-developed capillary network. Such a design limits the potential for gas exchange through the oropharyngeal mucosa.

We assume that the oropharyngeal papillae in *S. odoratus* are morpho-functional adaptations for gas exchange underwater. Their design should not significantly affect the potential of this species to suction feed. The oropharynx in this turtle, therefore, exhibits a dual functionality concerning feeding and underwater respiration. Future studies will examine the feeding behavior and oropharyngeal structures of other kinosternids to determine whether the dual functionality of the oropharynx found in *S. odoratus* is shared with other members of the family. Until we document the distribution of this trait within the Kinosternidae, we cannot determine whether the presence of respiratory oropharyngeal papillae and folds is an ancestral character shared with the Trionychidae or evolved independently in both groups.

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