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RESEARCH PAPER

Comparison of the lateral line and ampullary systems of two species of shovelnose ray

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Abstract The anatomical characteristics of the mechanoreceptive lateral line system and electrosensory ampullae of Lorenzini of *Rhinobatos typus* and *Aptychotrema rostrata* are compared. The spatial distribution of somatic pores of both sensory systems is quite similar, as lateral line canals are bordered by electrosensory pore fields. Lateral line canals form a sub-epidermal, bilaterally symmetrical net on the dorsal and ventral surfaces; canals contain a nearly continuous row of sensory neuromasts along their length and are either non-pored or pored. Pored canals are connected to the surface through a single terminal pore or additionally possess numerous tubules along their length. On the dorsal surface of *R. typus*, all canals of the lateral line occur in the same locations as those of *A. rostrata.* Tubules branching off the lateral line canals of *R. typus* are ramified, which contrasts with the straight tubules of *A. rostrata.* The ventral prenasal lateral line canals of *R. typus* are pored and possess branched tubules in contrast to the non-pored straight canals in *A. rostrata.* Pores of the ampullae of Lorenzini are restricted to the cephalic region of the disk, extending only slightly onto the pectoral fins in both species. Ampullary canals penetrate subdermally and are detached from the dermis. Ampullae occur clustered together, and can be surrounded by capsules of connective tissue. We divided the somatic pores of the ampullae of Lorenzini of *R. typus* into 12 pore fields (10 in *A. rostrata*), corresponding to innervation and cluster formation. The total number of ampullary pores found on the ventral skin surface of *R. typus* is approximately six times higher (four times higher in *A. rostrata)* than dorsally. Pores are concentrated around the mouth, in the abdominal area between the gills and along the rostral cartilage. The ampullae of both species of shovelnose ray are multi-alveolate macroampullae, *sensu* Andres and von Düring (1988). Both the pore patterns and the distribution of the ampullary clusters in *R. typus* differ from *A. rostrata*, although a basic pore distribution pattern is conserved.

Keywords Mechanosensory lateral line · Ampullae of Lorenzini · Shovelnose rays · Electroreception · Octavolateralis system

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Introduction

Visible in the skin of elasmobranchs are somatic pores belonging to two major sensory systems: the ampullae of Lorenzini and the lateral line system. When first described by Stenois in 1664, the pores were thought to belong to mucus producing organs (Raschi 1984). Historically the lateral line sense organs are thought to belong to the acousticolateralis system (Boord and Campbell 1977; Coombs and Montgomery 2005). Dijkgraaf (1963) divides the lateral line system of elasmobranchs into ordinary and ampullary organs. The former includes canal neuromasts, superficial neuromasts, vesicles of Savi and spiracular organs (Maruska 2001), and are mechanoreceptors displaying directional sensitivity distributed over the head, trunk and tail of elasmobranchs (Szabo 1974). The latter are the ampullae of Lorenzini, which are sensitive to electrical stimuli and restricted to the cephalic region and pectoral fins (Szabo 1974). Both the ampullae of Lorenzini and the lateral line system are innervated by branches of the anterior lateral line nerve (Boord and Campbell 1977).

Several types of mechanosensory lateral line organs occur in elasmobranchs. The sensory unit of all lateral line organs is the neuromast. Each neuromast comprises sensory hair cells and supportive cells and is covered by a cupula (Maruska 2001; Kasumyan 2003). The lateral line canal system forms a network of sub-epidermal pored or non-pored canals that possess a nearly continuous sensory epithelium located at the bottom of the canal (Maruska 2001). Pored canals connect to the surface via endpores and tubules branching off along the length of the canal. Tubules can be branched and do not contain a sensory epithelium (Maruska 2001). Pored lateral line canals enable elasmobranchs to detect acceleration of the hydrodynamic flow, whereas non-pored canals allow the detection of water velocity (Maruska and Tricas 2004). Superficial neuromasts (or pit organs) are neuromasts located either in surface grooves in rays or between modified scales in sharks (Maruska 2001). They encode water velocity and mediate rheotaxis (Peach 2001; Maruska and Tricas 2004). Vesicles of Savi are found in some benthic batoids (*Dasyatis* spp., *Narcine* spp. and *Torpedo* spp.). A large central and two smaller peripheral neuromasts are found in closed cavities located 0.5–2 mm under the skin surface, surrounded by a cartilaginous cover (Maruska 2001). Spiracular organs are located in a closed cavity in the hyoid arch region and may be proprioreceptors encoding movements of the hyomandible (Maruska 2001; Kasumyan 2003).

The ampullae of Lorenzini enable elasmobranchs to detect electric fields as low as 5 $nVcm^{-1}$ (Kalmijn 1974). Electroreception is used during navigation and the detection of mates, prey and predators (Kalmijn 1974; Bullock and Szabo 1986; Tricas et al. 1995; Wilkens and Hofmann 2005). Each ampulla consists of a somatic pore leading to a jelly-filled canal that proximally forms an ampulla comprising several alveolate bulbs embedded in subcutaneous tissue (Boord and Campbell 1977; Jorgensen 2005). The sensory epithelium is restricted to the inside of the alveoli (Waltman 1966; Murray 1974). Ampullae are clustered together in capsules of connective tissue enabling the suppression of interference from the animal's own electrical field, through restricting the received signals to those of non-common mode (Kalmijn 1974). Physiological response properties are linked to the passive electrical properties and structure of the ampullary organ (Kalmijn 1974). Each receptor is directional with best responses to fields oriented parallel to the canal (Murray 1962; Bodznick and Boord 1986). Andres and von Düring (1988) divide the electroreceptive structures of elasmobranchs into three groups, due to their overall size: (a) freshwater skates possess mini-ampullae, with canal lengths around 450 µm, (b) holocephalans and hexanchid sharks possess micro-ampullae restricted to certain cephalic regions with canals ranging from 1.5 to 10 mm in length, and (c) macro-ampullae are found in marine Chondrichthyes, with canals up to 20 cm long.

Rhinobatos typus (Bennett 1830), the giant shovelnose ray, is widely distributed in the Indo- Pacific, from India to Australia (Compagno and Last 1999). In Australasian waters this species is found from Shark Bay, Western Australia, to Forster, New South Wales, including the Northern Territory and Queensland (Cavanagh et al. 2003). Juveniles are common in mangrove systems and estuaries while adults are found on the continental shelf to depths of 100 m. Specimens have been found to live and breed permanently in freshwater (Compagno and Last 1999). This species reaches a maximum total length of 270 cm (Cavanagh et al. 2003) and feeds on shellfish and benthic prey (Compagno and Last 1999; Cavanagh et al. 2003).

Aptychotrema rostrata (Shaw & Nodder 1794), the eastern shovelnose ray, is endemic to the continental slope off eastern Australia, where it ranges from Moreton Bay, Queensland, to Halifax Bay, New South Wales (Compagno and Last 1999). Generally found in coastal waters to depths of 50 m, its diet is dominated by benthic crustaceans, mollusc and fish (Compagno and Last 1999; Kyne and Bennett 2002). A maximum size of 120 cm has been reported (Compagno and Last 1999).

Here, we compare the morphology of the lateral line system and ampullae of Lorenzini of *Rhinobatos typus* and *Aptychotrema rostrata*. Dominance of cryptic, benthic prey in the diet suggests a high probability of the use of mechanoreception and electroreception in prey detection. The occurrence of *R. typus* in both marine and freshwater habitats also makes this species of interest concerning the structure of the ampullae of Lorenzini, as only one omnihaline species of elasmobranch has been examined thus far (Whitehead 2002). By mapping the lateral line system and ampullae of Lorenzini, we assess general adaptations to the benthic lifestyle as well as adaptations to the specific habitat conditions. Rhinobatid rays were chosen for this study as they are locally abundant in southeast Queensland and because they are a poorly studied taxon amongst elasmobranchs (Last et al. 2004).

Materials and methods

All procedures of this study were approved by the University of Queensland Animal Ethics Committee (Permit No. CMS/420/04). *Rhinobatos typus* were collected under the MBMP Permit No.QS2004/CVL316, GBRMPA Permit No.G02/7121 and Queensland Fisheries Permit No.PRM02279I and *Aptychotrema rostrata* were collected under the Queensland Fisheries Permit No.PRM03951I.

Rhinobatos typus, Bennett 1830 (n = 6) and *Aptychotrema rostrata*, Shaw and Nodder, 1794 (n = 2) were caught by hand netting, in Shark Bay, Heron Island (23°31′ S, 152°1′ E) and off North Stradbroke Island (27°43′ S, 153°27′ E), Moreton Bay, Queensland, Australia (Table 1). Specimens were identified (Compagno and Last 1999) and euthanized with an overdose of tricaine methane sulfonate (MS222; 1:2000). The following measurements were taken (±1 mm): total length, precaudal length, disk width and disk length. The respective data on sex and collecting site of each specimen were also noted (Table 1).

Peripheral organisation of the mechanosensory lateral line and electrosensory ampullary systems

Dorsal and ventral tissue samples from *Rhinobatos typus* were examined with scanning electron microscopy (SEM) to identify differences in somatic pores belonging to the lateral line system and ampullae of Lorenzini. Tissue samples from four specimens (Table 1 No.2–5) were fixed and preserved in Karnovsky's (1965) formaldehyde- glutaraldehyde fixative. They were washed in three series of 0.1 M phosphate buffer, transferred into an ascending series of alcohol (20, 40, 60, 70% EtOH for 30 min each), critical point dried, mounted on 10 mm aluminium

Table 1 Specimens of *Rhinobatos typus* and *Aptychotrema rostrata* collected for the present study

Specimen number	Disk width (cm)	Disk length (cm)	Total length (cm)	Sex	Disk surface area (cm^2)	Collecting site
Rhinobatos typus						
1	14.0	18.0	43.0	m	–	Heron Island
2	13.5	17.0	39.5	f	–	Heron Island
3	16.1	18.4	46.9	m	155.6	North Stradbroke Island
4	17.2	21.0	49.5	f	178.5	Heron Island
5	14.4	19.2	45.0	m	141.5	Heron Island
6	15.5	19.7	43.3	f	142.6	Heron Island
Aptychotrema rostrata						
7	25.5	–	68.0	m	–	N. Stradbroke Island
8	22.4	–	64.0	m	–	N. Stradbroke Island

stubs and sputter coated with gold. Samples were viewed in a JEOL JSM 6400 F scanning microscope at 75 kV. Images were captured digitally and viewed with AnalySIS ver.3 by Soft Imaging System.

Morphological characteristics of the lateral line system and the ampullae of Lorenzini of four specimens of *Rhinobatos typus* (Table 1 No.3–6) and two specimens of *Aptychotrema rostrata* (Table 1 No.7 and 8) were compared. Specimens were preserved in neutrally-buffered formalin (10%) for 48 hrs and stored in 70% ethanol. The surface area of the pectoral disk was estimated (± 1 mm^2) by placing each specimen with the ventral side on a grid paper with 1 mm^2 squares and drawing an outline of the disk. A drawn line following the abdominal lateral line canal connected to the base of the pectoral fin was used to delineate the caudal margin of the disk. Possible changes in the size of animals due to preservation were presumed to be consistent for all specimens and between species. To visualize superficial sensory pores, specimens were stained with Methylene Blue solution (approximately 1%) applied to the skin under slight pressure. Specimens were viewed using an Olympus SZX9 stereomicroscope. To avoid double counting of the pores, a grid system made of nylon thread was superimposed on the skin surface. To further distinguish pores of the lateral line and ampullae of Lorenzini single pores were dissected out and the canals viewed. Pore fields of the ampulla of Lorenzini were identified for the purpose of general description. The location of the ampullary clusters was also identified. We define a cluster as an aggregation of ampullary bulbs, and a capsule as a cluster of ampullae surrounded by a common collagen sheath. Pit organs or free neuromasts of both species were verified by comparison with Peach (2003). Muscles and bones were identified after Wilga and Motta (1998), Compagno (1999), and Liem and Summers (1999). Terminology of the lateral line canals and ampullary clusters follows Garman (1888) in McEachran et al. (1996), Chu and Wen (1979) and Raschi (1984). Preliminary ampullary pore counts and disk surface area estimates were performed on ten additional specimens of *R. typus* in the collection of the Queensland Museum. As these specimens could not be dissected, a grid system was used as described above. All statistical methods follow Köhler et al. (2002) and Statsoft, Inc. (2004). As the mechanosensory lateral line canal system and electroreceptive ampullary system of *R. typus* are described in detail, only the major differences apparent in *A. rostrata* are reported.

Morphology of the ampullary organs of *Rhinobatos typus*

The general arrangement of ampulla of Lorenzini of the hyoid capsule and rostral tissue of *Rhinobatos typus* were analysed using standard histological methods on tissue samples from six specimens (Table 1 No.1–6). After collection, tissue samples were kept in neutrally-buffered formalin for several weeks. Samples containing denticles were decalcified in Gooding and Stewart's Fluid (Culling 1974) for up to four days, washed in water, dehydrated in an ascending alcohol series (70, 90, 100, 100% EtOH for 45 min each), transferred into 100% xylene and embedded in paraffin wax at 60°C in a vacuum oven. Sections (6 μm) were cut with a ''280'' Spencer microtome and stained with Mayer's Haematoxylin-Eosin (Culling 1974). They were viewed using an Olympus BX41 light microscope. Images were captured with a Nikon Coolpix 4500 digital camera.

Ampullary organs (Fig. 1) were classified according to the nomenclature defined in Andres and von

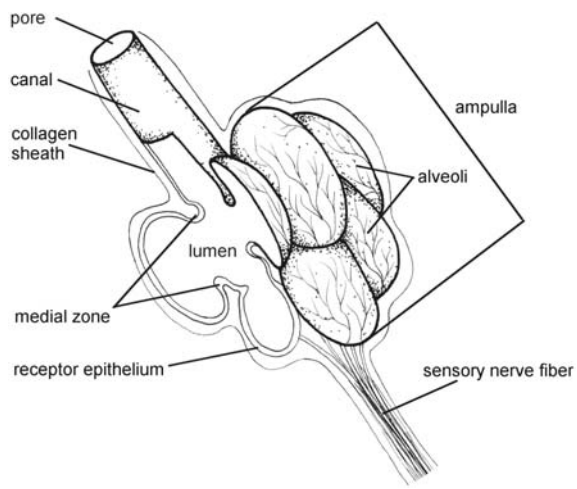

Fig. 1 Schematic representation of a single ampulla of Lorenzini of a rhinobatid shovelnose ray. From a somatic pore, the canal extends, widening proximally to an ampullary bulb. The ampulla is formed by several alveoli in a grape-like arrangement. The epithelium of adjacent alveoli and the canal is separated by the medial zone. A sensory nerve fibre extends from the proximal end of the ampulla

Düring (1988). Histological measurements were taken with a calibrated ocular (±1 ocular unit). Serial sections were produced for all ampullae and measurements were taken from the section showing the greatest circumference of the respective ampulla. As alveoli are elliptical in this species, the longest and shortest orthogonal diameters of the alveolar lumen were measured and the maximal area of cross-sections of alveoli calculated. Diameter of canals and ampullae were also measured. The diameter of the canal was measured immediately distal to the medial zone, where canals had not yet bifurcated. As the canals also appeared elliptical, two measurements were taken. For measurements of the ampullary diameter, cross sections were differentiated from longitudinal sections based on the presence of the ampulla's canal. All measurements are presented as mean ± standard deviation. In order to count the alveolar bulbs of each ampulla, all histological sections of the respective ampulla were drawn. All statistics follow Köhler et al. (2002) and Statsoft Inc. (2004). Skin layers were identified according to Kemp (1999) and Maruska (2001).

Results

Peripheral organisation of the mechanosensory lateral line and the electrosensory ampullary system

On the epidermal surface of *Rhinobatos typus*, structures belonging to two major sensory systems are visible: pores of the lateral line and the ampullae of Lorenzini (Fig. 2a, b) and canals of the lateral line (Fig. 2c). Pores of the lateral line vary in size and are of two types: the terminal pores of the canal are about equal in size to ampullary pores, whereas tubular pores are smaller (54 ± 2 µm in diameter). Pores of the ampulla of Lorenzini measure 114 ± 15 µm in diameter.

The lateral line system of *Rhinobatos typus*

The mechanosensory lateral line system forms a sub-epidermal bilaterally-symmetrical net on the dorsal and ventral surface of *Rhinobatos typus* (Fig. 3). Most canals are embedded in the fibrous layer of the dermis and contain a nearly continuous row of sensory neuromasts along their length, as reported for other chondrichthyans. Other canals are associated with the deep layer of the dermis. Canals are either non-pored or pored and pored canals are either connected to the surface through a single terminal pore or additionally possess numerous tubules along their length. Canals embedded in the fibrous layer can penetrate into the deep fascia of the dermis and become only loosely associated with the dermis. Some canals form an open groove containing free neuromasts.

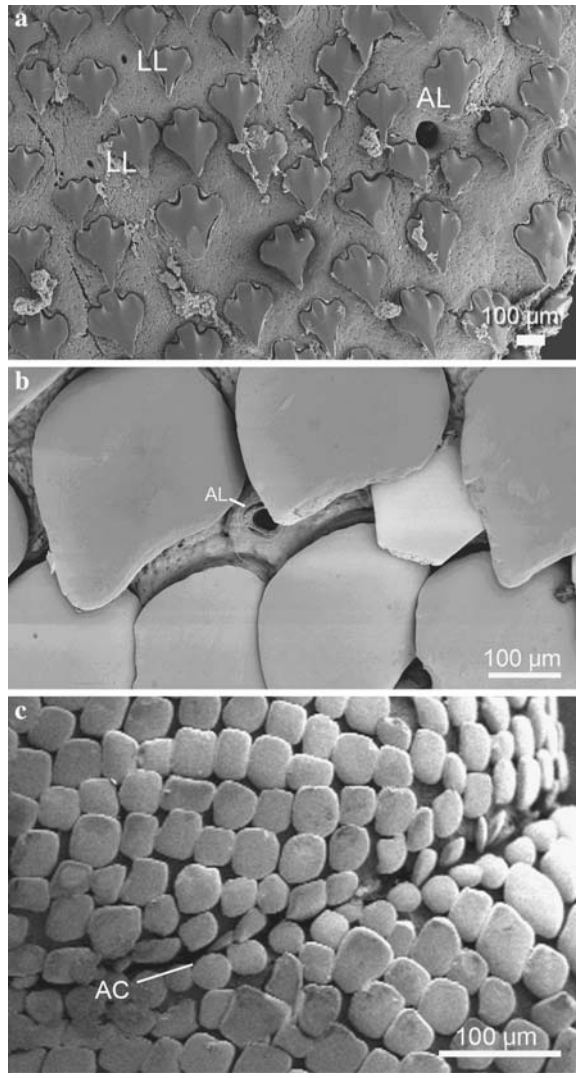

Fig. 2 The epidermis of *Rhinobatos typus* (Table1, specimen No.2 and 5), SEM. (**a**) dorsal side. (**b**), (**c**) ventral side. Pores of the lateral line system (LL) and ampullae of Lorenzini (AL) are visible, but differ in size. The abdominal lateral line canal (AC) forms an open groove

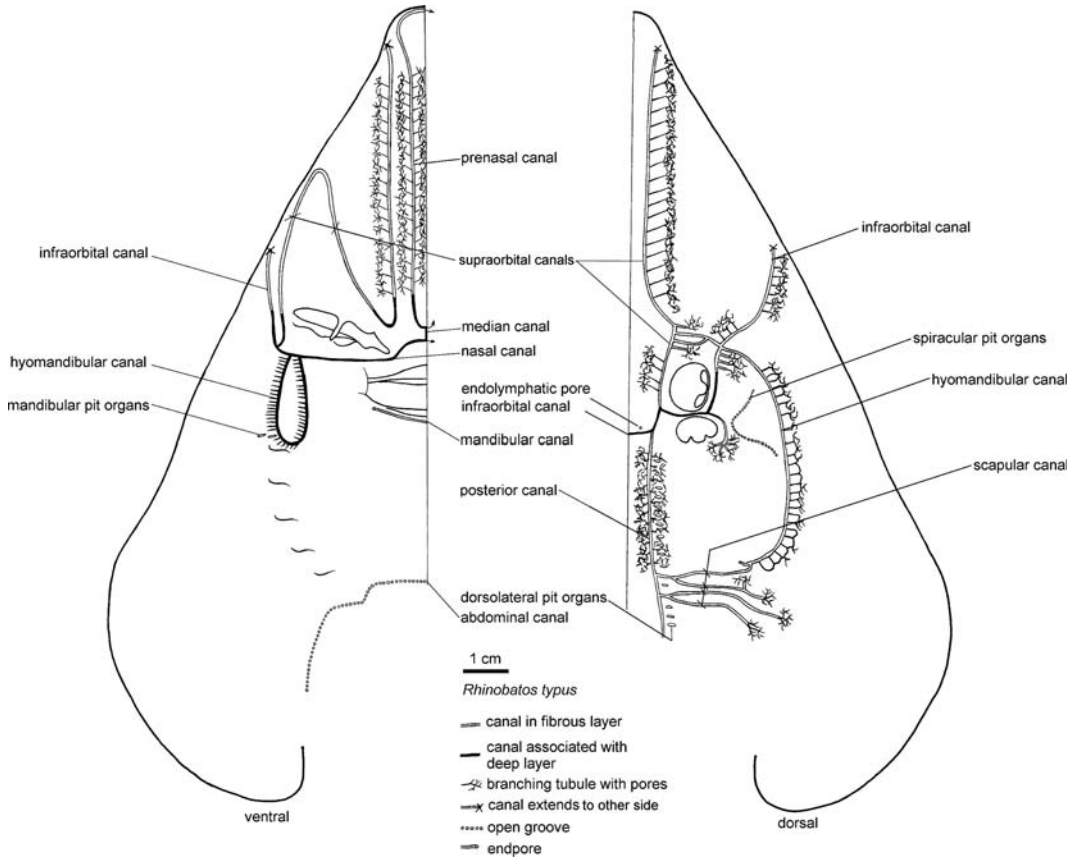

Fig. 3 Schematic representation of the mechanosensory lateral line canal system on the dorsal and ventral sides of *Rhinobatos typus*

Dorsally, the hyomandibular canal extends from an anterior branch of the scapular canal, loosely following the propterygial cartilage. It connects to both the infraorbital and supraorbital canals laterally and anterior to the eye, respectively. Tubules branch off the main canal and are mixed with the pores of the ampullae of Lorenzini. The dorsal infraorbital lateral line canal (DILC) connects bilaterally over the neurocranium anterior to the pores of the endolymphatic duct. From there it extends laterally between the spiracle and eye, being loosely associated with the deep fascia. Antero-lateral to the spiracle the DILC bifurcates where one branch runs to the caudo-lateral margin of the spiracle, where it terminates in branching tubules. The other branch passes lateral to the eye and the nasal capsule, extending to the rostral margin of the propterygium, where it penetrates to the ventral side. When passing laterally along the eye, the DILC is loosely connected to the deep fascia. Anterior to the eye it descends into the fibrous layer of the dermis and forms tubules on both sides. The dorsal supraorbital lateral line canal runs anteriorly along the rostral cartilage with branched tubules that extend laterally but not medially (Fig. 2). Lateral to the endolymphatic pore it connects with the infraorbital canal. Near the rostral appendix the supraorbital canal breaks through to the ventral side. The scapular lateral line canal forms four canals dorsally that extend from the posterior lateral line canal, above the pectoral girdle laterally, along the pectoral fins. The most rostral canal connects to the hyomandibular canal and the three others terminate in bifurcating tubules.

On the ventral surface, the hyomandibular canal forms a loop to the posterior between the lateral edge of the nasal capsule and the first gill opening, being connected to the skin surface through tubules along its entire length. Lateral to the nasal cartilage, the hyomandibular canal connects with the nasal lateral line canal. The ventral infraorbital canal extends from

the connection with the dorsal infraorbital canal to the junction with the supraorbital canal. This part lacks tubules or pores. Near the rostral appendix, the supraorbital canal breaks through to the ventral side, where it runs laterally to the prenasal lateral line canal along the rostral cartilage, with branched tubules extending laterally. When reaching the neurocranium, the ventral supraorbital canal forms a non-pored loop that extends to the lateral margin of the disk and returns to the lateral edge of the nasal capsule, where it connects to the infraorbital canal. The ventral suprorbital lateral line canal is embedded in the fibrous layer of the dermis and is only loosely associated with the deep fascia while crossing over the neurocranium. The mandibular lateral line canal runs across the midline passing posteriorly to the mandible. It is connected to the surface via terminal pores and lacks tubules. The abdominal lateral line canal in *Rhinobatos typus* forms an open groove (Fig. 2c) that follows the pectoral girdle and metapterygium. Scales surrounding this open grove are not specialized in their shape.

Superficial neuromasts or pit organs contain a sensory epithelium formed by free neuromasts embedded in grooves in the skin, as indicated by Peach (2003). In *Rhinobatos typus* the dorsolateral pit organs line the posterior lateral line canals from immediately posterior to the endolymphatic pores to the caudal fin. The grooves are oriented perpendicular to the rostrocaudal body axis. Dorsally, the spiracular pit organs form a continuous groove lateral to the spiracle and the eye. The terminations of this groove are in close proximity to the mandibular lateral line canal, where the spiracular pit organ bends towards the spiracle. On the ventral side, three mandibular pit organs are found rostral to the first gill opening.

The ampullary system of *Rhinobatos typus*

Pores of the ampullae of Lorenzini of *Rhinobatos typus* (Fig. 4) are mostly found on the cephalic region of the disk, extending only slightly onto the pectoral fins. Ampullary canals penetrate subdermally and are detached from the dermis. Ampullae occur in clusters that can be surrounded by connective tissue, forming a capsule. We divided the somatic pores of the ampullae of Lorenzini of *R. typus* into six areas dorsally (A–F) and six areas ventrally (G–L). These areas correspond to the innervation and cluster

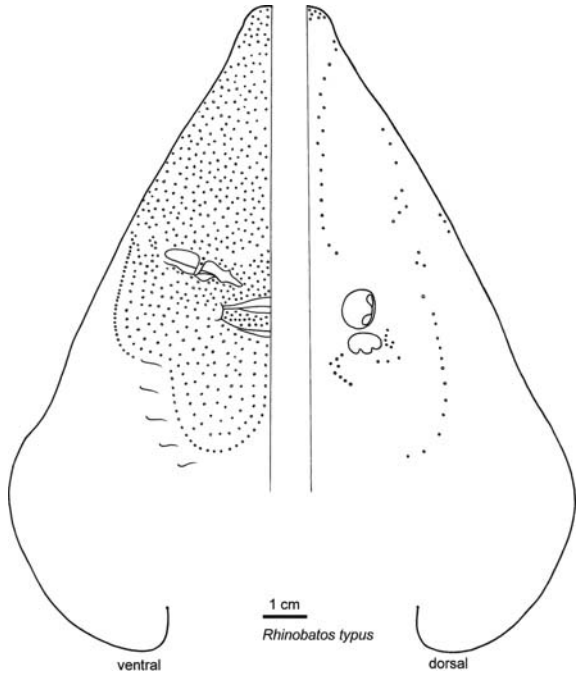

Fig. 4 Schematic representation of the pores of the ampullae of Lorenzini on the dorsal and ventral surfaces of *Rhinobatos typus*. This species possesses a mean of 75.1 ± 11.4 pores dorsally, and 452 ± 162.8 pores ventrally (n = 4)

formation (Fig. 5). To further clarify locations of ampullary clusters they are additionally presented in the context of muscles and cartilage, with dermis and connectives removed (Fig. 6).

The ampullary pores distributed on the dorsal surface within areas A–E (Fig. 5, Table 2) attach to sensory units of the hyoid capsule. Area A follows the hyomandibular lateral line canal from the pectoral girdle along the propterygium to the musculus quadratomandibularis in one row. Pores of area B form a semicircle medial and caudal of the spiracle. Area C lies lateral to the spiracle and between area A and B. The ampullary pores of areas D and E also lead to ampullae of the hyoid capsule lateral of the rostral cartilage. Pores of area D extend between the nasal capsule and the rostral tip of the propterygium and area E extends from the middle of the nasal capsule almost to the tip of the rostrum. The hyoid capsule is innervated by the hyomandibular branch of the anterior lateral line nerve. Ampullae of area F belong to the superficial ophthalmic capsule where their pores lie along the outer edge of the rostral cartilage and along the tip of the rostrum. Both the

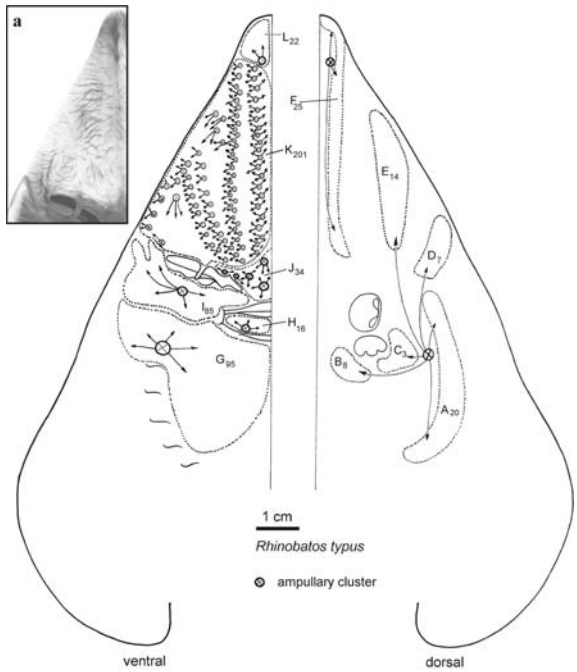

Fig. 5 Schematic representation of the dorsal and ventral pore fields and capsules of the ampullae of Lorenzini of a representative specimen of *Rhinobatos typus*. Each pore field is surrounded by a dotted line and assigned a letter. The number indicates the mean number of pores of the respective pore field ($n = 4$). Arrows indicate the main directions of the ampullary canals. (**a**) Ventral rostrum of *R. typus* with stained ampullary canals

dorsal superficial ophthalmic capsule and some of the ventral rostral clusters are innervated by the outer buccal branch of the anterior lateral line nerve.

On the ventral side of the disk of *Rhinobatos typus*, pores of the ampullae of Lorenzini are more numerous (Fig. 4, Table 2). Area G is formed by ampullae from the hyoid capsule where pores cover the whole abdominal area between the gills, the abdominal lateral line canal and the lower jaw. Laterally, the area is restricted by a row of pores running along the propterygium. Rostally, area G slightly overlaps with area I. Ampullae of area I are positioned in the outer buccal capsule located between the musculus quadratomandibularis, the nasal cartilage and the antorbital cartilage (Fig. 6). The pores of this capsule overlap caudally with the pores of area G and medially with the pores of area J. The most lateral and rostral pores are located on top of the propterygium. The outer buccal capsule and a few of the rostral clusters located anterior to the nasal cartilage are innervated by the outer buccal branch of the anterior lateral line nerve. Area H is formed by the mandibular capsule, positioned half way along each side of the mandible. The pores are situated on top of the lower mandible and restricted by skin folds on all sides. The mandibular capsule is innervated by the hyomandibular branch of the anterior lateral line nerve. Area J is formed by ampullae belonging to four nasal capsules. The capsules are positioned on top of the neurocranium between the palatoquadratum, the rostral cartilage and the nasal cartilage. Both the nasal capsules and some of the rostral clusters are innervated by the inner buccal branch of the anterior lateral line nerve.

The pores of area K are found in the transparent part of the rostrum, stretching from the rostral appendix to the rostral tip of the propterygium. Caudally, the area is restricted by the rostral edge of the nasal cartilage and the neurocranium. The ampullae of this area are found either detached or belonging to up to 85 clusters restricted to the same area. Each cluster contains 2–20 ampullae, but most clusters contain 1–5 ampullae. Clusters are lined up laterally along the loops of the infraorbital lateral line canal and laterally along the prenasal lateral line canal. Rostral clusters are innervated by the following branches of the anterior lateral line nerve: superficial opthalimic, outer buccal and inner buccal. Pores of the ampullae of Lorenzini belonging to the superficial ophthalmic capsule form area L where they are found from the caudal edge of the rostral appendix to the tip of the rostrum. No correlation was found between the surface area of the disk and the total numbers of pores (ventral $r^2 = 0.059$; dorsal $r^2 = 0.0238$; $n = 4$).

The lateral line of *Aptychotrema rostrata*

In *Aptychotrema rostrata*, on both the ventral and dorsal surfaces, all canals of the lateral line (Fig. 7) occur in the same locations as those of *Rhinobatos typus*. Therefore, only the main differences in canals will be described briefly. In *A. rostrata*, tubules end in one surface pore each instead of bifurcating and forming pore fields. Rostrally, the hyomandibular canal ends in a single surface pore and is not connected directly to the infraorbital canal but via three tubules. The scapular lateral line canal forms four canals, each one ending in a single surface pore without tubules. Lateral to the eye, the infraorbital canal bifurcates into a rostral and a caudal branch, the

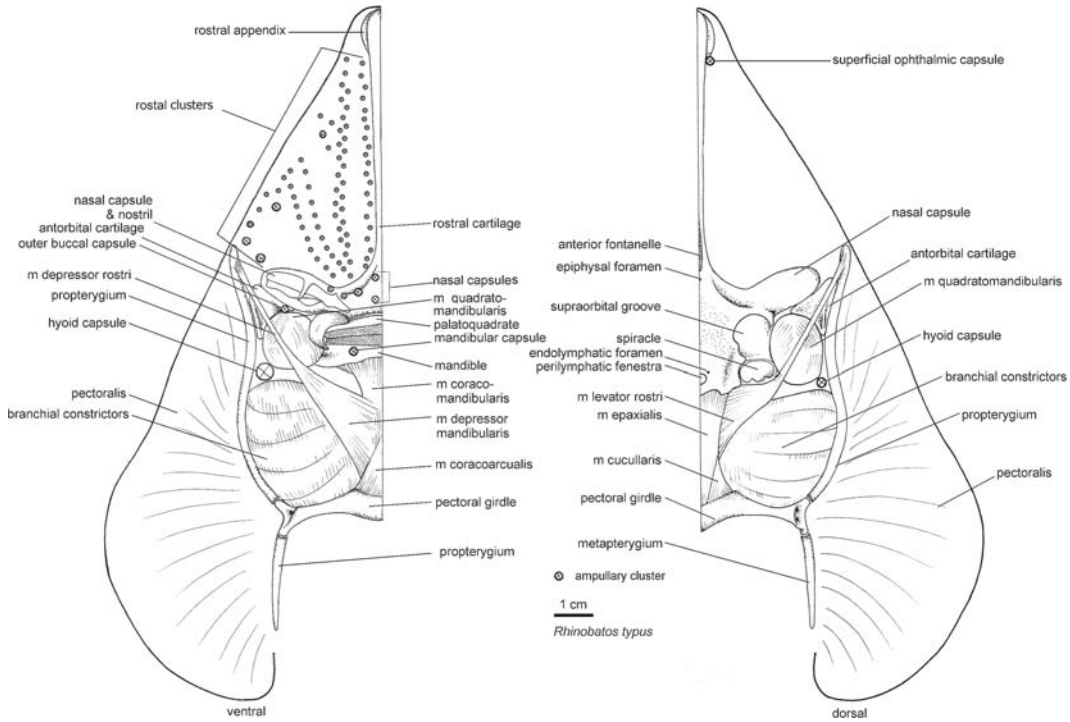

Fig. 6 Schematic representation of the right anterior dorsal and ventral surfaces of *Rhinobatos typus* with dermis and connectives removed. The position of the clusters of ampullae of the electrosensory system in respect to muscles and cartilages is shown

Table 2 Counts of the pores belonging to the dorsal and ventral pore areas of the ampullae of Lorenzini of *Rhinobatos typus* (n = 4, 43.3 −49.5 cm TL) and *Aptychotrema rostrata* (n = 2, 64.0–68.0 cm TL). See Fig. 4 and Fig. 8 for location of pore areas

Dorsal	A	B	C	D	E	F	Total
R. typus	19.5 ± 7.1	7.8 ± 1.8	2.5 ± 3.2	6.9 ± 2.6	13.5 ± 3.9	24.9 ± 5.1	75.1 ± 11.4
A. rostrata	41.7 ± 2.9	11.7 ± 1.5	0	18.7 ± 3.1	16.0 ± 1.0	24.7 ± 2.1	112.7 ± 3.1
ventral	G	H	I	J	K	L	total
R. typus	95.0 ± 47.0	15.8 ± 9.8	85.3 ± 16.0	34.3 ± 29.4	200.6 ± 67.0	22.3 ± 4.7	452 ± 162.8
A. rostrata	77.0 ± 1.0	13.3 ± 2.1	75.0 ± 7.1	35.5 ± 4.9	334.5 ± 24.7	0	461.5 ± 17.7

former branch ends in various ramifying tubules, whereas the latter possesses only straight tubules each terminating in a single surface pore. Unlike in *R. typus*, the supraorbital and infraorbital canals are not connected rostal to the eye. The dorsolateral pit organs are evenly distributed along the body axis in the area restricted by the supraorbital and posterior lateral line canals.

The ventral abdominal lateral line canal of *Aptychotrema rostrata* (Fig. 7) consists of a canal with tubules on one side and is not an open groove as in *Rhinobatos typus.* Both the prenasal and most medial supraorbital canals lack tubules.

The ampullary system of *Aptychotrema rostrata*

The overall distribution of ampullary pores in *Aptychotrema rostrata* (Fig. 8) is very similar to *Rhinobatos typus*. The dorsal pore fields of *A. rostrata* (Fig. 9, Table 2) differ from *R. typus* only slightly. In the first specimen examined, pores found in areas A to D all belong to the ampullae of the hyoid capsule, whereas in the second specimen pores of area D belong to a small cluster located on the rostral edge of area A. Pore field A is more elongated rostrally. Pore field B lies caudal of the spiracle and area D is half-moon shaped and lateral to the eye. Area C is lacking,

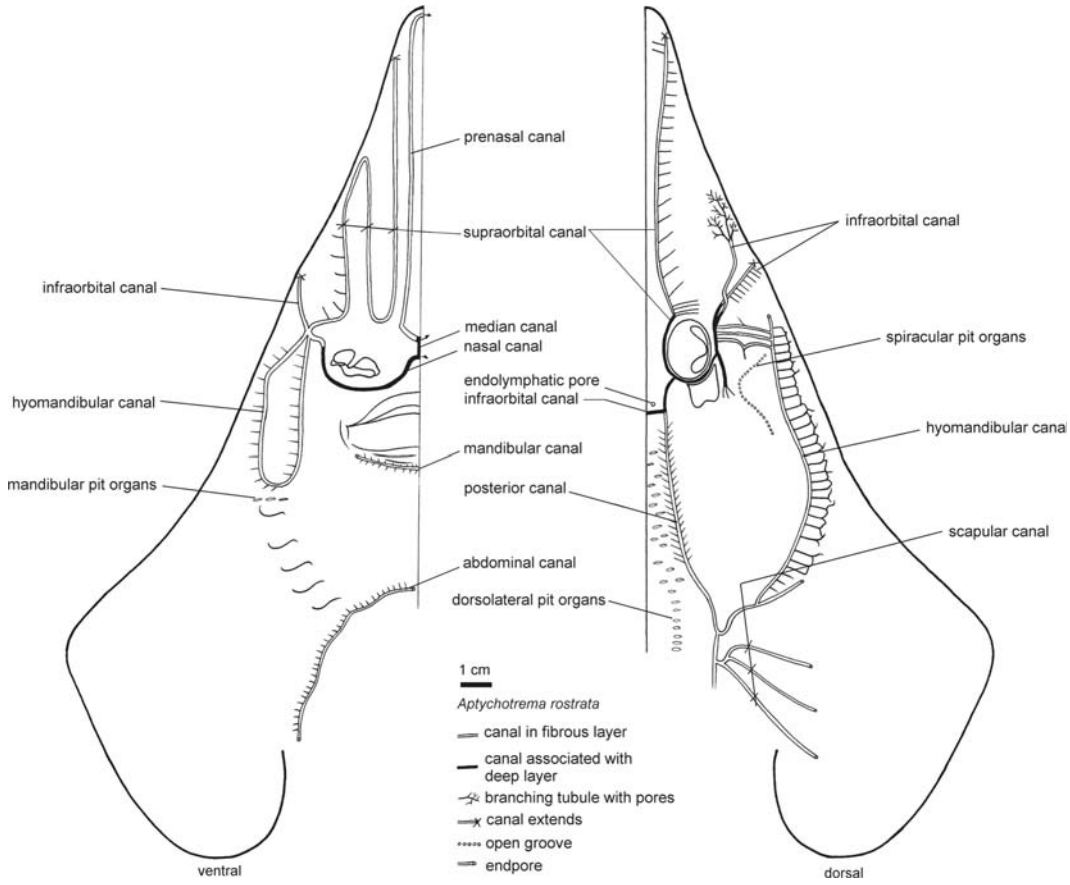

Fig. 7 Schematic representation of the mechanosensory lateral line canal system on the right dorsal and ventral disk surfaces of *Aptychotrema rostrata*

and pore field E is enlarged. Ampullae of area E are found detached and occur in two small clusters located underneath the pore field (Fig. 9). Ampullae forming area F are innervated by the superficial ophthalmic branch of the anterior lateral line canal. The innervation of the ampullary clusters forming area E could not be determined.

On the ventral side of *Aptychotrema rostrata*, area G is formed by the hyoid capsule, where the bilateral pore fields do not overlap along the body axis (Fig. 9). Area H is restricted to the lower jaw and area I is formed by four ampullary capsules located lateral to the nasal cartilage (Fig. 9). Ampullae of both capsules are innervated by the outer buccal branch of the anterior lateral line nerve. Area J is formed by four nasal capsules located on the neurocranium between the nasal cartilages. Ampullae of the rostral region are found detached or in small clusters containing a maximum of 15 ampullae. Contrary to *Rhinobatos typus*, all pores of the rostral region belong to rostral clusters. Ampullae of the superficial ophthalmic capsule do not form somatic pores on the ventral surface. Area K includes all pores on the rostrum of *A. rostrata.* The innervation characteristics of both species of shovelnose ray are similar.

Canal lengths of the ampullae of Lorenzini

Canal length increases linearly with total length in both species. The dorsal surface of *Aptychotrema rostrata* lacks area C. Area E is formed by ampullae of the hyoid capsule in *Rhinobatos typus* but several small ampullary clusters in *A. rostrata*. This difference is reflected in the length-range of ampullary canals (Table 3). Those in areas A and F are extremely variable, due to the location of the hyoid

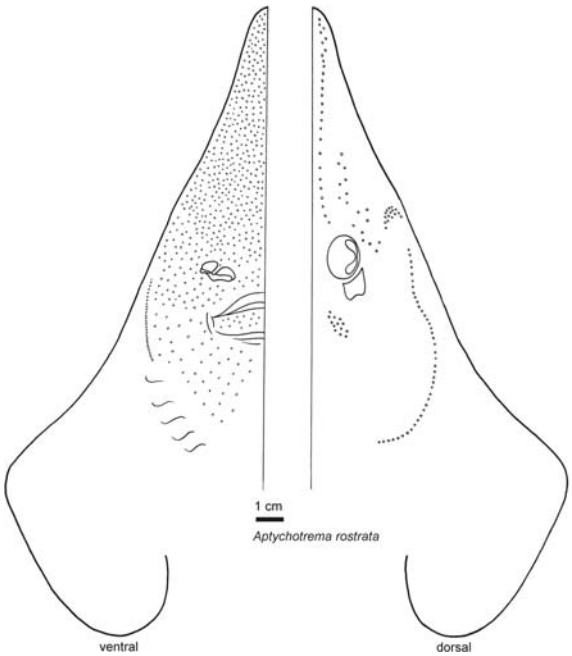

Fig. 8 Schematic representation of the dorsal and ventral pores of the ampullae of Lorenzini of *Aptychotrema rostrata*. All ventral pore fields contain a mean of 461.5 ± 17.7 pores and dorsally there are a mean of 112.7 ± 3.1 pores (n = 2)

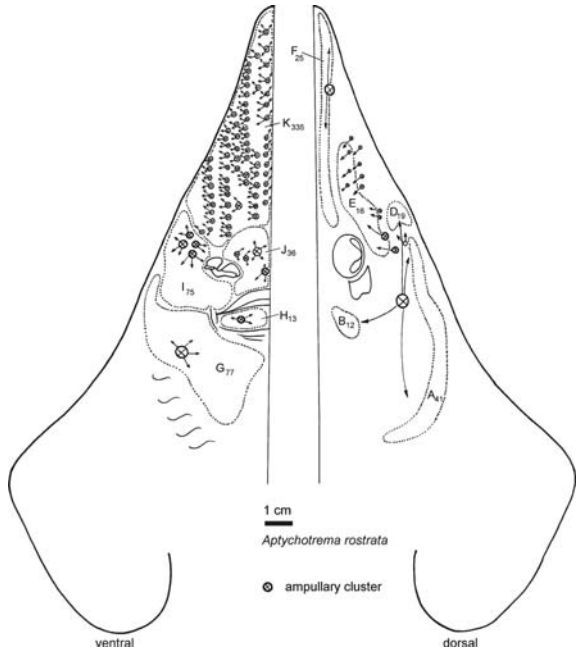

Fig. 9 Schematic representation of the dorsal and ventral pore fields and capsules of the ampullae of Lorenzini of one representative specimen of *Aptychotrema rostrata*. Each pore field is surrounded by a dotted line, and is assigned a letter. The number indicates the mean number of pores of the respective pore field (n = 2). Arrows indicate the main directions of the ampullary canals

capsule half way along the elongated pore field, resulting in a high standard deviation compared to area B, where pores are packed tightly in a small area distant from the ampullary capsule.

On the ventral side, numerous ampullary capsules and clusters distributed across the whole pore field form areas J and K, therefore canals are short with low variation. There are interspecific differences in the morphology of area I. In *Aptychotrema rostrata*, this area is formed by ampullae of four buccal capsules with short canals, whereas *Rhinobatos typus* possesses only a single buccal capsule. The canals of this area are shorter in *A. rostrata* than those in *R. typus.*

Morphology of the ampullary endings of *Rhinobatos typus*

Pores of the ampullae of Lorenzini of *Rhinobatos typus* are visible macroscopically. Each pore leads to a single jelly-filled canal of several cm in length that opens proximally to an ampullary bulb formed by several alveoli (for mean counts of hyoidal and rostral ampullae see Table 4). The sensory epithelium is restricted to the alveolus and appears twice as thick as the epithelial lining of the canal wall. Cells of the canal wall are elongated, whereas the cells of the receptor epithelium are oval with an oval nucleus.

The ampullae of *Rhinobatos typus* are multi-alveolate (*sensu* Andres and von Düring 1988), lack a central stage and are surrounded by several layers of collagen fibres. Shortly before opening up to the ampullary bulb, the ampullary canal internally bifurcates into several branches simultaneously, (Table 4) with branches being separated by a membrane. Each canal branch forms several alveolar bulbs (Fig. 1, Table 4). The external and internal structures of the alveoli differ. What externally appears to be one large alveolar bulb, internally comprises several alveolar bulbs. Internal divisions are created by the epithelium of the medial zone, which also separates the ampulla from the canal (Fig. 10A).

Ampullae of the rostral region of *Rhinobatos typus* occur either detached (Fig. 10B) or in small clusters of up to 20 ampullae (Fig. 10C). Ampullary clusters are embedded in a capsule of connective tissue (Fig. 10A), which also surrounds detached ampullae,

Table 3 Comparison of the mean canal lengths of the ampullae of Lorenzini of a specimen of *Rhinobatos typus* (49.9 cm total length) with a specimen of *Aptychotrema rostrata* (68.0 cm total length)

Dorsal pore fields	A	B	C	D	E	F
R. typus	22.5 ± 7.5	27.3 ± 1.7	7.6 ± 2.1	34.2 ± 7.3	53.4 ± 18.3	25.8 ± 17.9
A. rostrata	23.4 ± 9.6	35.1 ± 1.2	0	55.5 ± 1.6	9.6 ± 4.4	31.8 ± 14.2
ventral pore fields	G	H	I	J	K	L
R. typus	18.8 ± 8.9	6.7 ± 3.1	14.5 ± 5.6	8.2 ± 3.7	7.3 ± 2.8	8.3 ± 3.9
A. rostrata	22.4 ± 7.5	7.9 ± 1.7	9.8 ± 2.5	4.7 ± 1.6	8.9 ± 3.4	0

Table 4 (1) Measurements taken from the ampullae of the rostral tissue and the hyoid region of *Rhinobatos typus* (n = 4, Table 1 No.3–6). (2) Mean counts of ampullary structures of the rostral tissue and the hyoid region of *Rhinobatos typus* (n = 4, Table 1 No.3–6). All values are given as mean ± standard deviation

		Rostral	Hyoid
(1)	Alveolar lumen (10^{-8} m^2)	3.0 ± 1.3	3.7 ± 1.6
	Longitudinal ampullary area (10^{-8} m^2)	16.8 ± 5.4	33.0 ± 5.9
	Canal diameter (μm)	242.5 ± 55.2	283.3 ± 36.5
(2)	Alveoli per ampulla	9.3 ± 2.4	17.0 ± 5.8
	Alveoli per canal- branch	3.8 ± 1.4	5.1 ± 1.3
	Canal-branch per ampulla (median)	2.7 ± 1.0	3.6 ± 1.1

isolating them from the dermis. Connective tissue capsules are located in cavities of the deep fascia, between the fibrous layer of the dermis and the underlying connective tissue (Fig. 10D). Alveoli of different ampullae can be interdigitated since the layers of collagen surrounding individual ampullary bulbs are not very pronounced in ampullae of the rostral region, and ampullary canals bifurcate into several branches simultaneously.

Ampullary measurements from *Rhinobatos typus* (n = 4, Table 1 No.1–6) are presented in Table 4. No significant differences were found between individuals for each tissue for the three characteristics of the ampullary structure: number of alveoli per ampulla (hyoid: ANOVA, $F(4,21) = 1.860$, $P = 0.155$; rostral: ANOVA, $F(2,12) = 3.51$, $P = 0.063$), number of alveoli per canal-bifurcation (hyoid: ANOVA, $F(5,26) = 1.28$, $P = 0.303$; rostral: ANOVA, $F(2,12) = 1.52$, $P = 0.258$) and number of canal-bifurcations per ampulla (hyoid: Kruskal-Wallis test: $H(5,N = 32) = 8.618$, $P = 0.125$; rostral: Kruskal–Wallis test: $H(2,N = 15) = 4.05$, $P = 0.13$). Therefore, data from each tissue from all specimens were pooled. Hyoidal ampullae are larger, and structurally more complex, than ampullae of the rostral region and they possess significantly more canal branches per ampulla (Mann-Whitney U Test, $U = 132$, $Z = 2.465$, $P = 0.014$), more alveoli per canal branch (T-test, df = 45, $P = 0.0042$) and as a result also more alveoli per ampulla (T-test, df = 39, $P = 0.00002$).

Discussion

Peripheral organisation of the mechanosensory lateral line and electrosensory ampullary system

In the present study, the structures of the mechanoreceptive and electroreceptive sensory systems of two rhinobatid shovelnose rays were examined. As environmental cues that stimulate the visual, electroreceptive and mechanosensory systems are important for elasmobranch fishes during prey capture at close range (Hueter et al. 2004), the morphology of those three sensory systems allows us to draw conclusions on their specific function and use within this context.

The morphology and spatial distribution of the lateral line organs determine the receptive field, range and frequency response properties in elasmobranchs

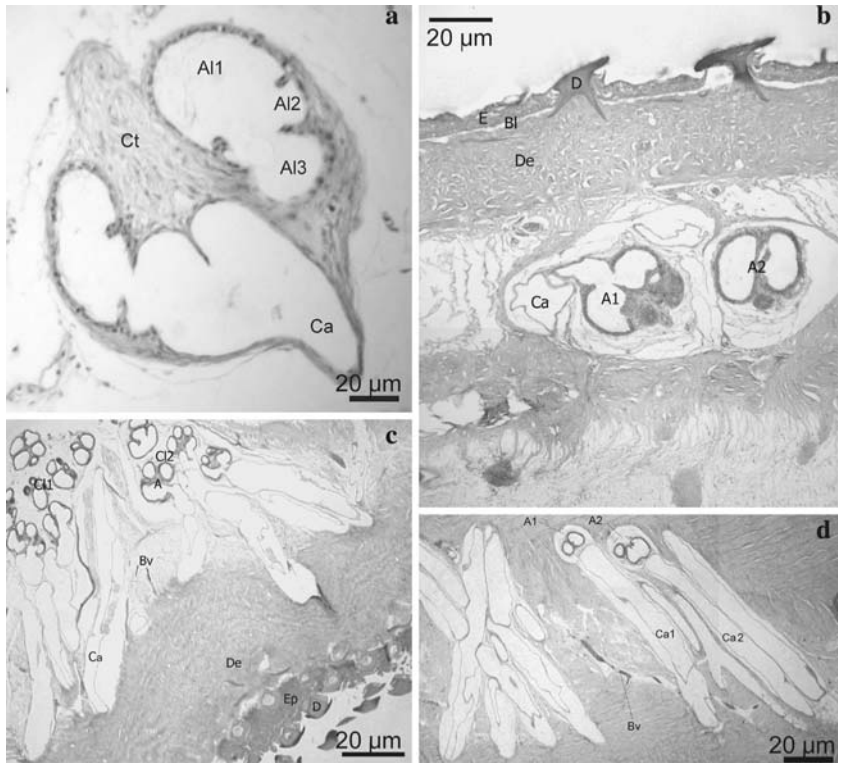

Fig. 10 (**a**) Light micrograph of a cross section of hyoid ampullae of Lorenzini of *Rhinobatos typus.* The ampulla consists of several alveoli (Al1, Al2, Al3), and is surrounded by a collagen sheath (Ct). Scale bar 5 µm. (**b**) Longitudinal section of the ventral rostrum of *Rhinobatos typus*. Rostral ampullae (A1, A2) are embedded in the dermis (De). Scale bar 15 µm. (**c**) Frontal section of the rostral tissue of *Rhinobatos typus* showing two ventral ampullary clusters (Cl1, Cl2). Scale bar 20 µm. (**d**) Frontal section of the rostral tissue of *Rhinobatos typus*. Two detached ventral ampullae (A1, A2) are visible. Ampullary canals radiate in two different directions, crossing over while permeating into deeper tissue layers. Scale bar 20 µm. (A, A1, A2) ampulla, (Al1, Al2, Al3) alveolus, (Bm) basement membrane, (Bv) blood vessel, (Ca, Ca1, Ca2) ampullary canal, (Cl1, Cl2) ampullary cluster, (Ct) collagen sheath, (D) denticle, (De) dermis, (Ep) epidermis

(Maruska 2001). For example, neuromast morphology determines the type of information processed by mechanoreceptors (Kroese and Schellart 1992; Maruska 2001). Differences in the characteristics of the lateral line systems of the examined species of shovelnose rays can be explained by their ecology. One major difference between the two species is found in the abdominal lateral line canal, which forms an open groove in *Rhinobatos typus*, but a closed canal with tubules in *Aptychotrema rostrata*. We hypothesize this difference to be functional and not systematic. Similar findings are evident in a morphological study on the lateral line and ampullary systems of elasmobranch taxa in Chinese waters, where the formation of an open groove (termed pit organ by Chu and Wen 1979) of the abdominal canal was only found in S*quatina japonica* and *Mustelus griseus* (Chu and Wen 1979). In contrast, all rhinobatids examined possessed a closed abdominal lateral line canal similar to that of *Aptychotrema rostrata*, except *Rhynchobatus djiddensis* (Rhynchobatidae) and *Scobatus granularis* (=*Rhinobatos granularis*, Rhinobatidae) which both lacked tubules (Chu and Wen 1979).

Tubules branching off the lateral line canals of *Rhinobatos typus* are ramified, which contrasts with the straight tubules of *Aptychotrema rostrata.* We hypothesize this to be an adaptation to the large body size of *R. typus*, but this hypothesis remains to be tested. As *R. typus* can obtain 270 cm in total length, lateral line pores of adults will be spaced further apart than in adults of *A. rostrata.* Increase in pore spacing causes a decrease in mechanosensory resolution that might be compensated by an increased number of pores per tubule.

The ventral prenasal lateral line canals of *Aptychotrema rostrata* are non-pored in contrast to the pored canals that possess branched tubules in *Rhinobatos typus*. Non-pored lateral line canals occur predominantly on the ventral side of batoids (Maruska and Tricas 2004), and may house specialised tactile mechanoreceptors, allowing the detection of stimuli from small infaunal organisms that do not stimulate pored canals (Maruska and Tricas 2004). The presence of pored canals on the ventral side of the rostrum of *R. typus* could indicate a dietary shift to more free moving prey with increasing size but there are no life history data to support this hypothesis. Stomach contents of *R. typus* from Western Australia do not reflect a dietary shift, but information on the maximum size of animals caught is only reported as >120 cm (White et al. 2004), which is less than half the maximum reported total length (Cavanagh et al. 2003). Non-pored prenasal canals of *A. rostrata* do reflect their diet, which is dominated by benthic crustaceans. A minor dietary shift is known for *A. rostrata*, where teleosts gain importance in larger individuals, but in adults crustaceans still comprise about 90% of the dietary importance (Kyne and Bennett 2002). The non-pored arrangement might enable this species to perceive tactile stimuli from infaunal prey while, simultaneously preventing contamination of the canals by sand intruding through the pores, as suggested by Maruska and Tricas (2004).

Interspecific variations in the morphological characteristics of the ampullae of Lorenzini of chondrichthyans can be explained by different ecological influences and life histories. Variations can occur in the following: distribution and total number of pores, number of alveoli per ampulla, average alveolous size and length of the canals. Moreover, the number of ampullae per cluster and the number of clusters themselves vary between species (Norris 1929; Raschi 1984, 1986).

The relationship between the visual and electroreceptive systems might explain morphological variations of the distribution of ampullary pores. In dorso-ventrally flattened batoids, the visual system does not provide the necessary input to guide the animal to its prey as the mouth is positioned ventrally and the eyes are positioned dorsally (Raschi 1984, 1986). Species feeding predominantly on slow, buried prey possess higher densities of pores ventrally, with the highest densities found around the mouth, compared to species feeding on mobile prey (Raschi 1984, 1986). This is supported by the present study, as the total number of ampullary pores found on the ventral skin surface of *Rhinobatus typus* is approximately six times higher than dorsally, *Aptychotrema rostrata* possesses four times more pores ventrally than dorsally. Pores are concentrated around the mouth, in the abdominal area between the gills and along the rostral cartilage. Electric fields created by cryptic prey are perceived by the electrosensors on the rostrum during forward movement and guide the shovelnose ray to the prey. Atlantic shovelnose rays *Rhinobatos lentiginosus* rapidly approach their prey when attacking and then press their bodies against the substratum to immobilize the prey. To reposition the mouth, the shovelnose ray slightly elevates the body, keeping the pectoral fins, pelvic fins, rostrum and tail pressed against the substratum (Wilga and Motta 1998).

Electroreceptive pore densities represent a measure of sensory system resolution, as each ampulla functions independently (Waltman 1966). Each ampulla is connected to a surface pore by a single canal. The total number of pores of an elasmobranch remains constant throughout development (Raschi 1978, 1984; Aadland 1992; Kajiura 2000), whereas body size increases. In the present study, no correlation was found between body size and the number of either dorsal or ventral ampullary pores, indicating that in rhinobatids the number of ampullae remains constant throughout much of their development. Pores of the right and left pore field G overlap in some specimens of *Rhinobatus typus*, but not in *Aptychotrema rostrata*. As bilateral pore fields do not overlap in the larger specimens of *R. typus*, which were still smaller than the examined specimens of *A. rostrata*, we assume that the overlap occurs only in juvenile individuals.

Norris (1929) mentions five ampullary clusters for rhinobatids, namely the supra-orbital, inner buccal, outer buccal, hyoidean and mandibular clusters. The five innervation areas of the anterior lateral line nerve were identified in both species. However, both rhinobatids we examined possess multiple clusters, especially along the rostral cartilage and in the triangle created by the rostal cartilage and the rostral end of the propterygium. Ampullae of this region are innervated by the outer buccal, inner buccal and

superficial ophthalmic branches of the anterior lateral line nerve, which divide and spread out to reach all of the small clusters containing mostly fewer than ten ampullae each.

The similarity of the electrosensory systems of these shovelnose rays is striking considering that *Rhinobatos typus* forms stable populations in freshwater (Compagno and Last 1999; Cavanagh et al. 2003), whereas *Aptychotrema rostrata* is restricted to saltwater. No miniampullae of freshwater rays (*sensu* Andres and von Düring 1988) were found. Canals of the rostral tissue are shorter and more uniform in length than the canals of ampullae of other regions. Nevertheless, these canals are about ten times longer than canals found in the obligate freshwater ray *Potamotrygon* (Szamier and Bennett 1980) and *Dasyatis garouaensis* (Raschi and Mackanos 1989).

Among species of rajoid, galeoid and carcharhiniform Chondrichthyes, basic pore patterns of the ampullary system are consistent among species, with the feeding ecology of each species influencing the number of pores and surface area of pore fields (Raschi 1984; Kajiura 2000). This pattern can be verified for rhinobatids by comparison of the present study with ampullary clusters described for other species of rhinobatids (Chu and Wen 1979). However, positioning and number of ampullary clusters is species-specific in rhinobatids. Both the pore patterns and the distribution of the ampullary clusters in *Aptychotrema rostrata* differ from those of *Rhinobatos typus*, although a basic pore distribution pattern is conserved. Small rostral clusters of two to ten ampullae have only been found ventrally in *R. typus* but do occur dorsally in *A. rostrata.*

The numerous ampullary clusters found in the rostral region of both species of rhinobatids permits us to speculate that the elongated rostrum may have developed to enhance sensory input. This theory corresponds to the enhanced electrosensory hypothesis for sphyrnid sharks. The laterally-expanded cephalofoil of sphyrnids allows electrosensory organs to be spaced out more widely compared to other sharks, increasing the sampling area (Kajiura 2000). Similarly the elongation of the rostrum of rhinobatids, a morphological feature unique for rhinobatids and rhynchobatids, could be explained by the high density of ampullary pores in this region. Comparison of total pore counts to the closely-related rajids was not considered, as ampullary canals of this group radiate to the edges of the disk (see Chu and Wen 1979), and pore fields occupy a significantly larger area.

A major difference between the two evolutionary developments of rhinobatids and sphyrnids is the length ranges of the canals. Rhinobatids possess multiple rostral clusters with short canals, whereas sphyrnids possess ampullary clusters located on the neurocranium with canals radiating to the edges of the cephalofoil (Chu and Wen 1979), and are therefore significantly longer. As the receptor epithelium is sensitive to voltage gradients created between the surrounding medium and the inside of the ampulla (Murray 1974), and the passive cable properties of the ampullary canals cause attenuation of high frequency signals (Waltman 1966), the sensitivity to voltage gradients increases with the length of the canal (Murray 1974). Therefore long canals on the pectoral disk of rhinobatids allow the detection of weak electric fields, whereas short canals of the rostrum have a lower sensitivity and allow the localisation of an intense field at close range during capture of prey (Tricas and New 1998).

A spatial interrelationship between the pores of the lateral line and ampullary pores is apparent in both species. In *Rhinobatos typus*, pores of the dorsal pore fields E and D are distributed along the infraoribtal lateral line canal and pores of pore area A run in close proximity to the dorsal hyomandibular canal. On the ventral side of the rostrum, ampullary clusters belonging to area K are distributed along the prenasal and supraorbital lateral line canals. The cause of this spatial relationship is unknown, but conforms to the widespread belief that both sensory systems share a common evolutionary origin (Coombs and Montgomery 2005). However, a study in the Oman shark, *Iago omanensis*, reported the development of the lateral line and ampullary system was not related and the authors assumed that the separation of the mechanosensory and electroreceptive systems occurred before the evolution of sharks (Fishelson and Baranes 1998). There is no evidence that the electrosensory ampullae evolved from the lateral line organs, rather that both sensory systems evolved in the earliest craniates (Coombs and Montgomery 2005). However, a functional relationship could connect both sensory systems. The spatial distribution of mechanosensory and electrosensory arrays is largely preserved in the central nervous system as

somatotopic maps (Coombs and Montgomery 2005). Further research is needed to identify whether different submodalities combine to form a more integrated picture (Coombs and Montgomery 2005).

Morphology of the ampullary endings of *Rhinobatos typus*

Rhinobatos typus possesses ampullae of Lorenzini classified as multi-alveolate macroampullae (*sensu* Andres and von Düring 1988). Macroampullae are commonly found in marine elasmobranchs. The ampullary bulbs lack a central stage, as found in other elasmobranchs such as *Carcharhinus leucas* (Whitehead 2002) or *Raja clavata* (Waltman 1966). Ampullary organs of the two regions of *Rhinobatos typus* were discriminated according to their complexity. Generally, ampullae of the hyoid region show more morphological differences between individuals than ampullae of the rostral region. Moreover, the hyoidal ampullae are more complex in structure, as the number of canal branches per ampulla, and hence the number of alveoli per ampulla, are significantly higher in this region.

Ampullae of the rostral region occur in small clusters with the connective tissue surrounding each ampulla being not as distinct as in the hyoid cluster. This, in addition to the bifurcations of the canal, leads to heavy interdigitating of the alveoli of different ampullae. This was not observed in the hyoid region, where ampullae are separated by a distinct collagen sheath surrounding each ampulla.

The structure of the ampullary organs in elasmobranchs seems to be a taxonomically significant character independent of the ecology of a species, but further investigations are needed. The multialveolate structure of the ampullary organs seems to be more often represented in skates (Waltmann 1966; Raschi 1984), whereas galeoid and carcharhinid sharks possess ampullary organs with a low number of alveoli in one concentric row surrounding the central stage (Raschi 1984; Aadland 1992). In lamnid sharks, a series of irregularly-shaped alveoli are found in a radial pattern within the terminal end of the ampulla (Aadland 1992). Aadland's (1992) description of each alveolus being further divided into smaller alveoli seems to hold true for the ampullae of *Rhinobatos typus*, where the divisions of the alveoli are evident by ridges of the medial zone.

This study reveals that the morphology of the ampullary system of shovelnose rays is unusual amongst elasmobranchs. The hypertrophy of the electrosensory system in shovelnose rays indicates its importance during foraging. Moreover, the morphological characteristics of the mechanosensory system of both species are described and related to feeding strategies. Although the morphology provides evidence for the use of both sensory organs during the close range of prey capture, behavioural experiments are needed to identify their exact roles in rhinobatids.

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