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# Sensory Systems in Sawfishes. 1. The Ampullae of Lorenzini

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**Key Words**
Electroreception · Pristidae · Sawfish · Rostrum · Ampullae of Lorenzini

**Abstract**
The distribution and density of the ampullary electroreceptors in the skin of elasmobranchs are influenced by the phylogeny and ecology of a species. Sensory maps were created for 4 species of pristid sawfish. Their ampullary pores were separated into pore fields based on their innervation and cluster formation. Ventrally, ampullary pores are located in 6 areas (5 in *Pristis microdon*), covering the rostrum and head to the gills. Dorsally, pores are located in 4 areas (3 in *P. microdon*), which cover the rostrum, head and may extend slightly onto the pectoral fins. In all species, the highest number of pores is found on the dorsal and ventral sides of the rostrum. The high densities of pores along the rostrum combined with the low densities around the mouth could indicate that sawfish use their rostrum to stun their prey before ingesting it, but this hypothesis remains to be tested. The directions of ampullary canals on the ventral side of the rostrum are species specific. *P. microdon* possesses the highest number of ampullary pores, which indicates that amongst the study species this species is an electroreception specialist. As such, juvenile *P. microdon* inhabit low-visibility freshwater habitats.



## Introduction

Electroreception is a phylogenetically old sensory modality, which is present in all early vertebrates [Wilkens and Hofmann, 2005]. The electroreceptive system of elasmobranchs is comprised of multiple ampullae of Lorenzini with pores distributed over the body surface. As ampullary canals penetrate the dermis and end in ampullary bulbs situated in the connective tissue or between adjacent muscles [Wueringer and Tibbetts, 2008], the receptor array is 3-dimensional [Tricas, 2001]. Localized weak electric fields produced by prey stimulate the receptors more strongly the closer they are to the source, thus providing the predator with a directional component for prey localization. The distribution and density of electroreceptors over the body surface of elasmobranchs is influenced by both the ecology and phylogeny of a species, as basic pore distribution patterns remain recognizable

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across different families of the same order [e.g. in sphyrnids and carcharhinids, Kajiura, 2000].

Four species of pristid sawfish inhabit Australian waters [Last and Stevens, 2009]. The unique body morphology of sawfish combines an elongated, shark-like body with the pectoral disk of batoids and an elongated rostrum that bears lateral teeth [Compagno, 1999a; Last and Stevens, 2009]. Here, we compare the distribution of their electroreceptive ampullae of Lorenzini. Complete sensory maps for each species are provided and results are compared to previous reports [Chu and Wen, 1979; Hoffmann, 1912]. Interspecific comparison sheds light on ecological adaptations and the feeding behaviour of each species and allows us to separate these from phylogenetic trends in this batoid family.

## Materials and Methods

All species of sawfish are listed in CITES Appendices I and II and 2 species are protected in Australia under the Environmental Protection and Biodiversity Conservation Act. Specimens were obtained through the QDPI&F (Queensland Department of Primary Industry and Fisheries) observer program or donated by other researchers. Specimens (table 1) were obtained frozen and thawed in 10% formalin in phosphate buffer for 24 h, and then transferred into another change of 10% formalin in phosphate buffer in which they were left for up to 2 weeks before being transferred into 70% ethanol.

The method of visualizing sensory pores followed Wueringer and Tibbetts [2008]. Specimens were stained with methylene blue solution (approximately 1%) applied to the skin. Specimens were viewed using a Heerbrugg Wild M650 or Olympus SZ40 stereomicroscope and images were taken using a Canon Powershot A620 camera. To differentiate lateral line pores from ampullary pores, single pores were dissected out and the canals exposed. Ampullary pore fields were drawn in Adobe Illustrator 14.0 (http://www.adobe.com). Incomplete pore fields were not included in pore counts. Ampullary counts are presented for both halves of the head. The right half of the head comprises the dorsal and ventral skin right of the mid-sagittal plane. This definition was chosen since ampullary canals from one cluster can radiate dorsally and ventrally.

To count ampullary pores on the rostrum, the rostrum length (RL, table 1; see Wueringer et al., 2011) was defined. Ampullary pores located in a 1-cm segment of the rostrum were counted in 3 locations (a = ½RL, b = basal ¼RL, c = rostral ¼RL) and the total number of ampullary pores of the rostrum (Σ) of *Anoxypristis cuspidata* and *Pristis clavata* were calculated with the equation

$$\Sigma = ((a + b + c) / 3) \cdot RL\ (cm),$$

which was modified for *P. microdon*

$$\Sigma = [((a + b + c) / 3) \cdot RL] + x\ (cm).$$

The variable x was introduced for *P. microdon*, since in *A. cuspidata* the pore fields V5 and D9 can be distinguished from V6 and D10, respectively, which is not possible in *P. microdon*. In *P. microdon,* pores located in areas of V5 and D9 possess clusters that are not spatially separated from rostral clusters. Therefore x represents a pore count for dorsally located pores lateral of the anterior fontanelle, which are part of D10 or for ventrally located pores medial of the anterior border of the nostril, which are part of V6.

The total length (TL) was not known for all specimens of *A. cuspidata,* so, based on the linear relationship between fork length (FL) and total length ($R^2 = 0.99$) of 7 juvenile specimens of *A. cuspidata* (TL 68.0–131.0 cm, B.E.W. unpubl. data) which were not dissected, it was calculated using the equation FL = 1.053763 · TL.

The location of all ampullary clusters was identified by tracing canals from the pore to the ampullary bulb. A cluster is defined as an aggregation of ampullary bulbs, and a capsule is a cluster surrounded by a collagen sheath [Wueringer and Tibbetts, 2008]. Names of clusters or capsules were based on their innervation [Raschi, 1986]. Ampullae were removed from the clusters, mounted on a slide and viewed under a Leitz Laborlux S light microscope, and images were taken using an Olympus DP70 camera.

**Table 1.** General measurements of pristids used for dissections of the ampullae of Lorenzini

| No. | Parts | TL | FL | RL | Sex | Collection site |
|---|---|---|---|---|---|---|
| *A. cuspidata* | | | | | | |
| 1 | H, P, S | *166.5* | 158.0 | 70.4 | M | – |
| 2 | H, S | *146.5* | 139.0 | 37.5 | F | Halifax Bay |
| 3 | H | *143.3* | 136.0 | | M | Halifax Bay |
| 4 | H | *140.8* | 133.6 | | M | Halifax Bay |
| 5 | H, P, S | 131.2 | 130.1 | 37.0 | – | Taylors Point |
| 6 | H, S | *124.3* | 118.0 | 33.5 | M | Bowling Green Bay |
| 7 | H, P | 121.3 | 111.9 | | F | – |
| 8 | H, S | 74.6 | *70.8* | 22.6 | F | – |
| 9 | H, P, S | 67.0 | *63.6* | 22.4 | F | – |
| *P. microdon* | | | | | | |
| 10 | H, P, S | 99.0 | 89.2 | 26.2 | M | Norman River |
| 11 | H, P, S | 142.0 | 131.7 | 35.4 | F | Norman River |
| 12 | H, P, S | 146.5 | 136.3 | 37.5 | M | Norman River |
| 13 | H, P, S | 149.5 | 136.0 | 37.4 | F | Norman River |
| 14 | H, P, S | 155.3 | 142.5 | 39.9 | F | Leichhardt River |
| 15 | H, P, S | 170.8 | 158.5 | 41.5 | M | Leichhardt River |
| *P. clavata* | | | | | | |
| 16 | H, P, S | – | | 33.7 | – | Ducie River |
| 17 | H, P, S | 77.0 | | 16.9 | F | – |
| 18 | H, P, S | 71.6 | | 17.4 | F | – |
| 19 | H, P, S | 150.0 | | 30.9 | M | Ducie River |
| 20 | H, P | 212.0 | | 39.8 | M | Ducie River |
| *P. zijson* | | | | | | |
| 21 | H, P | 287.0 | | 73.1 | F | Ducie River |

All specimens are juveniles. 'Parts' indicates if the specimen is complete with head (H), pectorals (P) and saw (S). Length measurements indicated in italics were calculated (see text). All animals were collected in North Queensland. All measurements are in centi-metres.

**Table 2.** Morphological characteristics of the ampullae of Lorenzini in pristid sawfish

**a** Number of pores of each pore area per body half (mean ± SD)

| Dorsal | D7 | D8 | D9 | D10 | Total dorsal | Total per body half |
|---|---|---|---|---|---|---|
| *A. cuspidata* | 23.3 ± 5.9 | 24.9 ± 6.0 | 16.1 ± 4.3 | 261.2 ± 40.1 | 326.9 ± 44.0 | 797.7 ± 54.5 |
| *P. microdon* | 24.0 ± 8.7 | 35.4 ± 7.6 | – | 474.0 ± 182.4 | 531.4 ± 187.0 | 1.580.4 ± 104.0 |
| *P. clavata* | 13.4 ± 2.4 | 15.6 ± 2.8 | 5.9 ± 1.9 | 212.6 ± 36.1 | 247.3 ± 37.5 | 721.3 ± 142.8 |
| *P. zijsron* | 15.5 ± 0.7 | 14.0 ± 2.8 | – | – | – | – |

| Ventral | V1 | V2 | V3 | V4 | V5 | V6 | Total ventral |
|---|---|---|---|---|---|---|---|
| *A. cuspidata* | 22.2 ± 5.8 | 13.1 ± 4.8 | 12.6 ± 3.2 | 21.9 ± 8.2 | 14.7 ± 7.1 | 384.8 ± 51.2 | 470.7 ± 49.0 |
| *P. microdon* | 49.6 ± 8.4 | 27.2 ± 10.7 | 34.7 ± 7.8 | 89.1 ± 27.3 | | 853.5 ± 198.8 | 1.049.0 ± 225.0 |
| *P. clavata* | 22.4 ± 4.5 | 15.0 ± 4.8 | 28.1 ± 5.0 | 39.1 ± 9.9 | 10.0 ± 6.3 | 363.4 ± 99.5 | 474.0 ± 114.6 |
| *P. zijsron* | 15.5 ± 0.7 | 28.0 ± 4.2 | 22.0 ± 2.1 | 23.5 ± 1.4 | – | – | – |

**b** Length of canals in mm (mean ± SD)

| Dorsal | No. | D7 | D8 | D9 | D10 | $D10_{max}$ | $V6_{max}$ |
|---|---|---|---|---|---|---|---|
| *A. cuspidata* | 5 | 25.3 ± 5.2 | 39.3 ± 12.9 | 13.8 ± 3.2 | Rostral canals (D10 and V6) | | |
| | 1 | 55.7 ± 9.1 | 85.4 ± 46.9 | 19.2 ± 4.8 | 13.8 ± 5.6 | | |
| *P. microdon* | 14 | 53.3 ± 10.6 | 87.8 ± 24.9 | – | 17.4 ± 6.0 | 30.2 | 28.8 |
| | 12 | 52.0 ± 13.1 | 88.0 ± 20.5 | | 14.6 ± 8.7 | 31.3 | 34.8 |
| *P. clavata* | 18 | 24.8 ± 9.7 | 24.4 ± 8.5 | 7.8 ± 1.2 | – | – | – |
| | 19 | 12.8 ± 2.6 | 30.3 ± 8.1 | 6.7 ± 2.5 | | | |

| Ventral | | V1 | V2 | V3 | V4 | V5 | V6 |
|---|---|---|---|---|---|---|---|
| *A. cuspidata* | 5 | 58.9 ± 16.4 | 10.0 ± 5.7 | 8.1 ± 1.8 | 30.0 ± 12.4 | 14.5 ± 3.4 | |
| | 1 | 89.7 ± 26.6 | 14.6 ± 7.5 | 21.5 ± 6.5 | 48.5 ± 29.5 | 23.1 ± 6.0 | |
| *P. microdon* | 14 | 66.7 ± 16.0 | 17.4 ± 2.3 | 21.2 ± 7.3 | 30.3 ± 8.9 | – | 19.2 ± 5.6 |
| | 12 | 50.2 ± 13.5 | 12.3 ± 5.8 | 15.2 ± 7.7 | 32.7 ± 10.5 | | 19.0 ± 10.4 |
| *P. clavata* | 18 | 28.4 ± 8.6 | 7.6 ± 2.9 | 8.0 ± 2.1 | 20.4 ± 11.1 | 9.9 ± 2.6 | – |
| | 19 | 30.5 ± 6.9 | 6.5 ± 2.2 | 8.8 ± 3.1 | 23.3 ± 12.2 | 10.2 ± 4.0 | |

Lengths of ampullary canals are presented for 2 specimens of each species. All canal length measurements represent means of actual lengths, except for rostral canal lengths, which represent minimum lengths. No. = Specimen number.

Ampullary canal lengths were measured in 2 specimens per species (table 2b). Measurements were taken along the path of the canal, but not following small meanders of less than 1 mm. To avoid measuring stretched canals, measurements were only taken from canals that were still attached to the skin or muscular tissue after removal of the skin. The rostral ampullary canal lengths presented give minimum values, as the delicate canals of the rostrum are embedded in cartilage or in connective tissue and no canal could be traced from the pore to the ampulla in this region.

Muscles and cartilage were identified [Compagno, 1999b; Liem and Summers, 1999; Wueringer and Tibbetts, 2008]. Terminology for the ampullary clusters follows Chu and Wen [1979] and Raschi [1984]. All statistical methods follow Sokal and Rohlf [1995].

## Results

All specimens of sawfish were juveniles to sub-adults (table 1). Data on *P. zijsron* is preliminary as only 1 incomplete specimen was dissected. However, no more specimen donations are expected. The ampullary bulbs of *A. cuspidata* are of the multi-alveolate type [Andres and von Düring, 1998] (fig. 1d), while those of *P. microdon* and *P. clavata* are of the centrum-cap type (fig. 2d, e). In all pristids, pores of the ampullae of Lorenzini are distributed over the head including the rostrum, extending slightly on the pectoral fins. Ampullary canals penetrate sub-

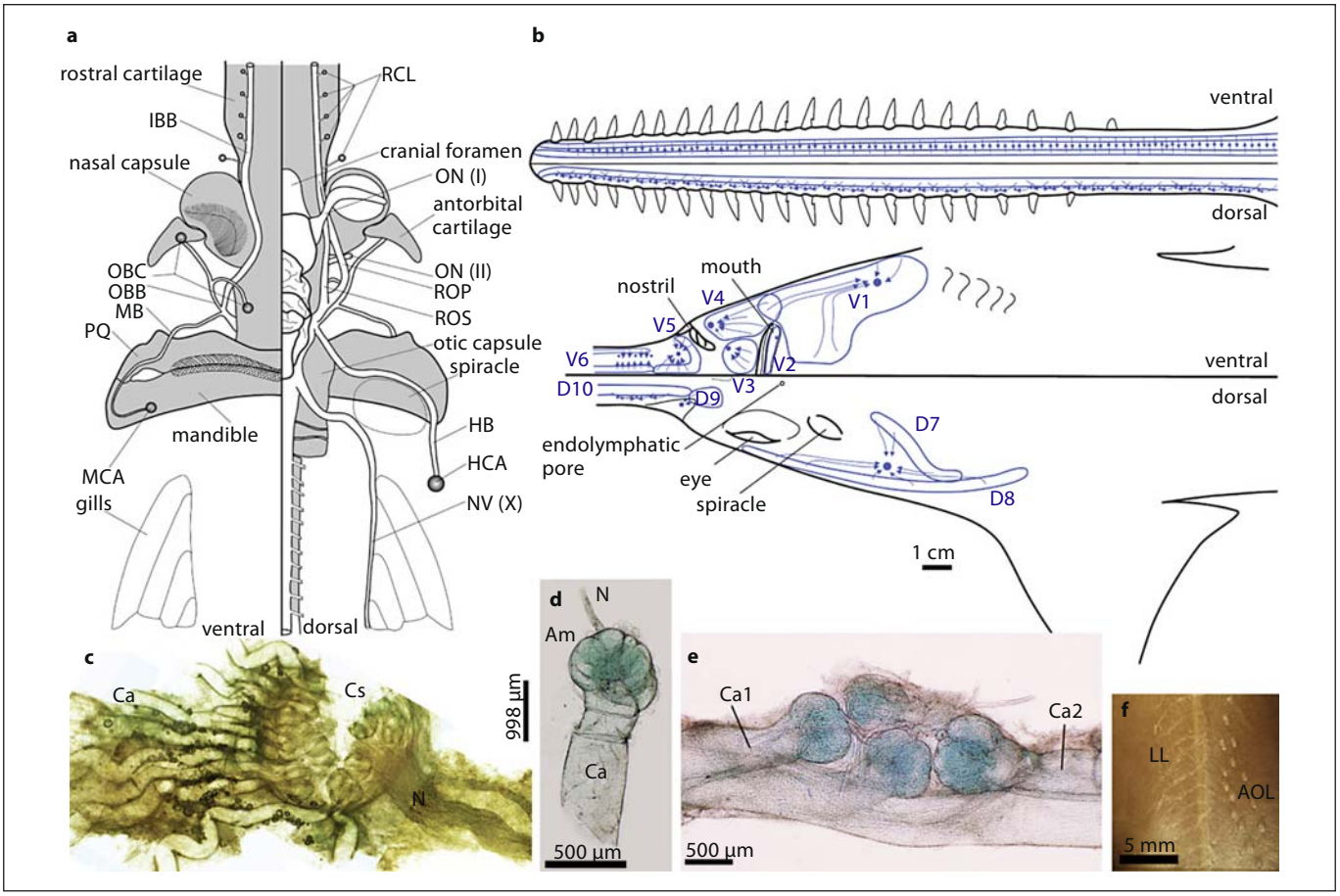


**Fig. 1.** Structures of the ampullae of Lorenzini of *A. cuspidata*. **a** Innervation of ampullary clusters and capsules by branches of the ALLN. Cartilages are indicated in grey. HB = Hyomandibular branch; HCA = hyoid capsule; IBB = inner buccal branch; MB = mandibular branch; MCA = mandibular capsule; NV(X) = nervus vagus; OBB = outer buccal branch; OBC = outer buccal capsules; ON(I) = olfactory nerve; ON(II) = optic nerve; PQ = palatoquadrate; RCL = rostral clusters; ROP = ramus ophthalmicus profundis; ROS = ramus ophthalmus superficialis. **b** Schematic representation of the ampullary pore areas. The border of each pore field is indicated. Arrows indicate directions of ampullary canals, drawing towards the ampullary clusters. **c** The outer buccal capsule (Cs) that sends ampullary canals (Ca) to area V3 is one of the smallest capsules. **d** A multi-alveolate ampulla (Am). N = Nerve. **e** Ampullae of areas D10 and V6 are situated inside rostral cartilage tubes, with canals (Ca1, Ca2) running from anterior to posterior and vice versa. **f** Pores of area D7 (AOL) slightly intermix with the lateral line (LL).

dermally and are detached from the dermis, unless otherwise mentioned. Ampullae occur in clusters or capsules, which are innervated by branches of the anterior lateral line nerve (ALLN). Ampullary pores were divided into 6 areas ventrally (V1–V6) and 4 areas dorsally (D7–D10). *P. microdon* possesses only 5 pore fields ventrally and 3 pore fields dorsally. In all sawfish the areas correspond to innervation (fig. 1a) and cluster formation.

*Ventral Pore Fields of the Ampullae of Lorenzini*

In all pristid species, ampullary pores are more numerous ventrally than dorsally (fig. 1b, 3, 4; table 2a). In all species of sawfish pores of area V1 belong to ampullae of the hyoid capsule, which is innervated by the hyomandibular branch of the ALLN. Area V1 extends over the area between the gills and the lower jaw. Its anterior border is lateral to the mouth, where it overlaps partially with the posterior border of area V4 in *A. cuspidata* and in the smaller specimens of *P. microdon* and *P. clavata*. The median extent of V1 is the smallest in *A. cuspidata* and the largest in *P. microdon*.

In all species of sawfish, the ampullary pores of area V2 are restricted to the lower mandible. In *P. zijsron*, area V2 extends only over the anterior half of the skin above

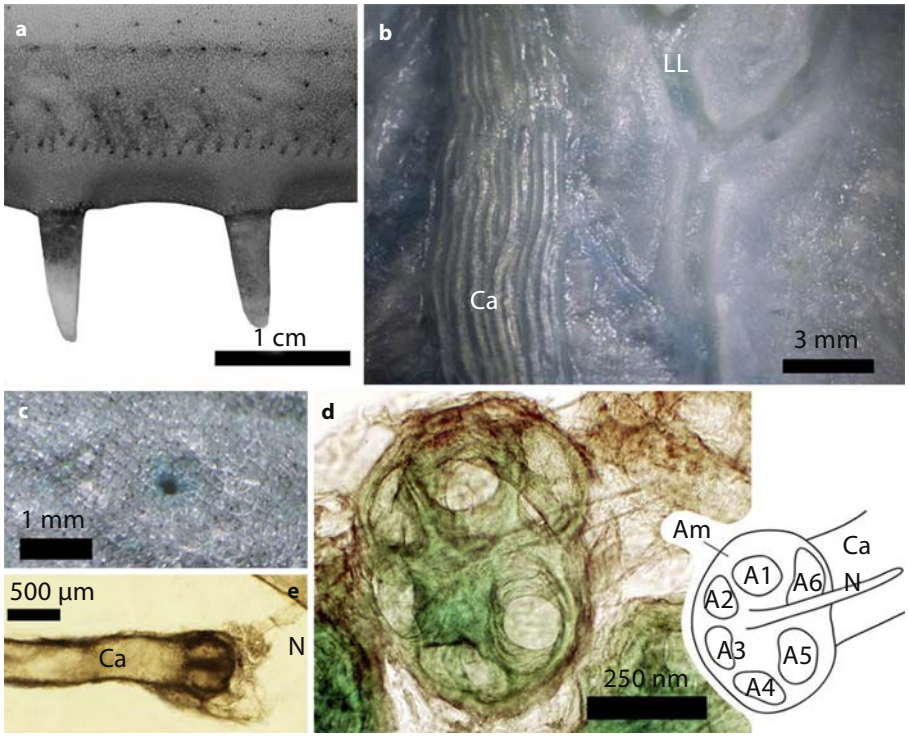


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**Fig. 2.** Structures of the ampullae of Lorenzini of juvenile *P. microdon*. **a** Stained ampullary pores of area V6 on the ventral side of the rostrum. **b** Ampullary canals (Ca) of cluster V4 draw parallel to various lateral line canals, lateral and anterior of the mouth. **c** Ampullary pore on the dorsal side surrounded by dermal denticles. **d** Centrum-cap-type rostral ampullae of area D10. The ampullary bulb (Am) comprises 6 alveoli (A1–A6). **e** A single ampulla of *P. clavata*. Ca = Ampullary canal, N = nerve.

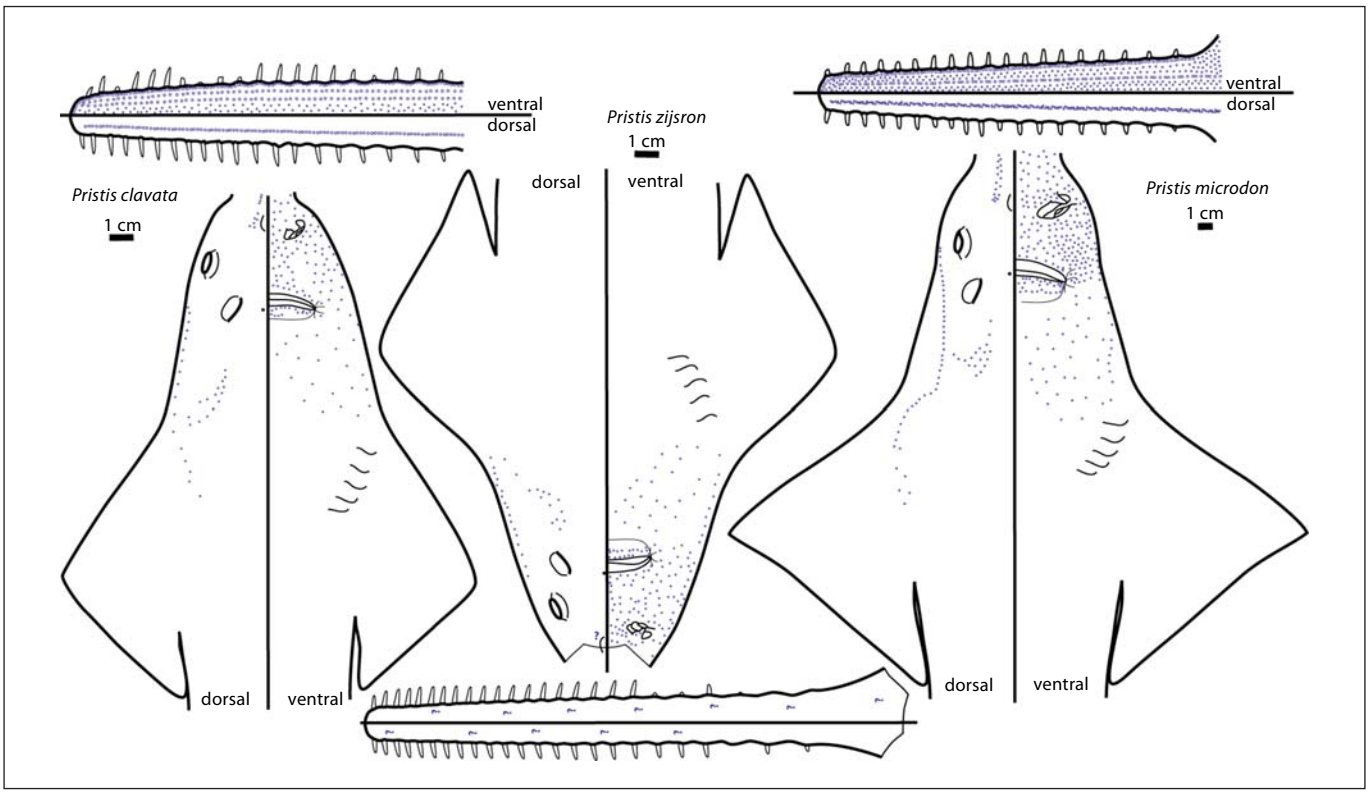


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**Fig. 3.** Schematic representation of the pore fields of the ampullae of Lorenzini of 3 species of *Pristis*. For description of pore areas and ampullary clusters, see text. A question mark indicates that the distribution of pores in this area is unknown. Each ampullary pore is indicated by 1 dot.

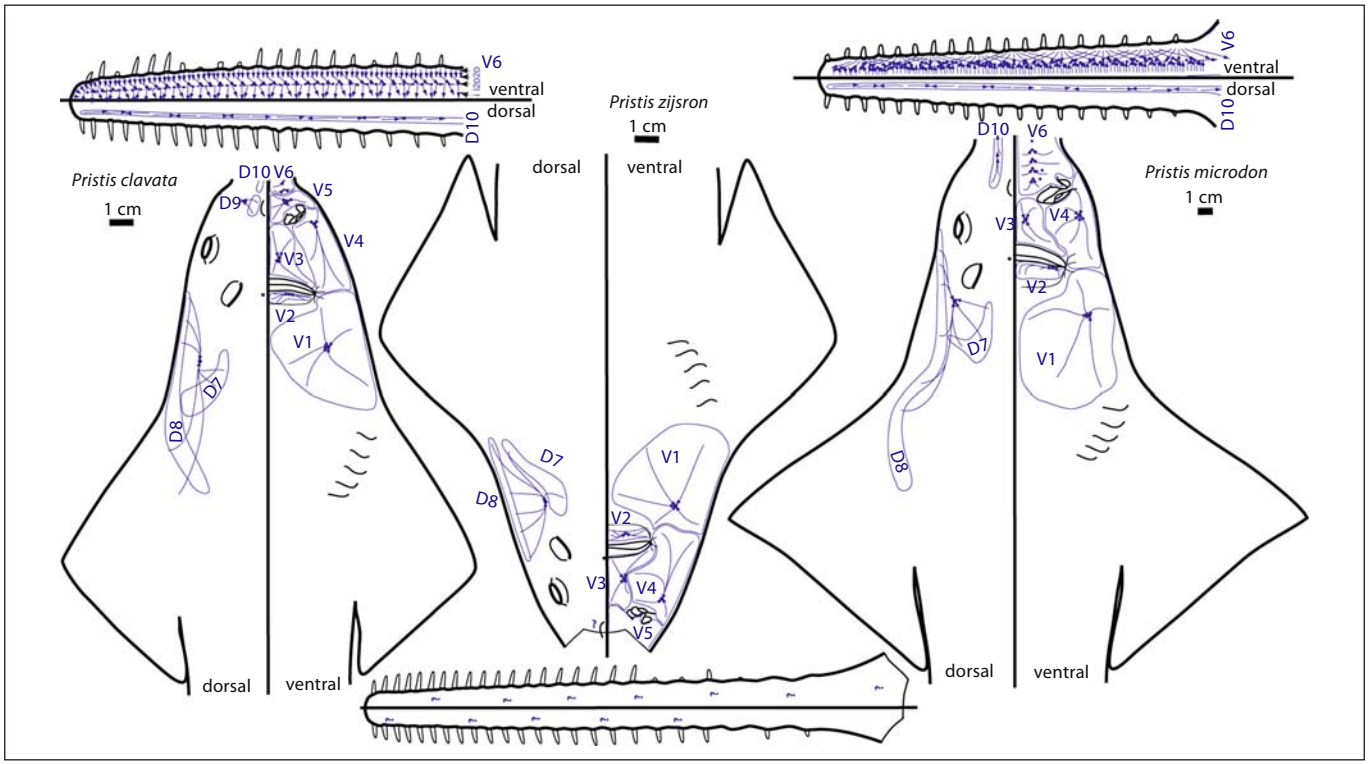


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**Fig. 4.** Schematic representation of the pore fields and ampullary clusters and capsules of the ampullae of Lorenzini of 3 species of *Pristis*. For description of pore areas and ampullary clusters, see text. The border of each pore field is indicated. Arrows indicate directions of ampullary canals, drawing towards the ampullary clusters. A question mark indicates that the distribution of pores in this area is unknown.

the lower mandible. This area is formed by the mandibular capsule, which is positioned close to the corner of the mouth in *A. cuspidata* and *P. microdon*, and halfway along the mandible in *P. clavata* and *P. zijsron*. It is innervated by the mandibular branch of the ALLN.

In all species of sawfish, the pores of area V3 belong to the ampullae of 1 of 2 outer buccal capsules, which are innervated by the 2 outer buccal branches of the ALLN. The area lies medially between the nasal capsule and the mouth. In *A. cuspidata* this capsule is very small (fig. 1c) and located halfway between the medial corner of the nostril and the mouth. In *Pristis* spp. the capsule is larger and located closer to the midline.

In all pristid species, area V4 is situated lateral to area V3. Its pores attach to ampullae of a 2nd outer buccal capsule, which is located between the musculus quadratomandibularis and the nasal cartilage, above the antorbital cartilage.

In *A. cuspidata*, the pores of area V5 are arranged in a semicircle, following the anterior border of the nasal capsule and along the base of the rostral cartilage. All canals converge on the most basal rostral ampullary cluster located in the connective tissue in the centre of the semicircle. In *P. clavata*, area V5 extends from medial of the nasal capsule to the base of the rostrum, where area V6 begins. There are no pores located on the nasal flaps. The ampullae of V5 and D9 belong to a small cluster located rostral of the nostril, which is innervated by the inner buccal branch of the ALLN that draws ventrally along the rostrum. In *P. microdon*, area V5 could not be distinguished and is included in area V6. The specimen of *P. zijsron* was missing the rostrum and descriptions of V5 and V6 are missing.

*Ampullae of the Rostrum*

Sawfish possess hollow tubes inside the rostral cartilage extending the whole length of the rostrum, but their number differs in *Anoxypristis* and *Pristis* (fig. 5), [Hoffmann, 1912; Wueringer et al., 2009]. The cartilage tubes are regularly perforated to allow the passing of ampullary canals and nerves.

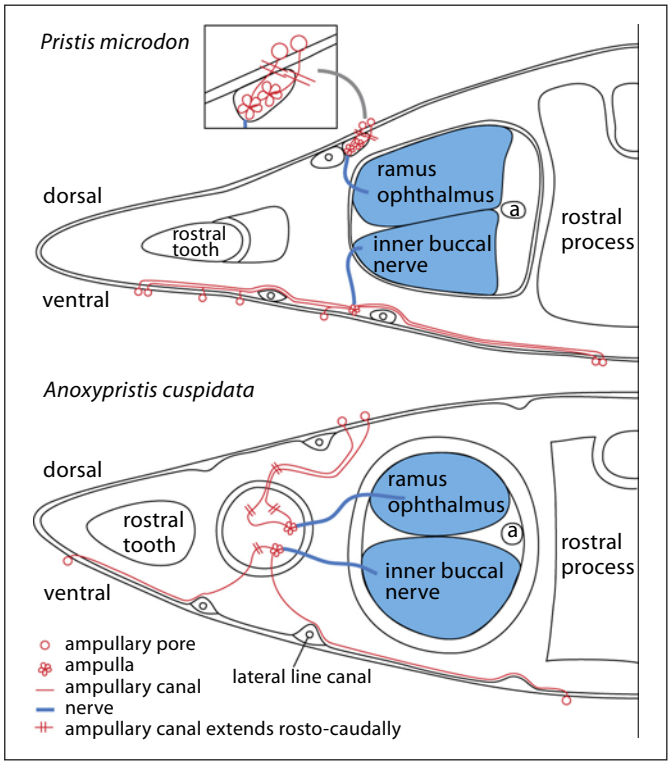


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**Fig. 5.** Cross section of the rostra of *A. cuspidata* and *P. microdon*. The locations of cartilage tubes, ampullary structures and their innervation are indicated. *A. cuspidata* possesses 5 hollow tubes in the rostral cartilage, while *Pristis* spp. possesses only 3 tubes. The ampullae of *Pristis* spp. are thus not located inside the cartilage but embedded in connective tissue. a = Rostral artery.

In *A. cuspidata*, ventral rostral pores of area V6 occur in 2 bilaterally symmetrical rows that extend from V5 to the rostrum tip. Underneath the dermis, ampullary canals extend from the pores perpendicular to the body axis towards the most lateral cartilage tube that contains ampullae.

In *P. microdon*, the pores of area V6 are evenly spaced along the whole length of the ventral side of the rostrum, with 1 row of denser pores located about one tenth of the rostrum width from its edge (fig. 2a). Area V6 commences anterior of the nostril and extends onto the nasal flap, and closely borders on areas V3 and V4. Its ampullary clusters form a straight line embedded in connective tissue along the length of the rostrum, lateral of the prenasal lateral line canal. At the base of the rostrum, clusters are also located in the loop formed by the ventral supra-orbital lateral-line canal. Underneath the dermis, canals of the medial pores extend perpendicular to the rostrum axis from the pores to the ampullae. Canals of laterally located pores extend in 7 different directions (fig. 4). The canals do not draw parallel to the rostrum axis before forming ampullae.

Pores of area V6 of *P. clavata* were separated into 4 rows (i, $i_2$, $o_2$ and o) that run parallel along the rostrum. All ampullary canals of 1 row draw in the same direction, which differs from the canal directions of the other rows (fig. 4).

In *A. cuspidata*, area D9 is compact and situated medial to the nasal capsule. All canals project to the outer buccal cluster, situated in the connective tissue anterior to the nasal capsule and lateral to the rostrum base. Dorsally on the rostrum of *A. cuspidata*, a row of ampullary pores forms area D10, which extends from D9 to the tip. Pores are situated between tubules of the dorsal supra-orbital lateral-line canal. Ampullary canals extend underneath the dermis rostrally and caudally (Sp. 2: rostral canals extend for 2.5–1.5 cm at the rostrum tip and 3.5–4.5 cm at its base) until entering the dorsal wall of the cartilage tube. Ampullary canals of V6 and D10 extend along the body axis inside the cartilage tube. Ampullary bulbs occupy the medial ventral region of this tube; the rest is filled with ampullary canals.

Dorsally along the rostrum, area D10 of *P. microdon* integrates the pores that in *A. cuspidata* belong to area D9. Its pores form 1 row that draws along the rostrum at about two thirds of its width from the lateral edge, above the dorsal supra-orbital lateral-line canal. Area D10 commences lateral to the anterior fontanelle. Ampullary canals extend from their pores underneath the dermis rostro-caudally and caudo-rostrally for a few centimetres. Ampullae form small clusters in the connective tissue lateral of the dorsal supra-orbital lateral-line canal and are innervated by the ophthalmic branches of the ALLN. In specimen 11, the ampullary clusters are spaced 1.0 cm apart.

Area D9 of *P. clavata* is located lateral to the anterior fontanelle. In *P. zijsron*, descriptions of D9 and D10 are missing.

*Dorsal Pore Fields of the Ampullae of Lorenzini*

In all species of sawfish, the ampullary pores of areas D7 and D8 attach to ampullae of the hyoid capsule, which is located between the muscles, halfway between dorsal and ventral. Canals of D7, D8 and V1 draw between the musculus quadratomandibularis and the branchial constrictors to the capsule. Canals of V1 form a bundle before entering between the muscles and bend sharply to dorsal and anterior. Area D7 is S-shaped in *A. cuspidata*, half-moon-shaped in *P. microdon* and lightly bent in *P. clavata* and *P. zijsron*. Area D7 commences posterior to the

spiracle, and in all species except *P. microdon* it connects to D8 about halfway along the length of D8.

In all pristids, area D8 forms 1 row of pores that follows along the propterygial cartilage, with pores located predominately lateral of the dorsal hyomandibular lateral-line canal, apart from the posterior section where in *Pristis* they can also occur medial to the lateral line. In *P. microdon* and *P. zijsron*, the ampullary pores are located between the tubules of the lateral line, whereas in *P. clavata* pores and tubules are separated. Caudally, area D8 is restricted by the junction of the propterygium and the pectoral girdle. The anterior end of area D8 is positioned halfway along the orbits in *A. cuspidata* and *P. microdon* but halfway along the spiracle in *P. clavata* and *P. zijsron*.

*Comparison of Pore Numbers*

The specimen of *P. zijsron* is excluded from statistical comparisons. In the other 3 sawfish species, the pores of the ampullae of Lorenzini are more abundant on the ventral side than on the dorsal side (paired-samples t test; *A. cuspidata*: $t(8) = -5.7$, $p < 0.001$; *P. microdon*: $t(11) = -4.5$, $p = 0.001$; *P. clavata*: $t(7) = 6.8$, $p = 0.000$; table 2a). However, in *A. cuspidata* this difference is the smallest. In all 3 species, rostral pore fields (V6 and D10) have the highest number of pores. The total number of pores is not significantly correlated to specimen size (Pearson correlation coefficient: FL in *A. cuspidata,* $C_p = -0.05$, $p = 0.93$; TL in *Pristis, P. microdon:* $C_p = -0.15$, $p = 0.78$; *P. clavata:* $C_p = 0.87$, $p = 0.33$), suggesting that the number of ampullary pores does not increase ontogenetically in sawfish. No significant difference exists in the total number of pores per body side in *A. cuspidata* and *P. clavata* (paired-samples t test; *A. cuspidata:* $t(3) = -0.55$, $p = 0.622$; *P. clavata:* $t(3) = 0.053$, $p = 0.96$). The number of pores per body side was only significantly different in *P. microdon* (paired samples T test, $t(5) = 2.99$, $p = 0.04$).

*Lengths of the Ampullary Canals*

The length ranges of ampullary canals were assessed separated by pore field (table 2b). Generally, small fields with pores positioned far from the ampullary cluster (e.g. D9, V2) show a smaller standard deviation (SD) in canal length than large fields with the cluster situated within the field (e.g. D8, V1). Comparison of ampullary canal lengths between the 2 specimens of *A. cuspidata* (excluding rostral canals) indicates that canals of the larger specimen are significantly longer than those of the smaller one (independent samples T test, $t(467.9) = -7.6$, $p < 0.01$). Thus canal lengths increase ontogenetically. In *P. microdon*, however, there was no significant difference in the ampullary canal lengths (except rostral canals) of the 2 specimens (independent samples T test, $t(167) = 0.62$, $p = 0.54$), which differed only 10 cm in total length. The same holds true for the 2 specimens of *P. clavata,* whose canal lengths (except rostral canals) did not differ from each other (independent-samples t test, $t(129) = 0.37$, $p = 0.51$), although the 2 specimens differed almost 70 cm in total length.

In *A. cuspidata*, lengths of rostral canals belonging to areas D1 and V6 were measured in 3 specimens, whereas in *P. microdon* they were measured in 2 specimens. They could not be measured in *P. clavata* or *P. zijsron*. Rostral canal lengths represent minimal canal lengths, indicating how far canals could be traced. As a result, there was no significant difference between the rostral canal lengths of the specimens of *A. cuspidata* (n = 3, 1-way ANOVA, $F_{2, 37} = 0.8$, $p = 0.5$) or of *P. microdon* (n = 2, independent samples T test, $t(36) = 0.68$, $p = 0.50$).

## Discussion

The ability to sense prey and hunt in the dark and in murky waters opens up a rich ecological predatory niche [Nelson, 2005]. The ampullae of Lorenzini are a close-range sensory system, which allows chondrichthyans to detect electric fields as weak as 0.025 $\mu Vcm^{-1}$ [Johnson et al., 1984; Kajiura, 2003; Kajiura and Holland, 2002]. In this study, the morphology of the ampullary system is compared between 4 species in 2 genera of sawfish, all of which possess a well-developed electroreceptive system, distributed over the head and rostrum.

In all species of sawfish, ventral pore counts are higher than dorsal ones. The same has been described for most species of sharks [Kajiura et al., 2010], various species of rajids [Raschi, 1986], and rhinobatids [Wueringer and Tibbetts, 2008]. Higher ventral pore counts are probably common for most batoids, which as a group possess a flattened bauplan with dorsally positioned eyes and a ventrally positioned mouth, and are unable to see their prey in the final stages of prey manipulation [Raschi, 1984, 1986].

Ampullary pores are concentrated both on the ventral and dorsal surfaces of the rostrum in all pristids. Additionally, although the hyoid capsule is the largest ampullary capsule in pristids, and it is also the largest one in other batoids, namely rhinobatids [Wueringer and Tibbetts, 2008] and rajids [Raschi, 1978], pristids possess significantly fewer pores located around the mouth than along the rostrum. As the number of ampullary pores equals the number of ampullae, which function as independent electroreceptors, an increased number of elec-

troreceptors provide increased resolution. We therefore hypothesize that the elongated rostrum provides pristid sawfish with a sensory advantage in their electroreceptive detection capabilities.

The fact that the total number of pores of *P. microdon* is twice as high as that of *A. cuspidata* or *P. clavata* indicates that *P. microdon* is an electroreception specialist. The habitat preferences within its distribution affirm this hypothesis, as juvenile *P. microdon* occur inshore and in freshwater beyond tidal reaches [Compagno and Cook, 1995; Thorburn et al., 2003; Wueringer et al., 2009] where visibility can fall below 25 cm, while *A. cuspidata* occur in clearer coastal and offshore waters [Peverell, 2006]. Similarly in carcharhiniform sharks, the number of ampullary pores and thus the relative importance of electroreception decrease with increasing water clarity [Kajiura et al., 2010]. *P. clavata* and *P. zijsron* occur predominately in marine waters, but not as far offshore as *A. cuspidata* [Thorburn et al., 2003]; their habitat preferences need to be confirmed.

Ecological differences between *P. microdon* and *P. clavata* are more subtle. Juveniles of both species occur in waters with salinities between 0 and 41 ppt [Compagno and Cook, 1995; Compagno and Last, 1999; Thorburn et al., 2003, 2007], with comparable visibilities recorded by Secchi disc: *P. clavata* 0–70 cm, *P. microdon* 5–170 cm [Thorburn et al., 2007, 2008]. Both species' prey is dominated by *Rhinomugil nasutus* and *Macrobrachium* sp., but juvenile *P. microdon* also feed on ariid catfish [Peverell, 2006; Thorburn and Morgan, 2005]. However, physiologically *P. microdon* is better adapted to freshwater than *P. clavata* [Ishihara et al., 1991; Otake, 1991]. In Western Australia, juvenile *P. clavata* prefer estuaries where salinities stay well above those of freshwater [Thorburn et al., 2004, 2008]. These waters transmit more short-wavelength light and are slightly clearer compared to the brown murky waters of rivers [McFarland, 1991], thereby increasing the usefulness of the visual system during foraging.

The ampullae of *P. microdon* and *P. clavata* are of the centrum-cap type that possesses a central stage, contrary to the ampullae of *A. cuspidata* which are multi-alveolate in a grape-like formation [Andres and von Düring, 1998]. Ampullae with a central stage possess fewer alveoli than multi-alveolate ampullae. An increase in alveoli number is correlated with decreasing light availability in rajids and sharks [Raschi, 1984]. An increase in alveoli number results in an increase in size of the ampullae and the sensory epithelium, and also the number of sensory cells located within, and thus in an increased sensitivity at lower stimulus strengths [Raschi, 1984]. Thus, if only the visibility in the respective habitats is considered, the comparative results for pristid ampullae types contradict previous results for elasmobranchs.

However, the centrum cap ampullae of *P. microdon* may be explained by the preference for oligohaline waters in juveniles. The only euryhaline elasmobranch so far studied – the bull shark *Carcharhinus leucas* – also possesses ampullae of the centrum-cap type [Whitehead, 2002]. Obligate freshwater rays possess mini-ampullae with reduced canals and alveoli [Andres and von Düring, 1998; Raschi et al., 1997; Szamier and Bennett, 1980]. Thus small ampullae may not be disadvantageous in juvenile *P. microdon*. As the animal grows, its ampullae increase in size and thus sensitivity, which may be more useful for adult *P. microdon* which move into saltwater [Thorburn et al., 2007].

The directions of the rostral canals differ between species. As ampullary canals are most sensitive to electric fields oriented parallel to the line between the ampulla and its pore opening [Bennett and Clusin, 1978; Kajiura and Holland, 2002; Murray, 1974; Tricas, 2001], directional differences have functional implications. In *Pristis* spp. dorsal ampullary canals of the rostrum extend along the body axis, whereas in *A. cuspidata* they draw in 2 directions at a 45° angle before extending inside the cartilage tubes. Ventrally, the canal arrangement is species-specific, and the number of angles between ampullary canals and the body axis increases from *A. cuspidata* (90°) to *P. clavata* (0°, ±25°, ±45°, 90°) and *P. microdon* (±45°, ±65°, ±75°, 90°). As canals of V6 in *A. cuspidata* extend inside cartilage tubes rostro-caudally, they are most sensitive to electric fields perpendicular to the rostrum axis. In *P. microdon*, canals of V6 do not extend rostro-caudally and thus there are 7 main axes of sensitivity. In *P. clavata* there are 5 main axes of sensitivity.

The array of hollow tubes inside the rostral cartilage is a phylogenetically important difference between *Anoxypristis* and *Pristis* which possess 5 and 3 tubes, respectively [for a review, see Wueringer et al., 2009]. Pristid sawfish share a common ancestor with rhinobatid shovelnose rays [Cappetta, 1974; Wueringer et al., 2009]. The presence of 5 hollow tubes in the rostral cartilage of *Anoxypristis* and their absence in *Pristis* and rhinobatids may indicate that sawfish are not monophyletic or that *Anoxypristis* is phylogenetically younger than *Pristis* [Cappetta, 1987; Wueringer et al., 2009].

The presence of the most lateral tube pair in *A. cuspidata* could be a functional adaptation. The arrangement of ampullae inside the cartilage tubes could have properties similar to capsules of connective tissue, which sup-

press interference from the animal's own electric field [Kalmijn, 1974], but this hypothesis remains to be tested. The presence of these tubes also reduces the weight of the rostrum, which is likely related to the more pelagic lifestyle of this species of sawfish, as pelagic elasmobranchs generally swim longer and faster than benthic species.

In an extensive study on the morphology of the ampullae of Lorenzini of elasmobranchs, Chu and Wen [1979] examined a specimen of '*Pristis cuspidatus* Latham'. The morphology of the rostrum identifies it as *A. cuspidata*, as the distance between the 1st rostral tooth and the base of the rostrum equals about one fifth of the rostrum length [Hussakof, 1912; Last and Stevens, 1994; Wueringer et al., 2009]. The presence of a posterior hook on the rostral teeth identifies it as an embryo or neonate [Herman et al., 1997].

In the specimen pictured by Chu and Wen [1979], rostral ampullary canals do not project into the cartilage tube and are thus significantly shorter than we found. We found rostral canals to extend inside the cartilage tubes for a minimum of one tenth of the rostrum length. Contrary to Chu and Wen [1979], the ampullae of Lorenzini are present on both sides of the rostrum, and not only ventrally. Moreover, Chu and Wen [1979] missed the lateral row of ampullary canals on the ventral side of the rostrum. The 2nd inner buccal capsule, which was found to be the smallest ampullary capsule that could easily be overlooked, is missing in Chu and Wen [1979].

In summary, our findings have serious implications for the electroreceptive abilities of *A. cuspidata*, which have previously been missed. Firstly, longer ampullary canals in the rostrum provide a greater sensitivity to voltage gradients [Murray, 1974]. Secondly, as rostral canals draw into cartilage tubes in the rostrum, the main direction of these ampullary canals is not perpendicular to the body axis, but parallel to it. Thirdly, the distribution of dorsal and ventral electroreceptors allows for a finer directional discrimination of electric fields both above and below the rostrum. Fourthly, the bias of pore distributions along the rostrum and the concomitantly low density of pores anterior of the mouth lead to the hypothesis that *A. cuspidata* uses its rostrum to detect and stun prey, as indicated for other species of sawfish [Breder, 1952; Irvine, 1947; Wueringer et al., 2009].

*Comparison of Canal Lengths*

The sensitivity of the ampullae of Lorenzini increases with the length of their canals [Murray, 1974]. As the number of ampullary pores of elasmobranchs remains the same ontogenetically, the pore density and therefore the electroreceptive resolution decrease as the animal grows, but sensitivity increases with growing canals. Therefore, the increase in sensitivity could counteract the decreasing resolution [Kajiura, 2000]. The canal lengths of *A. cuspidata* increase ontogenetically, which is in agreement with other species of elasmobranchs, e.g. carcharhinids and rhinobatids [Kajiura, 2000; Wueringer and Tibbetts, 2008]. In *P. microdon*, no differences in canal length between the 2 specimens were found; this can be attributed to a small difference in total length (<10 cm). At this stage, no explanation can be given for the finding that the lengths of ampullary canals of the 2 specimens of *P. clavata* do not differ despite the specimens themselves differing by 70 cm in total length. As ampullary bulbs are embedded in clusters or capsules, the result indicates that in larger specimens of *P. clavata* the ampullary pores are more concentrated in smaller pore fields.

The variations in the morphology of the ampullary systems of the 4 species of sawfish examined indicate variations in the relative importance of this sense in each species. The presence of ampullary pores on both sides of the rostrum in all species indicates that sawfish sense electric fields both above and below the rostrum. Behavioural studies are needed to determine the importance of electroreception during feeding.


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