

# Ultrastructure of the ampullae of Lorenzini of *Aptychotrema rostrata* (Rhinobatidae)

Barbara E. Wueringer · Ian R. Tibbetts ·  
Darryl L. Whitehead

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**Abstract** Small epidermal pores of the electrosensory ampullae of Lorenzini located both ventrally and dorsally on the disk of *Aptychotrema rostrata* (Shaw and Nodder, 1794) open to jelly-filled canals, the distal end of which widens forming an ampulla that contains  $6 \pm 0.7$  alveolar bulbs ( $n = 13$ ). The sensory epithelium is restricted to the alveolar bulbs and consists of receptor cells and supportive cells. The receptor cells are ellipsoid and their apical surfaces are exposed to the alveolar lumen with each bearing a single central kinocilium. Presynaptic bodies occur in the basal region of the receptor cell immediately proximal to the synaptic terminals. The supportive cells that surround receptor cells vary in shape. Microvilli originate from their apical surface and extend into the alveolar lumen. Tight junctions and desmosomes connect the supportive cells with adjacent supportive and receptor cells in the apical region. The canal wall consists of two cell layers, of which the luminal cells are squamous and interconnect via desmosomes and tight junctions, whereas the cells of the deeper layer are heavily interdigitated, presumably mechanically

strengthening the canal wall. Columnar epithelial cells form folds that separate adjacent alveoli. The same cells separate the ampulla and canal wall. An afferent sensory nerve composed of up to nine myelinated nerve axons is surrounded by several layers of collagen fibers and extends from the ampulla. Each single afferent neuron can make contacts with multiple receptor cells. The ultrastructural characteristics of the ampullae of Lorenzini in *Aptychotrema rostrata* are very similar to those of other elasmobranch species that use electroreception for foraging.

**Keywords** Ampullae of Lorenzini · Alveolar bulbs · Receptor cell · *Aptychotrema rostrata* · Electroreception

## Introduction

Ampullae of Lorenzini, the electroreceptors of elasmobranchs, detect animate and non-animate minute electrical fields in the environment (Kalmijn 1974; Zakon 1986). The biological roles ascribed to electroreception are prey detection, geomagnetic orientation and electro-communication (Dijkgraaf and Kalmijn 1962; Kalmijn 1974; Wilkens and Hofmann 2005).

Pores visible on the surface of the skin are opening into canals that lead to the sensory ampullae. The sensory epithelium, comprising receptor and supportive cells, is restricted to the alveolar bulbs of the ampulla (Waltman 1966; Jorgensen 2005). The canals of various lengths contain a species-specific gelatinous mucopolysaccharide similar in conductivity to the surrounding seawater (Waltman 1966; Murray 1974; Brown et al. 2002). In marine elasmobranch species, the length of the ampullary canals ranges from 5 to 20 cm (Brown 2002), and their ampullae are grouped into clusters by envelopes of connective tissue (Norris 1929; Jorgensen 2005).

B. E. Wueringer  
Department of Zoology, University of Vienna,  
1090 Vienna, Austria

I. R. Tibbetts · D. L. Whitehead  
Centre for Marine Studies,  
The University of Queensland,  
St Lucia, QLD 4072, Australia

### Present Address:

B. E. Wueringer (✉)  
Sensory Neurobiology Group (formerly Vision,  
Touch and Hearing Research Centre),  
School of Biomedical Sciences,  
The University of Queensland,  
St Lucia, QLD 4072, Australia  
e-mail: b.wueringer@uq.edu.au

This paper examines the ultrastructure of the electroreceptors of the shovelnose ray *Aptychotrema rostrata* (Shaw and Nodder, 1794). As no species of rhinobatid has been examined via electron microscopy to date, comparisons will be made to other species of elasmobranchs.

## Materials and methods

Rhinobatid rays are benthic suction-crushing feeders, with diets generally dominated by bottom-dwelling invertebrates and fish (Last and Stevens 1994; Kyne and Bennett 2002). *Aptychotrema rostrata* is endemic to eastern Australia, where it is found from Moreton Bay, Queensland to Jervis Bay, New South Wales. The species is generally found in shallow coastal waters to a depth of 50 m (Last and Stevens 1994; Kyne and Bennett 2002).

Two specimens of *Aptychotrema rostrata*, ranging from 650 to 755 mm total length, were captured via angling from Moreton Bay, Queensland, Australia (27°28'S, 153°02'E). The specimens were immediately euthanized with a lethal dose of tricaine methane sulfonate (MS222; 1:2000). Total length ( $\pm 1$  mm), disk width ( $\pm 1$  mm) and sex were recorded. Samples of epidermal tissue containing ampullae of Lorenzini were removed from the hyoid cluster and fixed in Karnovsky's (1965) formaldehyde–glutaraldehyde fixative in 0.1 M cacodylate buffer at 4°C for 3 days. The samples were processed in a Lynx Tissue Processor Unit using three rinses of buffer, each for 15 min, followed by 80 min postfixation in osmium tetroxide in 0.1 M cacodylate buffer (pH 7.2). After postfixation, samples were rinsed another three times in the buffer, each for 15 min, and then dehydrated in an ascending alcohol series. After dehydration, the samples were infiltrated with 50, 75% Spurr's epoxy resin (30 min each), followed by 30 min in 100% Spurr's epoxy resin before another change of Spurr's for 18 h. Then the samples were blocked in silicon molds and polymerized at 60°C overnight. Survey sections (1  $\mu$ m in thickness) were cut with a Nova Ultramicrotome LKB Bromma with a glass knife and stained with 3% toluidine blue in 0.1 M phosphate buffer. Ultrathin sections ( $\sim 100$  nm) were cut with a diamond knife, mounted on 1 mm  $\times$  2 mm single slot carbon-stabilized collodion grids, and stained with uranyl acetate and lead citrate, according to the method of Daddow (1986). Sections were viewed and photographed using both a JEOL 6400 and a JEOL 1010 transmission electron microscope at 80 kV.

Measurements of the ampullary tissues were made from images using AnalySIS ver.3 by soft imaging system and obtained from the male specimen (total length 755 mm), single axons of the sensory nerve fiber were measured, where Schwann cells surrounded them. The alveolar bulbs of single ampulla were counted. All measurements are

presented as mean  $\pm$  standard error. The results of ampullary morphology were compared to that described for *Amblyraja radiata* (Donovan, 1808), *Raja clavata* (Linnaeus, 1758) and *Dipturus batis* (Linnaeus, 1758) by Waltman (1966), *Scyliorhinus canicula* (Linnaeus, 1758) by Andres and von Düring (1988) and *Iago omanensis* (Norman, 1939) by Fishelson and Baranes (1998). All statistical methods follow Köhler et al. (2002) and Statsoft Inc. (2004).

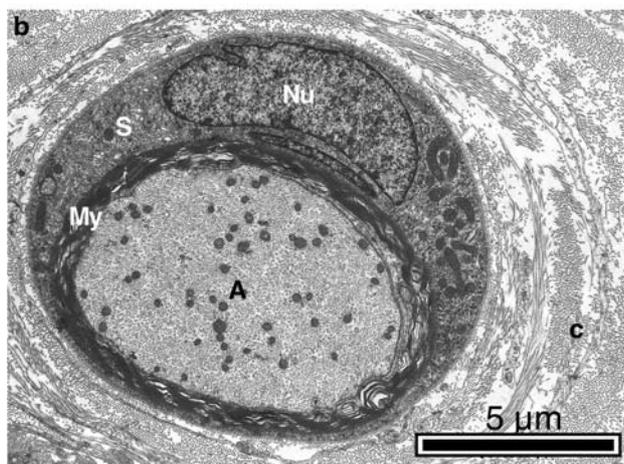
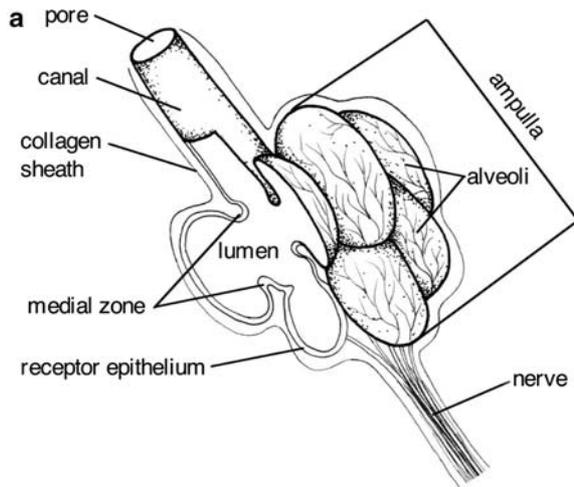
## Results

In *Aptychotrema rostrata*, as in other elasmobranchs, the ampulla of Lorenzini consists of two regions: the canal and the ampulla (Fig. 1a). Somatic pores are visible macroscopically because of their pigmentation and each one leads to one mucus-filled canal. Canals vary in length within one specimen, as ampullae are clustered together in tissue capsules in certain regions of the head. At the distal expansion of each canal, one ampulla comprising several alveolar bulbs is attached, with a mean of  $6 \pm 0.7$  ( $n = 13$ ) alveoli per ampulla.

Up to nine dendrites of the afferent nerve extend from the blind ending of each ampulla. At the point of attachment of the dendrite to the ampullary tissue, each dendrite divides into several collaterals. The collateral fibers spread out over the alveoli, forming synaptic terminals to communicate with the receptor cells. Each axon of the afferent fiber is surrounded by Schwann cells and a collagen sheath (Fig. 1b).

### Cells of the canal wall

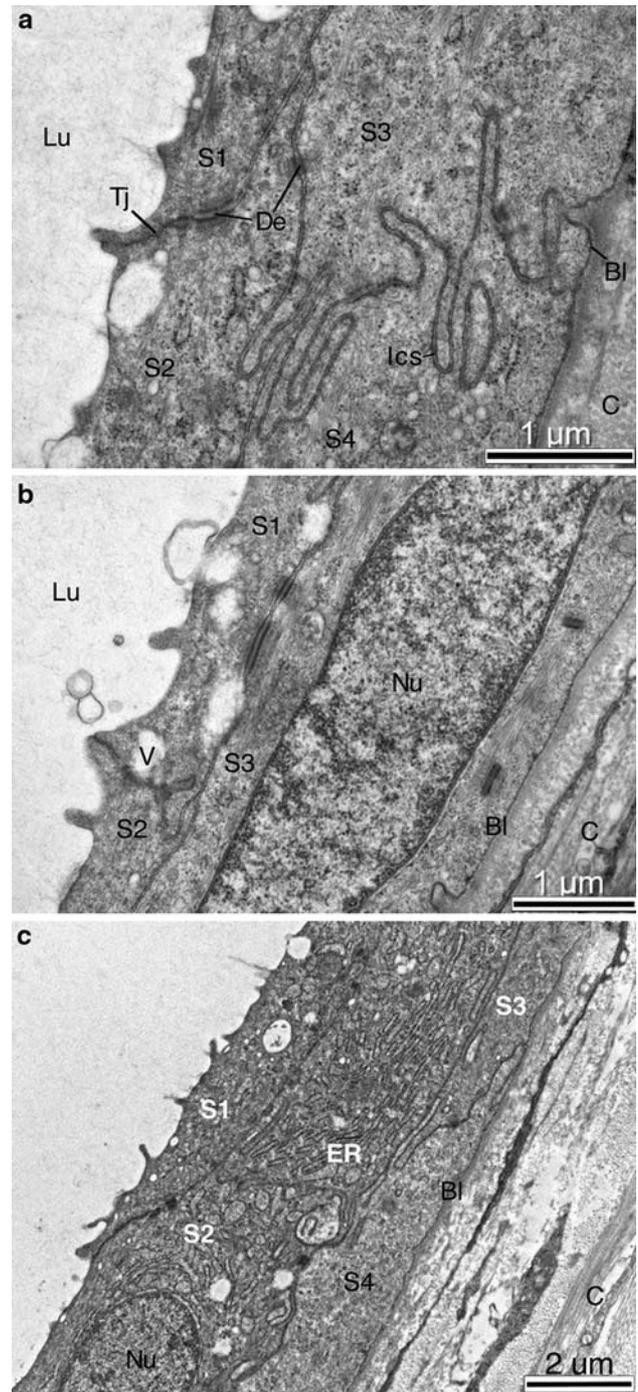
The epithelium of the canal wall is  $3.99 \pm 0.48$   $\mu$ m thick and consists of two layers of cells. Cells of the luminal layer of the canal wall differ from those of the basal layer. The luminal cells are squamous and less polymorphic than cells of the deep layer, as their membranes are less intertwined than membranes between adjacent cells of the deep layer. Luminal cells (Fig. 2) are connected by desmosomes and tight junctions. These connections are rarely visible in the cells of the deep layer. In the luminal region of the cells, vesicles are visible; they contain a substance of the same density as the lumen, and sometimes fuse with the luminal membrane of the cell, secreting the substance they carry into the canal lumen (Fig. 2c). Cisternae of the rough endoplasmic reticulum are common in the luminal cells (see Fig. 2c), as are the membranes of the Golgi apparatus. The nucleoli of the cells of both layers are elongate. Cells of the luminal layer of the canal wall measure  $2.15 \pm 0.23$   $\mu$ m in height. They are about 6  $\mu$ m wide, although no exact measurements could be taken.



**Fig. 1** **a** Schematic presentation of an ampulla of Lorenzini of the multialveolate type. The left side of the ampulla is opened to visualize epithelia of the canal, medial zone and alveoli. At the distal end the canal opens up to an ampulla, which comprises several alveoli. Dendrites spread out over the alveoli and synapse with the receptor cells. A sensory nerve extends from the distal end of the ampulla. A collagen sheath surrounds the canal, ampulla and nerve. Not drawn to scale. Reprinted with permission from Wueringer and Tibbetts (2008). **b** A single afferent nerve fiber of the ampullae of Lorenzini of *Aptychotrema rostrata*. TEM, cross section of a myelinated neuron. Several mitochondria are visible in the cytoplasm of the axon (A). A Schwann cell (S), with a nucleus (Nu), surrounds the axon, forming the myelin sheath (My). Neurilemmal collagen sheath (C)

Cells of the deeper layer are heavily intertwined (Fig. 2) and often contain a fibrous material in their cytoplasm (Fig. 2b). Compared to the cells of the luminal layer, cytoplasmic organelles are less abundant. The endoplasmic reticulum is not as prominent as it is in the luminal cells and contains fewer vesicles. Cells of the deeper layer of the canal wall are  $1.41 \pm 0.20 \mu\text{m}$  high and about  $6 \mu\text{m}$  wide; however, their heteromorphy precluded any useful measurements of their diameter.

On the proximal side, the deeper layer rests on the basal lamina, which separates the cells from a lamina of



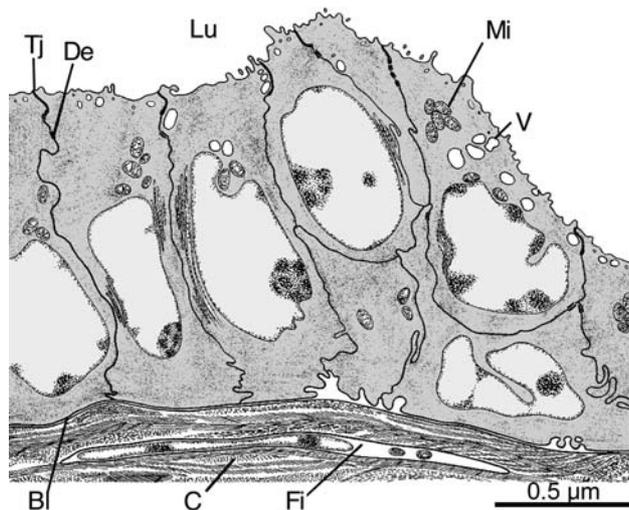
**Fig. 2** The canal wall of the ampullae of Lorenzini of *Aptychotrema rostrata*. TEM, to the left of the epithelium the canal lumen (Lu) is visible. The cells of the luminal layer S1, S2 are connected by desmosomes (De) and tight junctions (Tj), not found in the cells of the deeper layer S3, S4. The basal lamina (Bl) separates the two cell layers from a layer of connective tissue containing regularly oriented collagen fibers (C). **a** Cells of the deeper layer S3, S4 are intertwined heavily. **b** Vesicles (V) of the luminal cells contain a substance of the same density as that in the lumen. **c** The cells of the luminal layer contain vesicles (V) and an extensive rough endoplasmic reticulum (ER). The adjacent membranes of two cells S3, S4 of the deeper layer are heavily intertwined. Nu nucleus

connective tissue. This lamina contains several layers of collagen fibers, each oriented in a different direction (Fig. 2).

#### Cells of the medial zone

The medial zone (Fig. 3) forms the transition between the receptor epithelium and the cells of the canal wall. The canal wall is thinner than the receptor epithelium (height of the canal wall:  $3.99 \pm 0.48 \mu\text{m}$ ; height of the receptor epithelium:  $11.11 \pm 0.37 \mu\text{m}$ ), and consists of two layers of cells compared to the monolayered receptor epithelium. The medial zone consists of one layer of columnar cells that are about two and a half times higher than their width (i.e. height  $12.61 \pm 0.89 \mu\text{m}$ ; width  $4.75 \pm 0.11 \mu\text{m}$ ), with a centrally positioned nucleus similar to the nucleus of cells of the luminal layer of the canal wall and receptor cells. Vesicles occur on the apical surface of the cells exposed to the lumen. The walls of adjacent cells are interdigitated. Cells of the medial zone also create folds between the alveolar bulbs, separating the receptor epithelia of neighboring bulbs.

The cells of the canal wall adjacent to the cells of the medial zone differ in shape from other cells of the canal wall, as differences in height of the two epithelia are compensated. Cells of the deeper layer are consistent in height, whereas luminal cells expand in height from the side that borders the canal wall to the side that borders the receptor epithelium (see Fig. 3).



**Fig. 3** Semi-schematic presentation of the medial zone of the ampullae of Lorenzini of *Aptychotrema rostrata*. The cells of the medial zone connect with the single-layered sensory epithelium to the left and the double-layered canal wall on the right. Cells contain a large spherical nucleus (*Nu*) and are connected via tight junctions (*Tj*) and desmosomes (*De*) on the apical pole. Vesicles (*V*) are fused with the apical membrane. Underneath the basal lamina (*Bl*) are a collagen sheath (*C*) and fibroblasts (*Fi*)

#### Cells of the ampullary epithelium

The cells of the sensory epithelium measure  $11.11 \pm 0.37 \mu\text{m}$  in diameter ( $n = 5$ ), surrounding a lumen with a diameter of  $145.67 \pm 11.13 \mu\text{m}$ . An extracellular corpuscular layer, varying in thickness between 2.5 and  $5 \mu\text{m}$ , is found in the lumen overlying the sensory epithelium.

The alveolar epithelium of *Aptychotrema rostrata* exhibits two types of cells: elliptical receptor cells that are surrounded by supportive cells of various shapes (Fig. 4a). In both cell types a luminal, apical pole can be distinguished from a basal pole, restricted by the basal lamina. Underneath the basal lamina, a lamina of connective tissue contains several layers of collagen fibers.

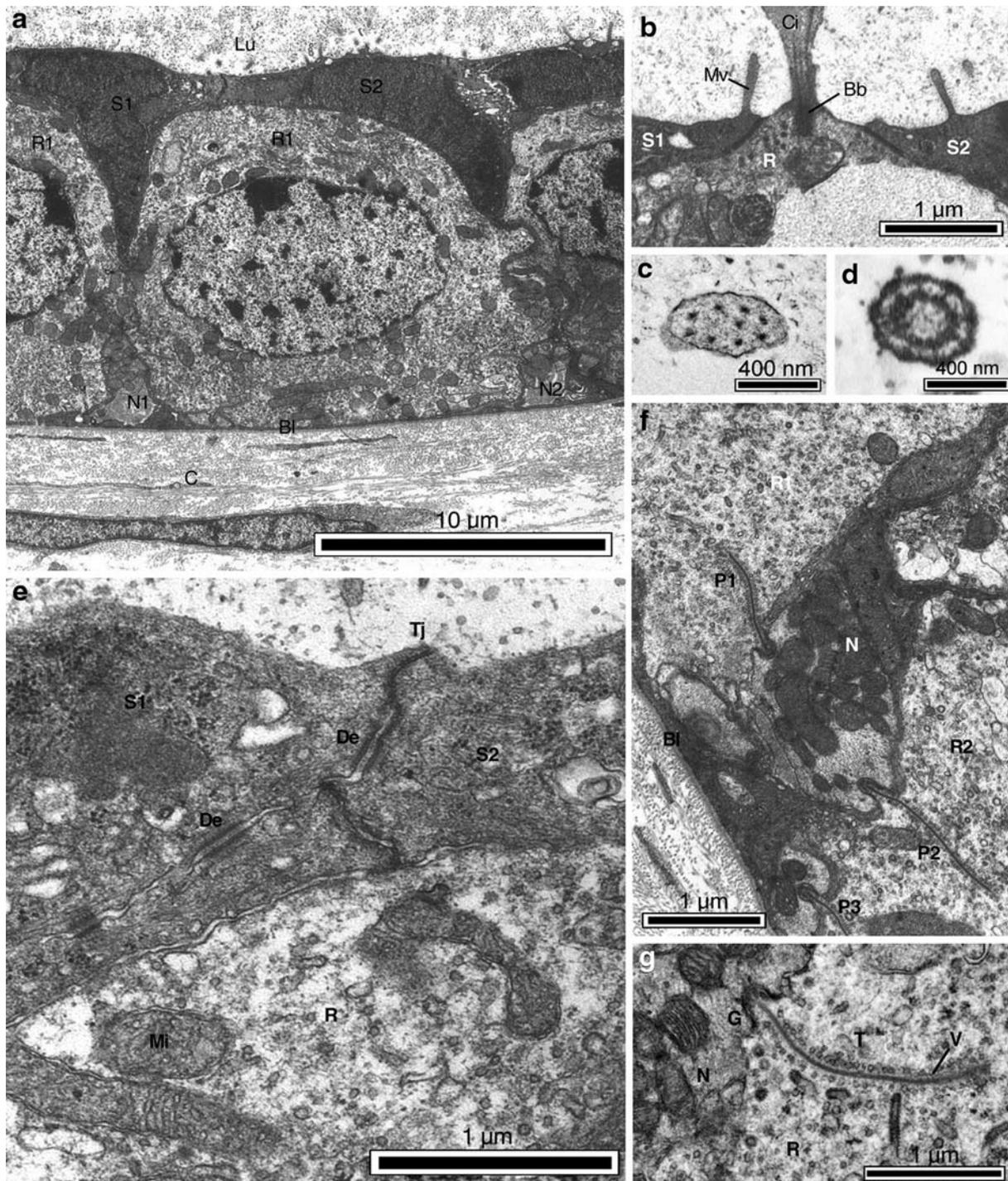
#### Receptor cells

The receptor cells are elliptical, extend from the basal lamina to the alveolar lumen and are  $10.72 \pm 0.48 \mu\text{m}$  high and  $11.22 \pm 0.62 \mu\text{m}$  wide. Each receptor cell contains an elliptical, centrally positioned nucleus measuring  $5.80 \pm 0.40 \mu\text{m}$  in height and  $7.23 \pm 0.24 \mu\text{m}$  in width. The apical surface of the cell exposed to the alveolar lumen, is  $1.32 \pm 0.11 \mu\text{m}$  in diameter and bears a single central kinocilium protruding into the lumen (Fig. 4b). The basal diameter of the kinocilium is  $441.40 \pm 72.05 \text{ nm}$ . The longest kinocilium measured  $4.2 \mu\text{m}$ , but it did not appear to be an exact cross section through the center. The arrangement of the microtubules in the kinocilia is very unusual; along the axoneme, microtubules are arranged in an 8 + 1 pattern (Fig. 4c), which was found up to  $4.2 \mu\text{m}$  away from the receptor cell membrane. In the basal region of the kinocilium the 9 + 0 structure (Fig. 4d) does not extend more than  $0.3 \mu\text{m}$  from the receptor cell. A basal body was found but no rootlet fibers. No microvilli extend from the apical surface of the receptor cells.

On the apical pole, tight junctions and desmosomes connect the receptor cell with adjacent supportive cells (Fig. 4a, e). In the apical cytoplasm of the receptor cells (Fig. 4e) there are numerous mitochondria, vesicles and the dictyosomes of the Golgi apparatus. The basal cytoplasm also contains many mitochondria and vesicles but few dictyosomes. In the basal region of the receptor cell, synaptic terminals are present between the nucleus and the basal lamina (Fig. 4f, g).

#### Supportive cells

As the supportive cells surround the elliptical receptor cells, they are quite variable in shape. In each supportive cell, the apical region extends to the alveolar lumen, whereas the proximal region abuts the basal lamina. Supportive cells measure  $11.71 \pm 0.56 \mu\text{m}$  in height and  $3.91 \pm 0.41 \mu\text{m}$  in



**Fig. 4** The ampullary epithelium of *Aptychotrema rostrata*. TEM, **a** An oblique section through a receptor cell (*R1*) that is surrounded by polymorphic supportive cells *S1*, *S2*. The apical pole of the receptor cell bearing a central kinocilium is not visible. Synaptic terminals *N1* and *N2* are formed above the basal lamina (*Bl*) between the receptor cells. A collagen sheath (*C*) surrounds the receptor epithelium. **b** The apical pole of a receptor cell (*R*) bears a single central kinocilium (*Ci*) extending into the lumen (*Lu*). Supportive cells *S1* and *S2* surround the receptor cells and are adjoined via tight junctions (*Tj*) at the apical pole. Microvilli (*Mv*) extend from the surface of the supportive cells. **c** Cross section through the tip of a kinocilium extending from the apical pole

of a receptor cell. Microtubules are arranged in an 8 + 1 pattern. **d** Cross section through the base of a kinocilium extending from the apical pole of a receptor cell, with microtubule arranged in a 9 + 0 pattern. **e** On the apical pole, supportive cells *S1*, *S2* connect via tight junctions (*Tj*) and desmosomes (*De*). **f** In the basal region of the receptor epithelium synaptic terminals (*N*) connect receptor cells with nerve cells. Presynaptic bodies *P1*, *P2*, *P3* are formed with two receptor cells. The cytoplasm of the nerve contains several mitochondria (*Mi*). **g** A groove (*G*) in the neural membrane surrounds the presynaptic body (*T*) (tongue) formed by the receptor cell. Microvesicles (*V*) are lined up along the tongue formation. *Bb* basal body of the kinocilium

diameter, although these measurements should be regarded as an estimate. The nuclei are more variable in shape than in receptor cells. On the supportive cell apical surface several microvilli extend into the lumen, encircling the central kinocilium of the receptor cell. They measure  $98.27 \pm 12.16$  nm in diameter and  $519.65 \pm 131.78$  nm in length. The apical surface of the supportive cells is coated in mucus, which is found in the alveolar lumen and secreted by exocytosis.

The synaptic terminals

In *Aptychotrema rostrata* each ampullary organ is innervated by an afferent nerve comprising up to nine nerve fibers. Each nerve fiber is surrounded by a myelin sheath (Fig. 1b), which is surrounded by a lamina of collagen fibers, that binds all nerve fibers together into a single nerve. The mean diameter of the nerve fiber is  $13.75 \pm 1.095$   $\mu$ m; the mean height of Schwann cells is  $5.36 \pm 0.74$   $\mu$ m.

In the basal region of the receptor cell, between the nucleus and the basal lamina, the cell connects with afferent dendrites (Fig. 4f, g), forming synaptic terminals. The synaptic terminals are unmyelinated, contain numerous mitochondria and form presynaptic bodies. One synaptic terminal can fuse with more than one receptor cell (Fig. 4f). Concomitantly, one receptor cell can possess multiple neural attachments. The tongue-and-groove formation (Fig. 4f, g) is created by a groove in the neural membrane in which the presynaptic body of the receptor cell extends, forming the tongue. Microvesicles occur along the length of the invagination of the receptor cell membrane within the tongue formation. Synaptic terminals measure  $2.37 \pm 0.60$   $\mu$ m in height and  $3.75 \pm 0.10$   $\mu$ m in width. A maximum of three tongue-and-groove formations per synaptic terminal was found ( $n = 18$ ).

## Discussion

The hyoid cluster of *Aptychotrema rostrata* is the largest cluster in rajids (Raschi 1978, 1986) and also in rhinobatids (Wueringer and Tibbetts 2008). As *Aptychotrema rostrata* is found in the marine environment and their ampullae of Lorenzini are macroscopic in the range of centimeters, the ampullary organs are classified as macroampullae sensu Andres and von Düring (1988) (Wueringer and Tibbetts 2008), compared to the microampullae of Holocephali species and the miniampullae of freshwater elasmobranchs, as described in *Potamotrygon laticeps* (Garman, 1913) and *Potamotrygon motoro* (Müller and Henle, 1841) (Andres and von Düring 1988). However, both stenohaline and omnihaline rhinobatid species are known to possess ampul-

lae that can be classified as macroampullae (Chu and Wen 1979; Wueringer and Tibbetts 2008).

Alveoli within an ampulla do not join at their distal ends as described for *Iago omanensis* (Fishelson and Baranes 1998), but are stacked like grapes (see Fig. 1a). Therefore, following the classification of ampullae by Andres and von Düring (1988), these of *Aptychotrema rostrata* belong to the multi-alveolate type ampulla of Jorgensen (2005), which is also found in another rhinobatid, *Rhinobatus typus* (Bennett, 1830) (Wueringer and Tibbetts 2008). The number of alveoli varies between species, as *Aptychotrema rostrata* possesses  $6 \pm 0.7$  alveoli per hyoid ampulla, whereas Raschi (1986) counted 20.5 to 8.3 alveoli per ampulla for the hyoid cluster of 40 different species of rajids, and *Iago omanensis* possesses seven to nine alveoli per ampulla (Fishelson and Baranes 1998). In rajids a low number of alveoli per ampulla correlates with a shallow habitat (Raschi 1986). Whether the same is true for rhinobatids remains to be tested.

The ampullary canal

The canal wall consists of two layers of cells, with the luminal cells being connected by tight junctions and desmosomes. Waltman (1966) rarely found tight junctions and desmosomes other than between the luminal ends of the inner cell layer. However, in *Aptychotrema rostrata*, desmosomes occur between adjacent cells of the deeper layer, as described for *Iago omanensis* (Fishelson and Baranes 1998). These occlusions of intercellular space form the functional base for electroreception. The insulation of the ampullary lumen enables the conduction of electric currents from the environment along the canal to the sensory epithelium (Waltman 1966; Jorgensen 2005). Furthermore, deep-layered cells of the canal wall are interdigitated. We hypothesize that these interdigitations provide mechanical strength to the canal, similar to that reported for cells of the small intestine (Ude and Koch 2002), but this hypothesis remains to be tested. Both the canal and ampulla are surrounded by multiple layers of collagen fibers, which provide mechanical support (Murray 1974). They are also present around the myelinated nerve, between and around the single nerve fibers. Such lamina of connective tissue have already been described for *Amblyraja radiata*, *Raja clavata* and *Dipturus batis* (Waltman 1966), as well as in *Scyliorhinus canicula* (Andres and von Düring 1988).

Canals 4.7–55.5 mm in length (*Aptychotrema rostrata* TL 68.0 cm, Wueringer and Tibbetts 2008) extend from the somatic pores and form the alveolar bulbs at their proximal end. The ampullae of rhinobatid species occur in five distinct clusters (Norris 1929), which facilitate the suppression of interfering signals created by the animal's own electric field (Kalmijn 1974) and do not change position ontogenetically.

Therefore, the length range of the canals depends on the size of the animal. Moreover, canal length range may be explained through the respective habitat of a species as it depends on the conductivity of the surrounding water (Kalmijn 1974; Bodznick and Montgomery 2005). In marine elasmobranchs, the body tissues are electrically less resistant than the surrounding water and longer canals are required to produce an effective potential difference that stimulates the receptor cells (Kalmijn 1974).

#### The medial zone

The morphology of the medial zone in *Aptychotrema rostrata* both between adjacent alveoli and on the border of the sensory epithelium and the canal wall seems to conform to the description of the epithelium of the centrum cap of *Scyliorhinus canicula* (Andres and von Düring 1988). However, *Aptychotrema rostrata* lacks the structure of a centrum cap and also brush-cells that border the centrum cap cells as described by Andres and von Düring (1988) for *S. canicula*.

#### The ampullary epithelium

The receptor cells of *Aptychotrema rostrata* are encased by supportive cells, as also observed in other species of elasmobranchs (see Waltman 1966; Murray 1974; Szabo 1974; Andres and von Düring 1988). In *Aptychotrema rostrata*, the apical surface of the receptor cell exposed to the alveolar lumen measures  $1.32 \pm 0.11 \mu\text{m}$  in diameter. The cell surface is approximately  $378 \mu\text{m}^2$  and the exposed surface measures  $1.37 \mu\text{m}^2$ , approximating 0.36% of the cell surface. This value should be regarded as an estimate. Murray (1974) found less than 1% exposed to lumen, whereas Andres and von Düring (1988) described 0.6% exposed to the lumen in *S. canicula*.

The structure of the kinocilium extending from the receptor cells of *Aptychotrema rostrata* is unusual, as microtubules are arranged in a 9 + 0 and 8 + 1 pattern. Waltman (1966) and Szabo (1974) describe an 8 + 1 arrangement of the microtubule in the axoneme, and mention finding a 9 + 0 arrangement in rajids without further specifying its spatial occurrence. Contrary to Andres and von Düring (1988) who report the 8 + 1 structure in the base and the 9 + 0 structure in the axoneme of the kinocilia of *Scyliorhinus canicula*, we found microtubular arrangements of 9 + 0 in the base and 8 + 1 in the axoneme of the kinocilia. These interpretations were made possible as some kinocilia were found attached to a receptor cell, while others were cut along the shaft. The exact length of the kinocilia could not be measured as we found no exact cross sections along the whole length of the shaft, but the minimum lengths of ampullary kinocilia of *Amblyraja radiata*, *Raja clavata*, *Dipturus batis* and *Scyliorhinus canicula* are 5  $\mu\text{m}$  (Waltman 1966; Andres and von Düring 1988).

Waltman (1966) reports neither rootlet fibers nor an accessory centriole of the kinocilium and neither were found in *Aptychotrema rostrata*. Fishelson and Baranes (1998) on the other hand report rootlet fibers in the kinocilia of *Iago omanensis*. They also describe a few low microvilli on the apical surface of the receptor cell surrounding the kinocilium, which do not exist in *Aptychotrema rostrata*.

In the basal region of the sensory epithelium, synaptic terminals connect with receptor cells. The unmyelinated dendrites form collaterals when attaching to the ampullary tissue. The tongue-and-groove formation (Waltman 1966) is created by the presynaptic body of the receptor cell (the tongue), which extends into the postsynaptic groove in the neural membrane (Fig. 4f, g). This structure is referred to as the ribbon and gutter structure by Murray (1974). In this study, receptor cells formed one to three presynaptic bodies per synaptic terminal, with a mean of  $1.61 \pm 0.18$  synaptic terminals per side. We observed a maximum of six presynaptic bodies per receptor cell. This value is regarded as an estimate, as only single sections of receptor cells were observed and receptor cells were not reconstructed three dimensionally. Murray (1974) found from two to seven separate synapses per receptor cell, whereas Andres and von Düring (1988) mention four to six synapses per receptor cell for *Scyliorhinus canicula*. As the ultrastructural characteristics of the electrosensory ampullae in *Aptychotrema rostrata* appear identical with those of *Amblyraja radiata*, *Raja clavata*, *Dipturus batis* and *Scyliorhinus canicula* (Waltman 1966; Andres and von Düring 1988), which use electroreception for foraging (see Kalmijn, 1974, 1978 for *Scyliorhinus* and *Raja*), it is assumed that this organ has a similar function in *Aptychotrema rostrata*. Although the morphology is indicative of this role, behavioral experiments are required to confirm the possible uses and the sensitivity of the ampullae of Lorenzini in this species of rhinobatid.

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