

# The “nasal barbel” of the halfbeak *Dermogenys pusilla* (Teleostei: Zenarchopteridae) – an organ with dual function

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## Abstract

Members of the taxon Zenarchopteridae (Beloniformes) possess external paired olfactory organs each consisting of a small cone-like papillae also called nasal barbel. We examined the structure of these barbels in the viviparous halfbeak *Dermogenys pusilla* using scanning (SEM) and transmission electron microscopy (TEM). Nasal barbels are covered by a typical epidermis characterized by ridged surface cells. Further, the epidermis contains goblet cells and small taste buds. The epidermis is interspersed with small depressions or pits (sensory islets) which contain the olfactory epithelium. Typically, taste buds consist of spindle-shaped dark cells with numerous apical microvilli, light cells with a thick microvillus each, basal cells and a rich nerve fiber plexus between receptor and basal cells. The olfactory epithelium at least contains two types of receptor cells, i.e. ciliated cells with a strikingly variable microtubular pattern and microvillous cells, and supporting and basal cells. An olfactory organ with an open groove and an elongated papilla is considered as synapomorphy of the Beloniformes (does not hold for the Adrianichthyoidei). Comparison of these olfactory organs suggests that *D. pusilla* and very probably all Zenarchopteridae may have the most uniform and least elaborated olfactory organs.

## Kurzfassung

Angehörige der Zenarchopteridae haben paarige, nach außen verlagerte Geruchsorgane. Jedes Geruchsorgan besteht aus einer länglichen, kolbenförmigen Papille, auch Nasalhörnchen genannt. Wir haben die Feinstruktur der Nasalhörnchen mittels Raster- (REM) und Transmissionselektronenmikroskopie (TEM) bei dem viviparen Halbschnabelhecht *Dermogenys pusilla* untersucht. Hier ist das Geruchsorgan überwiegend mit einer typischen Epidermis bedeckt, deren oberflächliche Zellen ein Mikroleistenmuster aufweisen, und in der Becherzellen sowie kleine Geschmacksknospen vorhanden sind. Zwischen den Epidermiszellen liegen Einsenkungen („Sinnesinseln“), deren Boden mit dem Riechepithel bedeckt ist. Die typischen Geschmacksknospen bestehen aus elektronendichten spindelförmigen Zellen mit zahlreichen kurzen Mikrovilli, elektronenleichten Zellen mit je einem dicken Mikrovillus, Basalzellen sowie einem dichten Nervenplexus oberhalb der Basalzellen. Das Riechepithel enthält mindestens zwei Typen von Rezeptorzellen, und zwar Cilienzellen mit Cilien, deren Mikrotubuli-Anordnung überraschend stark variiert, Zellen mit Mikrovilli, sowie Stütz- und Basalzellen. Ein Geruchsorgan mit offener Grube und verlängerter Papille gilt als Synapomorphie der Beloniformes (mit Ausnahme der Adrianichthyoidei). Vergleicht man die bisher beschriebenen Geruchsorgane der Beloniformes, scheinen diese bei *D. pusilla* und sehr wahrscheinlich bei alle anderen Vertreter der Zenarchopteridae relativ einheitlich und am wenigsten komplex zu sein.

## Key words

Halfbeaks, olfactory organ, taste buds, SEM, TEM.

## Introduction

The vast literature that is available on the organization, development and structure of olfactory organs in “fish” has been reviewed repeatedly (e.g. YAMAMOTO 1982; ZEISKE *et al.*, 1992; HANSEN & REUTTER, 2004; HANSEN & ZIELINSKI, 2005; ZEISKE & HANSEN, 2005). Concerning the atherinomorph fishes – taxonomy follows PARENTI (1983) and NELSON (1994) –, Atheriniformes and Cyprinodontiformes have olfactory organs, which consist of an olfactory chamber housing olfactory and non-sensory epithelia and are connected to the exterior by two nostrils. Within the Beloniformes, however, members of the Belonoidei (= Exocoetoidei) have olfactory organs that consist of a papilla-like protrusion arising from a groove; papilla and groove are covered by non-sensory and olfactory epithelium. This organisation called “beloniform pattern” in the following is considered a synapomorphy of the Exocoetoidei (see ZEISKE & HANSEN, 2005).

The unique organisation of the “beloniform” type of olfactory organs was mainly shown by gross morphology (e.g. C.P. SINGH, 1972; GUPTA & SHRIVASTAVA, 1973; S.P. SINGH, 1977; COLLETTE & SU, 1986). To our knowledge, the only beloniform species studied more detailed in this respect is the garfish *Belone belone* (THEISEN *et al.*, 1980; reviewed and illustrated with some additional SEM-pictures in ZEISKE & HANSEN, 2005). Authors briefly summarized previous anatomical and histological studies and, using TEM and SEM, described the olfactory organ of *B. belone* as an open groove, from which a papilla equipped with “sensory islets” protrudes; olfactory lamellae are entirely absent, but on the posterior face of the papilla irregularly arranged lobes are seen (THEISEN *et al.* 1980).

Within the Exocoetoidei the monophyletic Zenarchopteridae have been recently separated from the paraphyletic “Hemirhamphidae” (LOVEJOY *et al.*, 2004), which now include the internally inseminating Southeast-Asian genera *Zenarchopterus*, *Hemirhamphodon*, *Nomorhamphus*, and *Dermogenys*. They possess olfactory organs that consist of small elongate cones (called nasal barbels) protruding out of a small groove (= *fossa nasalis*). Presence of such obviously less elaborated olfactory organs has been proposed likewise as a synapomorphy of Zenarchopteridae (ANDERSON & COLETTE, 1991; for review and further readings see DOWNING MEISNER, 2001), but to our knowledge a closer description of these external olfactory organs is missing. SEM-micrographs available from literature show that the olfactory organ of the halfbeak *Dermogenys pusilla* protrudes from the head and is covered by a ridged surface epithelium interrupted by round sensory islets (see Fig. 8 c, d in GREVEN, 2006).

When studying the head morphology of several members of the Zenarchopteridae (see also CLEMEN *et al.*, 1997; GREVEN *et al.*, 1997), we detected taste buds interspersed between the epithelial components of the nasal barbel not documented yet. These findings prompted us to have a



**Fig. 1.** Head of *Dermogenys pusilla* from above with nasal barbels (from GREVEN 2006).

closer look to the nasal barbels of the most common half-beak *D. pusilla*. We herein do not focus on a detailed description of the ultrastructure of the olfactory epithelium and the taste buds, which correspond to the fine structure found in other fish and, thus, appear to be sufficiently known. Rather we used scanning and transmission electron microscopy to unequivocally show the coexistence of the olfactory epithelium and taste buds on nasal barbels. Concerning ultrastructure, we therefore cite largely summarizing literature (e.g. YAMAMOTO, 1982; ZEISKE *et al.*, 1992; HANSEN & ZIELINSKI, 2005; ZEISKE & HANSEN, 2005; HANSEN, 2005; REUTTER & HANSEN, 2005).

## Material and methods

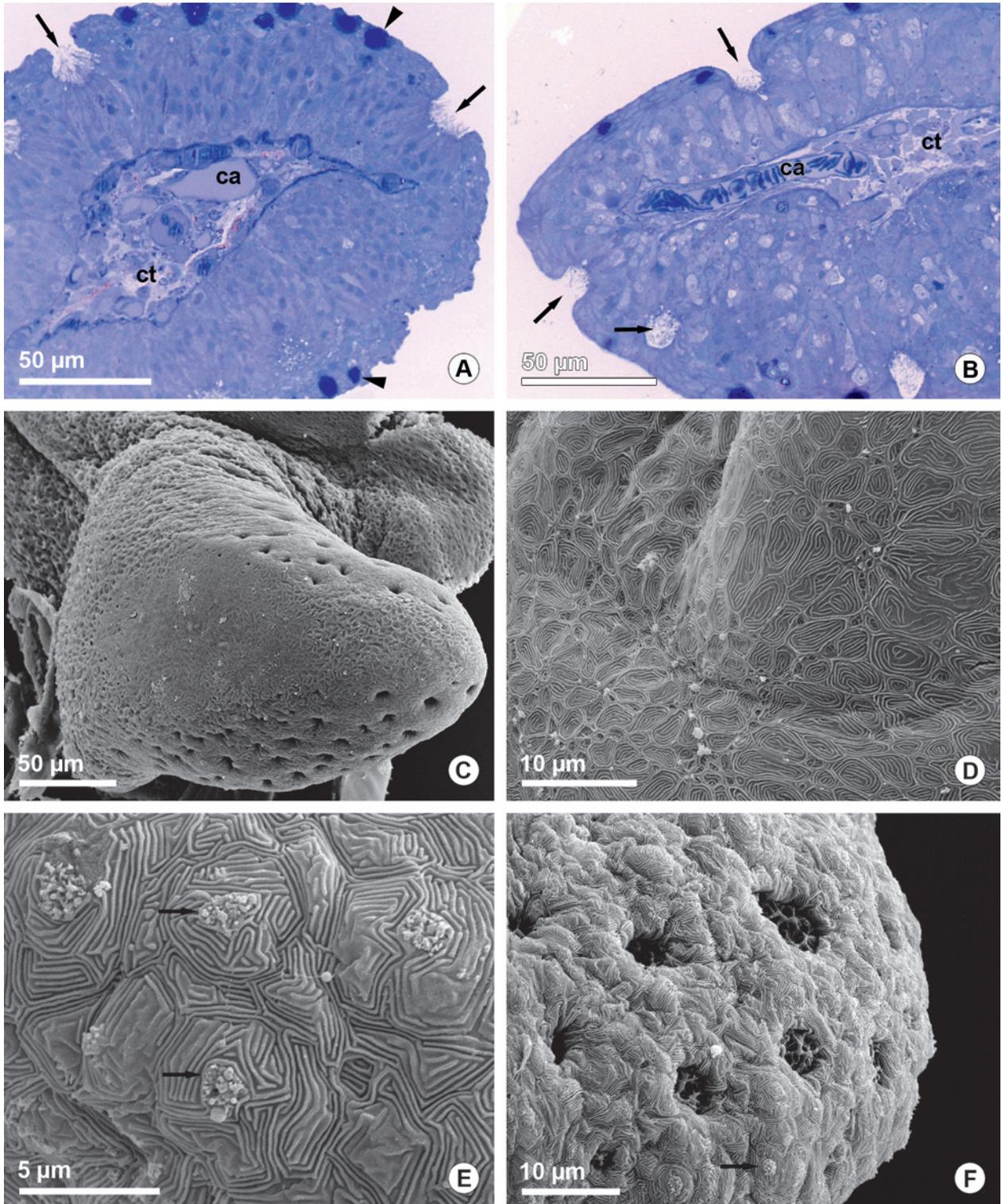
We used four specimens of *Dermogenys pusilla* (two males and two females) from a silver-coloured aquarium strain.

### Scanning electron microscopy (SEM)

Olfactory organs (two from males and two from females) were carefully excised and fixed some hours in 4% paraformaldehyde and 2.5% glutaraldehyde in 0.1 mol/l cacodylate buffer, pH 7.2, postfixed in 1% osmium tetroxide, dehydrated in a graded series of acetone, critical-point-dried (Leica EM CPD 030), mounted on aluminium stubs, coated with 25 nm gold (Cressington 108 auto) and examined in a Jeol JSM 35 CF scanning electron microscope.

### Transmission electron microscopy (TEM)

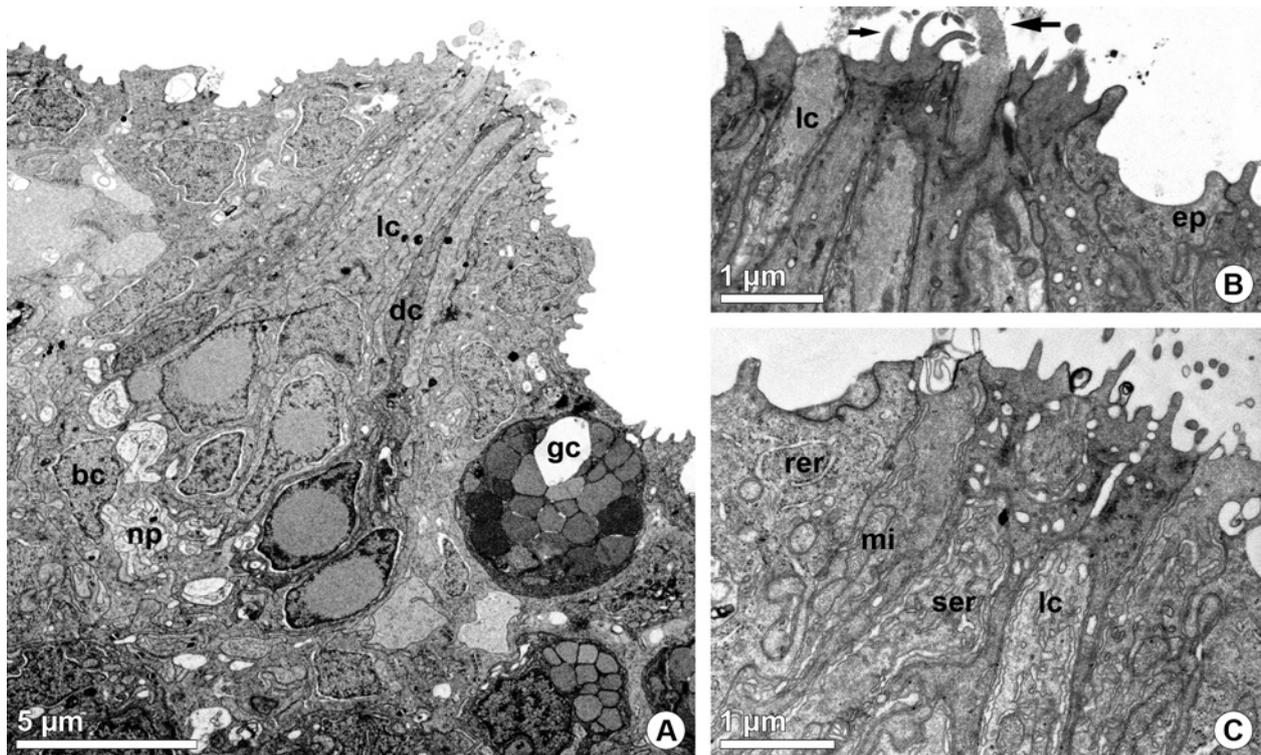
The remaining olfactory organs fixed in the same way as for SEM were embedded in Spurr's resin. For orienta-



**Fig. 2.** **A, B** Semithin sections; **C-F** SEM-micrographs. **A** Cross section of a nasal barbel. Note goblet cells (arrowheads) and olfactory pits (arrows). Capillary (ca), connective tissue core (ct). **B** Longitudinal section through the tip of a barbel. Note the connective tissue core (ct) with a capillary (ca). **C** Nasal barbel with numerous pits on its surface. **D** Posterior basis of the barbel lacking a distinct *fossa*. Note the ridged surface cells. **E** Small taste buds in the ridged epithelium covering the barbel (arrows). **F** Surface of the barbel with the nonsensory ridged epithelium (= epidermis) and pits containing the olfactory sensory epithelium; taste bud (arrow).

tion semithin sections (1 µm) were stained with toluidine blue-borax. Ultrathin sections were made with a diamond knife on a Reichert Ultracut, stained with lead-citrate and uranyl-acetate and examined using a Hitachi H 600

transmission electron microscope. Digital images were obtained with a Gatan Camera system, and the Digital Micrograph Software (Gatan, Munich).



**Fig. 3.** TEM of a taste buds on the nasal barbel and adjacent “non-sensory” epithelium. **A** Onion-shaped taste bud with electron dense (dc) and electron-light cells (lc). Note the rich nerve fiber plexus (np); basal cell (bc) and epidermis with a goblet cell (gc). **B** Apex of a taste bud showing light cells (lc) with a thick microvillus (large arrow) and dark cells with small apical microvilli (small arrow). **C** Detail of light cells (lc); mitochondrion (mi), smooth endoplasmic reticulum (ser); rough endoplasmic reticulum in an adjacent epidermis cell.

## Results

The paired olfactory organs of *Dermogenys pusillus* are situated just in front of the eyes lodged in a depression of the ethmoid bone. Each organ forms a small elongate papilla (= nasal barbel) arising immediately from the surface of the skin (Fig. 1). A prominent *fossa nasalis* is lacking in the specimens examined (see Fig. 2 D). Each nasal barbel is covered by a nonsensory epithelium, which does not differ from the adjacent epidermis. In between the epidermal cells epithelial depressions or pits are scattered, which house the sensory islets, i.e. the olfactory epithelium (Fig. 2 A, B, C, F). In addition, small taste buds are spread over the barbel (Fig. 2 E).

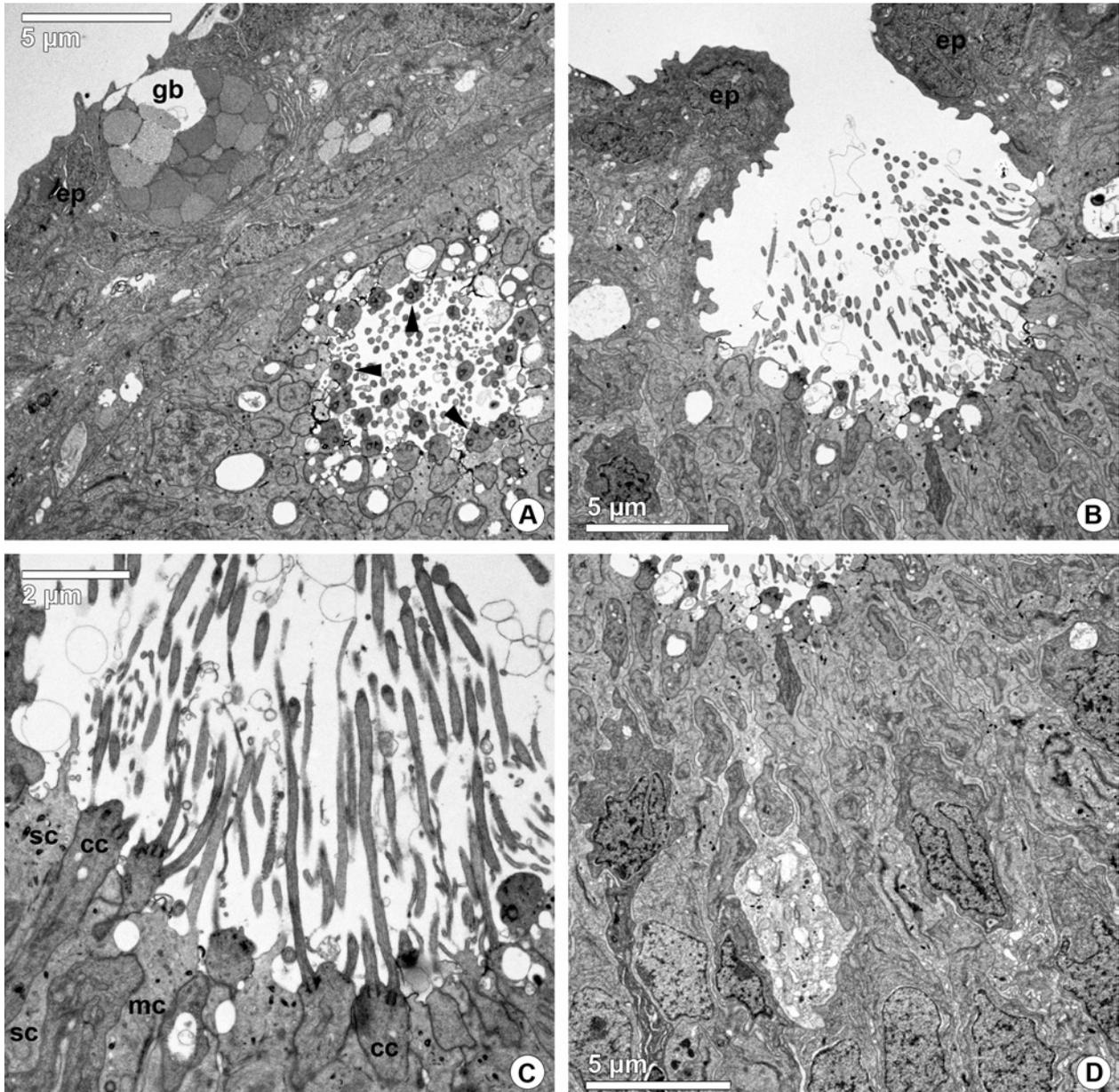
### Epidermis

The epidermis of the barbel (and the body) is a stratified squamous epithelium covering the dermis as well as connective tissue core of the barbel (Fig. 2 A, B). The superficial cells typically exhibit microridges on their surfaces (Fig. 2 D, E, F). The cytoplasm of epidermal cells contains the usual cell organelles and numerous tonofilaments. They are connected with adjacent cells by numerous spot desmosomes (maculae adhaerentes). Basal cells rest upon the basement lamellae (not shown). Epithelia are interspersed with mucous or goblet cells. Goblet cells

are roundish, mostly filled up with numerous secretory granules (Fig. see 3 A, 4 A).

### Taste buds

The intraepithelial small taste buds are irregularly distributed on the barbel (see Fig. 2 E). The receptor area (= endings of the apical microvilli of the receptor cell) measuring approx. 1 to 1.5 µm in diameter is slightly elevated above the surrounding epithelium (Fig. 2 E). In histological sections they can be hardly recognized. Low power electron microscopical images, however, show the typical shape of an onion spanning the width of the epithelium (Fig. 3 A). Three types of cells could be recognized by TEM: Vertically oriented elongated electron light and electron dark cells reaching a nerve plexus that is located between their basal parts and basal cells (Fig. 3 A). Light cells terminate apically in a single thick microvillus and dark cells in a tuft of microvilli (Fig. 3 A, B). Nuclei of both cell types are located basally. Cells are joined by small spot desmosomes (maculae adhaerentes). Light cells are rich in profiles of smooth endoplasmic reticulum and microtubules (Fig. 3 B, C). Dark cells contain numerous mitochondria, well-developed dictyosomes, also smooth endoplasmic reticulum and polyribosomes (Fig. 3 B, C). Processes of the dark and light cells are in contact with a well-developed nerve fibre plexus of unmyelinated dendritic axons above the ba-



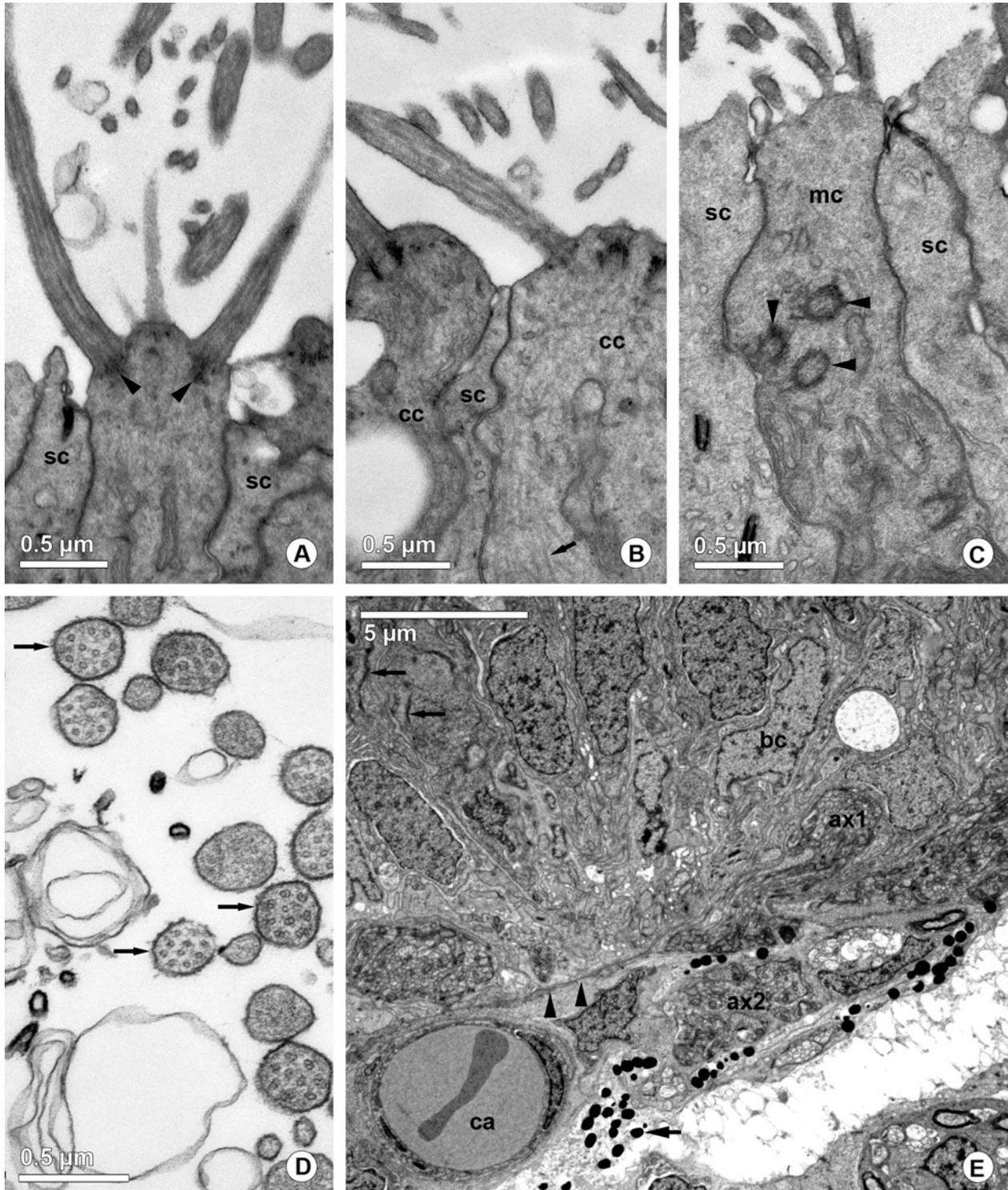
**Fig. 4.** TEM of the olfactory epithelium. **A** Horizontal section with the distal part of the olfactory epithelium extending into the pit; olfactory knobs with their basal bodies (arrowheads); adjacent epidermis (ep) with a goblet cell (gb). **B** Cross section showing the distal part of the olfactory epithelium. The rim of the pit is composed of epidermal cells (ep). **C** Distal part of the olfactory epithelium with ciliated (cc), microvillous (mc) and supporting cells (sc). **D** More proximal part of the olfactory epithelium showing the perikarya. Most of the light cells are supporting cells.

sal cells; the latter are oriented transversely to the bud's longitudinal axis (Fig. 3 A).

#### The sensory islets ("olfactory epithelium")

The largest portion of sensory islets seems to be concentrated in the upper third of the barbel (see Fig. 2 C). Generally, islets are submerged in the pits (Fig. 2 A, B, C, F; 4 A, B); they are rarely seen at the surface of the epidermis. The olfactory epithelium is pseudostratified. We recognized ciliated and microvillous receptor cells enclosed by supporting cells, and relatively small basal

cells (see Fig. 4 C, D, 5 E); ciliated nonsensory cells and so-called crypt cells could not be clearly identified. Receptor cells possess a distal (dendritic) swelling (= olfactory knob), from which the cilia or microvilli arise (Fig. 5 A-C). Microvillous cells show several centrioles beneath the olfactory knob (Fig. 5 C). Cilia show a variable arrangement of microtubules including the typical pattern of nine doublets surrounding two single microtubules (9 + 2 pattern), but obviously also a varying number of single microtubules (Fig. 5 D). Cells contain the usual cell organelles, rough endoplasmic reticulum, a relatively high number of mitochondria and more or less longitudinally arranged microtubules (= neurotubules).



**Fig. 5.** TEM of the olfactory epithelium. **A, B** The olfactory knobs of a ciliated receptor cell possess several cilia and basal bodies (arrowheads); supporting cell (sc); microtubules (arrow). **C** Sensory microvillous cell (mc) with centrioles (arrowheads) beneath the olfactory knob; supporting cells (sc). **D** Arrangement of microtubules in the cilia varies considerably (arrows). **E** Basis of the olfactory epithelium with nuclei mainly of the supporting cells and putative basal cells (bc), bundle of tonofilaments (long arrows). Note the basally situated unmyelinated axons (ax1) and axons (ax2) in the connective tissue core of the barbel; basal lamina (arrowheads); capillary (ca) with an erythrocyte; melanocyte (short arrow).

The perikarya of the receptor cells are located in the midregion of the epithelium (see Fig. 4 D). Supporting cells extend from the basal lamina to the surface of the olfactory epithelium and bear some short microvilli (if

at all), bundles of intermediate filaments (tonofilaments) and small electron granules (Fig. 4 C, D). Their perikarya are situated more basally (Fig. 5 E).

## Core of the nasal barbel

The connective tissue core of the barbel contains blood vessels, numerous unmyelinated nerve fibres (olfactory axons) and several chromatophores (Fig. 2A, B; 5E).

## Discussion

The present study shows that the nasal barbels of *Dermogenys pusilla* (Zenarchopteridae) are simple cone-like papillae covered by sensory and non-sensory epithelia. The non-sensory epithelium that separates several widely spaced depressions from each other housing the sensory islets, i.e. the olfactory epithelium, represents a typical epidermis; among its cells small, likewise widely spaced taste buds are interspersed. The epidermis of *D. pusilla* adjacent to the nasal barbel and the non-sensory epithelium covering the nasal barbel contains the cell types generally found in fish skin, i.e. basal cells, intermediary cells, superficial cells as well as the mucus-producing goblet cells and taste buds. Superficial cells bear the characteristic pattern of microridges generally suggested to be involved in maintaining an adherent mucous layer and /or epithelial rigidity or plasticity (e.g. WHITEAR, 1986; ZEISKE *et al.*, 1992).

Presence of taste buds, to our knowledge not yet described in the non-sensory epithelium of any olfactory organ of fish (see literature cited above) does not appear surprising in consideration of the development of olfactory organs from ectodermal olfactory placodes and the origin of the nonsensory epithelium from the epidermis (ZEISKE & HANSEN, 2005). Notwithstanding, a detailed study of the development of these unique olfactory organ would be of interest.

Regarding the ultrastructure only a few comments will be given, as taste buds and olfactory islets share the most distinctive characteristics reported for other fish species (e.g. HANSEN & REUTTER, 2004; REUTER & HANSEN, 2005). According to the characteristics of their cytoplasm and/or their position, taste buds contain at least three cell types, i.e. (1) light cells with a large, rod-shaped receptor villus at the apex surrounded by (2) dark cells with numerous small receptor villi, and (3) basal cells. Both, light and dark cells are considered as sensory cells and several subtypes, characterized by differently shaped receptor villi, have been described indicating that “no “common” type of TB exists in fish” (REUTER & HANSEN, 2005, p. 227).

The olfactory sensory islets are more or less sunken in the *D. pusilla* specimens examined herein, but in other Zenarchopteridae including *D. pusilla* (see Fig. 8 in GREVEN, 2006) they seem to reach the same level as the surrounding epithelium (unpublished). This varying depth of the sensory islet may also depend on the species, the developmental stages or simply on fixation. Receptor cells in the olfactory epithelium represent bipolar primary

neurons. The ciliated receptor cells seem to be strikingly variable concerning the axonemal complex, which has been so far described as the typical 9 + 2 or 9 + 0 arrangement of microtubules (for review see YAMAMOTO, 1982; ZEISKE *et al.*, 1992). The 9 + 0 pattern is also known from ciliated receptors of *B. belone* (e.g. THEISEN *et al.*, 1980; see also ZEISKE *et al.*, 1992). So-called crypt cells, i.e. ovoid cells without dendrites and with a crypt-like invagination that contains short cilia and microvilli, which are regarded as a common characteristic of all Actinopterygii (HANSEN & FINGER, 2000), were not unequivocally identified in the olfactory epithelium of *D. pusilla*; possibly these cells were not caught in our sections.

In both types of olfactory organs, i.e. the type with chambers and nostrils and the “beloniform” type, sensory regions (typically arranged in sensory islets that was considered as derived character of the Atherinomorpha by PARENTI, 1993) are either separated from each other by a non-sensory epithelium or the sensory epithelium is distributed continuously on the olfactory lamellae and sensory and non-sensory epithelia are located separately on each lamella. In a comparative approach HANSEN & ZIELIENSKI (2005) classified olfactory organs in teleosts according to the folding of the olfactory epithelium (OF) in the olfactory chamber. They distinguished (1) multi-lamellar (OF on a multi-lamellar structure); (2) flat (OF on a flat surface on the floor of the olfactory chamber); (3) OF on a single lamellar fold on the floor of the olfactory chamber; (4) the floor of the olfactory chamber contains a small rostral fold and a small caudal fold and is otherwise flat. Accordingly, olfactory organs of the Beloniformes are flat and unilamellar and the beloniform species *Oryzias latipes* (YAMAMOTO, 1982) and *Belone belone* (THEISEN *et al.*, 1980) and some other non-beloniform teleosts were given as examples. In the same year ZEISKE & HANSEN (2005) emphasized that the beloniform olfactory organ lacks an olfactory chamber and considered its special organisation as synapomorphy of the Exocoetoidei (see introduction). In the Beloniformes hitherto examined olfactory organs have been described as protruding from a relatively deep groove and the barbel itself as short and speculate, as a mushroom-shaped boss, or as fungi form with irregularly arranged lobes preferably on its posterior face (see citations above). Such olfactory organs appear more complex as the simple cones in *D. pusilla* (and other Zenarchopteridae), where the *fossa* is reduced (see also ANDERSON & COLETTE, 1991; DOWNING MEISNER, 2001) or even absent. Further, barbels are simple and straight cones with a large portion of nonsensory epithelium and widely spaced sensory islets (see in comparison figure 6 a in THEISEN *et al.*, 1980 with closely spaced islets in *B. belone*). A reduced *fossa* and an elongated barbel protruding out of the *fossa* have been proposed as synapomorphies of the internally-fertilizing halfbeaks (e.g. ANDERSON & COLETTE, 1991; DOWNING MEISNER, 2001). We think olfactory organs of Exocoetoidei may be further differentiated with the least complex (derived?) olfactory organs (in terms of the size of the lamellar surface, the size and spacing of sensory islets and depth of the *fossa*

*nasalis*) in the Zenarchopteridae. This assumption, however, has to be substantiated in further studies including a wider spectrum of species.

Information about the development of the “beloniform” type of olfactory organs is poor. THEISEN *et al.* (1980) described the anlage of the olfactory organ in *B. belone* as a smooth groove initially lined with a continuous sensory epithelium. Later the groove becomes triangular and a papilla arises from its bottom, which develops areas of nonsensory epithelium separating the sensory epithelium into islets. Ciliated non-sensory cells were found only in early stages of development, but not in the olfactory epithelium of adults (see also ZEISKE & HANSEN, 2005).

Effectiveness and adaptive value of the simple (relative to the chamber type) olfactory organs of Beloniformes are largely unexplored. ZEISKE & HANSEN (2005) cite some unpublished results from experiments in a laminar flow channel suggesting that the elongate nasal barbels in *Belone belone* are “an adaptation to the hydrodynamic situation” (p. 22). Simplicity of the organ has also been discussed as being indicative for a reduced olfactory sense (anosmic teleosts) most notably in fishes, in which eyes appear to be better developed than the nostril (S.P. SINGH, 1977; see TEICHMANN, 1954). There are, however, no studies that substantiate this assumption. Olfactory islets (as well as taste buds) of the nasal barbel are always exposed to the environmental waters. The lack of ciliated non-sensory cells, whose presence would enhance olfaction by creating a water flow around the barbel, may argue for an active swimming or other movements in *D. pusilla* to perceive odorants. Males of *D. pusilla* and other Zenarchopteridae check the receptivity of their females by nibbling with their jaws near the female’s genital opening. Therefore, the nasal barbel with their olfactory islets and taste buds (present in high numbers also on the lower jaw) may allow for a dual chemical control of the females (GREVEN, 2006, 2010).

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