

# Fine structure of the dorsal papillae in the holothurioid *Holothuria forskali* (Echinodermata)

D. VandenSpiegel\*, P. Flammang\*‡, D. Fourmeau\*, M. Jangoux†

**Abstract.** The dorsal surface of the holothurioid *Holothuria forskali* bears several longitudinal rows of modified podia called papillae. Each papilla consists of a conical stem topped by an hemispherical bud. Their gross tissue stratification is the same all along the papilla being made up of four tissue layers, viz. an inner mesothelium, a connective tissue layer, a nerve plexus and an outer epidermis. The latter is differently organized according to whether it belongs to the stem or to the bud. The epidermis of the bud is built up by ciliated cells that intimately contact the nerve plexus and have the classical structure of echinoderm sensory cells. The papillae are thus sensory organs involved in mechanoreception and possibly chemoreception.

**Keywords:** Ultrastructure, sensory organ, ambulacral system, holothurioid, echinodermata

## Introduction

Echinoderm ambulacral appendages are multifunctional organs. Indeed, they may be involved in locomotion, feeding, respiration and sensory perception (Lawrence, 1987). This variety of functions often comes with a variety of shapes. Aspidochirote holothurioids possess three types of ambulacral appendages: peltate appendages (the tentacles) surrounding the mouth, cylindrical appendages (the tube feet) covering most of the ventral surface of the individuals, and conical appendages (the papillae) occurring on the individual's dorsal surface. Tentacles and tube feet are used in relation to the substratum allowing the holothurioid either to handle it for feeding (tentacles) or to stick on it for locomotion and anchorage (tube feet). The papillae, on the other hand, are supposed to be sensory in function (Hyman, 1955). Whereas the ultrastructure of the tentacles and tube feet has already been described (e.g. Bouland et al.,

1982; McKenzie, 1988; Flammang and Jangoux, 1992 respectively), the morphology of the papillae has never been studied at the ultrastructural level.

The aim of this paper is to describe the fine structure of the dorsal papillae in the species *Holothuria forskali*, and to discuss their presumed sensory function by comparing them to other echinoderm organs known to be sensory.

## Materials and methods

Individuals of *Holothuria forskali* (Delle Chiaje, 1823) were collected by SCUBA diving in the Bay of Morlaix (Brittany, France) in October 1993. They were transported to the marine biology laboratory of the Mons University and kept alive in a closed circuit marine aquarium (13°C, 3.3% salinity).

For light microscopy, papillae were cut off individuals previously anaesthetized with propylene phenoxetol (0.2% in sea water), fixed in Bouin's fluid, embedded in paraplast, and cut into 7 µm thick sections. Sections were stained with Masson's trichrome and Mayer's hemalum coupled with phloxine and light green. Histochemical observations were performed using alcian blue pH 2.6 and the periodic acid-Schiff (PAS) tech-

\* Laboratoire de Biologie marine, Université de Mons-Hainaut, 7000-Mons, Belgium.

† Laboratoire de Biologie marine, Université Libre de Bruxelles, 1050-Bruxelles, Belgium.

‡ Senior Research Assistant, National Fund for Scientific Research, Belgium.

niques for the detection of mucopolysaccharides (Ganter and Jollès, 1969–70).

For scanning electron microscopy (SEM), papillae were fixed in Bouin's fluid for 24h (Lahaye and Jangoux, 1985). They were dehydrated in graded ethanol, dried by the critical point method (using CO<sub>2</sub> as transition fluid), mounted on aluminium stubs, coated with gold and observed with a Jeol JSM 6100 scanning electron microscope. Papilla spicules were cleaned off their associated soft tissues in 10% (v/v) common bleach. They were air-dried, mounted on aluminium stubs and processed as before.

For transmission electron microscopy (TEM), papillae were fixed by immersion in 3% glutaraldehyde in cacodylate buffer (0.1 M, pH 7.8) for 3h at 4°C. They were then rinsed in cacodylate buffer and postfixed for 1h in 1% osmium tetroxide in the same buffer. After a final buffer wash, they were decalcified according to the method of Dietrich and Fontaine (1975), dehydrated in graded ethanol, and embedded in Spurr. Sections were cut on an LKB V ultramicrotome, contrasted with uranyl acetate and lead citrate, and observed with a Zeiss EM 10 transmission electron microscope.

## Results

### External morphology and in vivo observations

Papillae are arranged in six longitudinal rows on the dorsal surface (bivium) of the holothurioids. Within each row, papillae organize grossly in 3 to 4 parallel series. Each papilla consists of a conical stem topped by a bud measuring ca. 80 µm thick and 200 µm wide (Figs 1,2). Two areas can be distinguished along the stem, a pigmented proximal part (ca. 8mm long) and a whitish distal part (ca. 2mm long).

When cleared of the cuticle, the surface of the papillae appears uniformly covered with the microvilli of epidermal cells. In addition, numerous cilia are observed on the surface of the bud. These are either short or long (Fig. 3). When the cuticle is preserved only the tips of long cilia are visible on SEM pictures.

Mechanical stimulation of the bud usually results in the contraction of the papilla, and the intensity of the reaction depends on the intensity of the stimulation. After a short stimulation (just touching the apical part of a papilla) the bud and the stem apical part (viz. the whitish part) retract into the stem basal part. Prolonged mechanical stimulation (pinching the apical part of the papilla with a forceps) results in the overall retraction of the papilla into the body wall of the individual, followed by retraction of adjacent papillae. When several papillae are stimulated simultaneously an overall contraction of the holothurioid's body is observed. This is sometimes followed by the expulsion of Cuvierian tubules (Cuvierian tubules are defensive organs; for more details see Vandenspiegel and Jangoux, 1987).

### Microscopic anatomy

Papillae are made of four tissue layers, each running along the entire length of the organ. These are, from the inside to the outside, a mesothelium, a connective tissue layer, a nerve plexus, and an epidermis covered by a well-marked cuticle (Fig. 6). The organization of the inner tissues is almost similar in the whole papilla whereas the epidermis shows conspicuous differences according to whether it belongs to the stem or to the bud.

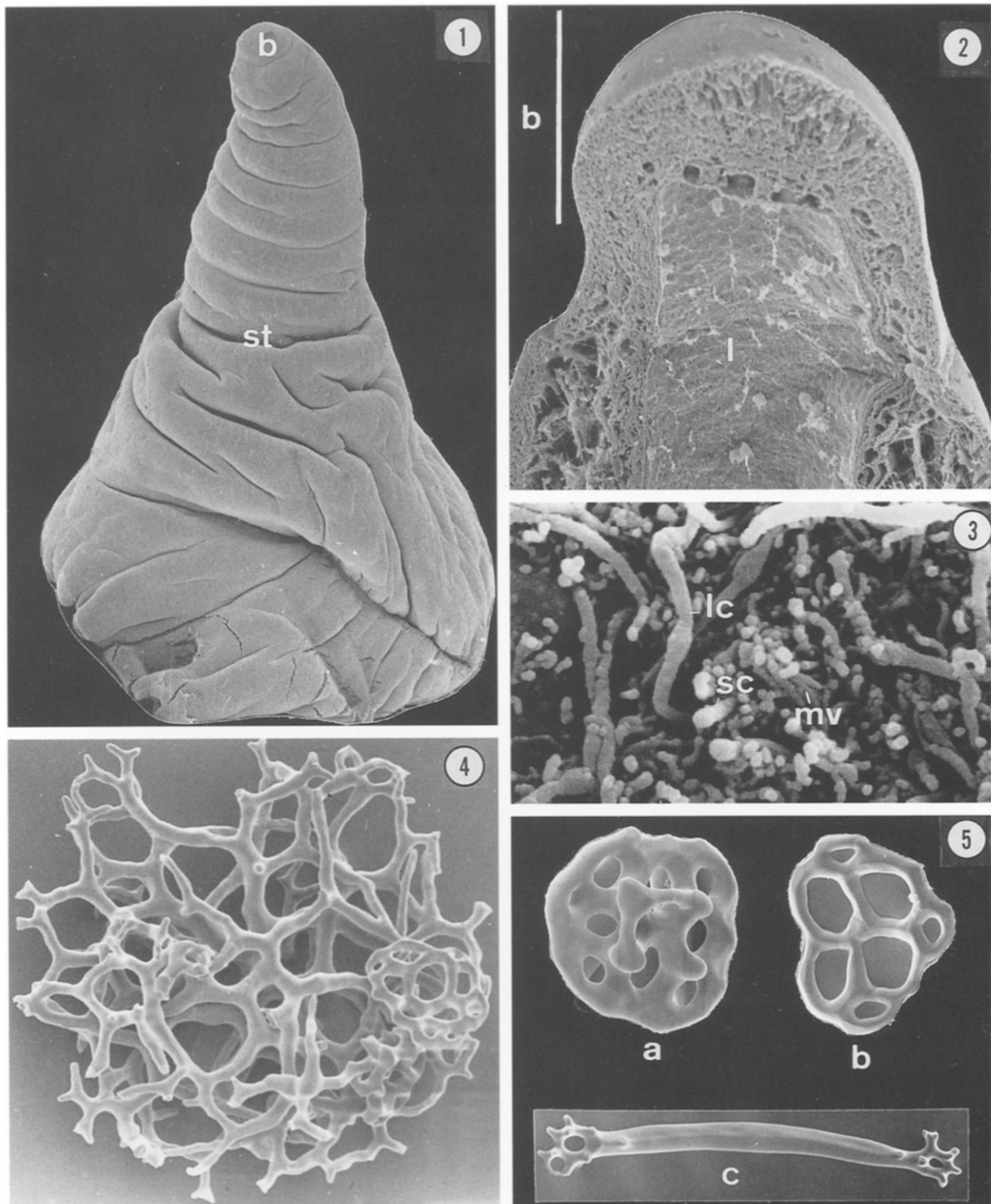
#### 2.1. Inner tissues

**Mesothelium.** The lumen of the papillae is lined by a mesothelium that is about 10 µm thick except at the vicinity of the papilla longitudinal nerve (Fig. 7) and in the bud, where it is thinner and measures only 5 µm in thickness. The mesothelium of the stem is pseudostratified and made up of two cell types, viz. adluminal cells and myoepithelial cells, while in the bud it is monostratified and only made up of adluminal cells.

Adluminal cells are T-shaped with a flattened apical part and a thin basal part (Fig. 8). They each bear one long vibratile cilium and many short apical microvilli (Fig. 9). Adluminal cells attach to each other through junctional complexes consisting of an apical zonula adhaerens and a subapical 'double-septum' septate desmosome (see Green, 1981). They attach to the basal lamina of the mesothelium through desmosome-like structures (Fig. 10). The nucleus is located in the apical part of the cell and the cytoplasm contains a juxtaneucleus Golgi apparatus, a few mitochondria, and a well developed RER (Fig. 8).

Myoepithelial cells never line the ambulacral lumen of the papillae, being overtopped everywhere by adluminal cells (Fig. 8). Myoepithelial cells contain a bundle of myofilaments associated with numerous mitochondria. Myofibrils are oriented longitudinally and form together a longitudinal muscle layer (viz. the retractor muscle of the papilla). Myoepithelial cells attach to each other and to the basal lamina through desmosome-like structures (Fig. 10).

**Connective tissue.** Three areas may be recognized in the connective tissue layer of the papilla stem, namely a thin and very dense internal layer (located under the mesothelium), a dense middle layer (which encloses the nerve plexus) and a loose external layer (located under the epidermis). In the bud the connective tissue layer is thinner than in the stem, and consists of only two layers, corresponding to the very dense and the dense layers of the stem. In both the stem and the bud, each layer contains striated collagen fibres that are mostly perpendicular to the long axis of the papilla. They also enclose spherulous coelomocytes and pseudopodial cells (fibrocyte-like cells). The most external layer sends outwards bundles of connective tissue fibres (Figs 6, 21) that insinuate themselves between the epidermal cells and



**Figs 1–5.** *Holothuria forskali*. Outer aspect of a papilla and of the spicules it includes. b: bud, l: papilla lumen, lc: long cilium, mv: microvilli, sc: short cilium, st: stem.

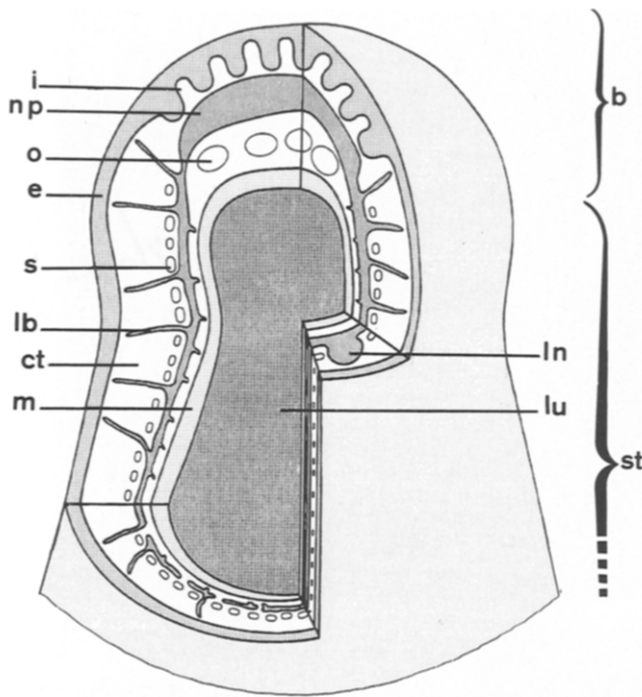
**Fig. 1** Entire papilla ( $\times 12$ ).

**Fig. 2** Longitudinal section through the apical part of a papilla ( $\times 200$ ).

**Fig. 3** Bud surface cleared of the cuticle ( $\times 9000$ ).

**Fig. 4** Bud supporting ossicle ( $\times 250$ ).

**Fig. 5** Stem supporting spicules ( $\times 300$ ). a: table, b: buton, c: rod.



**Fig. 6** *Holothuria forskali*. Schematic representation of the papilla bud and the upper part of the stem (the epineural sinus has not been represented – not to scale). b: bud, ct: connective tissue, e: epidermis, i: connective tissue indentation, lu: lumen, lb: lateral nerve branch, ln: longitudinal nerve, m: mesothelium, np: nerve plate, o: bud supporting ossicle, s: spicule, st: stem.

attach apically to the pigmented cells of the epidermis by way of hemidesmosomes.

In both the stem and the bud the dense layer encloses the skeleton of the papilla. In the stem this skeleton is located between the epidermis and the nerve plexus; it is made up of mixed spicules of three types: tables (Fig. 5a), buttons (Fig. 5b) and rods (Fig. 5c). In the bud, the skeleton is located between the mesothelium and the nerve plexus; it consists of a large rounded ossicle made of perforate stereom (Fig. 4) that is surrounded by a ring made up of mixed small spicules similar to those occurring in the stem (viz. tables, buttons and rods).

**Nerve plexus.** The nerve plexus is located in the dense connective tissue layer. It is similar to the one described by Flammang and Jangoux (1992) in the tube feet of *Holothuria forskali*. In the stem the nerve plexus looks like a cylindrical fenestrated sheet of nervous tissue, asymmetrically thickened to form a longitudinal nerve (Figs 6, 7), whereas in the bud it forms a plate of nervous tissue located just above the bud-supporting ossicle and intimately contacting the basal part of the epidermal cells (Fig. 6, 21). All along the stem the nerve plexus sends out short and long lateral branches to innervate the mesothelium or the epidermis, respectively (Figs 6, 7, 12). Branches that innervate the epidermis intimately contact the basal part of epidermal cells. On the contrary, branches directed towards the mesothelium never contact the mesothelial cells, they end at the level of the very dense connective tissue layer (Fig. 12).

Closely appressed to the outer side of the nerve plexus of the stem is a narrow sinus (the epineural sinus) which is lined by inner and outer adsinusal epithelia (Fig. 13). Each outer and inner adsinusal cell bears a single cilium that extends into the epineural sinus (Fig. 14). The cells are attached to each other by junctional complexes. The outer adsinusal cells are highly flattened (c.a. 1 to 1,5  $\mu\text{m}$ ) and rest upon the outer basal lamina of the nerve plexus. The cell body houses an ovoid nucleus, a Golgi apparatus, a few scattered mitochondria and a well-developed RER. It also contains one or several bundles of filaments that cross the cell and join its apical and basal membranes (Fig. 13). These particular structures basally bind the connective tissue by way of hemidesmosomes. The inner adsinusal cells rest upon the nerve plexus itself. They consist of a flattened cell body sending inward a slender basal process that traverses the whole nerve plexus (Figs 11, 13). The cell body is similar to that of the outer adsinusal cells. The basal process mainly consists of a bundle of intracellular filaments that extends from the apex of the cell body to the basal part of the cell process (Figs 11, 13). The basal process is attached to the inner basal lamina by hemidesmosome-like structure. Neither the epineural sinus nor the inner and outer adsinusal epithelia extend

**Fig. 7–14** *Holothuria forskali*. Fine structure of the inner tissues of a papilla. ac: adluminal cell, b: basal lamina, bf: bundle of filaments, c: cilium, ct: connective tissue, dct: very dense connective tissue layer, eac: external adsinusal cell, es: epineural sinus, hd: hemidesmosome like structure, iac: internal adsinusal cell, l: papilla lumen, lb: lateral nerve branch, lct: dense external connective tissue layer, ln: longitudinal nerve, m: mesothelium, mc: myoepithelial cell, mit: mitochondrion, my: myofibril, n: nucleus, np: nerve plexus, sd: septate desmosome.

**Fig. 7** Transverse section through the stem (semithin section) ( $\times 600$ ).

**Fig. 8** Transverse section through the mesothelium ( $\times 9000$ ).

**Fig. 9** Longitudinal section through the cilia of an adluminal cell of the mesothelium ( $\times 20\,000$ ).

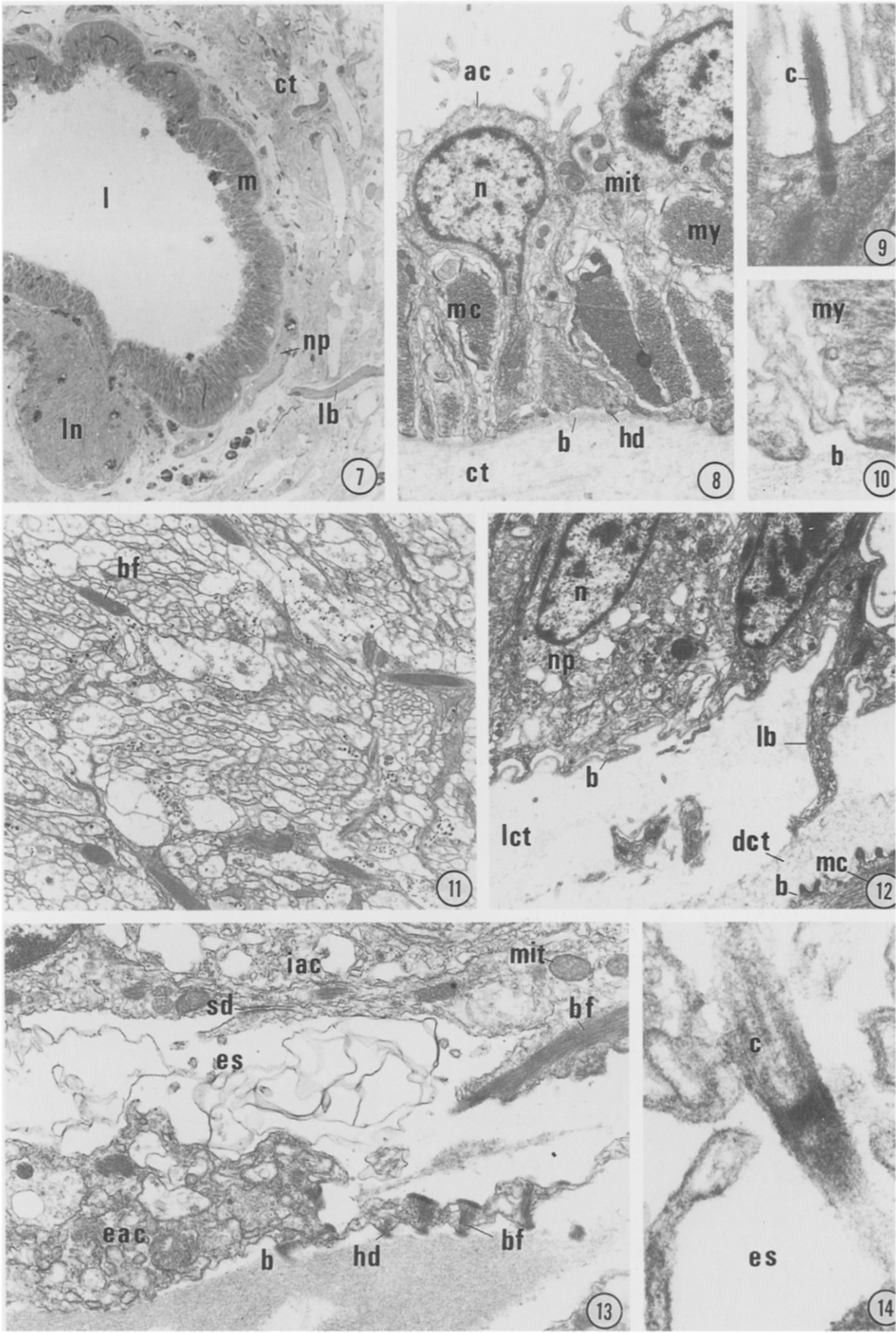
**Fig. 10** Detail view of the basal part of a myoepithelial cell ( $\times 30\,000$ ).

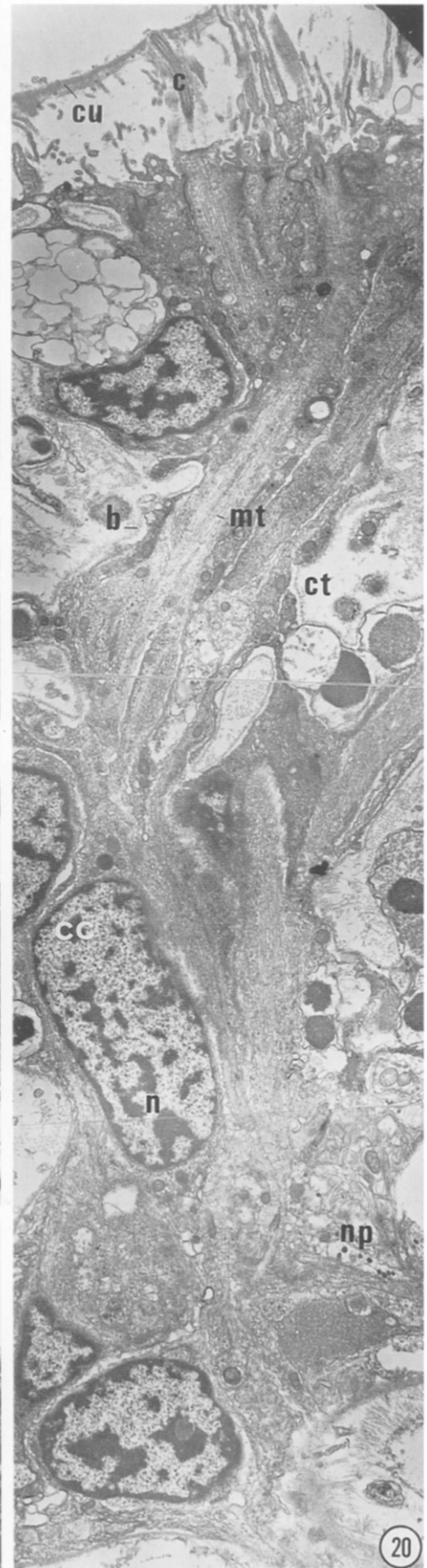
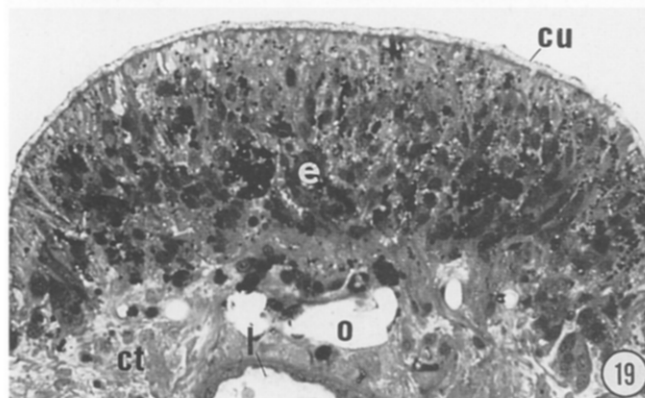
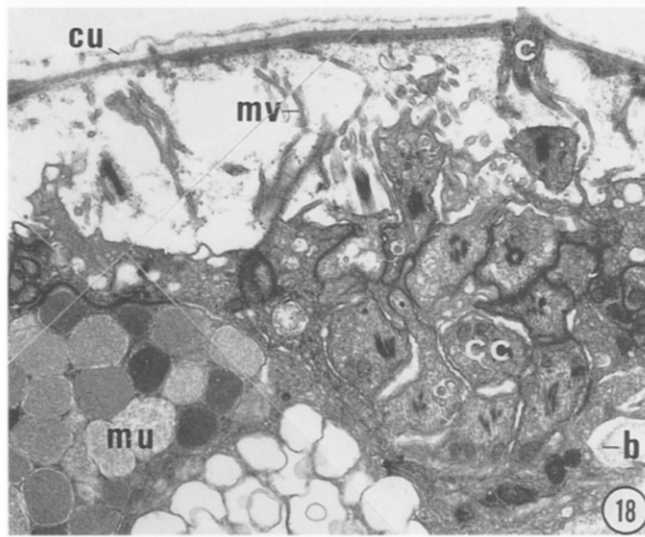
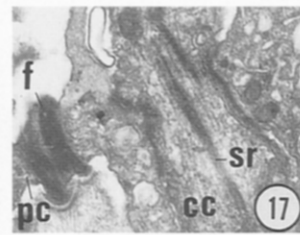
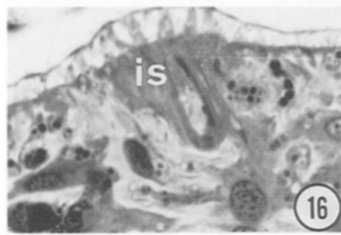
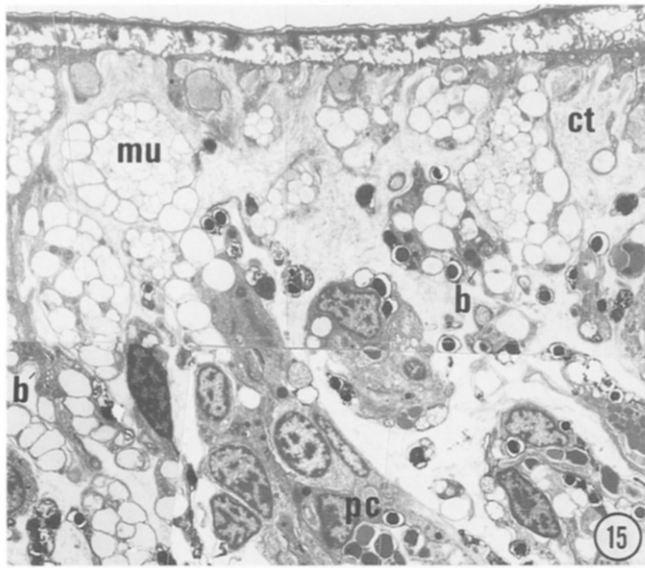
**Fig. 11** Transverse section through the longitudinal nerve ( $\times 20\,000$ ).

**Fig. 12** Transverse section through the internal part of the nerve plexus and a lateral branch ( $\times 10\,000$ ).

**Fig. 13** Epineural sinus ( $\times 20\,000$ ).

**Fig. 14** Detail view of the epineural sinus ( $\times 40\,000$ ).





into the bud or the lateral branches. A single continuous basal lamina lines the epidermis, the nerve lateral branches and the outer and inner surfaces of the stem nerve structures.

### Epidermis

The papilla epidermis is a monostratified epithelium covered by a well-marked cuticle. It is made up of four cell types: pigment cells, mucocytes and two types of ciliated cells which are all connected apically by junctional complexes. Although the four cell types occur all along the papilla, their proportions and, therefore, the epidermal organization are different according to the considered area of the papilla. In the stem epidermis, pigment cells are the most numerous and form a meshwork in which the other cell types are homogeneously distributed (Fig. 15). However, in the distal part of the stem (viz. the whitish part) pigment cells are less numerous and ciliated cells tend to aggregate in clusters of 10–15 cells (Figs 16, 18). (This is the only morphological difference between the two parts of the stem). On the contrary, the cells in the bud epidermis are grouped together within islets separated by connective indentations (Figs 19, 20, 21). In each islet, ciliated cells are the most numerous (about 5 times more than the other cell types). Ciliated cells generally occur in the middle of the islet being surrounded by mucocytes and pigment cells (Figs 20, 21). At the surface of the epidermis, pigment cells enlarge and join the mucocytes to form a continuous cellular layer (Fig. 21).

Pigment cells are T-shaped cells having a thin but extended apical area, a narrow neck and an enlarged nucleus-containing basal part (Figs 15, 21). The cytoplasm of pigment cells contains numerous granules, about 2 µm in diameter, sometimes enclosing very electron dense material. The apical part of these cells contains filaments that link the connective tissue fibres and the cuticle together by way of hemidesmosomes (Figs 17, 21).

Mucocytes are round to egg-shaped cells. The cytoplasm of these cells is filled with densely packed vacuoles containing Alcian Blue and PAS positive material (Figs 18, 21).

Except for the cilium length, which is 10 µm for the long cilia and 4 µm for the short cilia, the two types of monociliated cells have the same morphology. These are

elongated cells with a narrow neck, an enlarged middle part containing the nucleus and an elongated basal part. The latter consists of a thin process which is entangled in the axons of the nerve plexus (Figs 20, 21). The cytoplasm is electron dense and characterized by its richness in microtubules arranged parallel to the long axis of the cell (Figs 20, 21). It also contains a poorly developed Golgi apparatus and large mitochondria. Long and short cilia have both a regular 9×2+2 arrangement of microtubules and possess a long striated rootlet extending the length of the apical third of the cell. The cilium is surrounded by a ring of nine microvilli.

All along the papilla, the epidermis is covered by a multilayered cuticle (about 6 µm thick). This cuticle is separated from the epidermis by a subcuticular space crossed by the microvilli of the epidermal cells (Figs 15, 18, 20, 21). It is only traversed by the tips of the long cilia and is indirectly bound to the connective tissue indentations via the intracellular bundles of filaments of the pigment cells of the epidermis (Figs 15, 17, 21).

### Discussion

*Holothuria forskali* possesses, on its dorsal surface, several rows of conical projections, the papillae, each consisting of a contractile stem topped by a hemispherical bud. Papillae are morphologically similar to both the tentacles and the tube feet and have the same overall tissue stratification, that is, from the inside to the outside, a mesothelium, a connective tissue layer, a nerve layer and an epidermis (Bouland et al., 1982, Flammang and Jangoux, 1992). However, some ultrastructural differences occur which may be linked to the respective functions of these different ambulacral appendages. The peribuccal tentacles allow the holothurioids to handle the particles on which they feed. On the other hand, tube feet allow the holothurioids to stick to the substratum for locomotion and anchorage. In both types of ambulacral appendages, secretory cells of the apical epidermis account for stickiness while the stem provide a great motility. The papillae are not used in relation to the substratum and, indeed, their bud epidermis lacks specialized secretory cells. Moreover, they are only capable of protraction-retraction movements. Protraction is due to an increase of the hydrostatic

Fig. 15–20 *Holothuria forskali*. Fine structure of the epidermis of a papilla. b: basal lamina, c: cilium, cc: ciliated cell, ct: connective tissue, cu: cuticle, e: epidermis, f: filaments, is: islet of ciliated cells, l: papilla lumen, mt: microtubule, mu: mucocyte, mv: microvilli, n: nucleus, np: nerve plexus, o: bud-supporting ossicle, pc: pigment cell, sr: striated rootlet.

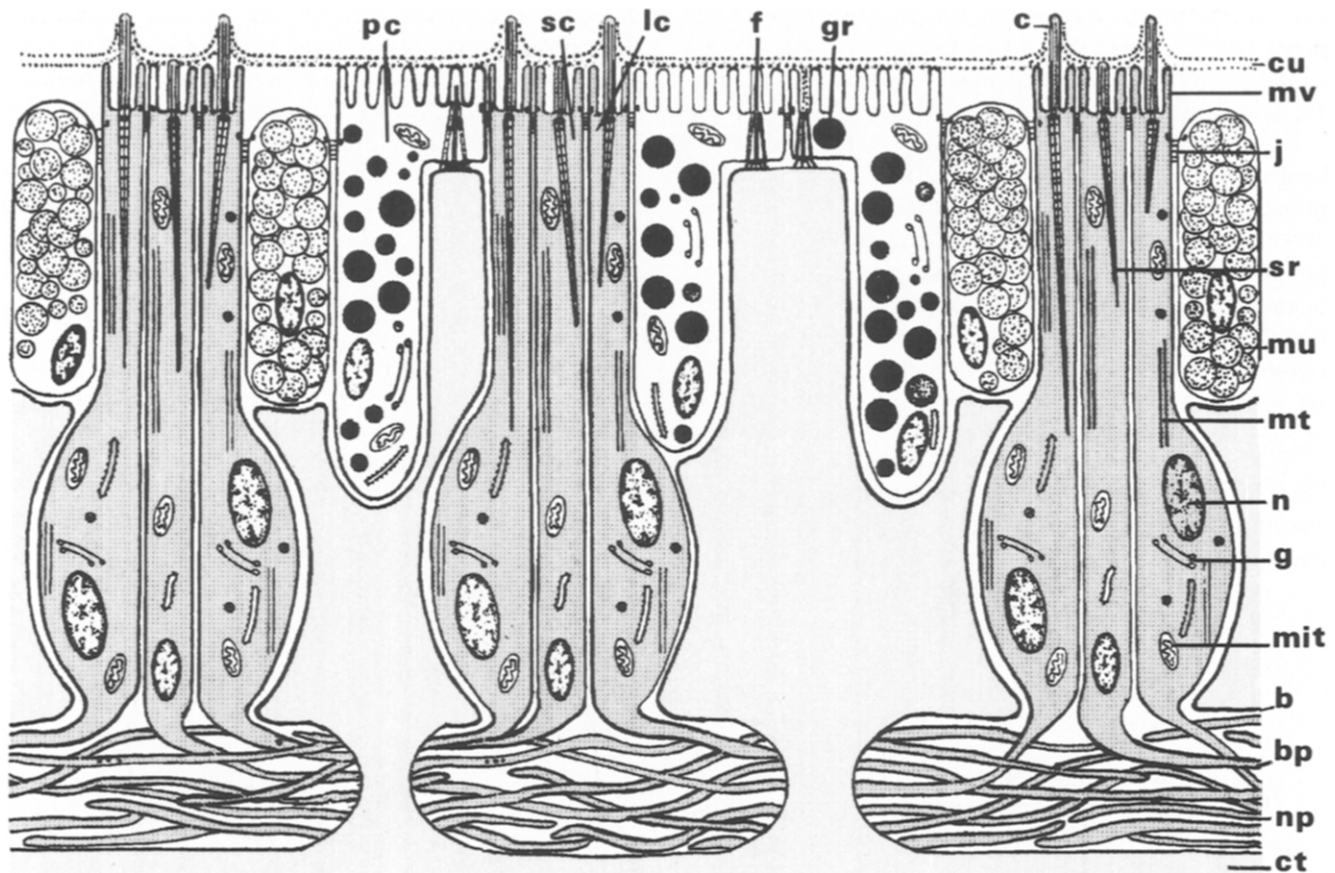
Fig. 15 Stem epidermis (× 2500).

Fig. 16 Semithin section through an islet of ciliated cells (× 1000).

Fig. 17 Longitudinal section through the apical part of a ciliated cell (× 25 000).

Fig. 18 Oblique section through the epidermis of the papilla (mucocytes and islet of ciliated cells) (× 18 000).

Fig. 19 Longitudinal section through the bud (semithin section) (× 110).



**Fig. 21** Reconstruction of a longitudinal section through the bud epidermis showing its relation with the nerve plate (not to scale). b: basal lamina, bp: basal process, c: cilium, ct: connective tissue, cu: cuticle, f: filaments, g: Golgi apparatus, gr: granule, j: junctional complex, lc: 'long cilium' ciliated cell, mit: mitochondrion, mu: mucocyte, mt: microtubule, mv: microvilli, n: nucleus, np: nerve plate, pc: pigmented cell, sc: 'short cilium' ciliated cell, sr: striated rootlet.

pressure in the papilla ambulacral cavity whereas retraction is due to the contraction of the retractor muscle of the papilla. This muscle is less developed in the papillae than in the tentacles and tube feet.

As in tentacles and tube feet, the apical part—viz. the bud—is the most specialized area of a papilla. The bud is clearly distinct from the stem in having an epidermis mostly built with elongated epidermal cells each bearing a cilium. These cells fit very well Holland's description (1984) of echinoderm sensory cells. They are columnar, typically bear an apical cilium arising from a basal body associated with a long ciliary rootlet; they also contain, associated with the ciliary rootlet, several dozen parallel microtubules. Above all they possess a basally produced axon intimately entangled with the nerve processes that is, according to Holland, the diagnostic feature for a sensory cell. The functions most commonly ascribed to superficial sensory cells of the type described here are mechanoreceptor and/or chemoreceptor (Laverack, 1974). According to Cobb (1987), it is not possible to separate these two modalities of perception ultrastructurally. Although, in *Holothuria forskali*, only mechan-

chemical perception cannot be ruled out. In this case, it is tempting to suggest that 'long cilium' sensory cells would be chemoreceptors and 'short cilium' sensory cells would be mechanoreceptors. Indeed, it is unlikely that chemicals traverse the cuticle to stimulate the short subcuticular cilia, while they can be detected by the long transcucular cilia. Furthermore, short cilium sensory cells are better candidates for a mechanoreception function, as the close association of their subcuticular cilium with the cuticle would presumably allow them to detect pressures applied anywhere on the cuticle.

Papillae of aspidochirote holothurioids are not the only echinoderm ambulacral appendages specialized for sensory perception. Such appendages also occur at the arm tip of asteroids and around the ambitus of spatangoid echinoids (Sloan, 1980; Nichols, 1959; respectively). Unfortunately, none of these sensory podia has been described at the ultrastructural level. However, echinoderms may show other sensory structures similar to the papilla bud. These structures include the sensory hillocks of the globiferous pedicellaria of some echinoids (Cobb, 1968; Oldfield, 1975; Ghyoot, 1991), the podial pits of

the 'stabchen' of ophiuroid spines (Whitfield and Emson, 1983). In almost all cases these structures are made up of ciliated sensory cells clumped into groups of 3–10 cells (ophiuroid stabchen, Whitfield and Emson, 1983; sensory hillock of globiferous pedicellariae, Oldfield 1975; present work). The sensory role of these cells is usually based on their morphological aspect, but Ghyoot (1991) has demonstrated that chemical and/or mechanical stimulation of the sensory hillock of globiferous pedicellariae of *Sphaerechinus granularis* induces the closure of the jaws and the venom expulsion.

*Holothuria forskali* thus possesses on its dorsal surface, numerous papillae that have a sensory function. When the ciliated sensory cells of a papilla are stimulated, an impulse is transmitted to the myoepithelial cells via the nerve plate and the nerve plexus (the transmitter released by the nerve plexus via the lateral branches probably

diffuse to the muscle through the internal connective tissue layer; Florey and Cahill, 1977). The contraction of the myoepithelial cells (the retractor muscle) then causes the papillae to retract. When several papillae are stimulated simultaneously the responses add up (presumably at the level of the radial nerve) and bring about the overall contraction of the holothurioid and sometimes the expulsion of Cuvierian tubules.

#### ACKNOWLEDGEMENTS

We thank Professor P. Lassere for providing facilities at the Observatoire Océanologique de Roscoff (Brittany, France); Professor J.A. Heuson-Stiennon for the use of transmission electron microscope; P. Postiau and A. Maes for technical assistance. Contribution of the 'Centre Interuniversitaire de Biologie Marine.'

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