

# The unique gravireceptor organs of *Pleurodasys helgolandicus* (Gastrotricha: Macrodasysida)

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**Abstract** The drumstick-like organs of the marine interstitial gastrotrich *Pleurodasys helgolandicus* Remane, 1927 were studied using optical and electron microscopy, in order to widen our knowledge of the sensory organs among gastrotrichs. The drumstick-like sensory organs are paired, symmetrical structures located on the dorsal side of the post-cephalic region of the body. Each sensory organ is formed by an outgrowth of the lamellar exocuticle covering the body surface, and it consists of an elongated, cylindrical hollow stalk surmounted by a hollow bulbous tip, housing in its cavity a dense spherical body. Compared with the three main sensory structures recognized among Gastrotricha, i.e., mechanoreceptors, photoreceptors, and chemoreceptors, the organization of the drumstick-like sensory organ matches that of mechanoreceptors. In particular, we suggest that the drumstick-like sensory organs of *P. helgolandicus* are gravireceptor organs, analogous to the orthopteran “plumb bob-like” receptors. This is the first description of a putative gravireceptor organ among gastrotrichs.

**Keywords** Sensory organ · Gastrotricha · Microscopy · Gravireceptors

## Introduction

*Pleurodasys helgolandicus* Remane, 1927 is a marine interstitial macrodasysidan gastrotrich widespread along the North Sea and the Atlantic European coasts. The species has also invaded the western Mediterranean sea, forming stable populations along the Spanish coast of the Alboran sea (Todaro et al. 2006), while single specimens have been found along the Catalan coast of France (Todaro and Hummon, unpublished) and the subtidal off of Leghorn, Italy (Todaro et al. 2001). The species seems present also along the south west coast of India (Govindankutty and Nair 1969).

The taxonomic status and systematization of *P. helgolandicus* has been debated. Remane (1927), in his original description of immature specimens collected in the Bay of Kiel (Germany) and surveyed under bright field and phase-contrast microscopy, assigned the newly established genus to the Macrodasysidae (Macrodasysida), according to the supposed position, at mid-pharynx, of the pharyngeal pores. Later, a second species, *P. megasoma* Boaden, 1963 was added to the monotypic taxon (Boaden 1963). The systematization of *Pleurodasys* within the Macrodasysidae remained unchanged until Hummon (1974), based also on the observation that the pharyngeal pores were located at the base of the pharynx, transferred the genus to the current family, the Lepidodasyidae. Recently, the same author, based on extensive investigations along European Northern shores, indicated *P. megasoma* as a junior synonym of *P. helgolandicus* Remane, 1927, recognizing therefore *P. helgolandicus* as the only known *Pleurodasys* species (Hummon 2007). We agree and accept the current systematization, with some concerns regarding the taxonomic status of the Indian specimens.

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With respect to the other lepidodasyid species, *P. helgolandicus* (length up to 1.8 mm, width up to 120  $\mu\text{m}$ ), is also characterized by an extremely elongated muscular pharynx that may reach half of the body length and by a pair of noticeable accessory adhesive organs made up of four (not three as previously reported) adhesive tubes, arising bilaterally next to the pharyngo-intestinal junction, toward the middle of the body. The most striking feature of this species is, however, the presence of a pair of peculiar drumstick-like organs located dorsally on the anterior region of the body, just beyond the grooves that separate the head from the trunk. Although never studied in detail, a sensorial function of these unusual organs, referred to also as pharyngeal knobs, has been hypothesized (Hummon 1974).

Sensory organs in gastrotrichs consist of modified ciliated cells, sometimes accompanied by supportive and pigmented cells, forming three main types of sensory structures: mechanoreceptors, cephalic photoreceptors and paired cephalic chemoreceptive capsules (Ruppert 1991). The three different types of sensory structures share a similar cellular organization, consisting of a variable number of monociliated bipolar receptor cells, with a modified cilium and a proximal segment extending in an axon probably joining a commissural fiber (Ruppert 1991).

The literature on gastrotrich sense organs is scarce: there are only few detailed ultrastructural descriptions of sensory organs in the group. Putative photoreceptor and chemoreceptors have been described as paired cephalic organs in two macrodasyidans: *Turbanella cornuta* (Teuchert 1977), and *Dactylopodola baltica* (Hochberg and Litvaitis 2003; Liesenjohn et al. 2006); sensory palps as putative chemoreceptors were described in the macrodasyidan *Tetranchyroderma papii* (Gagné 1980). Mechanoreceptors in gastrotrichs are known only as tactile sense organs, formed by sensory hair cells (sensu Teuchert 1977), occurring isolated or in groups, or associated with glandular adhesive organs in the body wall (Rieger et al. 1974; Teuchert 1977; Ruppert 1991; Hochberg 2001).

Although special mechanoreceptors working as equilibrium organs, and capable of perceiving the Earth's gravitational field evolved in virtually all animal groups (Barber 1968; Vinnikov 1974), to the best of our knowledge gravireceptor organs have never been described among Gastrotricha.

In this study we investigate the structure of the peculiar drumstick-like sensory organs of *P. helgolandicus* using optical and electron microscopy. Our aim is twofold: (1) to widen our knowledge of the gastrotrich sensory organs and (2) to describe, for the first time, the fine structure of a putative gravireceptor organ among gastrotrichs.

## Materials and methods

### Specimens collection

Sand samples containing *P. helgolandicus* Remane, 1927 were collected on 10 June 2005 at 2-m water depth from the bay of Getarez, Spain (36°05'54.8"N 05°26'32.2"E). Gastrotrichs were extracted from the sediment by the narcotization-decantation technique using isoosmotic (7%) magnesium chloride solution (Pfannkuche and Thiel 1988). The fauna-containing supernatant was then poured directly in a 5-cm diameter Petri dish and scanned for gastrotrichs at 50 $\times$  under a Wild M8 dissecting microscope.

### Microscopical techniques

For optical microscopy, the gastrotrichs were removed with a micropipette from the Petri dish, fresh-mounted on slides and observed using a Nikon Eclipse 90i equipped with Differential Interference Contrasts (Nomarski). During observation, the animals were photographed with a DS-5Mc Nikon digital camera and measured with the Nikon AcU2 software program.

For scanning electron microscopy, previously fixed specimens (5% buffered formalin) were rinsed in tap water, dehydrated through a graded ethanol series, critical point-dried using CO<sub>2</sub>, mounted on aluminium stubs, sputter coated with gold–palladium and observed with a Philips XL 30 scanning electron microscope.

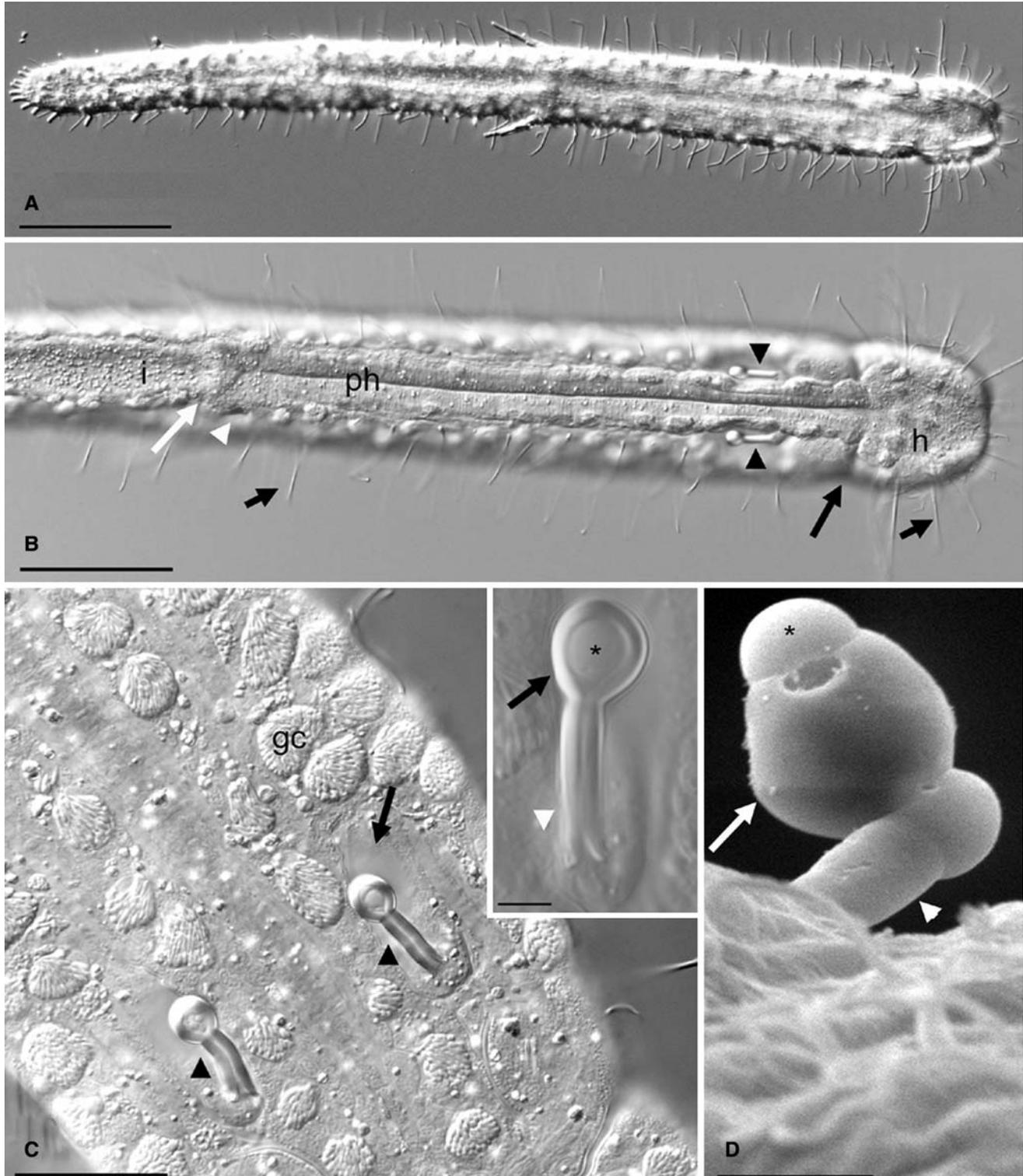
For transmission electron microscopy, the specimens were fixed for several days in a 0.1-M cacodylate-buffered paraformaldehyde–glutaraldehyde mixture in a saturated solution of picric acid with sucrose added (SPAFG, Ermak and Eakin 1976). Subsequently, the animals were washed in 0.1 M cacodylate buffer (pH 7.4), postfixed in 1% osmium tetroxide in the same buffer for

**Fig. 1** Light transmission and scanning electron microscopic images of *Pleurodasys helgolandicus*. **a** Habitus of a subadult specimen; note the peculiar accessory adhesive organs arising ventrolaterally at mid-body. **b** Dorsal view of the anterior body region of *P. helgolandicus*. Note the pair of drumstick-like sensory organs (arrowheads) just posterior to the grooves that separate the head from the body (long arrow), and the pharynx, which bear the pharyngeal pore at its base (white arrowhead). Short arrows point to sensory hair cells; white arrow points to the pharyngo-intestinal junction. **c** Higher magnification of the anterior dorsal body region. Note the drumstick-like sensory organs (arrowheads) and the elliptical superficial invagination devoid of epidermal gland cells around them (arrow). Inset, detail of a single sensory organ. Note the stalk (arrowhead), the bulbous tip (arrow) and the spherical body inside it (asterisk). **d** SEM image of a single drumstick-like sensory organ. Note the stalk (arrowhead), the bulbous tip (arrow) and the spherical body (asterisk) that, due to a fixation artifact, comes out from the apical portion of the bulbous tip. *h* head, *ph* pharynx, *i* intestine, *gc* gland cells. Scale bars: **a** 100  $\mu\text{m}$ , **b** 60  $\mu\text{m}$ , **c** 15  $\mu\text{m}$ , **c** inset, 6  $\mu\text{m}$ ; **d** 7  $\mu\text{m}$

2 h, washed in distilled water, stained en bloc overnight in 2% aqueous uranyl acetate, dehydrated in a graded ethanol series, and embedded in EPON resin. Thin sections were cut with a Reichert Ultracut E microtome, stained with lead citrate, and observed with a JEOL 100SX electron microscope.

## Results

The drumstick-like sensory organs of *P. helgolandicus*, are paired symmetrical structures located on the dorsal side of the postcephalic region of the body, just beyond the groove that separates the head from the trunk (Fig. 1b).



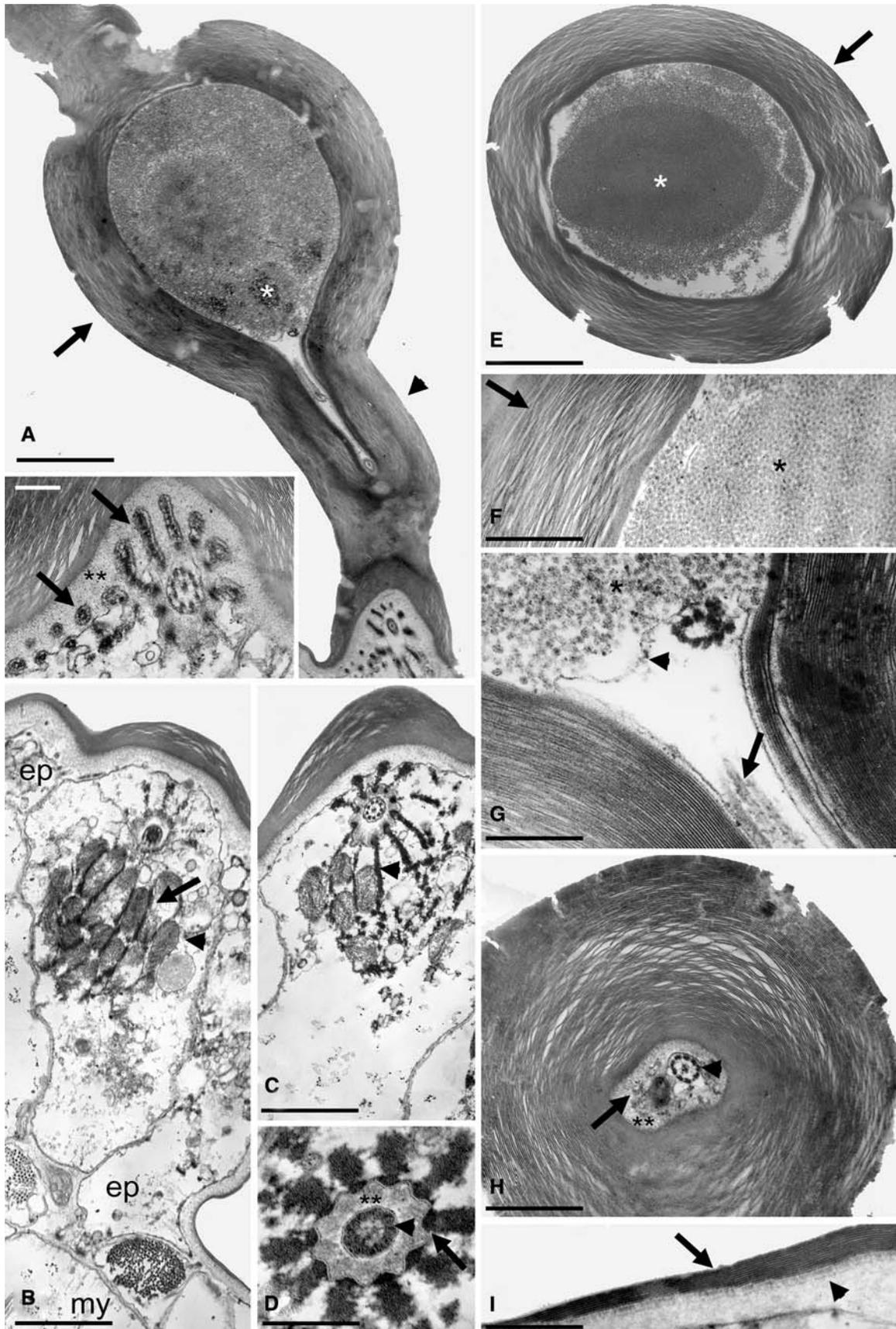
Each drumstick-like sensory organ consists of an elongated, cylindrical hollow stalk (length 12.5–22.5  $\mu\text{m}$ ; diameter 2.5–3.3  $\mu\text{m}$ ) containing a straight cylindrical canal, with an inner diameter of about 0.6  $\mu\text{m}$ , running through its entire length (Figs. 1c, 3). The stalk is surmounted by a hollow bulbous tip with a diameter of 5.0–6.6  $\mu\text{m}$  (Figs. 1c, d, 3), housing in its cavity a dense spherical body, clearly separated from the wall (Figs. 1c, 3). The dense spherical body may be extruded by some fixation techniques (Fig. 1d). Each drumstick-like sensory organ lies in a nearly elliptical superficial depression of the body wall, devoid of epidermal gland cells, and runs parallel to the main body axis, with its bulbous tip pointing toward the posterior body region (Fig. 1a, b). The base of the stalk is connected to the body wall, whereas the remaining portion stands up from the body surface, free to move (Fig. 1c, d).

Each drumstick-like sensory organ is formed by an outgrowth of the lamellar exocuticle covering the body surface (Figs. 2a, 3), formed by many tightly appressed exocuticular lamellae, of uniform thickness (thickness about 10 nm) (Fig. 2f, g). The lamellar exocuticle (thickness around 60 nm) covering the body wall, thickens gradually at the base of the sensory organ (Fig. 2a), reaching nearly 1.3  $\mu\text{m}$  (100 exocuticular lamellae) along the stalk and bulbous tip (Fig. 2e–h). The extracuticular lamellae are formed in the apical region of the granular endocuticle layer, where rows of electron-dense granules, putative exocuticular lamellar precursors, push outside the newly formed layers (Fig. 2i). The stalk wall is formed by more than 90 appressed exocuticular lamellae (thickness about 1.2  $\mu\text{m}$ ), concentrically arranged around a central nearly cylindrical cavity (Fig. 2h). The exocuticular lamellae run parallel to each other, and appear more densely packed close to the cylindrical cavity (Fig. 2h). The basal portion of the sensory organ's stalk forms a cup-like structure, housing the proximal portion of the receptor cell (Fig. 2a and inset).

A series of cross sections allowed us to reconstruct the ultrastructure of the receptor cell (Fig. 3). The sensory receptor is an elongated monociliated cell making contact, basally, with the longitudinal spindle-shaped myocytes surrounding the pharyngeal myoepithelial cells; the receptor is flanked, on both sides, by large epidermal cells (Fig. 2b). As in the conventional monociliated epidermal cells, the cilium of the receptor cell consists of a conventional  $9 \times 2 + 2$  axoneme arising from a shallow pit on the apical cell surface. The pit is formed by a shallow invagination of the cell membrane that deepens around the basal ciliary portion, and then extends outside tightly wrapping the axoneme main portion (Fig. 3f). Granular endocuticular electron-dense material fills the empty space between the pit wall and the axoneme plasma membrane (Fig. 2a inset, c, d). A palisade of several elongated mitochondria flanks the basal portion of the axoneme (Fig. 2b). Ridges of

**Fig. 2** Transmission electron microscope images of the drumstick-like sensory organ of *Pleurodasys helgolandicus*. **a** Sagittal section through a complete drumstick-like sensory organ showing the lamellar exocuticle forming the stalk (*arrowhead*), and the bulbous tip (*arrow*) that houses the spherical body (*asterisk*). Note the cup-shaped basal portion of the sensory organ housing the receptor cell, with its cilium extending through the stalk sub-cylindrical cavity. *Inset* higher magnification through the basal portion of the sensory organ. Note the finger-like extensions of the sensory receptor cell membrane into the granular endocuticle layer (*double asterisk*) to form the collar of ten microvilli radially arranged around the cilium (*arrows*). **b** Low magnification through the proximal portion of the sensory receptor cell contacting at its base the myocytes surrounding the pharyngeal myoepithelial cells (*my*), and it is flanked by large epidermal cells (*ep*). Note the palisade of several elongated mitochondria flanking the basal portion of the axoneme (*arrowhead*), and the electron-dense material among them (*arrow*); **c**, low magnification of the proximal portion of the sensory receptor cell showing the ridges of granular electron-dense material converging toward the basal portion of the cilium (*arrowhead*); **d** cross section of the ciliary basal portion showing a putative basal body tightly wrapped by the plasma membrane (*arrowhead*); the granular endocuticle materials filling the empty space between the pit wall and the axoneme plasma membrane (*double asterisks*), and the ten shallow invaginations of the pit wall plasma membrane in correspondence of the ten granular electron-dense ridges (*arrows*). **e** Cross section through the bulbous tip showing the exocuticular lamellar wall (*arrow*), and the spherical body inside it. Note the core of more densely packed vesicles inside the spherical body (*asterisk*). **f** Higher magnification of the bulb-like portion in longitudinal section. Note the epicuticular lamellae arranged parallel to form the continuous wall of the bulbous tip (*arrow*), and the small membrane-bound spheroidal vesicles inside it (*asterisk*). **g** Longitudinal section through the apical portion of the stalk. Note the cilium plasma membrane that widens in a funnel-like structure, contacting the basal portion of the spherical body (*arrowhead*), and an incomplete longitudinal section through the axoneme (*arrow*). **h** Cross section through the stalk showing the exocuticular lamellae concentrically arranged around a central cylindrical cavity housing the single cilium (*arrowhead*) and surrounded by the collar of electron-dense microvilli (*arrow*), and by the endocuticular granular layer (*double asterisk*); **i** High magnification of the body wall cuticle at the base of the sensory organ. Note the cuticular lamellae growing from the apical region of the granular endocuticle layer, where parallel rows of electron-dense granules (*arrowhead*), seem to push outside the newly formed layers (*arrow*). *ep* epidermal cells, *my* myocytes. *Scale bars*: **a** 2  $\mu\text{m}$ , **a inset** 0.25  $\mu\text{m}$ , **b**, **c** 0.7  $\mu\text{m}$ , **d** 0.3  $\mu\text{m}$ , **e** 1.5  $\mu\text{m}$ , **f**, **g** 0.5  $\mu\text{m}$ , **h** 0.6  $\mu\text{m}$ , **i** 0.4  $\mu\text{m}$

granular electron-dense material, present among the mitochondria of the palisade, converge toward the basal portion of the cilium (Fig. 2c). There, the electron-dense material contacts the pit wall plasma membrane, which forms ten shallow invaginations (Fig. 2a inset–d). In proximity of the pit apical margin these ten plasma membrane invaginations extend into the external granular endocuticle layer to form the low collar of ten short microvilli radially arranged around the cilium (Fig. 2a inset). Filamentous electron-dense material is visible inside the microvilli (Fig. 2a inset). Several microvesicular bodies, together with the nucleus, Golgi apparatus and rough endoplasmic reticulum are present inside the cytoplasm of the receptor cell.

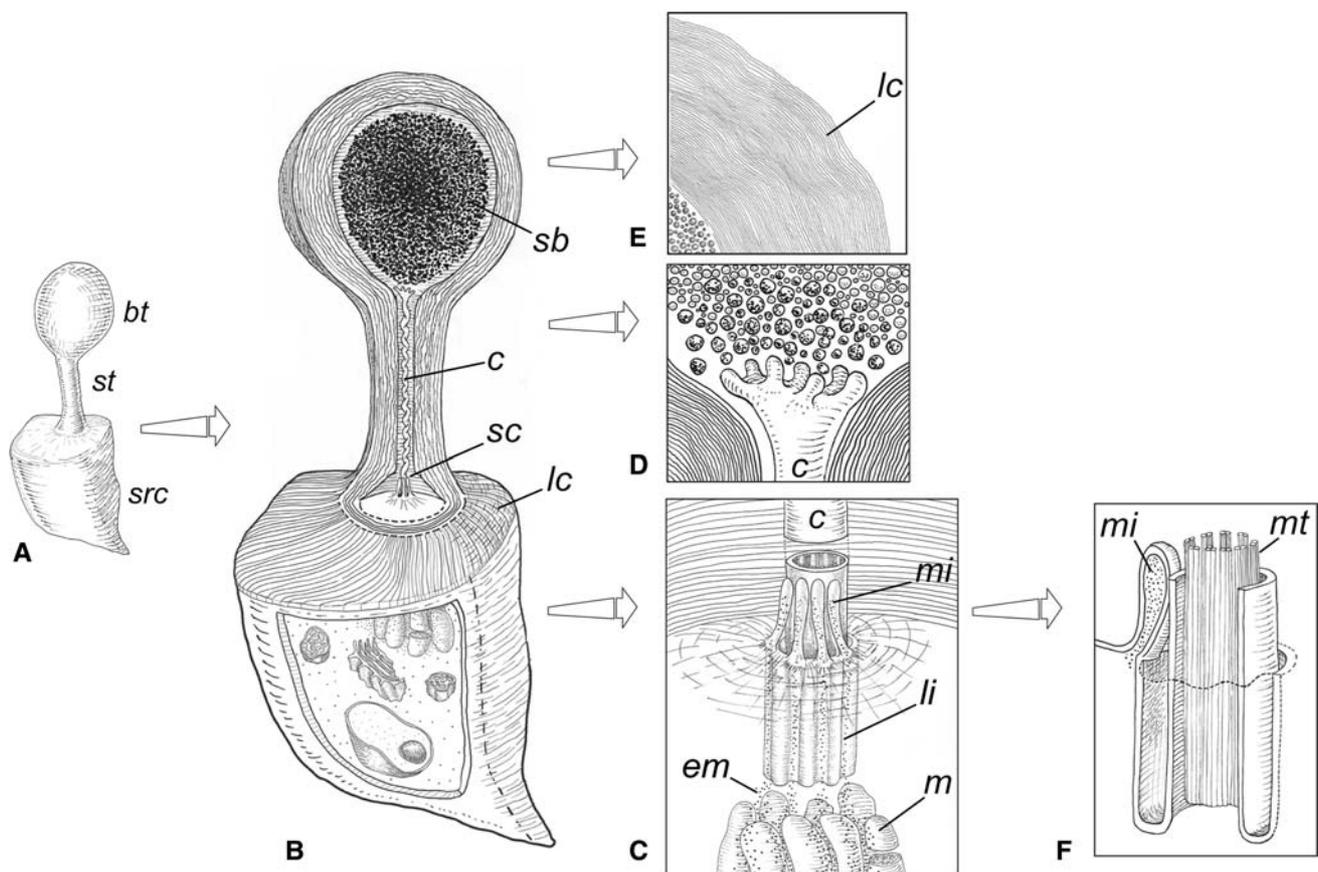


The single cilium of the receptor cell extends through the stalk cylindrical cavity for its entire length, twisting several times along its way (Figs. 2a, 3b). For a short tract along the stalk basal portion, the cilium is surrounded by the collar of ten electron-dense microvilli, and by the endocuticular granular cuticle (Fig. 2a inset, h). At the tip of the stalk, close to the bulb, the cilium plasma membrane widens in a funnel-like structure, containing several electron-dense granules that contact the basal portion of the spherical body (Figs. 2g, 3d). Here the cilium plasma membrane buds in several irregular digitations (Figs. 2g, 3). More than 70 epicuticular lamellae arranged subparallel to each other form the continuous wall of the hollow bulbous tip: they pack more densely at the inner layer of the bulb wall, forming a sharp edge bordering the cavity (Fig. 2e). A spherical body

not surrounded by any well-defined structure (Fig. 2e), formed by hundreds of small membrane-bound unconnected subspherical vesicles (average diameter 20 nm) filled with electron-dense material, lies in the center of the bulbous tip: only few short filaments are visible among the vesicles (Fig. 2a inset, e, f). A core of more densely packed vesicles is present inside the spherical body (Fig. 2e).

## Discussion

The paired postcephalic drumstick-like sense organs are characteristic of *P. helgolandicus*; similar sense organs are unknown among Gastrotricha and putatively related taxa (e.g., rotifers, gnatostomulids, flatworms, nematodes).



**Fig. 3** Three-dimensional reconstruction of the drumstick-like sensory organs of *Pleurodasys helgolandicus* with some details. **a** Three-dimensional reconstruction of the whole sensory organ. **b** Sagittal sections through the stalk and the bulbous tip. Note the cilium extending through the stalk sub-cylindrical cavity, and the spherical body inside the bulbous tip. Nucleus, mitochondria, multivesicular bodies and Golgi apparatus are visible inside the sensory receptor cell cytoplasm. **c** Detail of the distal portion of the sensory cell membrane. Note the collar of short microvilli radially arranged around the cilium (four out of ten microvilli shown), the corresponding longitudinal infoldings along the invaginated plasma membrane, and the electron-dense material. **d** Detail of the apical portion of the stalk. Note the

cilium plasma membrane widening in a funnel-like structure, and the spherical body electron-dense granules. **e** Section through the bulb. Note the epicuticular lamellae arranged subparallel to each other. **f** Schematic longitudinal section of the sensory cell plasma membrane surface surrounding the cilium. Note the plasma membrane that evaginates to form the microvilli (one out of ten microvilli shown), then, coming close to the cilium, it deepens around its basal portion, and then extends outside tightly wrapping a conventional  $9 \times 2 + 2$  axoneme. *bt* bulbous tip, *c* cilium, *em* electron-dense material, *lc* lamellar exocuticle, *li* longitudinal shallow invaginations, *m* mitochondria, *mi* microvilli, *mt* microtubules, *sb* spherical body, *st* stalk, *sc* stalk sub-cylindrical cavity, *src* sensory receptor cell

Some analogy can be found with the characteristic club-shaped sensory organ of tardigrades (Kristensen 1981).

Although peculiar in their external morphology, their cellular organization is congruent with the supposed ground pattern of Gastrotricha sensory organs (Ruppert 1991). Compared with the three main sensory structures recognized among Gastrotricha, i.e., chemoreceptive organs, photoreceptive organs and mechanoreceptors (Teuchert 1977; Gagnè 1980; Ruppert 1991; Liesenjohann et al. 2006), the fine organization of the drumstick-like sensory organ is more similar to that of gastrotrich mechanoreceptors.

Several characters argue against a chemosensory function for the drumstick-like sensory organs: the presence of a single receptor cell and the absence of microvilli protruding into the sensory organ cuticle, which instead consists of a thick and continuous exocuticular sheath preventing any connection of the organ to the environment. Likewise, the sensory organs under study cannot likely serve for photoreception. Although the spheroidal vesicles forming the spherical body are similar to the visual sensory filaments of the photoreceptive organs, and may derive from the proliferation of the ciliary proximal shaft membrane, this similarity is only superficial. Indeed, the vesicles of the spherical body differ from the visual sensory filaments of the photoreceptive organs due to their smaller size, the absence of axonemal microtubules inside them, and the complete absence of connections among the electron-dense vesicles of the spherical mass, essential to their work in case they were visual membranes. In addition, the thick and continuous multilamellar sheath of exocuticle covering the drumstick-like sensory organs forms a barrier for light penetration, thus conflicting with a probable photoreceptive function for the sense organs of *P. helgolandicus*.

Instead, the organization of the drumstick-like sensory organ matches that of gastrotrich mechanoreceptors, each sensory organ consisting of a single receptor cell, bearing at its distal segment a single, long, apical cilium, emerging from a shallow cup and surrounded by a collar of ten short microvilli symmetrically disposed around the cilium. The cilium passes through the endocuticle but not the exocuticle, which unsheathes it, while the microvilli remain below both layers of the cuticle.

A ten-part microvillar symmetry characterizes also the tactile sensitive hairs of the chaetonotidan *Lepidodermella squamata*, thus supporting the notion that this arrangement is apomorphic at least to the Gastrotricha mechanoreceptors, as suggested by Hochberg (2001). Indeed, among Gastrotricha, locomotory cilia have an eight-part microvillar symmetrical arrangement, and the sensory organ of Kinorhyncha (Kristensen and Higgins 1991; Neuhaus 1997), Loricifera (Kristensen 1991), Priapulida (Storch 1991) and Nematoda (Wright 1991) are characterized by an eight to nine-part symmetry.

Mechanotransduction, i.e., the cell's conversion of a mechanical stimulus into an electric signal, reveals vital features of an organism's environment. In general, mechanosensory transduction systems have one key feature: a specific ion transduction channel that detects the deflection of an external structure relative to an internal one, such as the cytoskeleton, and upon deflection opens rapidly and amplifies the signal by permitting the flux of a large number of ions (Gillespie and Walker 2001). In *P. helgolandicus*, as in many other invertebrates, the cuticle played a key role in the evolution of mechanoreceptors. Indeed, a wide range of cuticular structures has evolved in invertebrates for transmission of the various types of mechanical stimuli: sound, air current, touch, passive mechanical deformation, and gravitational forces (Keil 1997).

The peculiar shape of the drumstick-like sensory organs suggests that they probably are not merely tactile sensory organs, as the other numerous sensory hair cells present in the *P. helgolandicus* body wall (Fig. 1a, b), but mechanoreceptors specialized for a different function. The orientation of animals with respect to the Earth's gravitational field is affected, no matter how high their organizational level, by a "body-position transducer", represented in many invertebrates by a statocyst, formed by a "standard mass", i.e., the otolith, and by a system of receptors, as cilia or microvilli that, deflected by the standard mass, are capable of perceiving the position or movement of this mass within the organ (Vinnikov 1974). The drumstick-like sensory organs of *P. helgolandicus* are reminiscent of statocysts: the spherical body housed in their hollow bulbous tip acting as a standard mass, and the modified cilium contacting the basal portion of the spherical body functions as a receptor system. However, there are some key characters distinguishing the drumstick-like sensory organs from a typical statocyst. Indeed, as a general rule, in most invertebrates, the position of the statocyst is characteristically rigidly related to the position of the body. For example, in many free-living flatworms the statocysts are positioned inside the body, close to the brain (Ferrero et al. 1985; Elhers 1991). On the contrary, in *P. helgolandicus* the drumstick-like sensory organs are placed outside the body wall, and appear freely movable, thus their position is not rigidly related to the position of the body. In addition, the spherical body is a poorly compacted structure, uncrystallized and devoid of any membrane around it, unlike the otolith that is generally a dense crystalline structure consisting mostly of calcium carbonate or calcium phosphate, often coated by a thin layer of chitin (Vinnikov 1974). Besides, in a typical statocyst, the standard mass is freely movable within the limit of the organ, whereas in *P. helgolandicus*, the spherical body nearly completely fills the empty space of the bulb, thus having little freedom of movement within it.

Equilibrium organs signaling spatial position are well represented in virtually all major taxa in the Animalia; the outstanding exceptions are insects, where few receptor organs analogous to statocyst or otolith organs have been reported (Walthall and Hartman 1981). Indeed, in soil dwelling insects, such as orthopterans, new types of gravi-receptor organs have evolved (Hartman et al. 1979). The ventral surfaces of the cerci of burrowing cockroaches and crickets possess, in addition to sensory hairs and sensory bristles, sensory structures shaped like tiny plumb bobs. Each sense organ (sensillum) consists of a dense black-ridged sphere, the spheroid body, positioned at the distal end of a slender stalk, which inserts into a singly innervated socket (Roth and Slifer 1973; Hartman et al. 1979). The stalk appears to be freely movable; and the spheroid body has an outer surface covered with a cuticular layer, and its interior is filled with a dense nearly homogeneous material with a few irregular masses of different sizes and shapes scattered throughout it (Roth and Slifer 1973). These sensilla modified from trichobothria have a function similar to that of statocysts: the dense material filling the spheroid body weighs down the end of the sensillum and causes the stalk to move at its base, depending on the orientation of the cercus (Roth and Slifer 1973). Bischof (1975) and Hartman et al. (1979) confirmed this hypothesis, demonstrating that the two ascending giant interneurons in each of the two connectives of the ventral nerve cord of *Arenivaga* sp. (Blattodea: Polyphagidae) are activated by these receptors during roll and pitch of the insect; and named the plumb bob-like receptors “tricholiths”, to better reflect their function.

While being different in size (the tricholiths are about five times longer than the drumstick-like sensory organs), and in their cellular organization (Keil 1997), the two sensory organs are very similar in their external morphology, consisting of a freely movable outgrowth of the body cuticle, formed by a stalk-like portion, and surmounted by a spherical body. Therefore, our favored hypothesis is that, the drumstick-like sensory organs of *P. helgolandicus* are gravireceptor organs, analogous to the tricholiths of orthopterans. Similar in their external morphology, but different in their cell organization, probably the two structures represent convergent adaptations for detecting gravitational forces among organisms that dig or live in impermanent burrows or “swim” through quasi-liquid soil (orthopterans) or, as in *P. helgolandicus*, live interstitially among sand grains. Why a similar sensory organ has not evolved in other interstitial gastrotrichs remains an unsolved dilemma.

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