

Review



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Diversity of cilia-based mechanosensory systems and their functions in marine animal behaviour

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Sensory cells that detect mechanical forces usually have one or more specialized cilia. These mechanosensory cells underlie hearing, proprioception or gravity sensation. To date, it is unclear how cilia contribute to detecting mechanical forces and what is the relationship between mechanosensory ciliated cells in different animal groups and sensory systems. Here, we review examples of ciliated sensory cells with a focus on marine invertebrate animals. We discuss how various ciliated cells mediate mechanosensory responses during feeding, tactic responses or predator–prey interactions. We also highlight some of these systems as interesting and accessible models for future in-depth behavioural, functional and molecular studies. We envisage that embracing a broader diversity of organisms could lead to a more complete view of cilia-based mechanosensation.

This article is part of the Theo Murphy meeting issue ‘Unity and diversity of cilia in locomotion and transport’.

1. Introduction

Mechanosensory cells or mechanoreceptors are specialized cells detecting mechanical forces such as shear, compression or tension. Animals have evolved mechanosensory cell types with a large morphological diversity, such as the hair cells in the inner ear of vertebrates, the Merkel cells in the vertebrate skin or chordotonal-organ sensory cells in insects. The sensory morphology of mechanoreceptors and their association with supporting structures contribute to their sensory tuning [1]. In addition, mechanosensory cells express transmembrane channels that convert the force into a cellular signal, a process known as mechanotransduction. Members from unrelated protein families including Transient Receptor Potential (TRP) channels, Piezo, Transmembrane Channel-like proteins (TMCs) and DEG/ENaC channels have been implicated in this process [2,3].

One widespread structural feature of mechanoreceptors is the presence of one or more cilia in their sensory apparatus. These cilia—defined here as microtubule-containing organelles supported by a basal body—are ultrastructurally diverse and can be either motile or non-motile. The cilia are often surrounded by microvilli in various numbers and with a range of morphologies. It is not yet clear whether cilia are directly involved in mediating mechanosensation or have other functions such as maintaining the structure of the microvillar sensory apparatus. The biophysical details of how cilia may sense forces are also unclear and several possible models have been proposed [4,5].

The canonical ciliated mechanosensory cell is the hair cell of vertebrates (figure 1a). Hair cells occur in the ear and in the lateral-line neuromasts [11]. Hair cells typically have a single cilium (called the kinocilium; this is absent from the hair cells of the adult organ of Corti [12]) with a 9+2 axoneme. The central microtubule pair in hair cells is oriented perpendicular to the ciliary basal foot [13]. Opposite to the basal foot, there is a group of modified microvilli called stereovilli or stereocilia (for clarity we will use the term stereovilli [14]). The stereovilli have graded lengths, with the tallest stereovilli closest to the kinocilium (figure 1a). The hair cell is depolarized when the bundle is

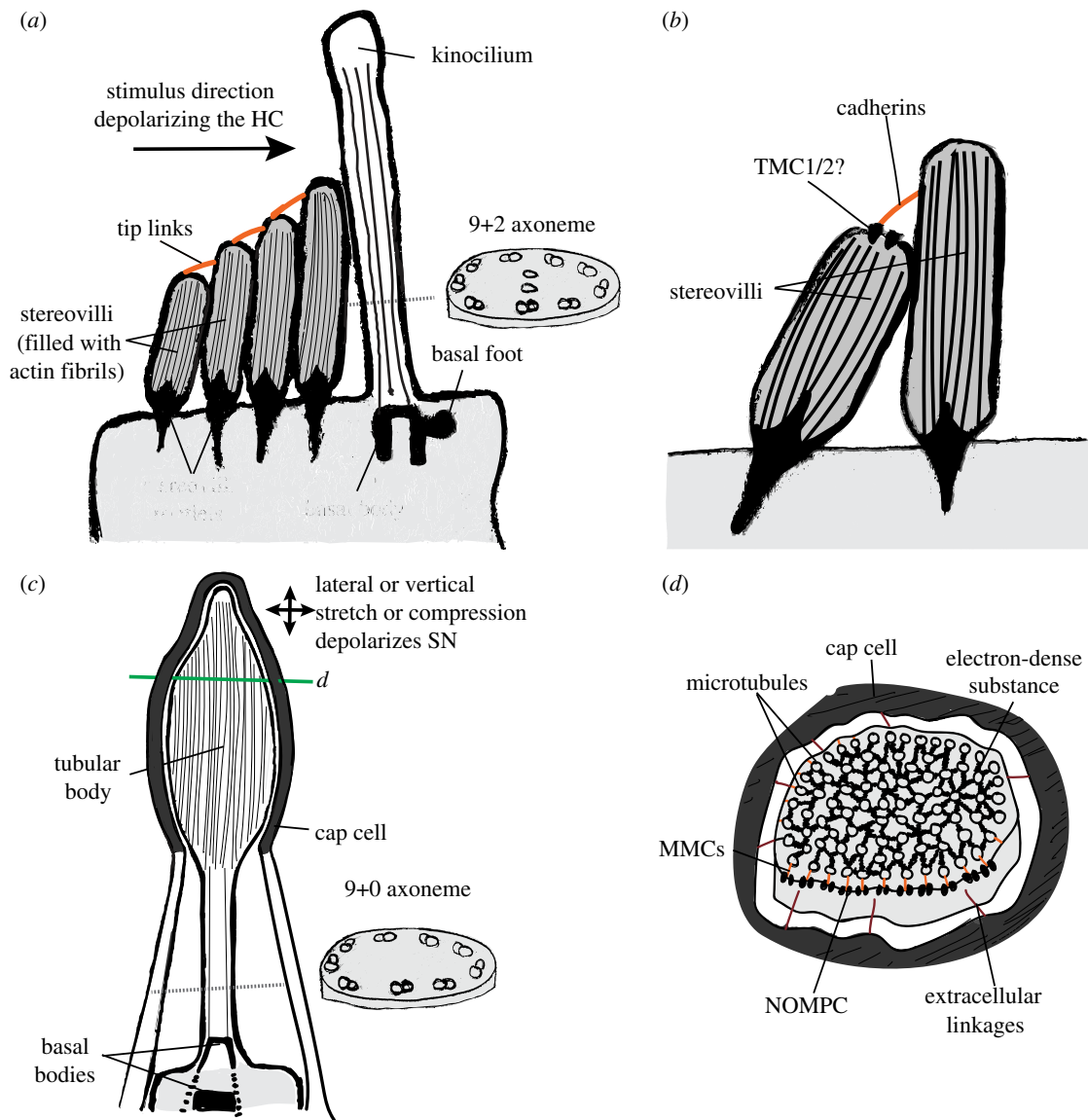


Figure 1. The ‘model’ ciliated mechanosensory cells. (a,b) The vertebrate hair cell (HC). (a) Sketch of the apical side of a hair cell showing stereovilli and kinocilium. Axoneme is shown in cross-section (along dotted line) to reveal the 9+2 axoneme. The central pair of microtubules is perpendicular to the basal foot. Depolarization of the hair cell occurs upon mechanical stimulation of the bundle towards the basal foot. (b) Mechanotransduction in the hair cells occurs at the stereovilli rather than at the kinocilium. A mechanotransduction channel (possibly composed of TMC1/2 channels) sits at the tip of a stereovillus and is indirectly opened by stretching the tip links attached to it. Cadherins are components of the tip links. (c,d) The arthropod type 1 organ sensory cell. (c) Sketch of the cilium of a type 1 organ sensory cell. Axoneme is shown in cross-section (along dotted line) to reveal a 9+0 axoneme at its proximal side. The axoneme increases in the number of microtubules at its distal side. Stretching or compressing at the tip of the cilium depolarizes the sensory neuron (SN). This region is known as the tubular body. The apical side is closely associated to a cap cell. (d) Cross-section of the tubular body (along solid line in panel c). Microtubules at the periphery show connections to the ciliary membrane (MMCs). The mechanotransduction channel NOMPC is localized to the ciliary membrane and is mechanically coupled to the microtubules via the MMCs. Extracellular linkages from the cap cell to the cilium are also shown. Sketches in a and b based on [6,7]. Sketches in c and d based on [8–10]. (Online version in colour.)

deflected towards the kinocilium and hyperpolarized when the stereovilli are pulled in the opposite direction [15]. In a classic study, Hudspeth and Jacobs demonstrated that the stereovilli, and not the kinocilium, are the site of mechanotransduction [16]. Fibrous connections called tip links were later found connecting the distal ends of shorter stereovilli to their taller neighbours [17]. Tip links are necessary for hair cell mechanosensitivity [18], probably by gating the mechanotransduction channel sitting at the tip of the stereovilli (figure 1b). Recent studies have pointed to TMC-1/2 channels as the likely molecule transducing the mechanical stimulus [19–21]. In agreement with this, TMCs are localized to the tip of the stereovilli and interact with cadherins and other components of the tip link [22–24].

Another model ciliated mechanosensory cell is the bipolar sensory neuron embedded in the type 1 organs of arthropods. These organs include sensory bristles, chaetae, campaniform sensilla and chordotonal organs [8]. In contrast to hair cells, the cilium in type 1 organ cells may play a more central role in mechanotransduction. The basic structure of the different type 1 organ mechanosensory cell types is similar [9], and thus the transduction apparatus likely follows similar working principles [8] (figure 1c). The cilium usually has a modified architecture with two basal bodies arranged in tandem leading to a 9+0 axoneme at the proximal side. The number of microtubules may either increase towards the distal part of the cilium (12–1000 tubules) forming a highly ordered array structure known in some cells as the

tubular body [9], or remain as a normal axoneme (e.g. some chordotonal organs). The tubules at the distal side of the cilium are connected to the plasma membrane via compliant structures known as membrane integrated cones [25] (recently renamed as microtubule-membrane connections (MMCs) [26]) (figure 1*d*). The ciliary membrane forms extracellular bridges with the surrounding dendritic sheath. By deforming, stretching or deflecting the organ, the force is transmitted via the extracellular bridges to the ciliary tip where the mechanotransduction apparatus likely sits. The TRPN channel NOMPC is expressed at the tip of the cilium [27–29], where it forms part of the MMCs [26,30] (figure 1*d*). NOMPC is a mechanotransduction channel with a long chain of ankyrin repeats (ARs) [31,32]. Through the binding of the ARs to microtubules, the channel in NOMPC may be opened upon deformation of the ciliary tip [33,34].

The vertebrate hair cell and the type 1 organ cells of arthropods are perhaps the best understood of all animal cells in terms of their physiology and molecular composition. However, it is not clear how these cells relate to each other in mechanistic and evolutionary terms, or which of them, if any, is more representative of how ciliated mechanosensory cells work in other animals. To tackle these questions, we need to know more about the molecular, structural and functional diversity of mechanosensory cells in the remaining major animal groups, most of which have an aquatic lifestyle. Putative mechanosensory cells in a wide range of aquatic organisms are structurally similar to the canonical vertebrate hair cell. This suggests a common origin that happened at the dawn of animal evolution [35], but a more nuanced view will likely emerge from mechanistic studies in underrepresented groups.

Here we review examples of putative and confirmed mechanosensory ciliated cells across marine invertebrates. We argue that a wider appreciation of the structural and functional diversity of mechanosensory ciliated cells in a larger range of organisms would help elucidate the mechanistic details and general principles of ciliary mechanosensation. The aquatic lifestyle of marine invertebrates relies heavily on motor and sensory cilia to generate feeding currents, propel the body or sense water movement and pressure. This makes marine organisms particularly relevant for the study of ciliary sensors and motor systems. The advent of genome editing and live imaging techniques now enable detailed mechanistic studies in some of these organisms. A broader sampling across phyla and more in-depth functional studies across diversity will also be needed to understand the evolutionary relationships of mechanosensory cells.

2. Ciliated mechanosensory cells in filter feeding

Filter feeding is widespread in both larval and adult forms of aquatic animals with motile cilia commonly generating the feeding currents [36]. While the flow pattern of the cilia-driven currents can account for the sorting and rejection of particles in some cases [37], filter feeders also use cilia to actively detect, sort or reject particles based on mechano- and chemosensation.

(a) Systems for particle retention

Ciliated sensory and motor systems for particle retention have primarily been studied in echinoderms (e.g. sea urchins, sea stars) and lophophorates (bryozoans, phoronids and

brachiopods). The planktonic filter-feeding larvae of sea urchins use local ciliary reversals to redirect particles towards the oral field [38]. Food particles can be detected by the locomotor cilia in the oral field and can induce a local reversal in the beat direction to deflect the particle towards the mouth. Ciliary reversals occur rapidly as they are electrically controlled [39]. They are triggered by particles of a certain size and are not influenced by the chemical composition of the particle [40]. The ciliary-band cells at the anterior tip of the larva are sensitive to mechanical cues and may themselves be the particle detectors [38,41]. In echinoderms and in some hemichordate larvae, the ciliary-band cells have a hair-cell like morphology with a single cilium surrounded by microvilli [42–48] (figure 2*a,b*; table 1). In fact, particle-induced reversals may occur in other echinoderm and hemichordate larvae [51,81]. There are additional unciliated sensory cells in close association with the ciliary band [49,50,82,83] (figure 2*c,d*), but it is still unclear whether these cells contribute to the detection of food particles.

Lophophorates use a different method of filter feeding called ciliary sieving [36,84]. These animals have stiff cilia on their tentacles (called laterofrontal cilia, LFC) that sense the drag created by food particles (figure 2*e–g*). Upon detecting the particle, LFC bend and start a ‘flick’ motion that pushes the particle into the feeding current towards the mouth [65–67]. They may also change the beating direction of adjacent cilia. Each laterofrontal cilium arises from a single sensory cell and is surrounded by thick microvilli [53,56,60–64,85,86] (figure 2*h*; table 1). The pilidium larva of nemerteans (ribbon worms) also has non-motile unciliated cells along the ciliary band [54,55,87] (table 1). These cells may be involved in sensing particles and regulate active capture by controlling ciliary band activity or the movement of the larval lappets.

(b) Systems for particle rejection

Ciliated mechanosensory cells can also detect large particles that could clog the filtering system. In the larval cephalochordate amphioxus (lancelet), bundles of cilia called oral spines emanating from unciliated sensory cells surround the mouth and initiate a cough response upon contact with debris [68] (table 1). Adult amphioxus also displays a cough response when mechanically stimulated from the anterior [88]. This response may be mediated by type I and type II ciliated mechanosensory cells located in a range of structures along the filtering system such as buccal cirri at the entrance of the channel [70,71] (figure 2*i,j*), or velar tentacles at the entrance of the digestive system (table 1). Velar tentacles are sensitive to touch [89,90] and harbour a group of cells with stiff cilia [70,71,91] that have 20 to 90 microtubules [70,71] (table 1). The cilium of a velar tentacle cell is surrounded by bulbous branched microvilli that reach half its length (type II cell in figure 2*l*).

Many ascidians or sea squirts (Tunicata, the sister group of vertebrates) are filter feeders. The inner side of the oral (inhalant) siphon has a ring of tentacles involved in detecting unwanted particles and triggering a rejection response [75,92,93]. Each tentacle has rows of mechanosensitive ciliated cells called the coronal cells. These cells are associated with non-ciliated supporting cells [72–74]. Coronal cells have one or more cilia (depending on the species) and either no or

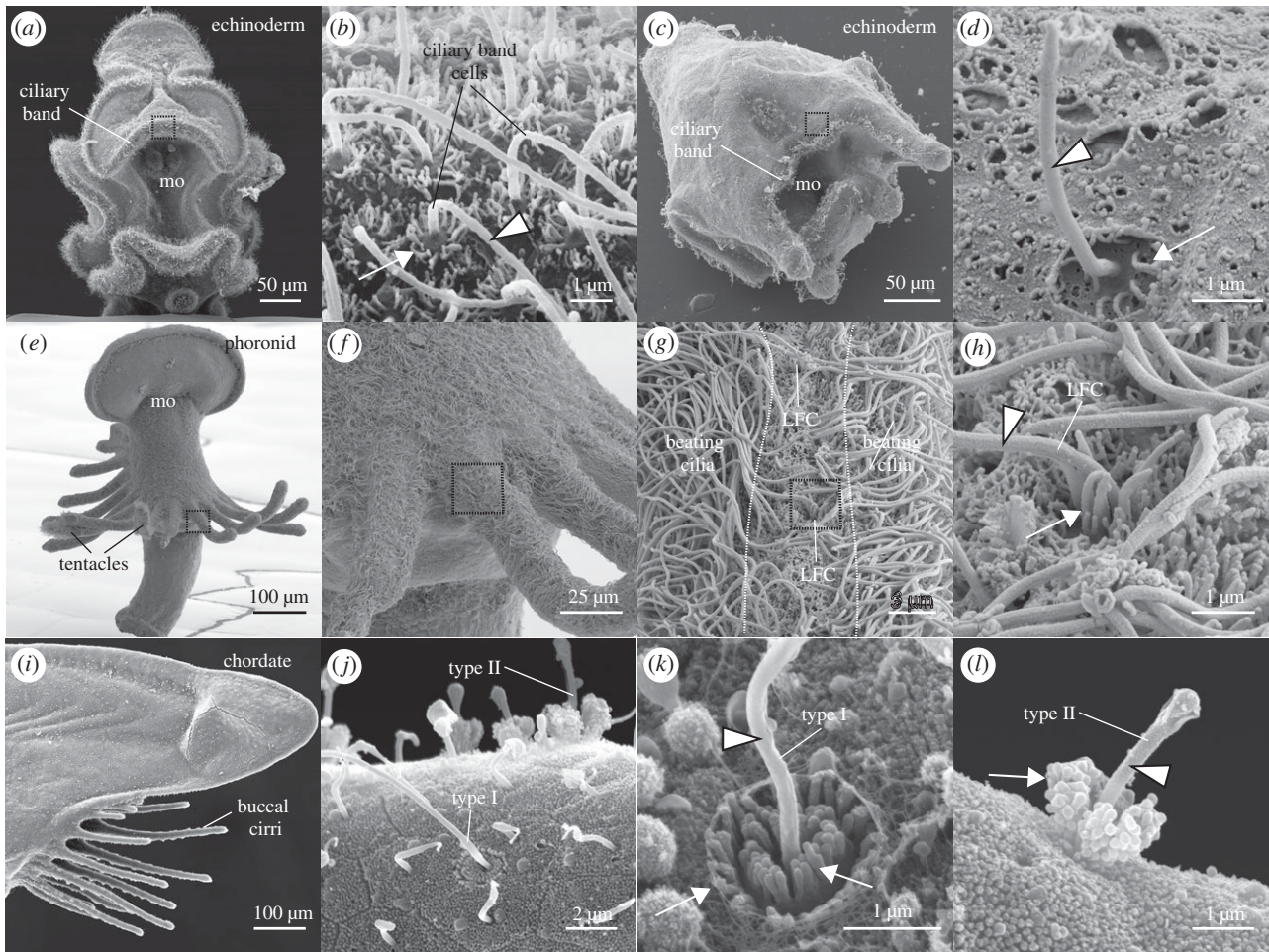


Figure 2. Cilia in invertebrate larvae involved in particle detection or rejection. (*a,c,e,i*) SEM images of planktonic larvae. (*a,b*) Sea star bipinnaria larva (*a*) has bands of unciliated cells, each with a collar of microvilli (*b*). Square in (*a*) shows approximate region of cells shown in (*b*). (*c,d*) Sea urchin pluteus larva (*c*) shows unciliated cells associated with the ciliary band (*d*). Square in (*c*) indicates approximate position of cilium shown in (*d*). (*e,f*) A phoronid larva has multiple ciliated tentacles that generate currents directed towards the mouth (*mo*). (*g*) Each tentacle has rows of laterofrontal cilia (LFC) between the fields of beating cilia. (*h*) LFC have collars of thick microvilli (stereovilli) that may sense particles and guide them to the mouth. Squares in (*e–g*) indicate blown up regions in the subsequent panel. (*ij*) Adult amphioxus has cirri at the mouth (*i*); each is covered with epithelial and type I and II unciliated sensory cells (*j*). (*k*) Type I sensory cells have two concentric collars of microvilli. (*l*) Type II cells have layered microvilli reaching half the length of the cilium. White arrows and black and white arrowheads in *b*, *d*, *h*, *k* and *l* point to microvilli/stereovilli and cilia, respectively.

numerous stereovilli [72,74–76,94] (table 1). Similar to mammalian hair cells, the stereovilli of some ascidian species are graded in length. There are also fibrous structures connecting the cilium to the stereovilli and the stereovilli to each other. Similar cells can be found in the oral field of larvaceans and thaliaceans, the other two major groups of tunicates [77,79,95,96] (table 1). Members in these taxa also display particle rejection behaviours [97,98].

Coronal cells in ascidians share a regulatory gene-expression signature with vertebrate hair cells and express the TRP channel TRPA, but not TRPN [78]. Whether TRPA is important for mechanosensation in the tunicate coronal cells is not known. Hair cells in the zebrafish lateral line express both TRPA and TRPN [99,100] but neither of these molecules is critical for mechanotransduction at the stereovilli [101,102].

In the examples above, particle rejection is mediated by the nervous system. Ciliated mechanosensory cells have also been described in the neuron-less sponges, animals that are also mostly filter-feeders. These animals also display behaviours triggered by particle accumulation. Some sponges have a slow ‘sneezing response’ that clears their system of

debris [103,104]. This response may be mediated by ciliated pinacocytes in the exhalant siphon (osculum) (table 1). Removal of either cilia or the osculum leads to the loss of this response [80]. Commonly used blockers of mechanotransduction in hair cells also reversibly inhibit the sneezing response. The ciliated cells may detect a reduction in water flow due to clogging to initiate the response [80,105–107].

3. Ciliated mechanosensory cells in prey and predator detection

Aquatic organisms generate a hydrodynamic signal as they swim. These signals can be used to locate potential prey or detect predators [108]. Mechanosensation through direct touch can also be involved in predator–prey interactions. Ciliated mechanosensory cells that likely mediate such behaviours have been described on the body surface of a large diversity of aquatic invertebrates [109]. These cells are tuned to different types of mechanical stimuli and can mediate prey location and approach, prey capture or defensive startle and escape responses.

Table 1. Ciliary mechanosensory cells in filter feeding.

animal group	species	stage	cell name (s)	evidence of mechanosensory modality	molecular data ^a	sensory neuron (SN) or secondary sensory cell (SSC) ^b	dilium features	actin or other structures	location of cells
Echinodermata	Echinodermata	brachiolaria larva,	prismatic cells,	fast local ciliary reversals	—	SSC	— uniliated	— collar of 9 to 12	— ciliary band
Hemichordata	<i>Asterias rubens</i> [44], <i>Pisaster ochraceus</i> [45,49], <i>Lytechinus pictus</i> [45], <i>Psammochinus millaris</i> [46], <i>Hemicentrotus pulcherrimus</i> [50]	pluteus larva, bipinnaria larva, tornaria larva, zooid stage	epaulette cells, ciliary band cells, oral field cells (Hemichordata)	induced by particle approach (in echinoderms) [51,52]	—	—	— 9+2 axoneme — diagonal rootlet — motile	regularly arranged microvilli — fibrous connections	— tentacles [48]
Hemichordata									
<i>Balanoglossus biminiensis</i> [45], <i>Tomaria ancoratae</i> [43], <i>Rhabdopleura compacta</i> [48]									
Echinodermata	<i>Pisaster ochraceus</i> [49,53], <i>Hemicentrotus pulcherrimus</i> [50]	pluteus larva, bipinnaria larva	type II bipolar cell (<i>P. och.</i>), ectoneural cell	—	—	SN	— uniliated — 20 µm long cilium	—	— transverse ciliary bands (<i>P. och.</i>) — preoral area
Nemertea	unidentified [54]	pillidium larva	uniliated cell	—	—	SN [55]	— uniliated	— collar of microvilli	— ciliary band
lophophorates (Phoronida, Bryozoa, Brachiopoda)	Phoronida <i>Phoronis</i> spp. [53,56–59], <i>Phoronopsis harmeri</i> [60]	actinotroch larva, cyphonautes larva, adult	laterofrontal cell	flick motion of cilia and induction of ciliary reversal (Brachiopoda and Bryozoa) [65–67]	—	SSC	— uniliated — multiple ciliary roots	— collar of 8 stereovilli	— lophophore tentacles — oral field — ciliated ridges (cyphonautes larva)
Bryozoa <i>Crisia eburnea</i> [61,62], <i>Membranipora membranacea</i> [63]									
Brachiopoda <i>Glattida pyramidata</i> [64], <i>Laqueus californianus</i> [60]									
Cephalochordata	<i>Branchiostoma floridae</i> [68]	larva	oral spine cell	direct touch of cilia induces a cough response [68]	Amphillac [69]	SSC	— uniliated	— no microvilli	— edge of mouth
Cephalochordata	<i>Branchiostoma</i> spp. [70,71]	adult	type I sensory cell [71]	—	—	SN	— uniliated — 9+2 axoneme	— collar of 9 stereovilli — outer collar of thinner microvilli	— buccal cili [70] — epidermis [71]

(Continued.)

Table 1. (Continued.)

animal group	species	stage	cell name (s)	evidence of mechanosensory modality	molecular data ^a	sensory neuron (SN) or secondary sensory cell (SSC) ^b	cilium features	actin or other structures	location of cells
Cephalochordata	<i>Branchiostoma</i> spp. [70,71]	adult	type II sensory cell	mechanical stimulation of velar tentacles induces cough response [70]	—	SSC	— unciolated — 9+ >90 microtubules axoneme — atypical rootlet — non-motile	— collar of 9 stereovilli — collar of stereovilli radially decreasing in length	— velar tentacles [70] — epidermis [71]
Tunicata	Ascidacea <i>Boryllus schlosseri</i> [72], <i>Styela plicata</i> [73], <i>Ciona intestinalis</i> [74], <i>Phallusia mammillata</i> [74], <i>Chelyosoma productum</i> [74], <i>Corella infata</i> [75], <i>Cavelina lepadiformis</i> [74], <i>Diplosoma listerianum</i> [74], <i>Malgula socialis</i> [76]	adult	conal sensory cell	removal of tentacles abolishes particle rejection response [75]	TRPA [78]	SSC	— unciolated in <i>B. sch.</i> , <i>S. pli.</i> , <i>M. soc.</i> , <i>P. atl.</i> , <i>D. nat.</i> — multiciliated (2–10 cilia) in <i>C. inf.</i> , <i>P. mam.</i> , <i>C. pro.</i> , <i>C. inf.</i> , <i>C. lep.</i> — 9+2 axoneme — non-motile — 4–5 µm cilium — poorly developed rootlets	— no microvilli in <i>P. mam.</i> , <i>C. lep.</i> — short microvilli in <i>C. inf.</i> , <i>C. pro.</i> , <i>C. inf.</i> , <i>P. atl.</i> , <i>D. nat.</i> — stereovilli in <i>B. sch.</i> , <i>S. pli.</i> , <i>M. soc.</i> — stereovilli can be of same or graded length — stereovilli eccentric or concentric to the cilium — fibrils connect microvilli and cilium	— oral tentacles (coronal organ) — oral flaps (coronal organ)
Tunicata (Larvacea)	<i>Oikopleura</i> spp. [79]	adult?	mouth sensory cell	—	—	SSC	— multiciliated — cilia radially graded in length — 9+2 axoneme	— no microvilli lip	— dorsal and ventral lip
Porifera	<i>Ephydata muelleri</i> [80]	adult	ciliated pinacocyte, epithelial ciliated cell	removal of cilia or osculum abolishes response [80]	—	—	— biciliated — 9+0 axoneme — non-motile	— no microvilli	— osculum (exhalant siphon)

^aOnly molecular data related to the expression of mechanotransduction-related components is included.

^bSecondary sensory cells lack a neurite projection (e.g. vertebrate hair cells).

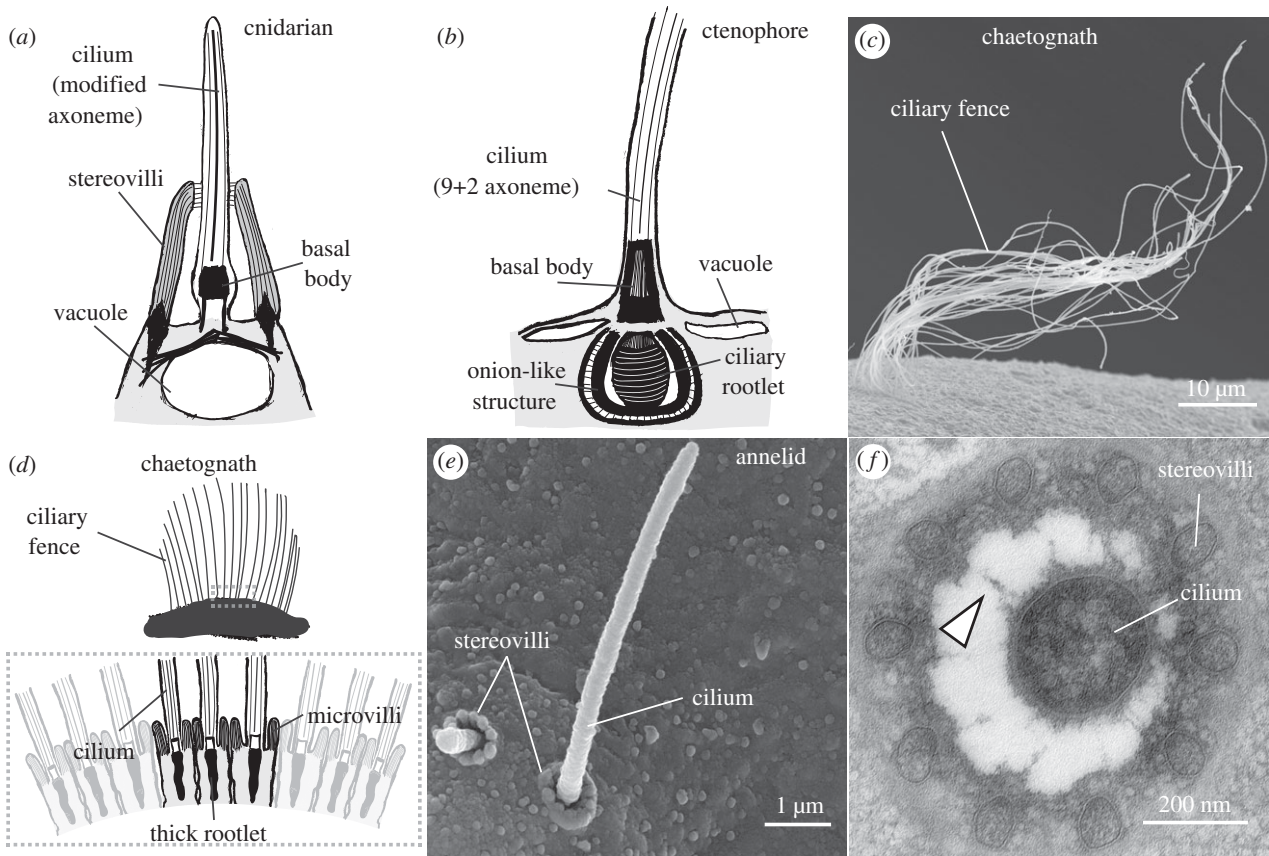


Figure 3. Structural diversity of vibration receptors. (a) Sketch of a cnidarian vibration receptor. The cilium has a modified axoneme, stereovilli and a vacuole at the base. (b) Sketch of a putative ctenophore vibration receptor. Note the absence of microvilli and the onion-like structure at the base. (c) SEM micrograph of a chaetognath ciliary fence. (d) (Top) Sketch of a ciliary fence in a chaetognath. Dashed rectangle highlights the region expanded below. (Bottom) Sketch of the ciliary fence receptors showing their collared cilia and their tight arrangement along the fence. (e) SEM micrograph of a collar receptor in the annelid *P. dumerilii*. (f) TEM micrograph of a collar receptor. Arrowhead points to fibres connecting the cilium and the stereovilli. Sketches in *a*, *b* and *d* are based on images/schematics in [112,116], [118–120] and [121,122]. Image in *f* is taken from [123].

(a) Prey location

Cnidarians, the sister group of bilaterians, have multiple ciliated sensory cell types and show varied behaviours in response to mechanical cues produced by their prey. Cnidarian polyps are attached to the substrate and capture their prey with tentacles around the mouth. Polyps respond to low-frequency vibrations or to touch by bending towards the source of the signal [110–112]. This behaviour could allow the polyp to catch passing prey and may be induced by collared unciliated sensory cells in the tentacles and other parts of the body [112–117] (figure 3*a*; table 2). In anthozoan polyps, sensory structures called hair bundles have stereovilli with radially decreasing length linked by fibrils at their tips in a similar fashion to vertebrate hair cell stereovilli [113,117] (table 2). Loose-patch recordings combined with flow stimulation induce negative or positive graded currents as a function of the intensity and direction of the stimulus [124], which may be due to the asymmetric arrangement of stereovilli. The stereovilli label with antibodies against a TRPA homologue [127] and a cadherin-23 homologue [125,126]. The latter molecule specifically localizes to the tip link-like structures [125]. Masking the cadherin with antibodies affected the structure and mechanosensitivity of the sensory bundle [126].

In addition to hair-cell like cells, cnidarians have evolved a highly specialized ciliated mechanosensory cell called the nematocyte. These cells are sensitive to vibrations and respond cell-autonomously by an explosive discharge of a

stinging capsule that injects toxins into their prey [151,152]. Mechanical stimulation drives action potentials in the cell [136,137], while coincident chemical stimuli can increase the probability of activation [153,154]. Nematocytes have a sensory part called the cnidocil apparatus, which is responsible for both sensory modalities. The cnidocil is a modified cilium associated with a bundle of microvilli that is connected by fibres to the cilium [115,130–133,135,155] (table 2).

Evidence points to a major role of the cilium in mechanotransduction at the nematocyte. First, deflection of the cnidocil induces mechano-electrical potentials independent of stimulus direction [137]. Second, removal of the cnidocil drastically reduces the receptor potential upon contact [154]. This process may involve the mechanotransduction channel NOMPC since at least one of the four NOMPC homologues in *Hydra* localizes to the cnidocil [138]. Moreover, MMCs such as those in the campaniform receptors of *Drosophila* (figure 1*d*) are also present in the cnidocil [131]. This suggests that MMCs may also form a gating spring to open the NOMPC channel upon cnidocil stimulation [138]. Cnidarians thus seem to have different mechanosensory cell types that rely more on stereovilli (hair bundles) or on cilia (nematocytes) for sensory transduction.

Ctenophores (comb jellies) have also evolved efficient mechanisms for prey detection [156–159]. Ctenophore prey detection likely depends on flow or contact sensitivity conferred by ciliated sensory structures. The lobate ctenophore *Eucharis* has multiple finger-like protrusions carrying ciliated neurons at

Table 2. Ciliary mechanosensory cells in prey–predator interactions.

animal group	species	stage	cell name (s)	evidence of mechanosensory modality	molecular data ^a	sensory neuron (SN) or secondary sensory cell (SSC) ^b	cilium features	actin or other structures	location of cells
Cnidaria (Hydrozoa and Cubozoa)	<i>Coryne pinniteri</i> [112],	polyp	mechanosensitive	vibration or touch of tentacles bearing these cells induces behaviour [112]	—	SSC (eg. in [116])	— unciolated	— collar of 7 to 9 stereovilli	— tentacles
	<i>Stauritiosarsia producta</i> [114],		ciliated cell type			— 2–70 µm non-motile cilium	— in some cases fibrous connection between stereovilli and cilium	— oral disc	
	<i>Carybdea marsupialis</i> [115],		concentric hair			— modified cilium with central dense fibril and periferal doublets	— stereovilli are joined intracellularly by pseudovilli		
	<i>Coryne tubulosa</i> [116]		cells [116]			— doublets connected to ciliary membrane at proximal side			
Cnidaria (Anthozoa)	<i>Diadumene lineata</i> [117],	polyp	anemone hair bundle	mechano-induced currents in HBs [124]	cadherin-23 [125,126],	SN	— unciolated	— collar of 5 to 10 stereovilli	— tentacles
	<i>Cerianthopsis americana</i> [113],		(HB) sensory neuron,			TRPA [127]	— 15 µm long cilium	— stereovilli with graded length surround the central collar and originate from supporting cells together forming the HB	— oral disc
	<i>Stomphia cocinea</i> [113]		ciliary cone sensory cell			— 9+2 axoneme	— length surround the central collar and originate from supporting cells together forming the HB		
Cnidaria (Hydrozoa)	<i>Aglantha digitale</i> [128,129]	medusa	ciliated comb pad (C) cell, T cell	responsiveness to short-range vibration (C cell) or to long-range vibration (T cell) [129]	—	SN	— unciolated	— collar of 7 microvilli	— velum/lumbrellar margin between tentacles (C cell)
						— 10–15 µm non-motile cilium	— microvilli graded in length (C cells)	— base of tentacles (T cell)	
							— 9+2 axoneme		
							— no rootlet		

(Continued.)

Table 2. (Continued.)

animal group	species	stage	cell name (s)	evidence of mechanosensory modality	molecular data ^a	sensory neuron (SN) or secondary sensory cell (SSC) ^b	cilium features	actin or other structures	location of cells	
Cnidaria (Hydrozoa and Cubozoa)	<i>Hydra</i> spp. [130–132], <i>Stauridiosarsia producta</i> [114], <i>Tubularia larynx</i> [131], <i>Carybdea marsupialis</i> [115], <i>Gonionemus vertens</i> [133], <i>Physalia physalis</i> [134], <i>Craspedacusta sowerbii</i> [135]	polyp, medusa, siphonophore	nematocyte	generator potentials upon mechanical stimulation [136,137]	NOMPC [138]	SSC	— unciolated — non-motile — multiple of 9 doublets at axoneme periphery — central axoneme modified with dense fibril filled with single microtubules or stacked plates — doublets connected to ciliary membrane at proximal side — large vacuole attached to basal body	— collar of 7 to 21 stereovilli — stereovilli of equal height — stereovilli forming a crescent shape at the proximal side of the ciliodocl and a ring at its distal side — stereovilli partially or fully covered by protrusions of surrounding epitheliomuscular cells — stereovilli connected to each other via intracellular and extracellular filaments	— tentacles	
	Ctenophora	<i>Eucharis multicornis</i> [139], <i>Lampetia panzerina</i> [140], <i>Callianira bialata</i> [140], <i>Pleurobrachia rhodops</i> [140], <i>Beroe cucumis</i> [119], <i>Pleurobrachia pileus</i> [141], <i>Euplokamis</i> sp. [118]	adult	sensory cell, Tastborsten	touch of the cilium and vibration induces prey-seeking response [139]	—	SN	— unciolated — up to 100 µm long non-motile cilium 9+2 axoneme — modified basal body and rootlet (layered in an onion-like fashion) — ER associated to the root — vacuolated surface	— no microvilli — in <i>Beroe</i> an actin peg is adjacent to cilium — microtubules surround the actin bundle	— finger-like protrusions (<i>Eucharis</i>) — tentacles — lip epidermis (<i>Beroe</i>) — statocyst epithelium in the aboral organ (<i>Pleurobrachia</i>) — tentilla (<i>Euplokamis</i>)

(Continued.)

Table 2. (Continued.)

animal group	species	stage	cell name (s)	evidence of mechanosensory modality	molecular data ^a	sensory neuron (SN) or secondary sensory cell (SSC) ^b	cilium features	actin or other structures	location of cells
Chaetognatha	<i>Spadella</i> spp. [121,122,142]	adult	ciliary fence receptors (CFRs) groups of >100, ciliary tuft receptors (CFRs) groups of <100	touch of the fence leads to escape response [143]	—	SN/SSC	— unciliated — up to 100 µm long cilium — 9+2 axoneme — central microtubule pair aligned to the long axis of the fence (but see [122]) — long striated rootlets (CFRs) — CFRs have an electron-dense basal apparatus (CFRs) — cilia of variable diameters	— collar of 9 microvilli — collar of stereovilli (microtrichien)	— across the body parallel to the anterior posterior body axis (CFRs) — across the body perpendicular to the anterior posterior body axis (CFRs)
Tunicata (Larvacea)	<i>Oikopleura</i> spp. [144]	—	Langerhans receptor	touch of the receptor evokes electric responses [144]	—	SSC	— unciliated — up to 70 µm long cilium — recessed cilium — no basal body — parallel microtubules — lateral rootlets	— no microvilli	— tail
Annellida	<i>Platynereis dumerilii</i> [123], <i>Lumbricus terrestris</i> [145], <i>Hirudo medicinalis</i> [146], <i>Eurythoe complanata</i> [147], <i>Ophryotrocha puerilis</i> [148], <i>Dinophilus gyrociliatus</i> [149]	nectochaete larva [123], adult [145–148]	CR [123], S hair [146], type 1 collar receptor [147], type 3 collar receptor [148], type la collar receptor [149]	short range vibration induces calcium spikes in the cells (<i>P. dum.</i>) [123]; sensilla show electrical responses to water-borne vibrations (<i>H. med.</i>) [150]	PKD1 and PKD2 [123]	SN	— unciliated — 10 µm long non-motile cilium — 9+2 axoneme — no rootlet	— collar of 10 oval-shaped stereovilli — dense matrix connects stereovilli — fibrils connect stereovilli to cilium	— sensory organs and epidermis across the body

^aOnly molecular data related to the expression of mechanotransduction-related components is included.

^bSecondary sensory cells lack a neurite projection (e.g. vertebrate hair cells).

their tips with a single long non-motile cilium and a highly modified root and basal apparatus [139] (figure 3*b*; table 2). The protrusions are sensitive to vibrations and this may underlie the ability of the animals to detect prey. Similar cells line the tentacles of cydippid ctenophores [118,140] and the lips of beroid ctenophores [119]. In the latter, the cilium is flanked by actin-microfilament-supported pegs.

Chaetognaths (arrow worms) are planktonic predators that can detect minute short-range vibrations generated by their prey [143,160,161]. This ability is likely conferred by numerous putative mechanosensitive organs called ‘ciliary fences’ [121,122,142,162] (figure 3*c*). These organs are mechanosensitive and are composed of parallel arrays of unciliated neurons each with regularly arranged collars of slender microvilli (figure 3*d*; table 2). The sensory arrays contain cells with cilia of different diameters and lengths in a defined arrangement within the array [122]. These structural features and their location along the body may account for the increased ability of these animals to locate the source of vibrations and respond in a defined frequency range [143,160].

(b) Predator detection

Planktonic organisms often rely on mechanical stimuli in order to detect approaching predators and display a defence response or escape.

The planktonic larvacean *Oikopleura* shows responses to touch or vibrations [163]. In its tail, there are mechanosensory cells called Langerhans receptors [144,164] that may mediate the escape response to touch in these animals [144,163]. The Langerhans receptors have a long process supported by multiple parallel microtubules—a modification also seen in the tubular body of insect type 1 mechanosensory organs and in the amphioxus type II cells (see above). Langerhans receptors have no associated microvilli and a highly modified basal apparatus that lacks a typical basal body (table 2). Ultrastructural studies of these receptors across development are needed to track how its unconventional sensory dendrite is formed.

The planktonic larva of the annelid *Platynereis* also shows a startle response upon water-borne vibrations [123]. The vibration receptors have a non-motile cilium and a collar of stereovilli (figure 3*e,f*). Collar receptors (CRs) with similar ultrastructure are present in other annelids (table 2; [145–149]). CRs in *Platynereis* express homologues of the Polycystin 1 and 2 gene families, which are important for the function and structure of ciliated mechanosensory cells in both vertebrates and invertebrates [165–168]. Polycystin-deficient *Platynereis* larvae generated by CRISPR/Cas9 mutagenesis are not sensitive to vibrations and are more easily captured by planktonic predators [123].

The larger planktonic jellyfish *Aequorea victoria* (phylum Cnidaria) also shows an escape response upon direct contact with a predator [169]. This animal has at least three types of ciliated mechanosensory cells implicated in responses to touch and vibrations. Collar cells or C cells are found in the velum and have a single cilium and a polarized collar of microvilli [128,129,170] (table 2). These cells connect to the giant axon system that triggers the predator escape response [170]. Laser ablation of the C cells eliminated neuronal activity in the giant axon induced by vibrational stimulation [129]. T cells and F cells are other ciliated mechanoreceptors found

in the velum [129] (table 2), but their exact sensory range and contribution to the response are still to be defined.

The detection of vibrations in the environment may have been among the first sensory functions of cilia in the last eukaryotic common ancestor. Ciliated unicellular organisms such as *Paramecium* and *Chlamydomonas* show fast escape responses triggered by contact and vibration [171,172]. These experimentally tractable systems are valuable to address the role of cilia in mechanosensation and to trace the evolution of this sensory modality. In *Paramecium*, frontal contact of the cell with an obstacle leads to ciliary arrests followed by reversal of the ciliary stroke. Although cilia are in principle stimulated in this response, deciliated cells still retain depolarizing receptor potentials, thus indicating that the site of mechanotransduction is at the cell rather than at the ciliary membrane [173]. The long *Chlamydomonas* cilia (commonly referred to as flagella) are mechanosensitive [174] and suppression of a TRPV channel located in the proximal side of the cilium leads to a reduction in avoidance responses [175]. Another unicellular green alga, *Pyramimonas octopus* shows high sensitivity to contacts to its locomotory cilia, upon which a fast escape response is enacted [176]. Such enhanced sensitivity may be achieved by micrometer-scale movements of its cilia during non-swimming periods. Thus, at least in algae, cilia may have an active role in sensing mechanical cues.

4. Ciliated mechanosensory cells in orientation and navigation

Orientation or navigation guided by mechanical signals is common in aquatic organisms. In this section, we review examples where ciliated mechanoreceptors have been implicated in various forms of orientation and navigation responses, including gravitaxis, flow and pressure sensation.

(a) Gravitaxis

Many aquatic organisms can orient relative to the gravity vector. In some cases, orientation is passive due to the shape and density distribution of the animal. In other cases, orientation is active and depends on sensors in the body. Statocysts are the most common type of gravisensory organs, and they often contain ciliated mechanosensory cells and a small concretion or statolith.

In cnidarian medusae, the statocysts are located at the edge of the velum and contain a concretion that likely stimulates mechanosensory cilia when the animal turns upside down [128,177–183]. Different types of ciliated cells either with or without stereovilli can be found in the cnidarian statocyst, even in a single species (table 3). The individual contributions of these cells to mechanosensation has not been elucidated [179] and may also include sound perception [210].

The aboral sense organ of ctenophores contains a statocyst involved in controlling body posture [211]. The statocyst contains one statolith in the middle that is attached to four groups of ciliated cells (called the balancers) [184,185], one in each quadrant of the animal (table 3). Each balancer has several cilia that sporadically beat as a unit. When the statolith presses the cilia upon a change in posture, their beating frequency changes as a function of statolith load (figure 4*a*) [184,186]. The balancer cilia are hydrodynamically coupled to the locomotor ciliary comb plates. Changes in ciliary

Table 3. Ciliary mechanosensory cells in posture and orientation.

animal group	species	stage	cell name (s)	evidence of mechanosensory modality	molecular data ^a	sensory neuron (SN) or secondary sensory cell (SSC) ^b	cilium features	actin or other structures	location of cells	
Cnidaria	<i>Halistaura cellularia</i> [179], <i>Aegina citrea</i> [179], <i>Salmisus marshalli</i> [179], <i>Cumina lativenis</i> [182], <i>Rhopalomena velatum</i> [182], <i>Geryonia proboscidalis</i> [182], <i>Aurelia aurita</i> [183], <i>Aqantha digitale</i> [128]	medusa	type A–C sensory cells [179], type I receptor [183], ciliated sensory cell	removal of statocyst leads to loss of righting behaviour [180]	—	SN	— unciliated — 10–15 µm long non-motile cilium — 9+2 axoneme — no rootlet (type A, B) to strong rootlet (type C)	— no microvilli (type A) — unorganized microvilli (type C) — collar of 7 to 15 stereovilli	— statocyst	
	<i>Pleurobrachia pileus</i> [184,185], <i>Bolinopsis</i> sp. [184]	adult	balancer ciliated cell	deflection of a balancer increases or decreases beating frequency [184,186]	—	—	— unciliated — 50–100 µm long cilium — 9+2 axoneme — dense striated rootlet — cilia tips embedded in folds of lithocytes — central pair oriented at right angles to beating direction	— no microvilli	— statocyst (aboral sense organ)	
	Bivalves <i>Pecten</i> sp. [187,188]	adult	hair cell	generator potentials recorded in statocyst cells upon mechanical displacement or statocyst rotation (nudibranchs [198], gastropods [199,200] cephalopods [201])	—	SN/SSC	— multiciliated — 9+2 axoneme — basal feet in a single cell point in the same direction (cephalopods and some other molluscs [187,189,194,196,197]) — non-motile cilia (cephalopods) — motile cilia (at least some gastropods, and nudibranchs) — basal feet radially arranged (i.e. no hair cell polarization [187,188,190,192–195]) — striated rootlet opposite basal foot	— ring of microvilli around each cilium [187,189,194,196] — few dispersed microvilli [187,188,192,197] — no microvilli [193]	— statocyst — in cephalopods also found in neck [202] and lateral line [203]	
	Gastropods <i>Pomacea paludosa</i> [189], <i>Aplysia californica</i> [190,191], <i>Pleurotrachea</i> sp. [187], <i>Lymnaea stagnalis</i> [192], <i>Biomphalaria glabrata</i> [193]									
	Nudibranchs <i>Rostanga pulchra</i> [194], <i>Hemisserida crassicornis</i> [195]									
	Cephalopods <i>Octopus vulgaris</i> [196], <i>Sepia officinalis</i> , <i>Loligo vulgaris</i> [197]									

(Continued.)

Table 3. (Continued.)

animal group	species	stage	cell name (s)	evidence of mechanosensory modality	molecular data ^a	sensory neuron (SN) or secondary sensory cell (SSC) ^b	cilium features	actin or other structures	location of cells
Tunicata	Ascidacea	swimming	statoyst-associated cells,	statolith-ablated larva (<i>Ciona</i>) fails to show gravitaxis [208]	—	SN	— unciliated — cilium filled with vesicles (<i>O. dioica</i>)	— several microvilli (<i>D. mac</i>) — laminar microvillar extensions (<i>B. sch.</i>)	— sensory vesicle
	<i>Diplosoma macdonaldi</i> [204], <i>Ciona</i> spp. [205], <i>Boryllus schlosseri</i> [206]	larva (ascidian)	antenna cells, S1 cells				— cilium contacts statolith (<i>O. dioica</i>) — striated rootlet		
	Larvacea								
	<i>Oikopleura dioica</i> [207]								
Cephalochordata	<i>Branchiostoma floridae</i> [209]	12.5-day larva	ciliary bulb cell	—	—	SN	— unciliated — enlarged distally and filled with a dense matrix — rootlet	—	— infundibular region of cerebral vesicle

^aOnly molecular data related to the expression of mechanotransduction-related components is included.

^bSecondary sensory cells lack a neurite projection (e.g. vertebrate hair cells).

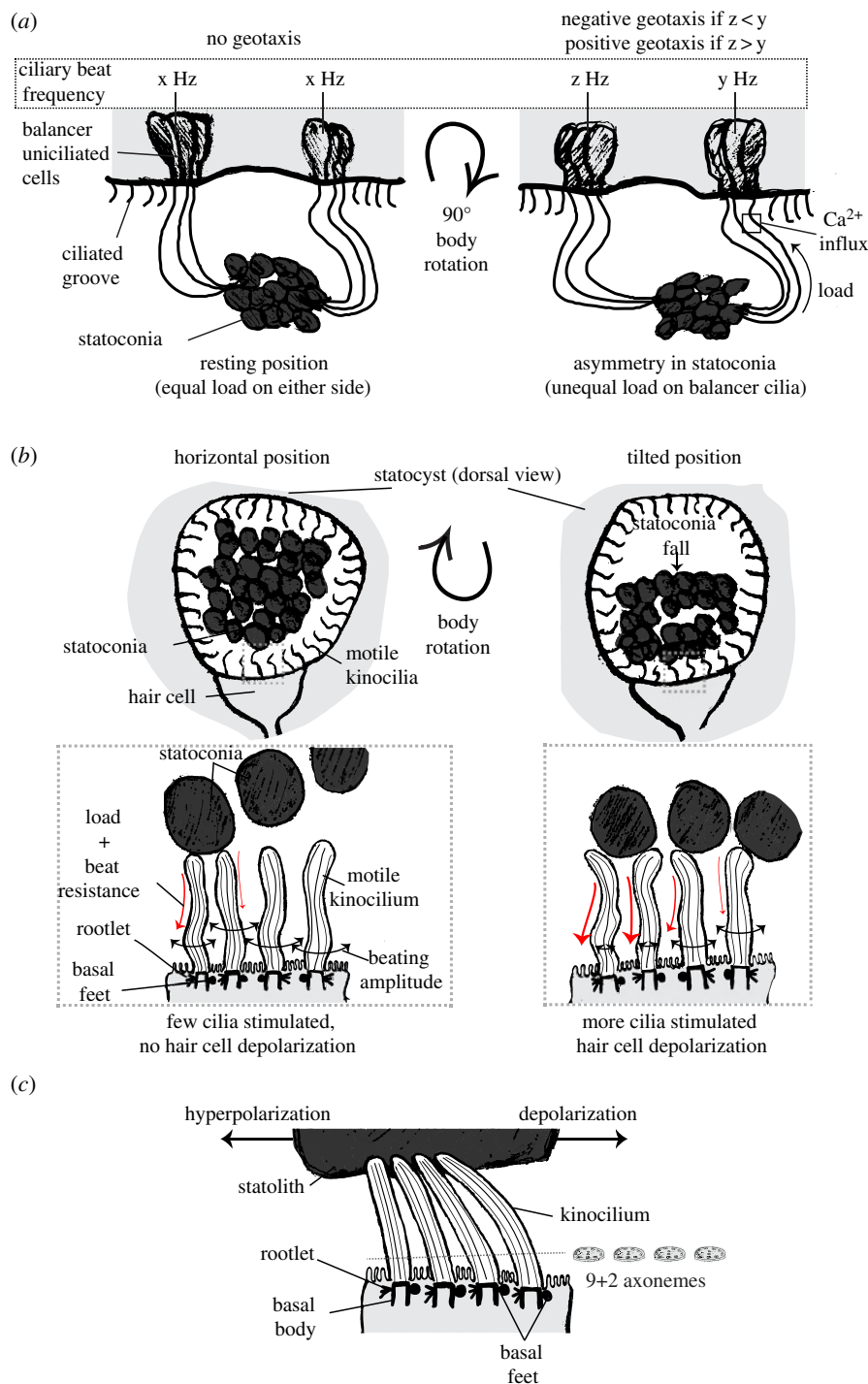


Figure 4. Diversity in function and structure of ciliated statocysts. (a) (Left) Sketch of a ctenophore statocyst in its resting position (i.e. animal in vertical position). Water surface is to the top. Balancer cilia on opposite sides have the same beating frequency (x Hz). (Right) Upon body rotation the statoconia attached to the balancer cilia exert more load on one group of balancers (arrow). For clarity, the statocyst is not rotated in the sketch. This leads to an asymmetry in stimulation, and thus a consequent difference in beat frequency (z and y). The sign of geotaxis depends on the relative beating frequencies of each balancer. Beating only occurs at the base of the cilia (square) and it depends on Ca^{2+} . (b) (Upper left) Sketch of a non-cephalopod mollusc statocyst in its resting position (i.e. animal in horizontal position). View from the dorsal side. (Lower left) Close-up view of a multiciliated hair cell in resting position. Basal feet are not oriented in the same direction. Some of the motile kinocilia sporadically contact statoconia, thus affecting their beating amplitude. This leads to an increase in voltage noise in the cell, but still below the firing threshold. (Upper right) Upon tilting, statoconia redistribute to one side, thus increasing the chance of cilia colliding with them. (Lower right) More cilia make contact with statoconia, causing depolarization of the cell. (c) Sketch of a cephalopod multiciliated hair cell. Kinocilia are not motile and are attached to the overlying statolith. All basal feet are oriented in the same direction, which is perpendicular to the central pair of the 9+2 axoneme. The cell is depolarized when the cilia are deflected in the direction towards the basal feet and hyperpolarized when bent in the opposite direction. Sketches in *a*, *b* and *c* are based on [184,212], [195,213,214] and [197,215], respectively. (Online version in colour.)

beat frequency have been suggested to propagate through this coupling and cause a turning response [184]. The deflection-induced ciliary beating in the balancer cells is dependent on influx of Ca^{2+} at the base of the cilium [212]. Ca^{2+} levels

are probably modulated by mechanically induced electrical changes in the membrane of balancer cells [184].

Molluscs also have statocysts and show gravitactic responses [192,216]. The statocysts have mechanosensory

cells with multiple cilia (e.g. 30–40 in *Pomacea paludosa*) and small microvilli arranged in rings or irregularly among the cilia [187–194] (table 3). In non-cephalopod molluscs, cilia are often motile and statoliths or statoconia can move freely upon changes in the animal's posture (figure 4*b*, top). Direct contact of the motile cilia with the statoconia depolarizes the mechanosensory cells [198–200] (figure 4*b*, bottom). The responses are graded according to the magnitude of stimulus [217,218] and are not dependent on stimulus direction [219]. The motility of the cilium in these mollusc hair cells leads to a constant fluctuation in voltage due to random contacts with the statoconia [220–222]. A change in the orientation of the animal leads to more cilia contacting the statoconia, which in turn leads to a summed and concerted change in voltage of the cell by the activation of the mechanotransduction apparatus in each cilium [213,214,223] (figure 4*b*, bottom right). Cilium motility may serve two purposes in these cells. First, it may amplify the signal by the combined effect of statoconia loading and the resistance to beating. Second, it may be a mechanism to actively monitor statoconia load by sustained depolarization events due to the constant interactions caused by the beating cilia [214]. Cilium-motility-driven modulation of mechanotransduction (or active mechanosensing) is also known from chordotonal organs in insects [224,225].

In cephalopods, the statocyst is embedded in a complex equilibrium organ with analogous functions to the vertebrate ear [226–230]. Like other molluscs, mechanosensory hair cells in the cephalopod statocyst have several kinocilia (up to 200 in decapod cephalopods) and short microvilli [196] (table 3). The kinocilia in cephalopods are not motile and connect to each other at their tips by membrane junctions [231]. The basal feet of the cilia in a single cell are oriented in the same direction [196,197]. Recordings from the statocyst afferent nerves have shown maximal directional sensitivity to vibrations that are parallel to the axis of the morphological polarization of the hair cells [201,232,233] (figure 4*c*). The polarization of cilia in cephalopod hair cells thus has similar functional consequences to the polarization of stereovilli in vertebrate hair cells.

Some planktonic tunicates are geotactic and also have a statocyst with ciliated sensory cells [206,207,234–236]. The sensory vesicle of the ascidian larva hosts a pigmented statocyst composed of a cellular otolith and associated ciliated sensory cells [204] (table 3). When the otolith is ablated, the larva loses the ability to swim towards the surface [208]. Gravitaxis may rely on the stimulation of the ciliated cells by the otolith [204,237,238]. In *Ciona* larvae, the ciliated sensory cells (called antenna cells) are glutamatergic [239]. Their neuronal circuitry down to the muscle effectors was recently reconstructed by serial electron microscopy [205].

A less conventional ciliated statocyst was found in the amphioxus larva [209,240]. Although no geotactic response has been reported in this animal, a balance organ may be responsible for its hovering swimming behaviour [241]. A putative balance organ was found at the posterior side of the cerebral vesicle. This organ is composed of a group of 'ciliary bulb' cells, each with a single cilium filled at its distal end with a dense bulky matrix (table 3). Adjacent to these highly modified cilia there are slender cilia emanating from accessory cells. In theory, the dense bulbous cilia would be moved by gravity, thereby activating the accessory cells by contacting their cilia. This may allow the larva to monitor its body orientation [209].

Several other invertebrate planktonic animals, including bryozoan larvae and chaetognaths, show geotactic responses albeit these animals lack a statocyst [242–244]. In at least some cases, these are active responses, as shown by centrifugation experiments [242]. The gravisensory organ in these animals has not yet been found, but as suggested for amphioxus, it may lie in the different modified ciliated structures reported in these animals [86,121,245].

(b) Detection of flow

Detection of flow (rheoreception) is common among aquatic animals and it is often used for orientation [246]. In fish, lamprey and tadpoles rheoreception is mediated by hair cells in the lateral line [247]. Aquatic invertebrates such as nudibranchs, brittle stars and flatworms also respond to the effects of turbulence and flow [248–255]. Ciliated sensory cells have been proposed as potential flow receptors in these and other animals [256,257] but, to our knowledge, direct physiological evidence is still lacking. Some of these animals also respond to chemicals delivered by the flow [258], which highlights the need of carefully controlling for such confounding effects in rheotaxis experiments.

Cephalopods have an organ with functional similarities to the vertebrate lateral line. These 'epidermal' lines are composed of multiciliated sensory cells similar to the cells lining the statocyst [203] (see above). Electrophysiological recordings from the epidermal line nerve indicate that the organ is sensitive to small water movements [215,259]. Chemical ablation of the epidermal line in squid reduces its ability to detect a fish predator [260,261]. Whether the organ is also involved in navigation and orientation like the lateral line in fish has not been studied.

Sponges also have ciliated sensory cells implicated in flow sensation. The cone cells or apopylar cells are unciliated cells in the excurrent pore (apopyle) of the choanocyte chamber [105,262–264]. These cells have a 'fringe' of microvilli oriented towards the choanocyte chamber [263]. Cone cells may detect flow and help control its direction.

Small planktonic larvae are exposed to local flow variations caused by waves, filter feeders or turbulence [265–268] and can respond by changing their swimming behaviour [269–272]. Such responses usually involve vertical movements in the water column to enter or exit particular flows [273]. For example, different mollusc larvae can either sink, or actively swim downwards or upwards in response to different flow environments [270,274–279]. Arthropod larvae also swim upwards in response to increased turbulence [280]. In oyster larvae, the internal ciliated statocyst is thought to mediate responses to waves and turbulence [276,281]. Sea urchin larvae lack a statocyst but are able to adjust their swimming speed according to turbulence levels [282].

(c) Pressure sensation

The locomotory response to changes in hydrostatic pressure is termed barokinesis [283,284]. Barokinesis has been documented in various marine animals, including ctenophores [285], annelids [286,287], cnidarians [286,288], molluscs [289–291] and arthropods [286,289,292–294]. The response usually involves an increase in swimming activity with increasing pressure. Pressure is an indicator of depth and responding to pressure can enable an animal to counter

downwelling and upwelling currents [295]. Pressure changes may also entrain tidal clocks [296–298].

Fish sense hydrostatic pressure and this ability is likely mediated by receptors lining the swimming bladder [299]. Animals without a swimming bladder may use ciliated sensory cells to detect changes in pressure. Dogfish hair cells increase their firing frequency under increased hydrostatic pressure [300]. Crabs use instead a modified type 1 organ in their statocysts to detect pressure changes. It consists of a long cuticular hair attached to ciliated sensory cells at its base. Upon changes in pressure the thread hair serves as a piston pressing against the sensory cilia, thereby causing cell depolarization [301]. Putative ciliated pressure receptors have been described in ctenophores [120,285], tunicates [206,235], amphioxus [302–304] and barnacles [305]. These cells usually have branched cilia with a 9+0 axoneme and bulbous tips protruding into an internal liquid-filled cavity. In support of the involvement of such a type of ciliated cell in pressure detection, we recently found in *Platynereis* a branched ciliated neuron showing a correlated increase in activity with increases in pressure (LA Bezares-Calderón and G Jékely 2016, unpublished). One hypothetical mechanism to explain how cilia sense small pressure changes is basal body movement by fluid displaced from the tip of the bulbous cilium [306].

5. Ciliated mechanosensory cells in larval settlement

The majority of marine invertebrates have a biphasic life cycle with a larval planktonic stage and an adult benthic stage. During settlement, planktonic larvae need to find a suitable substrate.

They achieve this by integrating multiple cues, primarily chemical but also mechanical, about the substrate and the flow environment. In this section, we highlight a few cases where there is potential involvement of ciliated mechanosensory cells in regulating settlement.

(a) Topography-based settlement

The mechanical detection of the substrate may allow larvae to detect appropriate surfaces. Echinoderm larvae that already contain the adult rudiment use their tube feet to scan the substratum [307]. This direct contact together with chemical cues is required to induce settlement. At the end of the tube feet, the larvae have unciliated sensory receptors with a collar of microvilli that may work as substrate sensors [308].

Substrate topography can also influence settlement. Some coral and sponge larvae prefer to settle on surfaces with holes of a particular size [309]. Both sponge and coral larvae have diverse ciliated sensory cells including cells with a long cilium and a collar of microvilli [310–317]. Ascidian larvae also have a preference for particular substrates [318,319]. These larvae use adhesive papillae at their anterior end to find a suitable substrate for settlement and metamorphosis [234,320]. Ciliated sensory cells in the papillae may be used to detect the mechanical properties of a particular substrate [321–328]. That said, the settlement preference for a particular surface topography may in some cases be an indirect effect of the flow environment created by it and detected by the larva (see below) [329].

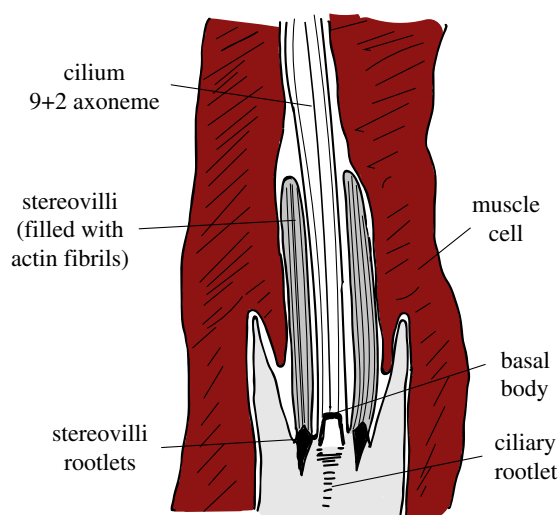


Figure 5. Sketch of a cnidarian proprioceptor. The sensory dendrite including the cilium and the stereovilli are embedded in a muscle cell. Muscle contraction may stimulate the cilium and/or the stereovilli and depolarize the cell. Sketch based on [349]. (Online version in colour.)

(b) Flow-based settlement

Flow sensation has been shown to influence larval settlement in several animal groups [266,267,330]. Cnidarian, barnacle and annelid larvae are able to settle under different flow regimes by integrating flow and settlement cues [331–335]. In some larvae, flow detection alone can recruit larvae to the substrate where they are more likely to encounter chemical cues [336]. For example, oyster larvae stop swimming and sink in response to the turbulent layer near the substrate (*ca* 1 cm from the surface) [278]. In some echinoderm larvae, turbulence may induce competence to settle [273,337,338].

The flow-sensory mechanisms have not been identified in these larvae. Sensory cells regulating settlement are often found at the anterior tip of larvae in a structure known as the apical organ. Some of these cells have long cilia exposed to the flow environment [42,245,339–341]. Chemical disruption of the apical organ cilia in sea urchin larvae leads to swimming defects [342]. The *Platynereis* larva has sensory cells in the apical region with a motile cilium and a collar of microvilli that respond to changes in flow ([343]; LA Bezares-Calderón and G Jékely 2015, unpublished). Apical organ cells express different ion channels that are associated with mechanosensation in vertebrates. For example, cells in the apical organ of sea urchin, *Platynereis* and cnidarian larvae express ASIC, and/or TRP channels such as NOMPC or TRPV [343–346]. Whether and how these cells contribute to substrate or flow sensation is yet to be explored.

6. Ciliated mechanosensory cells in proprioception

Proprioception is a sensory ability to monitor mechanical stress, load and tension on different parts of the body. Proprioceptive systems have mostly been studied in arthropods and mammals [347], but they also occur in other animals to control active locomotion and body posture (e.g. [348]). While mammalian proprioceptors are non-ciliated sensory cells, some arthropod proprioceptors have a cilium, such as the sensory cells in the chordotonal organs or campaniform sensilla.

Table 4. Ciliary mechanosensory cells in proprioception.

animal group	species	stage	cell name (s)	evidence of mechanosensory modality	molecular data ^a	sensory neuron (SN) or secondary sensory cell (SSC) ^b	cilium features	actin or other structures	location of cells
Cnidaria	<i>Hydra</i> spp. [350–352]	polyp	sensorimotor interneuron	—	—	SN	<ul style="list-style-type: none"> — unciliated — recessed cilium — cilium partially exposed to the muscle-epithelial cells — thick rootlets — acellular cavity at the ciliary neck/axone region — 9 doublets plus 6 singlets microtubule-membrane connections (MMCs) 	<ul style="list-style-type: none"> — three concentric rings of microvilli arise opposite to the cilium — fibrous connections between cilium and microvilli 	<ul style="list-style-type: none"> — tentacles — hypostome
Cnidaria	<i>Ceriantheopsis americana</i> [349]	polyp	bipolar mechanoreceptor	—	—	SN	<ul style="list-style-type: none"> — unciliated — 9+2 axoneme — >16 µm long cilium — embedded in muscle-epithelial cell — MMCs — long-thick rootlet 	<ul style="list-style-type: none"> — collar of 6–8 stereocilli — sensory apparatus and dendrite interdigitates with the epitheliomuscular cell 	<ul style="list-style-type: none"> — body wall
Nematoda	<i>Deontostoma californicum</i> [353]	—	proprioceptor metaneme [353]	—	—	SSC	<ul style="list-style-type: none"> — unciliated — 9+0 axoneme — 3.5 µm long cilium — thick long rootlet, sometimes extending into the cilium 	<ul style="list-style-type: none"> — 6–7 fibrous lobes surrounding cilium and arising opposite the cilium — ridges fuse near base of cilia — filaments connecting lobes and cilium 	<ul style="list-style-type: none"> — hypodermal lateral nerve cords

^aOnly molecular data related to the expression of mechanotransduction-related components is included.

^bSecondary sensory cells lack a neurite projection (e.g. vertebrate hair cells).

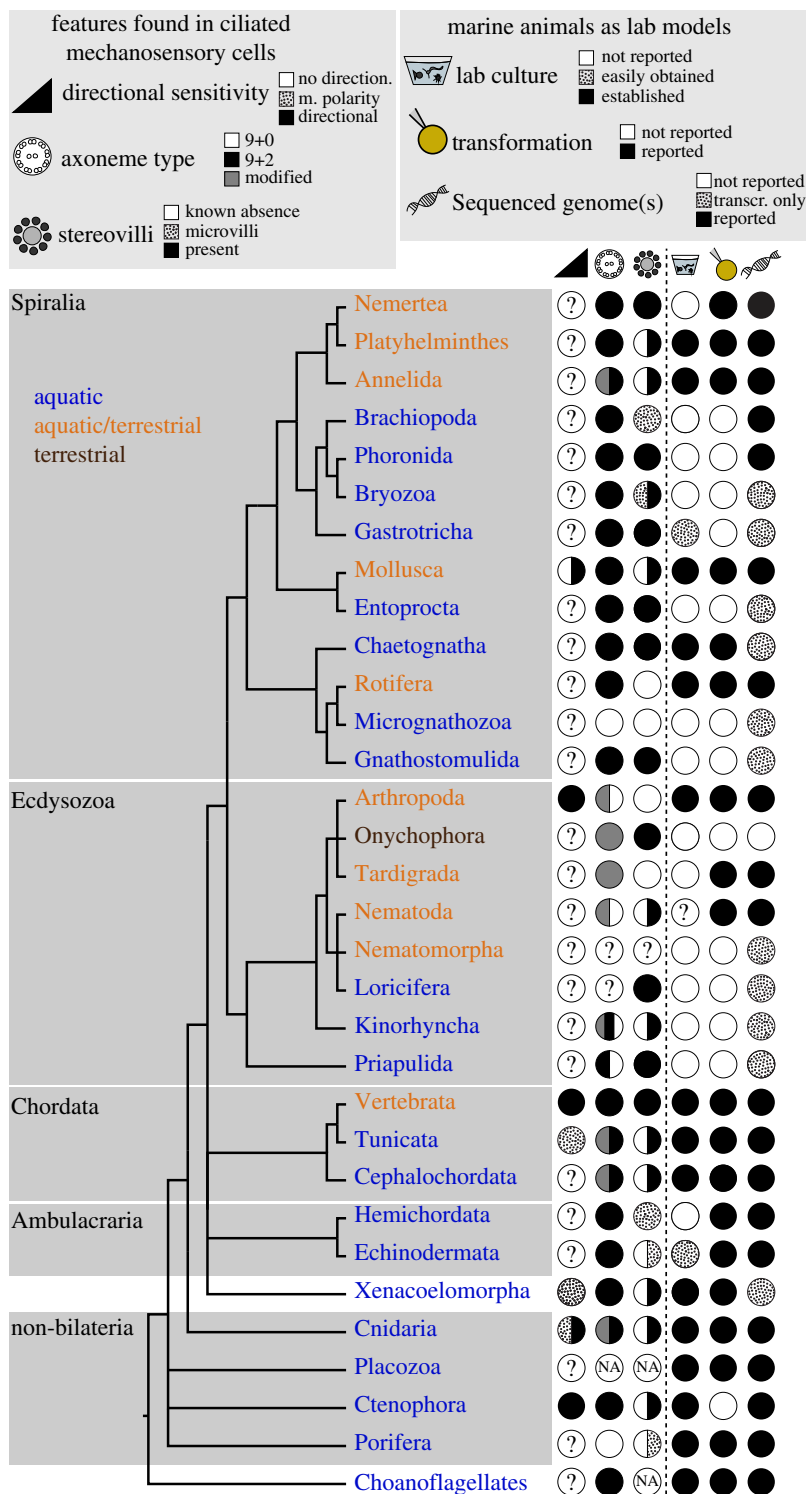


Figure 6. Animal phylogeny shown to indicate main features of ciliary mechanosensory cells and the degree of current experimental accessibility of each major taxon. First column: evidence of directional sensitivity, morphological polarity (m. polarity) or of no directionality. Second column: type of axoneme found in mechanosensory cells. Third column: presence/absence of cells with stereovilli. Fourth column: marine species that can be reared in the laboratory (dotted circle: a species cannot be bred in the laboratory but can be regularly obtained from the wild). Fifth column: transformation techniques available (e.g. microinjection or electroporation). Sixth column: genome sequence reported (dotted circle: only transcriptome assembly reported). Note that other groups of marine organisms not covered in this review (e.g. Rotifers, Platyhelminthes) also offer good opportunities for experimental analyses. Phylogeny is based on [359–361]. See electronic supplementary material, table S1 for references and further details. (Online version in colour.)

There are only a few known examples of ciliated proprioceptors outside the arthropods and vertebrates, mostly in cnidarians. For instance, cerianthid cnidarians have sensory cells with both cilium and stereovilli embedded in a muscle cell [349] (figure 5, table 4). This cell has afferent and efferent connections with fibres controlling muscle activity, perhaps forming a basic proprioceptive circuit. *Hydra* has in its

tentacles a putative proprioceptive ciliated neuron enclosed by epitheliomuscular cells and with its cilium and stereovilli parallel to the mesoglea [350–352] (table 4). Cubozoan medusae also have cilia associated with circular muscle in the epidermis [354] (table 4). Finally, a species of marine nematode has sensory cells with the cilium tightly associated with muscle fibres [353] (table 4).

A highly sophisticated ciliated proprioceptor system was reported in squids. These animals are able to move their head independent of the rest of the body. To achieve a fine control of head movements, squids have a series of ciliated proprioceptors in the 'neck' region with similar morphology to those receptors in the statocyst [202]. These cells are oriented at different angles on the neck surface. Depending on the angle of movement of the head a defined subset of cells is stimulated.

Proprioceptive neurons, neuronal units and behaviours in other marine animals such as sea stars, molluscs or annelids have been reported [252,355–357]. Most of the identified or proposed proprioceptors have a non-ciliated (i.e. multidendritic) morphology similar to spindle receptors in vertebrates [358]. Although more comprehensive ultrastructural descriptions would be needed to rule out the presence of cilia in some of these cases, ciliary mechanoreception does not seem to be generally required for proprioceptive functions.

7. Promising avenues to study ciliary mechanosensation

The examples reviewed here illustrate the diversity in structure and function of ciliated mechanosensory cells across animals (figure 6). Our knowledge of the physiology and function of most of the examples discussed here is fragmentary. Exploring some of these systems further could open up new perspectives in understanding the mechanisms of ciliary mechanosensation and the evolution of mechanoreception.

There are many interesting unanswered questions regarding the function and physiology of ciliary mechanoreceptors. These questions could now be revisited with state-of-the-art techniques in the emerging marine experimental systems. For example, one could test whether the Langerhans receptors or the coronal organ cells in tunicates are

mechanosensitive, as in these and many other cases physiological and genetic evidence is still lacking (tables 1–4). The ultrastructural diversity of putative mechanoreceptors—sometimes even within the same animal—suggests functional and sensory specializations.

Recent developments in genomics, imaging, serial electron microscopy and genome editing have enabled functional studies in several marine organisms. Genetic transformation and the generation of gene knockouts is now feasible in many of the animals discussed above (figure 6) [362]. This is complemented by an ever-increasing number of marine invertebrates that can be reared in the laboratory and that have a genome sequence available. Further progress in understanding the function of ciliated mechanosensory cells will nonetheless require more detailed and quantitative behavioural studies. These approaches could be combined with high-resolution serial electron microscopy reconstruction of sensory structures and neural circuits, as has been possible in *C. elegans* [363] and more recently in marine larvae [123,205].

The structural diversity of mechanosensory cilia in marine invertebrates has long been recognized [364], as well as the rich treasure trove of behavioural mechanisms to be found in marine organisms [365]. We believe the time is ripe to functionally address these aspects in order to have a more unified view of cilia-based mechanosensation.

Data accessibility. This article does not contain any additional data.

Authors' contributions. G.J. collected plankton samples; J.B. prepared and acquired the SEM data; L.A.B.-C. compiled the literature, drew the sketches and assembled the figures; L.A.B.-C. and G.J. wrote the manuscript.

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