

## First record of the freshwater bryozoan *Pectinatella magnifica* in north-west Russia with a description of sensory structures

Z.I. Starunova<sup>1</sup>, K.V. Shunkina<sup>1</sup>, E.A. Genelt-Yanovsky<sup>2</sup>,  
A.V. Kucheryavyy<sup>3</sup>, N.V. Polyakova<sup>3</sup>, Y.A. Danilova<sup>4</sup>, T.A. Ivanova<sup>4</sup>,  
V.V. Starunov<sup>1,5</sup>, O.V. Zaitseva<sup>1\*</sup>

<sup>1</sup> Laboratory of Evolutionary Morphology, Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia. E-mails: Zinaida.Starunova@zin.ru, Ksenia.Shunkina@zin.ru

<sup>2</sup> Department of molecular systematics, Laboratory of Theriology, Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia. E-mail: Evgeny.Genelt-Yanovskiy@zin.ru

<sup>3</sup> Laboratory of behavior of lower vertebrates, A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky pr. 33, Moscow, 119071 Russia. E-mails: scolopendra@bk.ru, nvpnataty@yandex.ru

<sup>4</sup> Baltic Fund for Nature (ICPO Biologists for nature conservation), 24 liniya V.O. 3-7, Saint-Petersburg, Russia. E-mails: suillus@mail.ru, ivanova.baltic@gmail.com

<sup>5</sup> Department of Invertebrate Zoology, Faculty of Biology, Saint Petersburg State University, Universitetskaya nab. 7/9, Saint Petersburg, 199034 Russia. E-mail: Victor.Starunov@spbu.ru

\* Corresponding author: ovzaitseva@inbox.ru

**ABSTRACT:** Colonies of the freshwater bryozoan *Pectinatella magnifica* (Leidy, 1851) were found in north-west Russia for the first time. As the colonies have been observed in Vuoksi river connecting Saimaa and Ladoga lakes, most likely this is a result of the downstream migration from Finland. Details of the general morphology of *P. magnifica* and distribution of sensory structures on the lophophore and colony surface were studied using scanning electron microscopy. Three types of sensory structures were recorded. Two rows of presumably immobile cilia were found on the latero-frontal surfaces of tentacles, and this type is common in Bryozoa. One-two sensory cilia with bases surrounded by short microvilli were detected on the abfrontal surface of the tentacles as well as on the outer and inner surfaces of the lophophoral arms. The mechanosensory function of both these types was assumed like in other bryozoans. Sensory structures of the third type were microvillous ‘knobs’ situated on the colonial body wall surface. They were described for the first time in Bryozoa. Their possible photosensory function is discussed.

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**KEY WORDS:** aquatic invasion, freshwater Bryozoa, sensory structures, scanning electron microscopy.

## Первая находка пресноводной мшанки *Pectinatella magnifica* на северо-западе России с описанием сенсорных структур

З.И. Старунова<sup>1</sup>, К.В. Шунькина<sup>1</sup>, Е.А. Генельт-Яновский<sup>2</sup>,  
А.В. Кучерявый<sup>3</sup>, Н.В. Полякова<sup>3</sup>, Ю.А. Данилова<sup>4</sup>, Т.А. Иванова<sup>4</sup>,  
В.В. Старунов<sup>1,5</sup>, О.В. Зайцева<sup>1\*</sup>

<sup>1</sup> Лаборатория эволюционной морфологии, Зоологический институт Российской академии наук, Университетская наб., 1, Санкт-Петербург, 199034 Россия. E-mails: Zinaida.Starunova@zin.ru, Ksenia.Shunkina@zin.ru

<sup>2</sup> Отделение молекулярной систематики, Лаборатория териологии, Зоологический институт Российской академии наук, Университетская наб., 1, Санкт-Петербург, 199034 Россия. E-mail: Evgeny.Genelt-Yanovskiy@zin.ru

<sup>3</sup> Лаборатория поведения низших позвоночных, Институт проблем экологии и эволюции им. А.Н. Северцова Российской академии наук, Ленинский проспект 33, Москва, 119071 Россия. E-mails: scolopendra@bk.ru, nvrnataly@yandex.ru

<sup>4</sup> Балтийский фонд природы (МБОО Биологи за охрану природы), 24-я линия В.О. 3-7, Санкт-Петербург, Россия. E-mail: suillus@mail.ru, ivanova.baltic@gmail.com

<sup>5</sup> Кафедра зоологии беспозвоночных, Биологический факультет, Санкт-Петербургский гос. университет, Университетская наб., 7/9, Санкт-Петербург, 199034 Россия.

\* Адрес для корреспонденции: ovzaitseva@inbox.ru

**РЕЗЮМЕ:** Колонии пресноводной мшанки *Pectinatella magnifica* (Leidy, 1851) были впервые обнаружены на северо-западе России. Поскольку колонии обнаружены в реке Вуокса, соединяющей озера Сайма и Ладога, скорее всего, это результат миграции с территории Финляндии. Детали общей морфологии и распределение сенсорных структур на лофофоре и поверхности колонии *P. magnifica* были изучены с помощью сканирующей электронной микроскопии. На поверхности зооидов и колонии были обнаружены три типа сенсорных структур. Два продольных ряда, предположительно неподвижных ресничек, были обнаружены на латеро-фронтальных поверхностях щупалец и типичны для мшанок в целом. Одна-две сенсорные реснички, окруженные короткими микровиллями находятся на абфронтальной поверхности щупалец, особенно в их основании, а также на фронтальной и абфронтальной поверхностях рук лофофора. По аналогии с другими видами мшанок предполагается механосенсорная функция этих структур. Третий тип сенсорных структур представляет собой микровиллярный бугорок и был обнаружен на поверхности стенки колонии и описан впервые для пресноводных мшанок. Для этого типа нами рассматривается возможная фотосенсорная функция.

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**КЛЮЧЕВЫЕ СЛОВА:** водные инвазии, пресноводные мшанки, сенсорные структуры, сканирующая электронная микроскопия.

## Introduction

Bryozoans are aquatic sessile colonial invertebrates that occupy various substrates and play an important role in benthic communities (Wood, Okamura, 2005; Schwaha, 2021). Phylum Bryozoa comprises of three classes, Gymnolaemata, Stenolaemata and Phylactolaemata. All Stenolaemata and most Gymnolaemata are marine, while Phylactolaemata are exclusively freshwater. Whereas feeding and behavior was described in many marine bryozoans (reviewed in Winston, 1977, 1978; Ostrovsky, Shunatova, 2002; Ostrovsky *et al.*, 2002; Winston, Migotto, 2021), relatively few studies were specifically focused on the freshwater species (Antipenko, 1999; Riisgård *et al.*, 2004, 2010; Tamberg *et al.*, 2014; Tamberg, Shunatova, 2016).

Research on the mechanisms of bryozoan feeding and accompanying phenomena (e.g. Riisgård, Manríques, 1997; Shunatova, Ostrovsky, 2001, 2002; Riisgård *et al.*, 2010) triggered the renewed interest to the studies of the nervous system and sensory structures (e.g. Schwaha, Wanninger, 2012; Temereva, Kosevich, 2016, 2018; Shunkina *et al.*, 2015; Shunkina, Zaitseva, 2017; Worsaae *et al.*, 2019, reviewed in Schwaha *et al.* 2020). Although first observations of putative sensory structures on bryozoan tentacles go back to the first half of the XIX century (Lister, 1834), and this work was continued after invention of the histological staining technique (e.g. Silbermann, 1906; Gerwerzhagen, 1913; Lutaud, 1955; Brien, 1960), information on this topic was generally scant till recent (reviewed in Winston, 1978; Ostrovsky, Shunatova, 2002). Invention of the scanning and transmission electron microscopy (SEM and TEM elsewhere in the text) and modern staining techniques (among them glyoxylic acid-induced fluorescence) greatly added to our understanding of the bryozoan sensory structures (e.g. Gilmour, 1978; Nielsen, Riisgård, 1998; Shunatova, Nielsen, 2002; Riisgård *et al.*, 2004, 2010; Shunkina *et al.*, 2014a; 2015; Shunkina, Zaitseva, 2017; Tamberg, Shunatova, 2017). Currently, ciliary cells with presumed sensory function are known on the tentacles and the

introvert (eversible part of the body wall) in both marine and freshwater bryozoans.

The freshwater bryozoan “jelly brain” — *Pectinatella magnifica* (Leidy, 1851), is a widespread North American species actively spreading across Europe in during recent decades including Danube (Szekeres *et al.*, 2013), Elbe (Balounová, *et al.*, 2011) and other river systems. In 2010 *P. magnifica* was noticed in the lake Saimaa (Finland) near the border with Russia (I. Kuznetsov, personal communication). Vuorio with co-authors (2018) described the invasion history and dispersion of *P. magnifica* in Finland suggesting that this species has been most likely introduced by international shipping 10–15 years ago. Here we report the first finding of *P. magnifica* in the Vuoksi river, and describe its general morphology and sensory structures on the surface of the lophophore (feeding apparatus) and the colony wall.

## Materials and Methods

Colonies of *Pectinatella magnifica* (Fig. 1A, B) were collected in July–August 2020 from single location at Vuoksi-Virta (location coordinates 60.75, 29.78). Colonies were abundant at sites with slow water flow and up to 2–3 meters deep, usually near the water surface, being attached to rigid stems of aquatic macrophyte vegetation like *Phragmites australis*, *Potamogeton natans*, *Eleocharis spp.* mostly along the shore region.

Species identification was carried out based on general morphology of the colony, zooidal and statoblasts morphology using guidebooks (Kluge, 1949; Lacourt, 1968; Gontar, 2012). Colonies were photographed using Olympus OM-D E-M5 II digital camera, and colony details were further studied using stereomicroscope Leica M205C equipped with a Leica DFS405 camera.

For scanning electron microscopy, the groups of zooids without gelatinous mass were dissected from colony, relaxed by adding drop by drop 7% solution of MgCl<sub>2</sub>, and fixed in 1.25% glutaraldehyde in 0.05 M phosphate buffer (PB, pH 7.2). After fixation, the specimens were rinsed 1–3 times in PBS and dehydrated in an

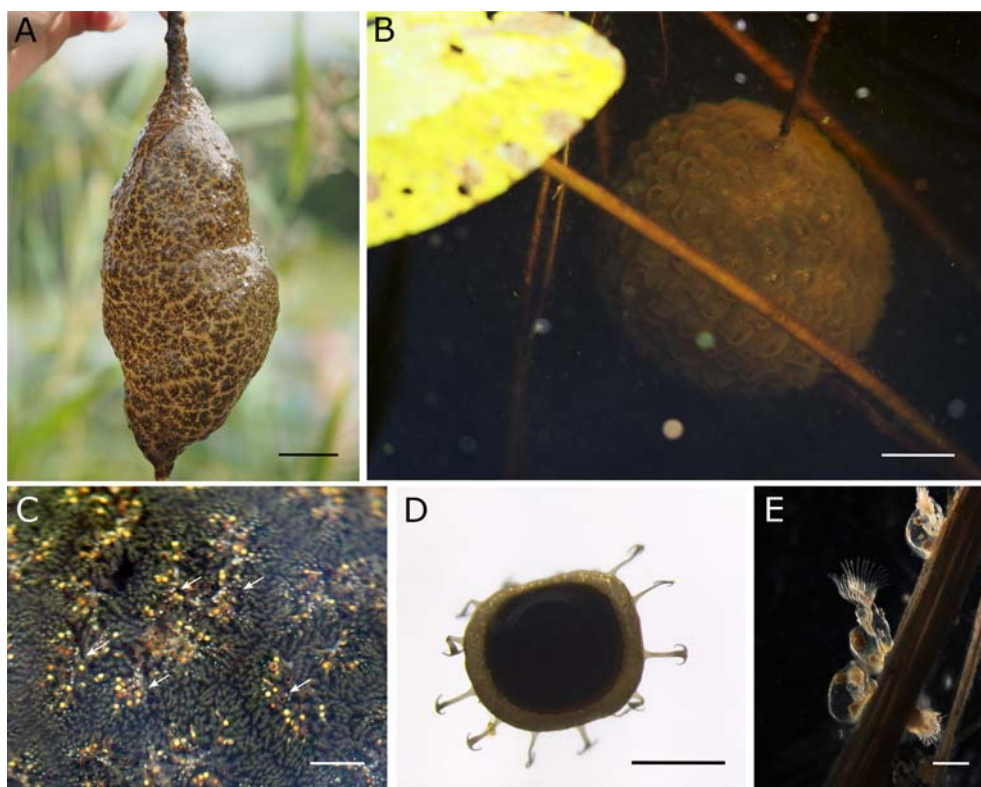


Fig. 1. Freshwater bryozoan *Pectinatella magnifica* found in Vuoksi-Virta, Leningrad oblast, Russia. A — colony pulled out of the water; B — submerged colony; C — part of the colony with expanded lophophores and statoblasts (arrows) visible inside colony; D — statoblast; E — young colonies developed from statoblasts (photo by V. Khabibulina).

Scale bars: A, B — 3 cm; C, D — 0.5 cm; E — 0.1 cm.

Рис. 1. Пресноводная мшанка *Pectinatella magnifica* из Вуокса-Вирта, Ленинградская область, Россия. А — общий вид колонии, извлеченной из воды; В — общий вид колонии под водой; С — часть колонии с лофофорами и статобlastами (отмечены стрелками); D — статобlast; E — молодые колонии, развивающиеся из статобlastов (фото В. Хабибулиной).

Масштаб: А, В — 3 см; С, D — 0,5 см; E — 0,1 см.

acetone series of increasing concentration, critical point dried, coated with platinum, and examined under a FEI Quanta 250 scanning electron microscope (FEI Company, The Netherlands). Measurements were performed (not less than 10 measurements for each type of cells and cilia) using Fiji (Schindelin *et al.*, 2012).

## Results

The observed colonies of *Pectinatella magnifica* were fusiform or spherical (Fig. 1A, B), attaching to various aquatic vegetation, tree

branches or, sometimes, stones. They were 10–30 cm in length/diameter, the largest having a weight up to 2 kilograms. The gelatinous mass covered by hundreds of ‘rosettes’ of various forms, each formed by several zooids (Fig. 1C). Formation of the dormant asexual stage (statoblasts) began in August. Statoblasts have a round shape and one row of anchor-like thorns around the edge of the disc (Fig. 1D). Colonies disappeared at the end of the summer. Under laboratory conditions it was possible to grow young colonies (Fig. 1E) from the statoblasts without freeze-thawing cycle.



Zooids of *Pectinatella magnifica* have a massive horseshoe crown of tentacles (lophophore) consisting of two arms bearing 40–50 ciliated tentacles (Fig. 2A, B). Each tentacle possesses three ciliary bands: two lateral and one frontal with densely spaced motile cilia (Fig. 2C). Lateral multiciliary epithelial cells were about 4–5  $\mu\text{m}$  in diameter in fixed material and bore about 20 cilia, each about 15  $\mu\text{m}$  long (Fig. 2D). On either side of the frontal ciliary band the rows of latero-frontal cilia, presumably immobile, were situated (Fig. 2E, F). The bases of these cilia were surrounded by tiny folds that may presumably be interpreted as microvilli. We were not able to recognize the cell borders corresponding to them. Cilia of these cells were thinner towards the distal end and were longer than the cilia of the epithelial cells, reaching at least 20  $\mu\text{m}$  (Fig. 2F).

On the surface of the lophophore arms and abfrontal surfaces of the tentacles the borders of non-ciliated epithelial cells are clearly visible. The apical surfaces of these cells have an irregular polygonal shape being about 10–15  $\mu\text{m}$  in size (Fig. 3). Among them the ciliary cells (presumably sensory) were recorded on both the abfrontal surface of tentacles (Fig. 3C) and randomly on the outer (faced to outside) and inner (faced to another arm) surfaces of the lophophore arms. Apical surfaces of these cells were smaller in size than neighboring epithelial cells. They had an irregular triangle-like shape with size about 1–1.5  $\mu\text{m}$  (Fig. 3A, B, D–G). These cells were mostly monociliated, but sometimes biciliated (Fig. 3G) with a cilium 8–10  $\mu\text{m}$  long, having the same diameter along the entire length, and basal part surrounded by several short microvilli, about 0.5  $\mu\text{m}$  long (Fig. 3D–G). Such cells were sometimes grouped by two (Fig. 3D), but most were single (Fig. 3E, F).

Epithelial cells of the introvert had an irregular shape being 20–30  $\mu\text{m}$  in size (Fig. 4A–C), and bore no cilia or microvilli. Colony body-wall was composed of different-sized cells similar to the cells of an introvert. Among them some had microvillary apical surfaces that looked like knobs (size 5–7  $\mu\text{m}$ ), densely covered with 1–2  $\mu\text{m}$  long microvilli (Fig. 4D–F). They were

sparsely spread on the colony wall being usually situated close to the bases of the introverts.

## Discussion

### Lifespan and ways of invasion

Invasions and distribution patterns of alien species affect local biodiversity and aquatic environments (Orlova *et al.*, 2006). There are some possible ways how the recent invader *Pectinatella magnifica* could enter the Russian inland waters. According to the data from the Danube river and the known rate of invasion (Zorić *et al.*, 2015), we would expect that *P. magnifica* could actively spread across the territory of Russia from the southern regions. Such an assumption was made by Kluge, who did not find *Pectinatella* in the former USSR, however (Kluge, 1949). In more recent list of bryozoan species of the Pontic–Caspian fauna, *P. magnifica* was mentioned among the freshwater bryozoans of the Danube-Don area (Vinogradov, 2003). However, our recent finding of *P. magnifica* in Vuoksi river system currently is the only record of this species in Russia.

Leningrad oblast at the north-west of Russia is known to be the gate for invasions by non-indigenous species. It is situated at the border of two climatic zones: subarctic and temperate being influenced by the temperate zone in summer and the subarctic in winter (Orlova *et al.*, 2006). The Leningrad oblast and Saint Petersburg are also important transport shipping centers, and the ballast waters are one of the potential means of introduction of non-native aquatic species. All these factors may afford the alien species to spread into new areas and provide new opportunities for distribution of water animals.

Inland waters of Finland are not readily available for non-indigenous species because of low water pH and temperature and low nutrient concentrations. These conditions form natural barrier against invasions (Vuorio *et al.*, 2018). According to Vuorio with co-authors, there are three main factors of the *P. magnifica* invasion in the Vuoksi River watercourse: the shipping

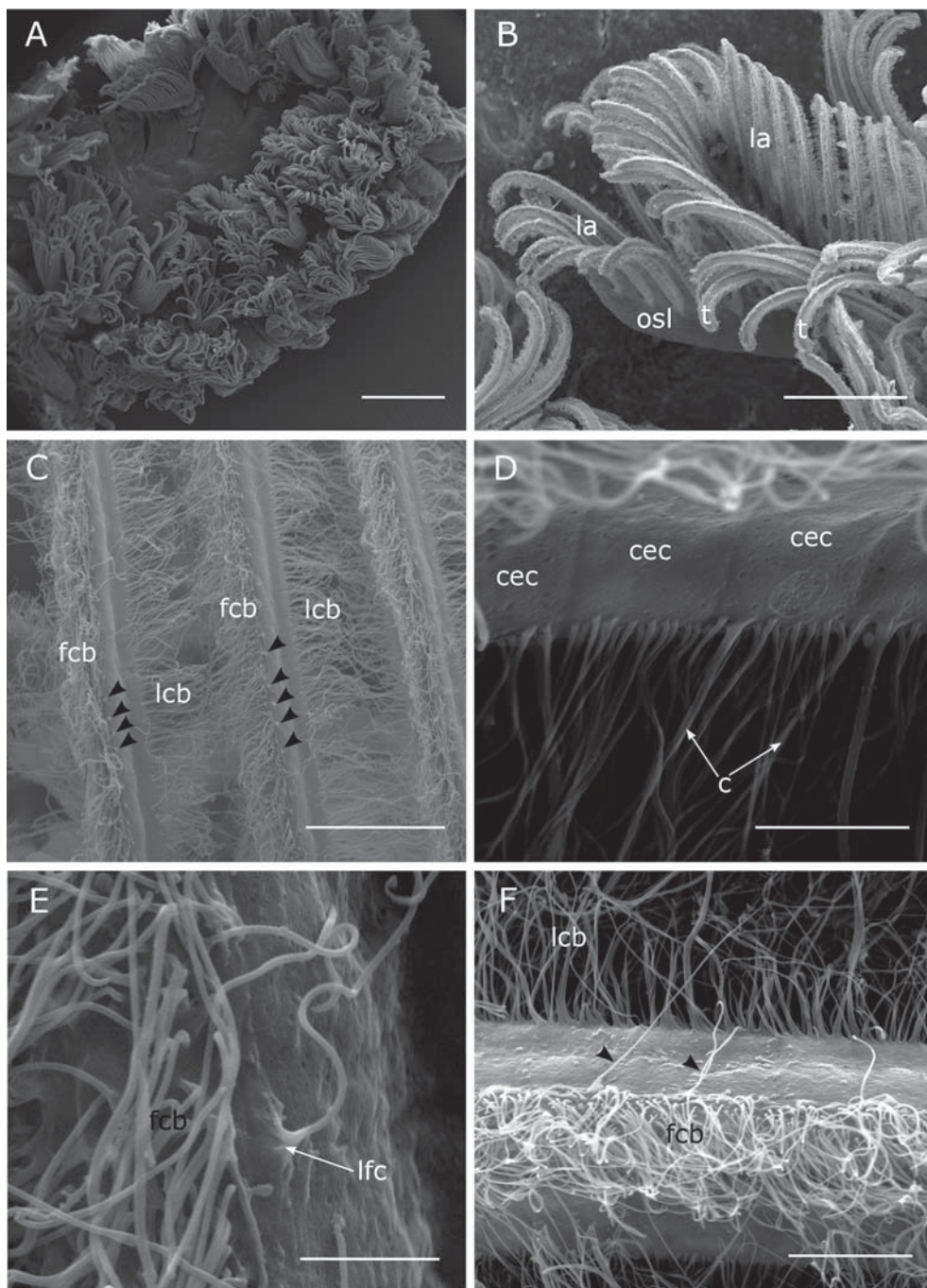


Fig. 2. Scanning electron micrographs of a colony fragment, lophophoral arms and tentacle surface in *Pectinatella magnifica*. A — general view of a colony fragment with expanded lophophores; B — part of horseshoe-shaped tentacular crown (lophophore); C — arrangement of ciliary bands on tentacles; D — ciliary epithelial cells of lateral ciliary band (frontal ciliature in the upper part of image); E — close up of latero-frontal cilium near frontal ciliary band; F — latero-frontal cilia visible between frontal and lateral ciliary bands. Arrowheads indicate latero-frontal cilia.

waterways, recreational boating, and the most likely waterbirds. The Vuoksi is running through two countries: Finland and Russia. There are three dams on it, one in Imatra (Finland) close to the border, two others in Russia. These dams prevent any shipment and recreational boating across the border. Thus, possible methods for migration of *P. magnifica* from Finland's part of the Vuoksi River to its Russian part is a statoblast transport by the water birds and the river flow itself. For instance, statoblasts of another freshwater bryozoan *Cristatella mucedo* were transported over long distances (more than 300 kilometers) in the digestive tract of waterfowl (Charalambidou *et al.*, 2003).

Water temperature is one of the main environmental factors that control growth and reproduction of *Pectinatella magnifica* (Joo *et al.*, 1992). Similar to all other freshwater bryozoans, it can survive winter only as a dormant stage (statoblasts). The temperature limitation for the growth and reproduction could be the possible explanation why the colonies occurred only at 3.5 km of the coastline in the semi-isolated Vuoksi-Virta and the species was not observed in the most part of the 150km riverbed of Vuoksi. Phylactolaemates in the Ukrainian part of the Danube River delta start to form new colonies at the beginning of the summer, and the destruction of the colonies begins in the second decade of October-November (Aleksandrov *et al.*, 2014). In the Leningrad oblast, the duration of the colony life of *C. mucedo* is about the same (K. Shunkina, personal communication). Unfortunately, there are no data about timespan of the colonies of *P. magnifica* in Finland. Howev-

er, according to our observations, it is noticeably shorter, possibly because of lower water temperature most of the year. Colonies of *P. magnifica* in the Leningrad oblast reach the size up to 30 cm in diameter in August but are found only during two summer months, and vanish before autumn. In other words, in the north-west Russia (and, obviously, Finland) for 10 months *P. magnifica* exists as statoblasts.

### Sensory structures

Tentacles of *Pectinatella magnifica*, like those of the other phylactolaemates (Mukai *et al.*, 1997; Riisgård *et al.*, 2004, 2010; Shunkina *et al.*, 2015; Tamberg, Shunatova, 2017), have three broad ciliary bands formed by multiciliary epithelial cells: one frontal and two lateral. The cilia are motile and generate water currents that deliver food particles to the mouth. The length of these cilia varies from 9 to 30  $\mu\text{m}$  in different bryozoan species. The average cilia length in *P. magnifica* is 15  $\mu\text{m}$ . There are also two rows of latero-frontal cilia situated on either side of the frontal ciliary band (Figs 2C; 5). Although we were not able to recognize the cell borders around them, we believe that these cilia correspond to the latero-frontal monociliary cells known in the tentacles all bryozoans studied so far (reviewed in Mukai *et al.*, 1997 and Ostrovsky *et al.*, 2002).

Concerning phylactolaemates, initially monociliary "sensory cells" were described on the tentacles of *Cristatella mucedo*, *Lophopus cristallinus* and *Plumatella fungosa* using histological sections (Gerwerzhagen, 1913; Marcus, 1926a), and Brien (1960) was the first who

Abbreviations: c — cilia; cec — ciliary epithelial cells; fcb — frontal ciliary band; la — lophophoral arm; lcb — lateral ciliary band; lfc — latero-frontal cilia; osl — outer surface of lophophore; t — tentacles. Scale bars: A — 1 mm; B — 0.1 mm; C — 30  $\mu\text{m}$ ; D — 5  $\mu\text{m}$ ; E — 3  $\mu\text{m}$ ; F — 10  $\mu\text{m}$ .

Рис. 2. Фрагмент колонии, руки лофофора и поверхность щупалец у *Pectinatella magnifica*, сканирующая электронная микроскопия. А — общий вид участка колонии с лофофорами; В — часть подковообразного лофофора; С — расположение рядов ресничек на щупальцах; D — ресничные эпителиальные клетки латеральной ресничной полосы (сверху реснички фронтальной полосы); E — латерофронтальные реснички в фронтальных ресничных рядах; F — латерофронтальные реснички около фронтальной ресничной полосы. Реснички латеро-фронтальных рядов указаны стрелками. Обозначения: c — реснички; cec — ресничные эпителиальные клетки; fcb — фронтальный ресничный ряд; la — руки лофофора; lcb — латеральный ресничный ряд; lfc — латеро-фронтальные реснички; osl — внешняя поверхность лофофора; t — щупальца. Масштаб: А — 1 мм; В — 0,1 мм; С — 30 мкм; D — 5 мкм; E — 3 мкм; F — 10 мкм.



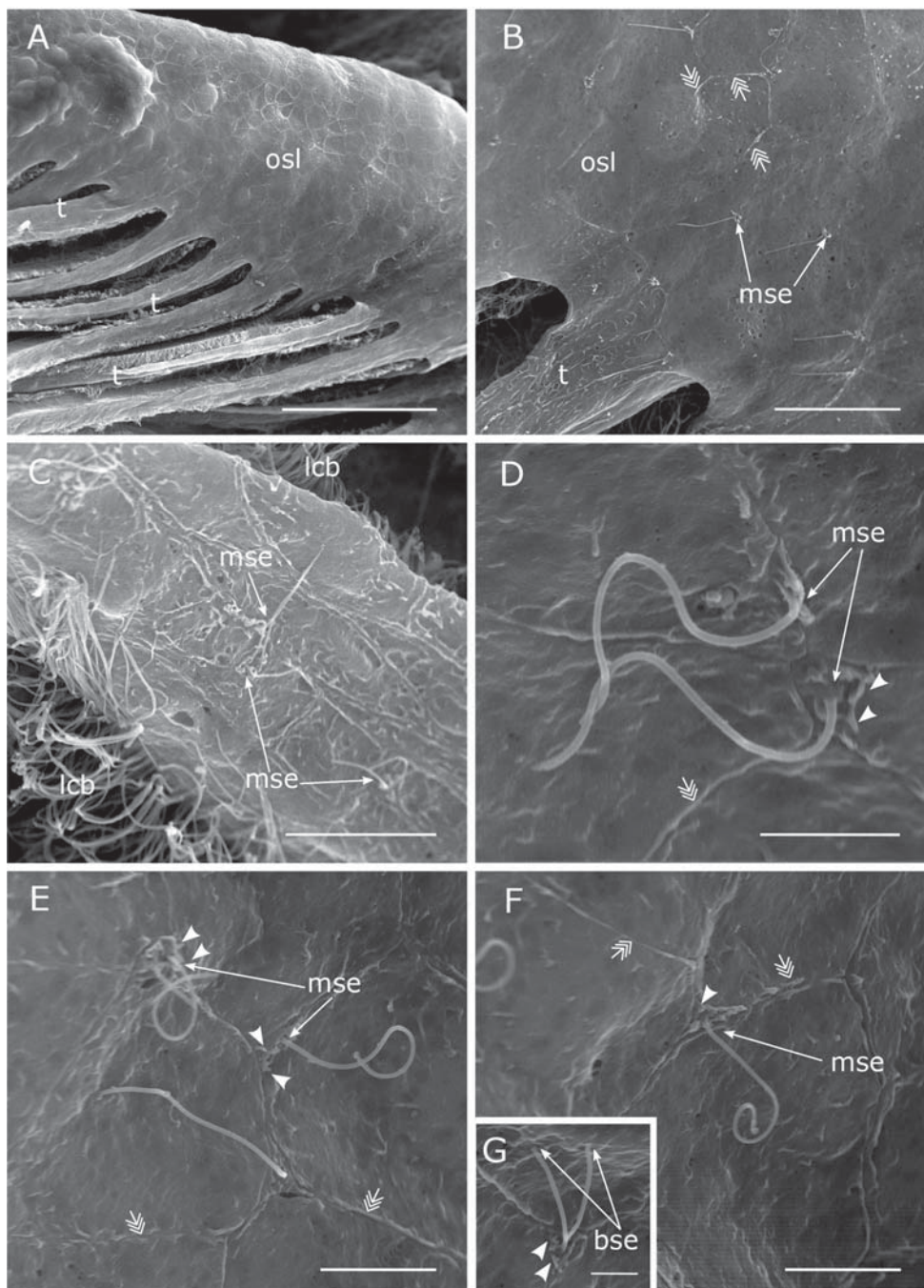


Fig. 3. Scanning electron micrographs of lophophoral arms and abfrontal tentacle surface with sensory structures in *Pectinatella magnifica*. A — basal part of lophophore arm with outer tentacle row; B — outer surface of the lophophore arm showing sensory cilia; C — cilia on abfrontal tentacle surface; D, E — close up of the second type of monociliary sensory structures on the outer surface of the lophophore arm; F — close up of inner surface of the lophophore arm with sensory structure; G — biciliary sensory structure. Arrowheads point to microvilli around the ciliary bases. Triple arrows show the borders of epithelial cells.



precisely indicated their latero-frontal position. Gilmour (1978) found these cells in *Plumatella* sp. using transmission electron microscopy (TEM) and mentioned that the ciliary base is surrounded by rings of microvilli. He also wrote that basally the latero-frontal cells have “synapses with the nerves running along the tentacles” (p. 2152). This corresponds to the data of Shunkina with co-authors (2014b, 2015) on *C. mucedo*. According to this description the latero-frontal cells basally have axons extending into the latero-frontal nerves. The number of cilia was not indicated, however. TEM study by Tamberg & Shunatova (2017) did not mention any connection between the latero-frontal cells and corresponding nerves below them in three studied phylactolaemates, however. Several SEM works showed the presence of the latero-frontal cilia in *P. repens*, *P. fungosa*, *C. mucedo* and *Fredericella sultana*. In all species the base of each cilium was surrounded by a circle of microvilli (Riisgård *et al.*, 2004, 2010; Tamberg, Shunatova, 2017).

In *P. magnifica* the latero-frontal cells have a single cilium, each narrowed to the distal end, which is usually characteristic for the sensory cells (Croft *et al.*, 2018). The presence of surrounding microvilli is also highly probable. However, the quality of material did not allow us to confirm or deny this suggestion without additional studies. Following previous authors, we suppose that latero-frontal monociliary cells have a sensory function (first type of sensory structures) in this species. In addition, study on feeding *Plumatella repens* (Riisgård *et al.*, 2004) showed that stiff sensory latero-frontal cilia act

as a mechanical sieve, as previously described in marine bryozoans (discussed in Riisgård *et al.*, 2004 and Ostrovsky *et al.*, 2002).

The second type of sensory structures was found in *P. magnifica* on the abfrontal surface of tentacles, as well as the outer and inner surfaces of the lophophore arms (Fig. 5). Each such structure includes 1–2 cilia surrounded by several microvilli and associated with a small area (1–1,5 µm in diameter) presumably representing an apical narrowed part of sensory cell(s) or its dendrite, also termed as sensory endings (Zaitseva, Bocharova, 1981; Schlawnny, 1991a).

Both mono- and multiciliary cells with immobile cilia were described on the abfrontal tentacle side and introvert in marine Bryozoa (Shunatova, Nielsen, 2002; reviewed in Mukai *et al.*, 1997 and Ostrovsky *et al.*, 2002). In Stenolaemata all of them were monociliary, while in Gymnolaemata, bi- or multiciliary sensory cells alternate with monociliary ones (Shunatova, Nielsen, 2002). As to phylactolaemates, 5–10 pairs of ‘setae’ have been found on the abfrontal surface of the tentacles in *P. repens* (Bullivant, 1968) although SEM studies by Riisgård with co-authors (2004) revealed bundles of 4 cilia (surrounded by microvilli) in this species. Later on, presumed abfrontal sensory structures including 1–4 cilia (with the basal parts surrounded by microvilli visible on Fig. 8, Riisgård *et al.*, 2010) were described in *F. sultana*, *L. cristallinus* and *C. mucedo*. Single ‘abfrontal cilia’ were also illustrated by Gilmour (1978) who studied *Plumatella* sp. by TEM. Finally, TEM-study of Tamberg and Shunatova (2017) showed presence of the abfrontal ciliary

Abbreviations: bse — biciliated sensory structure; lcb — lateral ciliary band; mse — monociliary sensory structure; osl — outer surface of the lophophore arm; t — tentacles.

Scale bars: A — 100 µm; B — 20 µm; C — 10 µm; D — 3 µm; E — 5 µm; F — 5 µm, G — 2 µm.

Рис. 3. Основание рук лофофора с сенсорными структурами у *Pectinatella magnifica*, сканирующая электронная микроскопия. А — основание лофофора и наружный ряд щупалец; В — поверхность рук лофофора с моноцилиарными клетками; С — реснички на абфронтальной поверхности щупалец; D, E — моноцилиарные сенсорные структуры второго типа на наружной поверхности рук лофофора; F — внутренняя поверхность лофофора с сенсорными структурами; G — двуресничная сенсорная структура. Микроворсинки показаны наконечниками стрелок. Тройными стрелками показаны границы эпителиальных клеток.

Обозначения: bse — двуресничные сенсорные структуры; mse — моноцилиарные сенсорные структуры; osl — наружная поверхность лофофора; t — щупальца. Масштаб: А — 100 мкм; В — 20 мкм; С — 10 мкм; D — 3 мкм; E — 5 мкм; F — 5 мкм, G — 2 мкм.

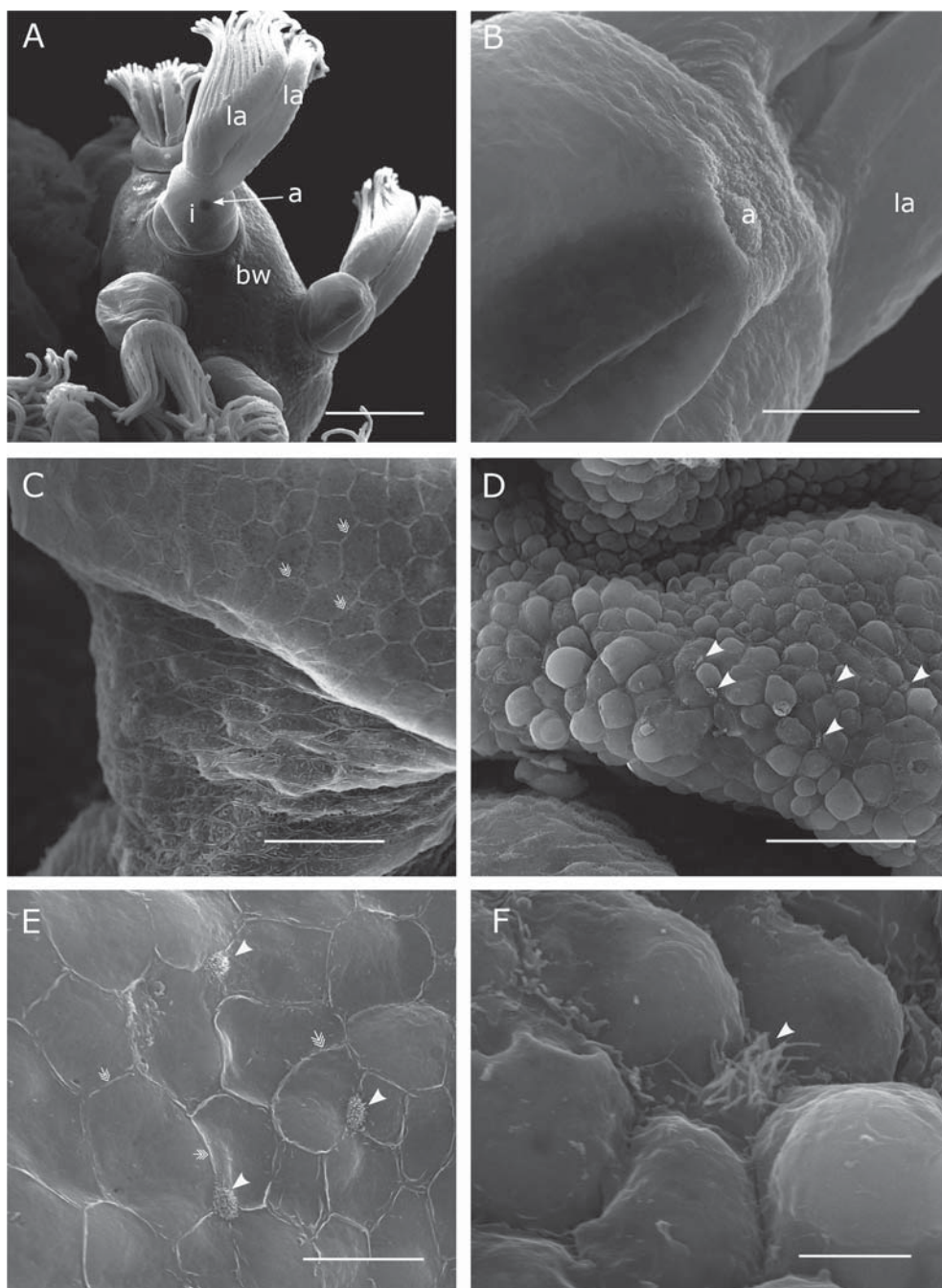


Fig. 4. Scanning electron micrographs of the colony surface and expanded lophophores in *Pectinatella magnifica*. A — general view of a part of the colony with protruded lophophores; B — part of lophophore viewed from the anal side; C — surface of introvert (above the lophophore arms); D, E, F — various magnifications of the third type of sensory structures (arrowheads) on the colony surface. Triple arrows show the borders of epithelial cells.

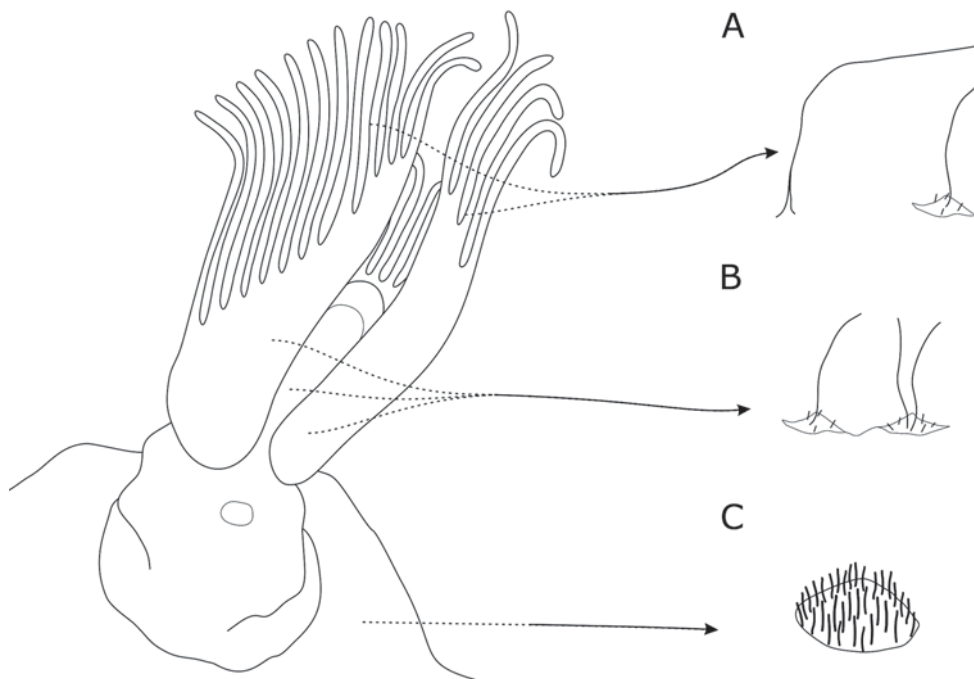


Fig. 5. Schematic drawings of three types of sensory structures in *Pectinatella magnifica*. A — first type on latero-frontal side of tentacles (from the left) and second type on abfrontal side of tentacles (from the right); B — second type on the lophophore; C — third type on the colony wall.

Рис. 5. Схема распределения трех типов сенсорных структур у *Pectinatella magnifica*. А — первый тип на латеро-фронтальной стороне щупалец (слева) и второй тип на абфронтальной стороне щупалец (справа); В — второй тип на внутренней и наружной сторонах рук лофофора; С — третий тип на стенке колонии.

‘tufts’ with microvillar ring around ciliary bases in *P. fungosa*, *C. mucedo* and *F. sultana*. Importantly, each such ‘tuft’ was formed by a pair of monociliated and/or biciliated cells that was considered as specific feature to Phylactolaemata. Mono- and/or biciliated, presumably sensory cells (never in pairs) with basal microvilli were also found externally on the intertentacular membrane in all three species studied. In contrast to all discussed examples, in

*P. magnifica* the abfrontal sensory cilia were usually single. In addition, they were situated not only on the abfrontal side of the tentacles, but also on the outer and inner surface of the lophophore arms.

Observations and experiments on living bryozoans together with ultrastructural research led researchers to suggest that both latero-frontal and abfrontal sensory cells perceive tactile stimulation (Lutaud, 1955; Dick, 1984; Lutaud,

Abbreviations: a — anus; bw — body wall; la — lophophoral arm; i — introvert. Scale bars: A — 500  $\mu\text{m}$ ; B — 100  $\mu\text{m}$ ; C — 40  $\mu\text{m}$ ; D — 50  $\mu\text{m}$ ; E — 20  $\mu\text{m}$ ; F — 5  $\mu\text{m}$ .

Рис. 4. Общий вид поверхности колонии и расправленных лофофоров у *Pectinatella magnifica*, сканирующая электронная микроскопия. А — общий вид части колонии с расправленными лофофорами; В — участок лофофора и интроверт с анусом; С — поверхность интроверта (сверху руки лофофора); D, E, F — третий тип сенсорных структур (указаны при помощи наконечников стрелок) на поверхности колонии. Тройными стрелками показаны границы эпителиальных клеток.

Обозначения: а — анус; bw — стенка тела; la — руки лофофора; i — интроверт. Масштаб: А — 500 мкм; В — 100 мкм; С — 40 мкм; D — 50 мкм; E — 20 мкм; F — 5 мкм.



1993; Nielsen, Riisgård, 1998) thus being mechanosensory cells (discussed in Mukai *et al.* 1997). This is confirmed by the ultrastructural studies showing presence of the long rootlets of the cilia (Shunatova, Nielsen, 2002; Tamberg, Shunatova, 2017), which is one of the characteristic features for mechanoreception (Windoffer, Westheide, 1988). In addition, most of the tentacular sensory cilia in the studied bryozoans are immobile (but see Gordon 1974), which also testifies in favor to their mechanosensory function. Thus, it can be assumed that the sensory structures of the 1st and the 2nd types found in *P. magnifica* most likely belong to mechanosensory cells.

Behavioral experiments have shown that mechanical stimulation plays a more important role in the behavior of zooids than chemical (food) stimulation (Shunatova, Ostrovsky, 2001, 2002; Ostrovsky *et al.*, 2002; Tamberg, Shunatova, 2016). Nevertheless, it is premature to assume that bryozoans have no chemical sensitivity (Shunatova, Ostrovsky, 2001). It has been shown that water quality as well as the concentration of oxygen and chlorophyll  $\alpha$  play an important role in the distribution of *P. magnifica*. Also, this bryozoan tend to prefer certain plant species over others as a substrate for attachment (Joo *et al.*, 1992; Vuorio *et al.*, 2018). But if there is chemical sensitivity in bryozoans, what kind of sensory cells provide it?

The third type of the putative sensory structures was detected in *P. magnifica* on the colony wall surface near the base of the expanded lophophores. They have specialized microvillary knobs with diameter 5–7  $\mu\text{m}$  (Figs 4D–F; 5), and have not been reported in bryozoans before. It is unlikely that these structures are mechanosensory since the such type of cells have cilia with a special rootlet system (Shunatova, Nielsen, 2002; Tamberg, Shunatova, 2017) or long stereocilia (as in the spiral organ of Corti) in both invertebrates and vertebrates (Schlawny, 1991a, b). Chemosensory function of the bryozoan colony wall is also unlikely, since chemoreception should most likely be used by lophophores to provide effective feeding and filtration by the tentacles. It should be

noted that the structure of the sensory cells of *P. magnifica* colony wall is most similar to the photosensory cells of gastropods (Bobkova, 1998; Zaitseva, 1998, 2016). In addition, some freshwater bryozoans are known to be sensitive to light, although it is not clear how they can perceive it. For example, the mobile colonies of *C. mucedo* (Marcus, 1926b; Ryland, 1977; reviewed in Shunkina *et al.*, 2015) and young colonies of *P. magnifica* (Joo *et al.*, 1992) move away from the light and prefer the shady sides of substrates. In the attached bryozoan colonies, the photosensory cells of the colony wall can be involved in the regulation of seasonal or circadian biorhythms like in planktonic animals (Coesel *et al.*, 2021). To answer this and other questions regarding the sensory system in Bryozoa, new studies are needed.

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**Conflict of Interest.** The authors declare that they have no conflict of interest.

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