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RESEARCH ARTICLE

Histological organisation of the bathypelagic species *Protoheterokrohnia bogutskayae* (Chaetognatha: Tokiokaispadellidae) in the trunk–tail region

Гистологическое строение батипелагического вида *Protoheterokrohnia bogutskayae* (Chaetognatha: Tokiokaispadellidae) в туловищно-хвостовой области

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Abstract. A histological study of the unique bathypelagic species *Protoheterokrohnia bogutskayae* Kassatkina, 2016 (Chaetognatha: Tokiokaispadellidae) was conducted. Specimens were collected from the near-bottom layers of the Laptev Sea in the deep Arctic waters. The structure of the trunk–tail region was examined, revealing that large lateral fields are characteristic of this plankto-benthic species. The intestinal structure differs from that of other chaetognaths, with the intestinal epithelium containing secretory cells with an unusual secretion containing crystal inclusions. The composition and location of the female and male gonads were also studied. The longitudinal muscles were investigated using immunocytochemical method, which revealed the presence of type IV collagen in the extracellular matrix at the base of the muscle layer. The structure and location of the transverse muscle bundles and their attachment points were described in detail. Fins and fin rays were analysed through histological sections, showing that fin rays are located within the cytoplasm of the fin epithelial cells as cytoplasmic inclusions containing proteins. The fin rays are notably long, as illustrated in the longitudinal sections. The dense arrangement of the rays is characteristic of the species examined.

Резюме. Проведено гистологическое исследование уникального батипелагического вида *Protoheterokrohnia bogutskayae* Kassatkina, 2016 (Chaetognatha: Tokiokaispadellidae). Экземпляры были собраны в придонных слоях моря Лаптевых (глубоководная часть Арктики). Изучено строение туловищно-хвостового отдела. Для этого планкто-бентического вида характерны протяженные латеральные поля. Кишечник по своему строению отличается от такового других щетинкочелюстных. Кишечный эпителий содержит железистые клетки с необычным секретом, имеющим кристаллические включения. Изучены строение и локализация женских и мужских гонад. Исследованы продольные мышечные тяжи; иммуноцитохимическим методом выявлено наличие коллагена IV типа во внеклеточном матриксе в основании мышечного слоя. Описаны строение и локализация тяжей поперечной мускулатуры, точки их прикрепления. Изучены плавники и плавниковые лучи на гистологических срезах. Установлено, что плавниковые лучи локализуются в цитоплазме эпителиальных клеток плавника и представляют собой цитоплазматические включения, содержащие белки. Они имеют значительную длину, что можно видеть на продольных срезах лучей. Плотное расположение лучей характерно для изученного вида.

Key words: chaetognaths, bathypelagic species, morphology, histology, fin rays, Tokiokaispadellidae

Ключевые слова: щетинкочелюстные, батипелагические виды, морфология, гистология, плавниковые лучи, Tokiokaispadellidae

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Introduction

Chaetognatha are elongated, bilaterally symmetrical marine animals that can be either planktonic or benthic. The size of mature individuals ranges from 2 to 120 mm (Kapp, 1991). The body of chaetognaths is divided into three sections: the head, trunk, and tail, with the tail located behind the anus. Most species have lateral and tail fins. A distinctive characteristic of the Chaetognatha is the combination of a simple general organisation and highly differentiated tissues. Chaetognaths lack certain organs, such as permanent oviducts and seminal canals, as well as excretory and respiratory systems. Their recently discovered hemal system (Shinn, 1997) has a simple structure (Malakhov & Berezinskaya, 2001) and functions solely to transport nutrients, rather than oxygen. A unique feature of chaetognaths is the presence of a stratified skin epithelium with unusual intercellular junctions (Duvert et al., 1984; Stolyarova & Kassatkina, 1988, 2001, 2019; Shinn, 1997). According to the most recent molecular genetic analyses, Chaetognatha are considered a sister group to Gnathifera or an ingroup of gnathiferans (Marlétaz et al., 2019; Vinther & Parry, 2019).

The unique structures of Chaetognatha are fin rays. According to Ghirardelli (1968), these rays are suggested to contain elastoidin, while some authors, such as Kapp (1991), consider them to be chitinous structures. Fin rays were previously believed to be a specialisation of the extracellular matrix (Hyman, 1959; Welsch & Storch, 1983). However, Duvert & Salat (1990) and Shinn (1997) demonstrated using transmission electron microscopy that the rays are, in fact, intracellular structures located within the cytoplasm of the fin epithelial cells. There are few studies on fins and fin rays, and the rays have not been adequately examined at the histological level. Additional histological research is necessary to determine the distribution of the rays in the fins, their morphology in different sectional planes, and their affinities to specific dyes.

Despite the increasing number of molecular biological studies and investigations into the nervous system and embryonic development of the Chaetognatha, a significant challenge in studying chaetognaths is the lack of information regarding the general organisation of the various species within this group (Kapp, 1993). Research on chaetognath morphology has primarily focused on the ultrastructural level of epiplanktonic species, particularly representatives of the family Sagittidae (Duvert & Salat, 1979, 1990; Welsch & Storch, 1983; Stolyarova & Kassatkina, 1988, 2001; Bone & Duvert, 1991; Duvert & Casanova, 1993; Shinn, 1997; Malakhov & Berezinskaya, 2001; Müller et al., 2019). The histological features of many chaetognath species remain insufficiently investigated. Furthermore, there is a lack of data on the histological structure of representatives of the family Tokiokaispadellidae, which includes species exhibiting plesiomorphic characters.

The aim of this study was to perform a histological examination of the body wall, internal organs, and fins, including a detailed description of the fin rays in a bathypelagic species of Tokiokaispadellidae.

Material and methods

This research is based on the material collected during the joint Russian and German expedition aboard the R/V Polarstern in 1993, which explored the northern part of the Laptev Sea, a challenging high-latitude deep-sea region of the Arctic. Plankton was collected using a specially designed device, the benthopelagic sampler, which was attached to the frame of an Agassiz trawl (Sirenko et al., 1996). This setup enabled the capture of near-bottom layers of plankton. Chaetognaths were extracted from plankton samples that had been preserved in a 4% formalin solution. Specimens were meticulously retrieved using bent-end

forceps, a technique specifically designed for handling chaetognaths to prevent deformation of their soft tissues. Three specimens of the species later described as *Protoheterokrohnia bogutskayae* Kassatkina, 2016, were found in good condition.

The fixed material (the paratype of *P. bogutskayae* at stage II of maturation with a body length of 25 mm) was dehydrated and embedded in paraffin using a standard technique. The material did not undergo any mechanical manipulation during the processes of dehydration and embedding in paraffin. Serial histological sections, with a thickness of 5–7 μm, were stained with Mayer's hematoxylin and eosin. High-quality histological sections were utilised. The localisation of type IV collagen, characteristic of the extracellular (basal) matrix, was studied using peroxidase immunocytochemistry. To detect type IV collagen, mouse monoclonal antibodies (clone CIV 22, Dako, Denmark) were diluted 1:400 and subjected to high-temperature treatment in citrate buffer, followed by the application of secondary antibodies, EnVision anti-mouse (Dako, Denmark). Visualisation of the reaction product was achieved using the chromogen DAB+ (Dako, Denmark). The histological preparations were examined under a Leica DME light microscope (Leica, Germany), and images were captured using a Leica EC3 digital video camera (Leica, Germany).

Results

Phylum **Chaetognatha**

Class **Sagittoidea**

Subclass **Eukrohniones**

Order **Biphragmoeukrohniformes**

Family **Tokiokaispadellidae**

Genus ***Protoheterokrohnia*** Kassatkina, 2016

Protoheterokrohnia bogutskayae
Kassatkina, 2016
(Figs 1–4)

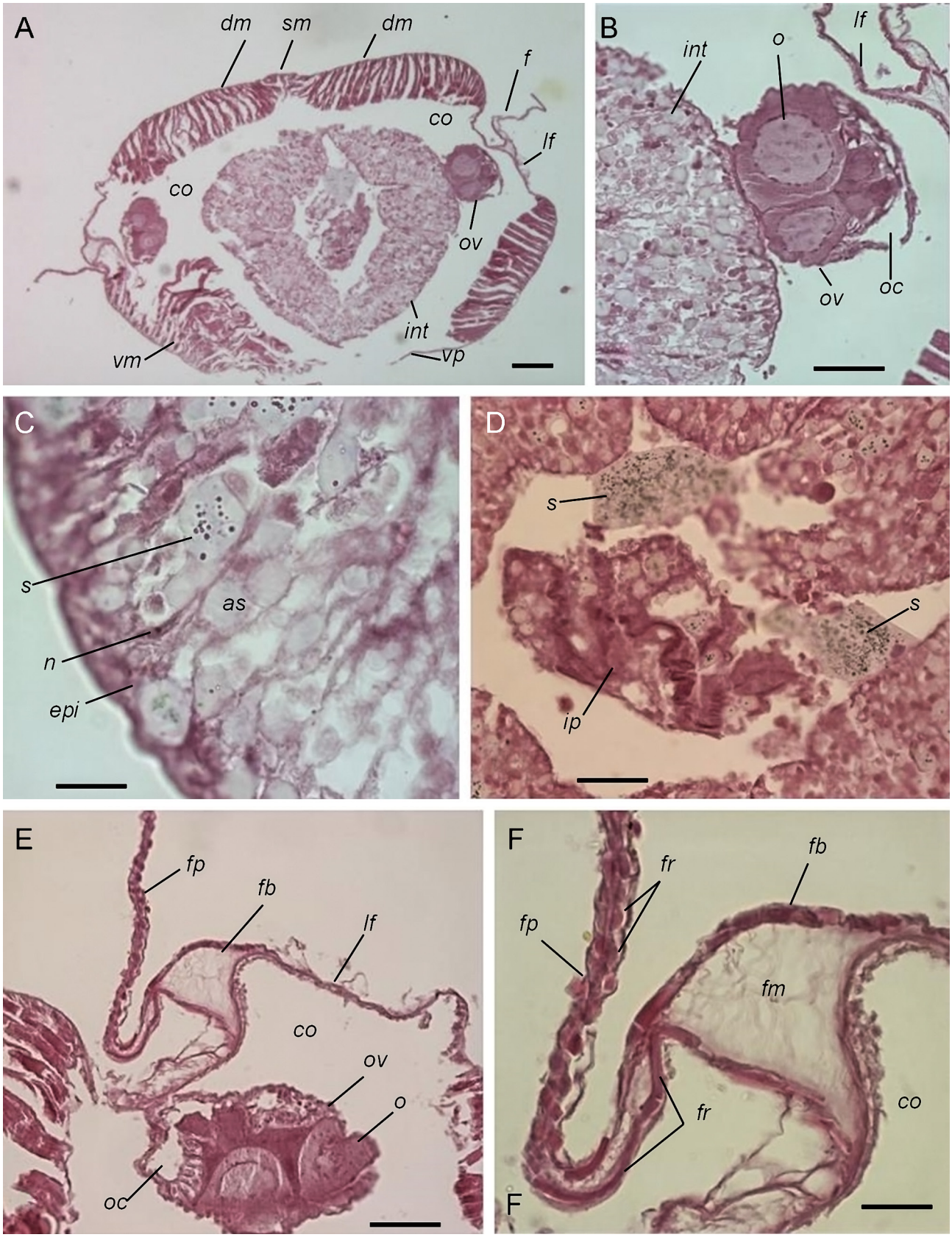
Material examined. **Russia**, *Laptev Sea*, 77°41.4′ N 125°55.1′ E, depth 1992–1993 m, 10 Sept. 1993, coll. B.I. Sirenko, 1 paratype of *P. bogutskayae* (stage II of maturation) (collection of V.I. Il'ichev Pacific Oceanological Institute, Far East Branch of the Russian Academy of Sciences, Vladivostok).

Histological organisation. The current description of the histological organisation of *P. bogutskayae* primarily focuses on the trunk–tail region.

Trunk division. In cross-sections at the end of the trunk, the longitudinal dimension of the body measures approximately 1.100 μm, while the transverse dimension is about 800 μm. Dorsal and ventral muscle bands, along with thin lateral fields of considerable length, are visible. The length of the lateral fields (approximately 300 μm) is similar to that of the muscle bands (400–450 μm) (Fig. 1A). The fins, measuring approximately 200 μm in length, are situated near the midpoint of the lateral fields. At the centre, there is a rounded intestine with a diameter of approximately 600 μm. The ovaries are located laterally to the intestine, near the level of the fins.

The intestinal epithelium consists of tall cells with poorly defined borders (Fig. 1B, C). Their nuclei are small, contain a nucleolus, and are located in the basal part of the cells (Fig. 1C). The cytoplasm is filled with numerous large, teardrop-shaped amorphous inclusions, some of which contain small crystalline structures. Additionally, there are cells containing small oxyphilic granules, and in the areas surrounding the anus, cells with large oxyphilic granules are also present. In the lumen of the intestine, the food organism, likely a copepod, is being digested (Fig. 1A, D). Individual dense structures are visible within it. On all sides, it is covered with clots of amorphous secretion that contain crystals. This secretion likely contains enzymes that metabolise the tissues of the captured prey. Nutrients may be stored within the cells of the intestinal epithelium. The ovarian wall is in contact with the surface of the intestine (Fig. 1B), indicating the significance of the gut as a source of nutrients for maturing oocytes.

Longitudinal muscle bands, consisting of two dorsal and two ventral bands, are composed of muscle elements (Fig. 4A) that closely intertwine to form groups of very tall columns, which correspond to "primary muscle", type A, according to Duvert & Salat (1979). Within each column, four thin muscle bundles can be distinguished: the outer two slightly bend toward the surface, while the inner two form serrated, zipper-shaped interconnections (Fig. 4D). Such connections are possible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when individual "fibers" extend from one bundle to another or when they possess branches that create these links. Between the compact muscle columns, there are muscle elements (presumably cells) or their thin bundles, which are of considerable height. They extend to the surface, bending in a wavy manner and contacting the adjacent columns ("primary muscle", type B). Noticeable spaces are observed between the muscle bundles within the muscle bands (Figs 1A, 4A–D), which likely arise under the influence of intensive geophysical impacts (Kassatkina & Stolyarova, 2016), a phenomenon characteristic of the Laptev Sea (Avetisov, 1993). In the area of the lateral fields, low cells with rounded nuclei are present. At the level of light microscopy, no myofibrils are detected within these cells.

Dorsal muscle bands are closely positioned to one another, while the ventral bands in the specified area (the end of the trunk) are separated by a significant interval. The body wall in this region is represented by a thin plate (Figs 1A, 4A, B), which disappears in the tail division (Fig. 4C). Between the dorsal muscle bands, there is a triangular piece of muscle tissue (Fig. 1A) that differs in structure and appears to correspond to the "secondary muscle" (according to Duvert, 1991). Type IV collagen is revealed through immunocytochemical method in the extracellular matrix at the base of the muscle layer (Fig. 4E), which is characteristic of the basement membrane of epithelial tissues.

The ovaries are located in the trunk (Fig. 1A), with their posterior portions terminating at the beginning of the tail division (Fig. 4B, C). In specific regions of the trunk, the ovarian wall contacts the surface of the intestine (Fig. 1B), while in other areas, it connects the ovaries to the body wall (Fig. 1E). In the tail division, the ovaries are in contact with both the body wall and the wall of the testes (Fig. 4B). Within the trunk, the ovaries contain single large oocytes, while the ovarian cavity is small.

Fins have a broad base and a slender plate (Fig. 1E, F). In a cross-section of the body, the width of the fin at the base in the dorsoventral direction measures approximately 50 μm. The matrix of the fin, referred to as the fin core, consists of an amorphous substance that contains fibrous structures (Figs 1F, 2A–E). The fibers exhibit a wavy appearance and form a dense layer approximately 2.0 μm in width at the periphery of the fin core (Fig. 2A, B). The extracellular matrix fibers are not separated from the layer of collagen fibers in the body wall and are likely composed of collagen. No cells typical of connective tissue were observed.

Fin rays are present within the epidermis that covers the fins. They are oval or elongated in cross-section and are intensely oxyphilic (Figs 1F, 2A–F, 3A). The rays are present on both the dorsal and ventral surfaces of the fin. The rays on the dorsal surface are larger, with many protruding above the surface (Fig. 2A). Their dimensions in cross-section typically range from 4.5 to 5.5 μm in length and 2.5 to 3.3 μm in width; however, smaller rays measuring 2.0 to 3.0 μm in length and 1.5 to 2.0 μm in width can also be found. In contrast, the rays on the ventral surface are smaller and flattened, measuring 3.0 to 4.0 μm in length and 1.5 to 2.2 μm in width. Occasionally, rays in cross-section may exhibit a cubic shape (Fig. 2E, F). The rays are located at the base of the epithelium.

It can be observed at high magnification that fin rays are present in the cytoplasm of epithelial cells as intracellular inclusions (Fig. 2B, D). The nucleus of the ray-forming cell is clearly visible in some sections (Fig. 2B, D). The nuclei of the ray cells are small, measuring 1.7–2.0 μm in diameter. The presence of some nuclei on the surface of the epithelium suggests that there is a secondary layer of flattened surface cells. The rays are situated

Fig. 1. *Protoheterokrohnia bogutskayae* Kassatkina, 2016, hematoxylin and eosin staining. **A**, cross-section of the trunk region; **B**, contact of the wall of the ovary (*ov*) with large oocytes (*o*) and the wall of the intestine (*int*); **C**, epithelium of the intestine [the nucleus (*n*) of epithelial intestinal cell (*epi*) and secretion with crystals (*s*) are visible]; **D**, ingested prey (*ip*) surrounded by secretion; **E**, contact of the ovary wall and the body wall; **F**, cross-section of the lateral fin. Other abbreviations: *as* – amorphous secretion; *co* – coelom; *dm* – dorsal muscle bands; *f* – lateral fin; *fb* – fin base; *fm* – fin matrix; *fp* – fin plate; *fr* – fin rays; *lf* – lateral field; *oc* – ovarian cavity; *sm* – secondary muscle; *vm* – ventral muscle bands; *vp* – ventral plate. Scale bars: 100 μm (A), 50 μm (B, D, E), 20 μm (C, F).

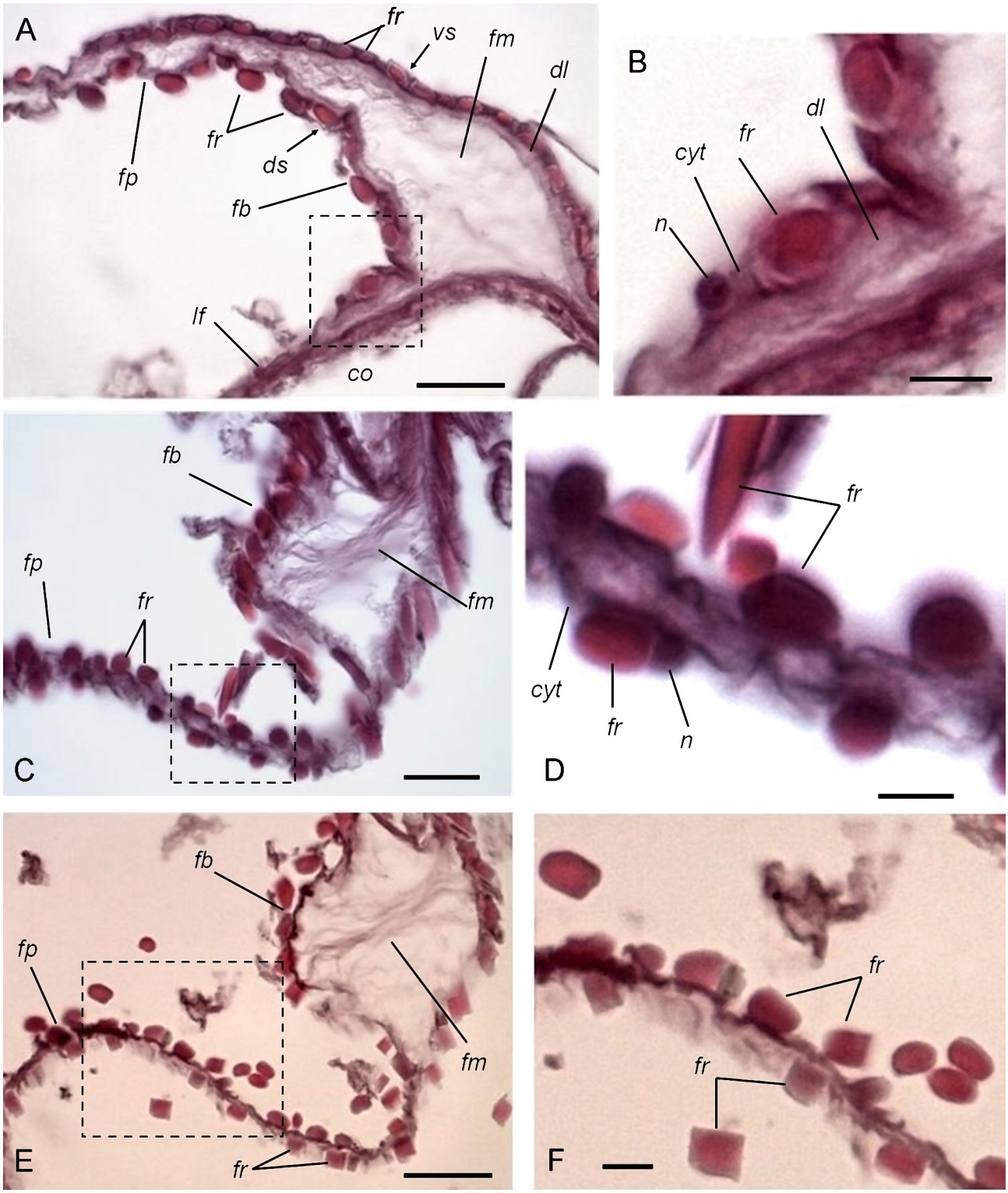

Fig. 2. *Protoheterokrohnia bogutskayae* Kassatkina, 2016, cross-section of the trunk region, hematoxylin and eosin staining. **A**, **C**, **E**, lateral fins in cross-section; **B**, **D**, **F**, portions of fins indicated by dashed box in A, C, and E, respectively. Oxyphilic fin rays (*fr*) are round, oval or cubic in cross-section. Other abbreviations: *co* – coelom; *cyt* – cytoplasm; *dl* – dense layer; *ds* – dorsal surface; *fb* – fin base; *fm* – fin matrix; *fp* – fin plate; *n* – nucleus; *vs* – ventral surface. Scale bars: 20 μm (A, C, E), 5 μm (B, D, F).

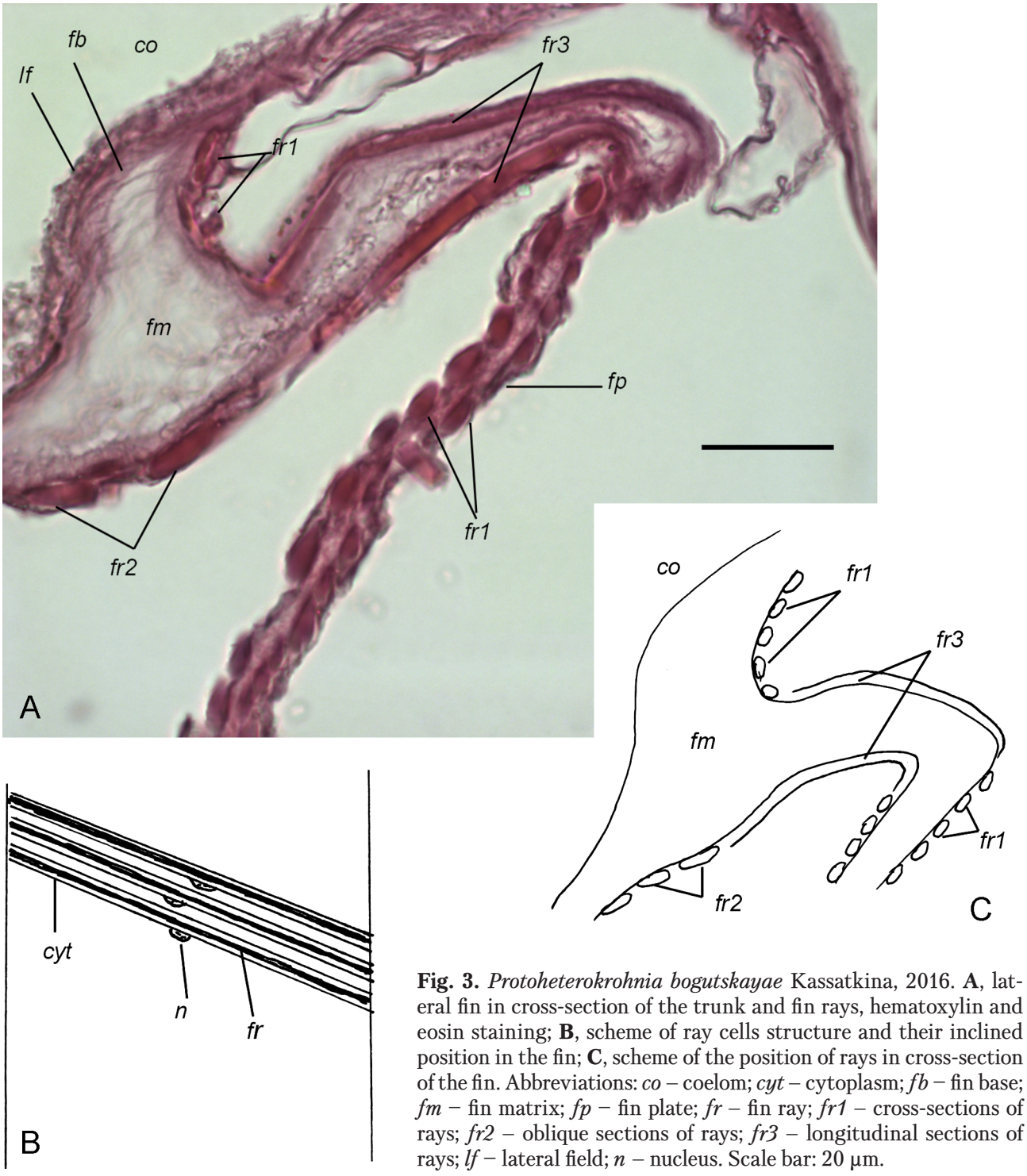

Fig. 3. *Protoheterokrohnia bogutskayae* Kassatkina, 2016. **A**, lateral fin in cross-section of the trunk and fin rays, hematoxylin and eosin staining; **B**, scheme of ray cells structure and their inclined position in the fin; **C**, scheme of the position of rays in cross-section of the fin. Abbreviations: *co* – coelom; *cyt* – cytoplasm; *fb* – fin base; *fm* – fin matrix; *fp* – fin plate; *fr* – fin ray; *fr1* – cross-sections of rays; *fr2* – oblique sections of rays; *fr3* – longitudinal sections of rays; *lf* – lateral field; *n* – nucleus. Scale bar: 20 μm.

very close to one another, leading to the assumption that many cells in the basal layer of the fin epithelium contain such inclusions. The oxyphilic staining of the rays indicates their proteinaceous nature. The rays exhibit a distinct difference in staining and a significantly higher density compared to the surrounding cytoplasm, allowing them to be considered as secretory protein inclusions. Therefore, each ray represents a dense mass of protein secretion synthesised by the cell.

The rays appear to be parallel to the fin surface and are oriented at an angle to the longitudinal

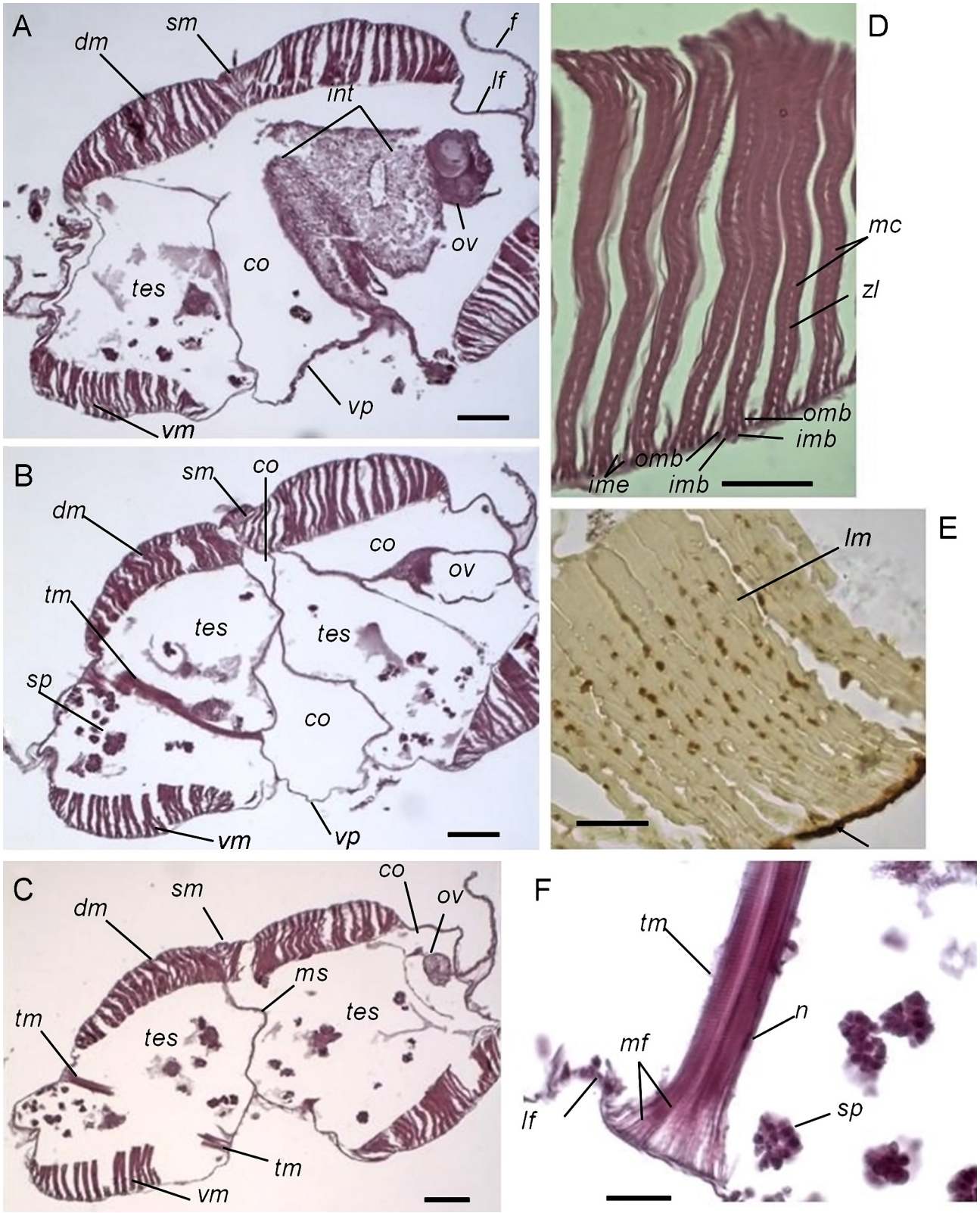

Fig. 4. *Protoheterokrohnia bogutskayae* Kassatkina, 2016, hematoxylin and eosin staining (A–D, F), and peroxidase immunocytochemistry reaction (E). **A**, cross-section of the posterior portion of the trunk [intestine (*int*), one ovary (*ov*) and one testis (*tes*) are in the plane of section]; **B**, cross-section of the anterior portion of the tail posterior to the intestine [one ovary, two testes and bundle of transverse muscle (*tm*) are in the section]; **C**, cross-section

axis of the body. Oblique sections reveal that the rays are elongated (Fig. 2C, D). Longitudinal sections of the rays demonstrate that they are lengthy and situated beneath the surface of the fin, bending in accordance with its contours (Fig. 3A). A ray cell is presumably a highly elongated cell that contains a nucleus located peripherally and an inclusion shaped like a ray (Fig. 3B). The appearance of the ray in histological preparations depends on its orientation relative to the plane of section; it may appear oval if the ray cell is cut transversely or very elongated if the ray cell is cut longitudinally (Fig. 3A, C). The ray cells appear to be quite long, consistent with the length of the fin rays.

The ends of the fins are directed dorsally (Fig. 4A–C). This positioning is functionally determined; when a fertilised egg is released into the environment, it falls on the dorsal surface of the fin and settles within its curvature. The fin subsequently develops into a brood chamber (marsupium) around the egg, which is typical of bathypelagic species (Kapp, 1991; Kassatkina & Stolyarova, 2010).

Tail division. The testes resemble irregularly shaped sacs with very thin walls. They are represented by aggregations of developing spermatocytes dispersed within the tail coelom (Fig. 4A–C). Their parts are observed at the end of the trunk (Fig. 4A) and subsequently at the beginning of the tail division (Fig. 4B). Further caudally in the tail division, they occupy the general coelomic cavity, converging along the midline to form a medial septum (Fig. 4C).

Transverse musculature is present at the beginning of the tail division (Fig. 4B, C) and is also found in the trunk division of certain Chaetognatha, specifically within the families Tokiokaispadellidae and Heterokrohniidae. The bundles of transverse muscle fibers are oriented at approximately a 45° angle to the dorsoventral axis of the body. Each bundle has a considerable thickness of 12.6 μm and crosses the coelomic cavity obliquely, attaching to the area of the lateral fields above the fin on one side and to the medial wall of the tail coelom in its lower part on the other side. At the point of attachment, the bundle forms a fan-shaped expansion, where individual fibers can be distinguished (Fig. 4E). Cross-striation is evident within the bundle, and individual flattened dark nuclei measuring 4 μm in length are visible (Fig. 4E). The bundles appear to consist of closely packed and very long cross-striated muscle cells. Notably, the muscle bundles lack a sheath, and groups of spermatocytes are observed surrounding them.

A notable asymmetry in the positioning of the ovaries and testes, as well as in the bundles of transverse musculature, is evident (Fig. 4A–C). For example, transverse musculature was observed only on one side of the body in the cross-sections (Fig. 4B, C). In some cross-sections, only one ovary (Fig. 4A–C) or one testis (Fig. 4A) was present out of the two typically found. This asymmetry may suggest variability in the lengths of the gonads on the right and left sides of the body. Ovaries can extend into the tail region and may be observed in the same section as the testes (Fig. 4B, C), while the testes may be located at the posterior end of the trunk (Fig. 4A).

Discussion

Due to its presence in the near-bottom layers of the sea, *P. bogutskayae* can be defined as plankto-benthic. A characteristic feature of the trunk–tail region in *P. bogutskayae* is the significant extent of the lateral fields, along with a gap between the ventral muscle bands, where the body wall is represented by a thin plate. Consequently, the body of the animal has a trapezoidal shape in cross-section. Well-developed bundles of

of the tail more caudally to B [remnant of the ovary, two testes, medial septum (*ms*), and one bundle of transverse muscle are visible]; **D**, **E**, transverse sections through the longitudinal muscle bands (*lm*) [D, muscle columns (*mc*) with inner (*imb*) and outer (*omb*) muscle bundles, zipper link (*zl*) and intermediate muscle elements (*ime*); E, localisation of the product of immunocytochemical reaction on type IV collagen at the base of muscle band (black colour, arrowed)]; **F**, portion of the bundle of transverse muscle with striated muscle fibers (*mf*). Other abbreviations: *dm* – dorsal muscle bands; *f* – lateral fin; *lf* – lateral field; *sm* – secondary muscle; *sp* – spermatocytes; *vm* – ventral muscle bands; *vp* – ventral plate. Scale bars: 100 μm (A, B, C), 50 μm (D), 10 μm (E), 20 μm (F).

transverse musculature in the tail region extend diagonally, originating from the upper point of the lateral fields and terminating at the medial wall of the testes, thereby connecting the dorsal and ventral surfaces of the body. These structural features of *P. bogutskayae* may be associated with its near-bottom lifestyle, at least during one stage of its life cycle. The presence of transverse musculature in both the trunk and tail is generally linked to a near-bottom lifestyle and the ability to move laterally. The extended lateral fields are present in *Eukrohnia hamata* (Möbius, 1875) (Bone & Duvert, 1991), which has a transverse musculature in the trunk. The large lateral fields known in certain species (Duvert & Casanova, 1993) may represent a significant morphological character that warrants further investigation.

In contrast, many chaetognaths possess relatively short lateral fields, lack transverse musculature, and have bodies that are either rounded or slightly flattened dorsoventrally. Examples of these include *Aidanosagitta macilenta* Kassatkina, 1971, *Sagitta bedoti* Beraneck, 1895, *S. bipunctata* Quoy et Gaimard, 1827, *S. elegans* Verrill, 1873, *S. friderici* Ritter-Záhony, 1911, *S. hexaptera* d'Orbighy, 1843, *S. marri* David, 1956, *S. megalophtalma* Dallot et Ducret, 1969, *S. minima* Grassi, 1881, *S. neodisipiens* Tokioka, 1959, *S. planctonica* Steinhaus, 1896, *S. setosa* Müller, 1847, and *S. zetesios* Fowler, 1905 (Kuhl, 1938; Dallot, 1970; Duvert & Salat, 1979; Duvert, 1991; Perez et al., 2001; Kassatkina & Stolyarova, 2008). These species, which belong to the family Sagittidae, are primarily epiplanktonic. Epiplanktonic species can only move in the dorsoventral direction.

Type IV collagen revealed at the base of the longitudinal muscle layer of *P. bogutskayae* indicates the presence of a basement membrane, which is characteristic of epithelial tissues. An electron microscopy study of *A. macilenta* has demonstrated that the contractile elements of muscle bands are represented by myoepithelial cells. The basal portions of these cells are located on the basal matrix, while their apical portions reach the surface (Stolyarova, 2012). This basal matrix obviously serves as an attachment site for the transverse muscle bundles. At the histological level, the structure of the muscle bundles in the transverse musculature has been examined, revealing elongated nuclei that presumably belong to the cross-striated muscle cells.

The intestinal epithelium in *P. bogutskayae* differs in its structure from that of other representatives of chaetognaths. Notably, it lacks vacuolised cells that contain large sac-like vacuoles, which are characteristic of some species within the family Sagittidae (Dallot, 1970; Bone et al., 1987; Bone & Duvert, 1991; Perez et al., 2001). Instead, there are granular cells that contain both small and large oxyphilic granules, as well as numerous secretory cells that produce a specific type of amorphous secretion. Of particular interest is a special amorphous secretion that contains crystal structures and appears to harbor enzymes. Identifying specialised absorptive cells can be quite challenging. In contrast, other chaetognath species have been documented to possess absorptive and granular cells (Parry, 1944; Welsch & Storch, 1983; Kapp, 1991). The structure of the intestinal epithelium in *P. bogutskayae* also differs from that in *A. macilenta*, where the intestinal epithelial cells do not contain granules but instead produce flake-like secretions while simultaneously functioning as absorptive cells (Stolyarova, 2012). It is possible that some epithelial cells in *P. bogutskayae* may play a role in absorption. The vacuolated absorptive cells (A-cells) described in certain deep-sea species of *Sagitta* Quoy et Gaimard, 1827 are considered a significant adaptation for buoyancy in deep and cold-water environments (Perez et al., 2001; Müller et al., 2019) due to the high concentration of NH_4^+ ions in vacuolar fluids. The absence of vacuolated cells in *P. bogutskayae* may indicate an alternative adaptive strategy (Bone & Duvert, 1991; Perez et al., 2001), which involves a reduction in trunk musculature (with lateral fields being very thin and elongated) to decrease specific gravity and enhance buoyancy. Other species of the genus *Protoheterokrohnia* also lack such cells (Kassatkina, 2016).

The data obtained are consistent with the conclusion of Duvert & Salat (1990) regarding the intracellular position of the fin rays. At the same time, the present research provides information on some characteristics of the fin rays. The distinct oxyphilic staining of the rays indicates their protein composition. The rays exhibit a marked

contrast to the surrounding cytoplasm due to their intense staining and significantly high density, which allows them to be considered as cytoplasmic protein inclusions synthesised by the cells. The presence of rays with varying diameters suggests that they are formed in the cytoplasm as inclusions, which may gradually increase in size. Therefore, each ray can be considered a dense mass of protein secretion synthesised by the cell. This conclusion aligns with the results of the electron microscopic investigation of *Sagitta setosa* and *S. friderici* (Duvert & Salat, 1990), which indicate that fin rays are flexible structures produced by specialised cells. These authors describe the filamentous nature and the paracrystalline structure of the rays, which are composed of cytoskeletal filaments. In thick fin rays, the central portion (core) consists of loosely arranged filaments, while the periphery (cortex) features a more regular arrangement of filaments. A comparison of histological and electron microscopic data suggests that the filamentous structures with a paracrystalline character found in the rays at the ultrastructural level are composed of proteins. This composition accounts for the flexibility of the rays and their function as supportive structures in the fins.

Intracellular secretory inclusions of a proteinaceous nature have been found in some invertebrates. They form large oxyphilic globules within the goblet cells of the skin epithelium of Nemertini and Enteropneusta (Atamanova, 1978; Stolyarova, 2012). Some of these inclusions possess an internal structural order, which can be detected at the ultrastructural level (Stolyarova, 2012). The elongated structures with a paracrystalline pattern found in the ray cells of *Spadella cephaloptera* (Busch, 1851) (Müller et al., 2019) correspond in diameter and arrangement to the fin rays. It has been demonstrated that these structures are connected to the base of the epidermal cells by a special amorphous material (Müller et al., 2019).

Our results demonstrate that fin rays are densely arranged on both surfaces of the fin, which is a characteristic feature of the species examined. It has been shown that the fin rays curve at the points where the fin bends, indicating a degree of flexibility. These findings support the notion that the rays have a specific architecture at the ultrastructural level (Duvert & Salat, 1990). Furthermore, we can conclude that the rays serve as supporting structures for the fin plate. This conclusion is supported by the observation that, under the influence of radiation, the fin plate is destroyed while the rays remain intact, causing their ends to protrude beyond the fin plate (Kassatkina et al., 2017). It is likely that the fins play a crucial role in maintaining the balance of the animal due to their horizontal orientation.

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