Invertebrate Zoology, 2025, 22(1): 21–29

Myoanatomy and nervous system of a swimming-type larva *Barentsia gracilis* (Entoprocta: Coloniales)

A.O. Borisanova

Faculty of Biology, Lomonosov Moscow State University, Leninskie Gory 1-12, Moscow 119991 Russia. Anastasia Borisanova: borisanovaao@mail.ru ORCID https://orcid.org/0000-0002-9700-6446

ABSTRACT: The organization of the musculature and nervous system of the larvae of Entoprocta is still poorly investigated. Only a few species have been studied using methods of immunocytochemistry and confocal microscopy. Previously investigated larvae belong to creeping-type larvae or swimming-type larvae with a completely reduced foot. This study describes the myoanatomy and nervous system (α-tubulin labeling) of the larva of *Barentsia gracilis*, the swimming-type larva with a partially reduced foot. The musculature of *B. gracilis* includes the muscles of the apical organ, various longitudinal and transverse muscles of the episphere, the musculature of the foot rudiment, the ring and longitudinal muscles of the prototroch, and the musculature of the hyposphere. The nervous system includes the apical and frontal ganglia connected by apico-frontal connectives, paired foot knob nerves, foot nerves and frontal nerves, several fine transverse nerves of the episphere, and the nerve ring of the prototroch.
How to cite this article: Borisanova A.O. 2025. Myoanatomy and nervous system of a swimming-type larva *Barentsia gracilis* (Entoprocta: Coloniales) // Invert. Zool. Vol.22. No.1. P.21–29. doi: 10.15298/invertzool.22.1.02

KEY WORDS: Kamptozoa, trochophore-type larvae, immunocytochemistry, α-tubulin, phalloidin, confocal laser-scanning microscopy.

Организация мускулатуры и нервной системы планктонной личинки *Barentsia gracilis* (Entoprocta: Coloniales)

А.О. Борисанова

Биологический факультет Московского государственного университета имени М.В. Ломоносова, Ленинские горы 1-12, Москва, 119991, Россия. E-mail: borisanovaao@mail.ru

РЕЗЮМЕ: Организация мускулатуры и нервной системы личинок Entoprocta до сих пор остается малоизученной. Методами иммуноцитохимии и конфокальной микроскопии исследовано лишь несколько видов. Ранее изученные личинки относятся к ползающим личинкам или планктонным личинкам с полностью редуцированной ногой. В данной работе описана организация мускулатуры и нервной системы (окрашивание антителами к α-тубулину) планктонной личинки *Barentsia gracilis* с частично редуцированной ногой. Мускулатура *B. gracilis* включает мышцы апикального органа, различные продольные и поперечные мышцы эписферы, мускулатуру рудимента ноги, кольцевые и продольные мышцы прототроха, а также мускулатуру гипосферы. Нервная система включает апикальный и фронтальный ганглии, соединенные апико-фронтальными

Devoted to memory of Claus Nielsen.

коннективами, парные нервы передней части ноги, нервы ноги и фронтальные нервы, несколько тонких поперечных нервов эписферы и нервное кольцо прототроха.
Как цитировать эту статью: Borisanova A.O. 2025. Myoanatomy and nervous system of a swimming-type larva *Barentsia gracilis* (Entoprocta: Coloniales) // Invert. Zool. Vol.22. No.1. P.21–29. doi: 10.15298/invertzool.22.1.02

КЛЮЧЕВЫЕ СЛОВА: Kamptozoa, трохофорные личинки, иммуноцитохимия, α-тубулин, фаллоидин, конфокальная лазерная сканирующая микроскопия.

Introduction

Entoprocts have a pelago-benthic life cycle with a benthic adult stage and a trochophore-type larva (Ivanova-Kazas, 1986). The larval body consists of an episphere and a hyposphere, separated by a prototroch; the apical organ is located at the apex of the episphere. Two types of larvae are distinguished: creeping-type larvae and swimming-type larvae (Wanninger, 2015). Creeping-type larvae have a well-developed sensitive frontal organ at the anterior edge of the episphere and a ciliated foot on the ventral side of the hyposphere. In swimming-type larvae, the frontal organ and foot are partially or completely reduced.

The anatomy of entoproct larvae remains poorly studied. Some details of the structure of the nervous and muscular system of larval stages have been described using electron microscopy methods (Sensenbaugh, 1987; Haszprunar, Wanninger, 2008; Borisanova, Ivanova, 2024), but without reconstructing the total anatomy of these organ systems. Only a few species have been studied using fluorescence labeling and confocal scanning laser microscopy. The organization of the musculature was studied in the creeping-type larva of *Loxosomella murmanica* (Nilus, 1909) (Merkel *et al*., 2015) and in two species of the swimming-type larvae with a completely reduced foot — *Barentsia discreta* (Busk, 1886) (Borisanova *et al*., 2012) and *Loxosomella atkinsae* Bobin et Prenant, 1953 (Fuchs, Wanninger, 2008). The organization of the serotonergic nervous system was studied only in the creeping-type larva of *L. murmanica* (Wanninger *et al*., 2007) and the swimming-type larva of *L. atkinsae* (Fuchs, Wanninger, 2008).

The present study was aimed at investigation of the organization of the nervous and muscular systems of the swimming-type larva of *Barentsia gracilis* (Sars, 1835) with a partially reduced foot and a partially reduced frontal organ.

Material and methods

Material was collected in the Velikaja Salma Bay ("Great Salma strait"), Kandalaksha Bay, White Sea (66°34′ N, 33°08′ E) in August 2023. Specimens of *Barentsia graiclis* with larvae in atrial cavity were fixed in 4% PFA in 0.1 M PBS overnight at 4 °C, then washed six times for 20 min in the 0.1 M PBS. For α-tubulin labeling, the material was first preincubated in 0.1 M PBS with 0.03% NaN3 and 5% Triton X-100 during one day at 4 °C, and then incubated in 1% Bovine Serum Albumin (BSA) in 0.1 M PBS with 0.03% NaN_3 and 1% Triton X-100 during nine hours at 4 °C to block unspecific binding sites. Incubation in the first antibodies was carried out using a mixture of mouse anti-tyrosinated α-tubulin and mouse anti-acetylated α-tubulin antibodies in 0.01 M PBS with 0.03% NaN_3, 1% Triton X-100 and 1% BSA during 18 h at 4 °C. After six washes in 0.1 M PBS with 0.03% NaN_3 and 5% Triton X-100 the secondary antibodies (anti-mouse donkey) was applied for 16 h at 4 °C. Then the material was washed up six times in the 0.1 M PBS. For phalloidin labeling, the material was stained with Alexa Fluor 488 phalloidin in 0.1 M PBS with 0.03% NaN_3 and 5% Triton X-100 for two hours at 4 °C and then two hours at room temperature. The material was embedded in a mixture of 90% glycerol and 10% PBS with DABCO. Optical sections were digitally recorded using a Nicon A1 confocal laser-scanning microscope. Images were processed using ImageJ and Amira software.

Results

Morphology of larva

The larvae of *Barentsia gracilis* are about 150 microns in size. The shape of the larval body resembles a bell. A large non-ciliated episphere and a low ciliated hyposphere are separated by a prototroch. The prototroch is located on a fold of the body called the prototrochal fold (Fig. 1A). A ciliated apical organ lies at the apex of the episphere (Fig. 1A, B). It can retract into the episphere, forming an apical pit. A ciliated frontal organ lies on the anterior side of the larval body,

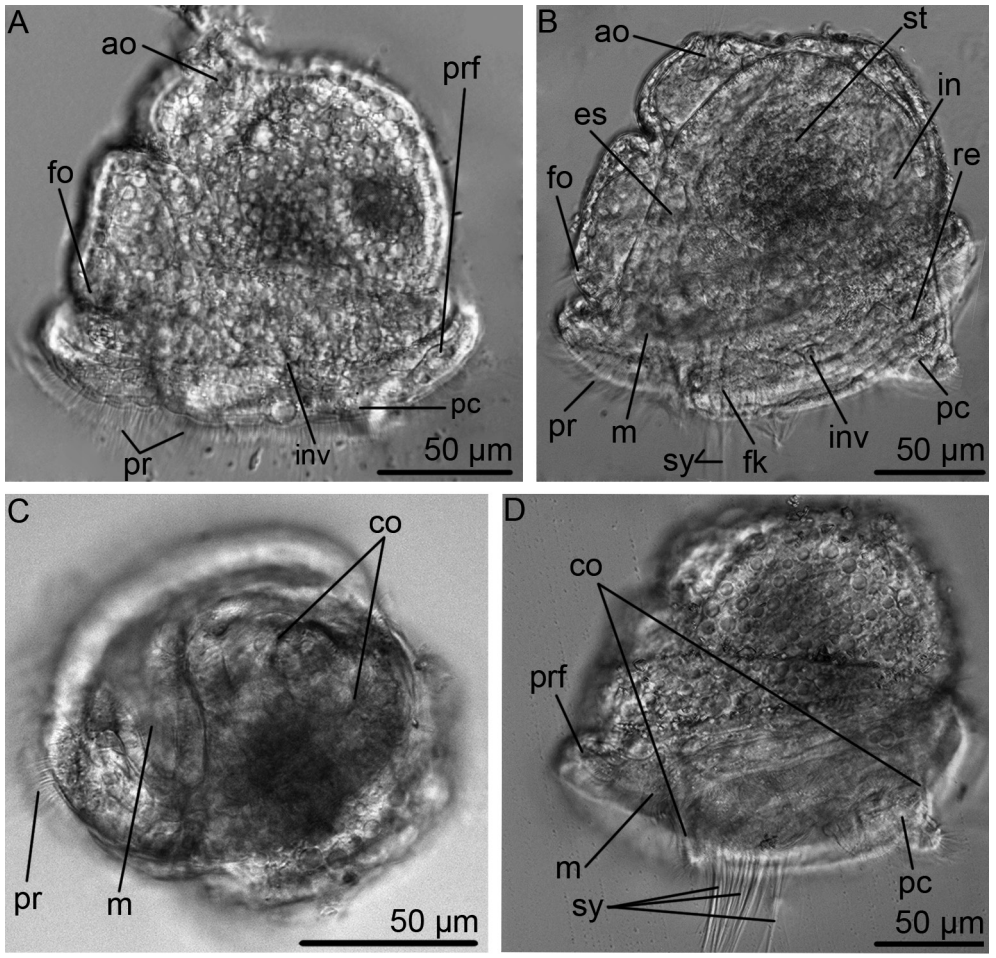

Fig. 1. Morphology of *Barentsia gracilis* larvae. A — lateral view with a focus on the prototrochal fold (prf); B — lateral view with a focus on a foot rudiment (fk, inv and pc); C — view on the hyposphere of a larva with a retracted foot rudiment showing the central opening of the hyposphere (co); D — laterofrontal view on a larva with partly extend foot rudiment.

Abbreviations: ao — apical organ; co — central opening of hyposphere; es — esophagus; fk — foot knob; fo — frontal organ; in — intestine; inv — foot invagination; m — mouth; pc — pedal cone; pr — prototroch; prf — prototrochal fold; re — rectum; st — stomach; sy — syncilia.

above the prototrochal fold (Fig. 1A, B). Like the apical organ, the frontal organ can retract into the episphere. A slit-shaped mouth opens at the anterior margin of the hyposphere (Fig. 1C). In the central part, the hyposphere has a trapezoidal shape with a central opening through which the foot rudiment may partially extend (Fig. 1C, D). The foot is a ciliate invagination in the center of the hyposphere with a foot knob in the anterior part and a pedal cone in the posterior part (Fig. 1B, D). The foot knob bears several bundles of cilia, syncilia. The anus opens on the pedal cone.

Musculature

The musculature of the larva of *B. gracilis* includes the musculature of the body wall, musculature of the apical organ, longitudinal musculature of the episphere and hyposphere (Figs 2A, B; 3). Numerous fine *body wall ring muscles* surround the episphere (Fig. 2B–D). Ring and longitudinal muscles are connected with the apical organ (Fig. 2C). The *ring muscles of the apical organ* run in the body wall in several groups under each other. Six *longitudinal muscles of the apical organ* are located deeper than the

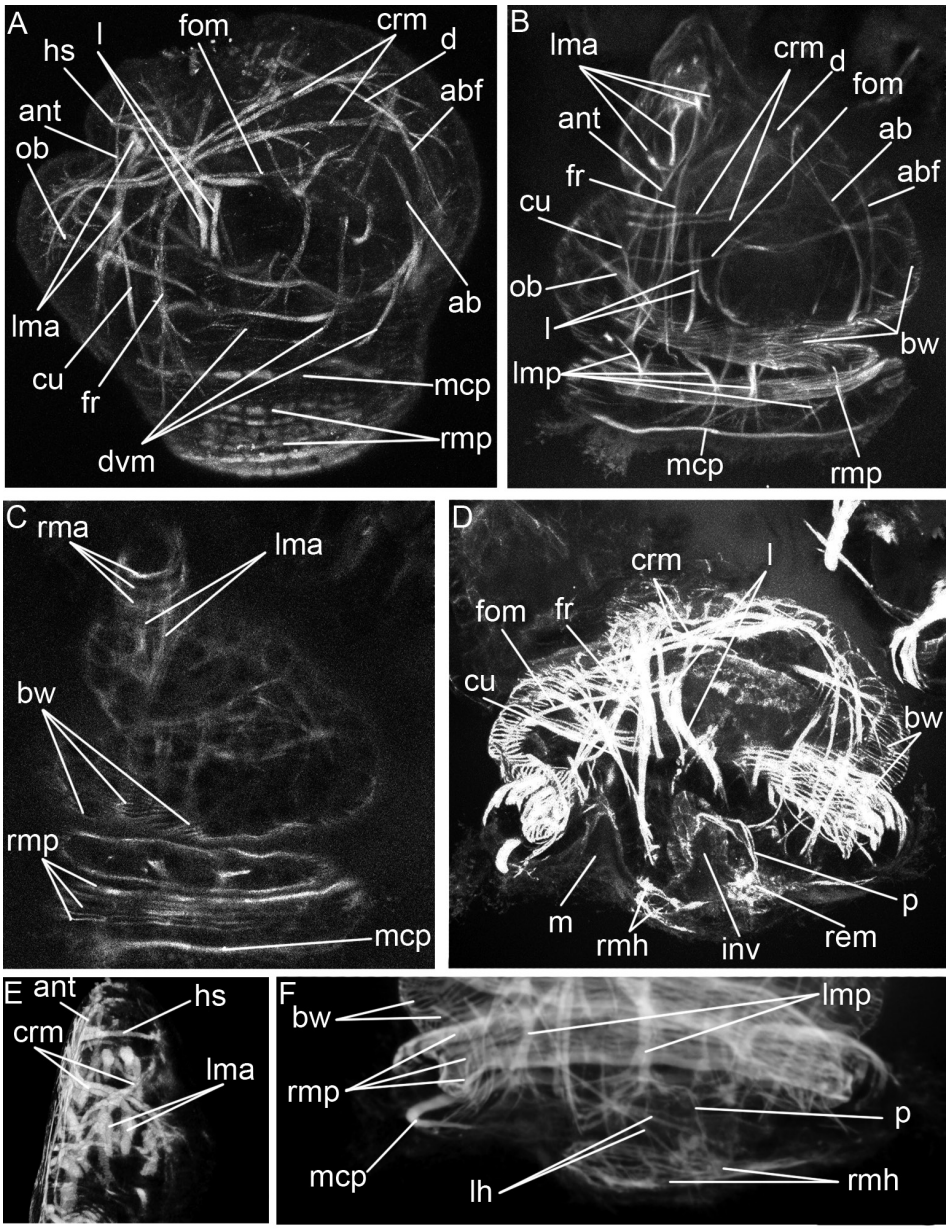

Fig. 2. Musculature of *Barentsia gracilis* larvae, CLSM. A — lateral view of the contracted larvae; B — lateral view of the relaxed larvae; C — lateral view of the larvae showing ring muscles of the apical organ (rma); D — lateroventral view on the hyposphere and episphere showing pedal muscle (p) and rectal musculature (rem); E — frontal view on the larva showing crossing of cross muscles (crm); F — lateral view on the musculature of the hyposphere and prototroch.

Abbreviations: ab — aboral muscle; abf — abfrontal muscle; ant — anterior longitudinal muscle; bw — body wall ring muscles; crm — cross muscle; cu — curved muscle; d — dorsal muscle; dvm — dorsoventral muscle; fom — muscle of frontal organ; fr — frontal muscle; hs — horseshoe-shaped muscle; inv — foot invagination; l — lateral muscle; lh — longitudinal muscle of hyposphere; lma — longitudinal muscle of apical organ; lmp — longitudinal muscle of prototroch; m — mouth; mcp — main constrictor of prototroch; ob — oblique muscle; p — pedal muscle; rem — rectal musculature; rma — ring muscle of apical organ; rmh — ring muscle of central opening of hyposphere; rmp — ring muscle of prototrochal fold.

ring muscles (Fig. 2B, C, E). These muscles form a kind of basket around the apical organ. They are relatively short and end in the upper third of the episphere. In the contracted larva, a *horseshoe-shaped muscle* is visible in the apical part of the episphere, with its arc directed forward (Fig. 2A, E). A pair of longitudinal *anterial muscles* insert in front of the arc of the horseshoe-shaped muscle (Fig. 2A, B, E). They end at the level of the middle of the episphere. The paired *curved muscles* originate near the mouth opening (Fig. 2D), run obliquely upward to the episphere, and end in the body wall in the area above the frontal organ (Fig. 2A, B). A pair of *oblique muscles* protrudes from the area above the frontal organ below the curved muscles and extends toward the posterior wall of the esophagus (Fig. 2A, B). The paired *frontal muscles* run from the foot knob (Fig. 2D) to the posterior part of the apical organ, where it splits into two bundles (Fig. 2A, B). The paired *dorsal muscles* originate behind the apical organ and run to the aboral side of the larva's body. A pair of *abfrontal muscles* runs at the posterior part of the larval body in the upper half of episphere (Fig. 2A, B). The paired *aboral muscles* insert with small branching fibres at the upper part of the posterior side of the body, run parallel to the abfrontal muscles and end at the border between the episphere and hyposphere (Fig. 2A, B). Two pairs of *cross muscles* run from the frontal to the abfrontal side of the larval body at the level above the middle of the episphere (Fig. 2B, C). These muscles cross each other on the frontal side of the body (Fig. 2E). The paired *muscles of frontal organ* insert at the sides of frontal organ, first go upward, and then turn laterally and run toward the abfrontal side of the body (Fig. 2A, B). Three pairs of *dorsoventral muscles* are located on the sides of the larval body in its posterior half (Fig. 2A, D). They run from the hyposphere to the middle part of the episphere. Two pairs of *lateral muscles* insert above the foot invagination (Fig. 2D) and run upward and laterally, wrapping around the stomach (Fig. 2A, B). In the digestive tract, the muscular elements are identified in the lower third of the rectum, near the anus — *rectal musculature* (Fig. 2D).

The prototrochal fold contains a broad band of ring muscles — a sphincter of the prototroch (Figs 2A–C; 3). The sphincter includes a number of muscle fibers located close to each other,

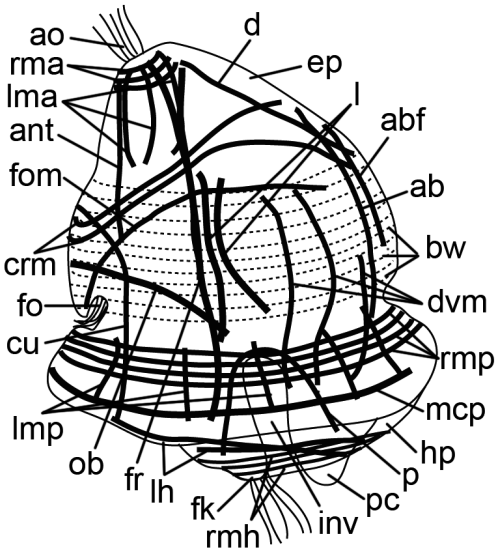

Fig. 3. Schematic diagram of the musculature of *Barentsia gracilis* larvae.
Abbreviations: ao — apical organ; ab — aboral muscle; abf — abfrontal muscle; ant — anterior longitudinal muscle; bw — body wall ring muscles; crm — cross muscle; cu — curved muscle; d — dorsal muscle; dvm — dorsoventral muscle; ep — episphere; fk — foot knob; fo — frontal organ; fom — muscle of frontal organ; fr — frontal muscle; hp — hyposphere; inv — foot invagination; l — lateral muscle; lh — longitudinal muscle of hyposphere; lma — longitudinal muscles of apical organ; lmp — longitudinal muscles of prototroch; mcp — main constrictor of prototroch; ob — oblique muscle; p — pedal muscle; pc — pedal cone; rma — ring muscles of apical organ; rmh — ring muscles of central opening of hyposphere; rmp — ring muscles of prototrochal fold.

the *ring muscles of prototrochal fold*, and one thick muscle fiber below them — the *main constrictor of prototroch* (Fig. 2B, C). The main constrictor is unclosed on the abfrontal side. In the contracted larva, the main constrictor is located above the ring muscles of prototrochal fold. The *longitudinal muscles of the prototroch* insert with small branching fibres near the main constrictor of prototroch and extend into the episphere, ending in its lower third (Fig. 2B). Longitudinal muscles of prototroch are located along the periphery of the body at approximately equal distances from each other.

In the central part of the hyposphere there is a group of *ring muscles of hyposphere* surrounding the central opening through which the foot rudiment extends (Fig. 2E). The *longitudinal muscles of hyposphere* run from the area of the central opening to the anterior end of the body

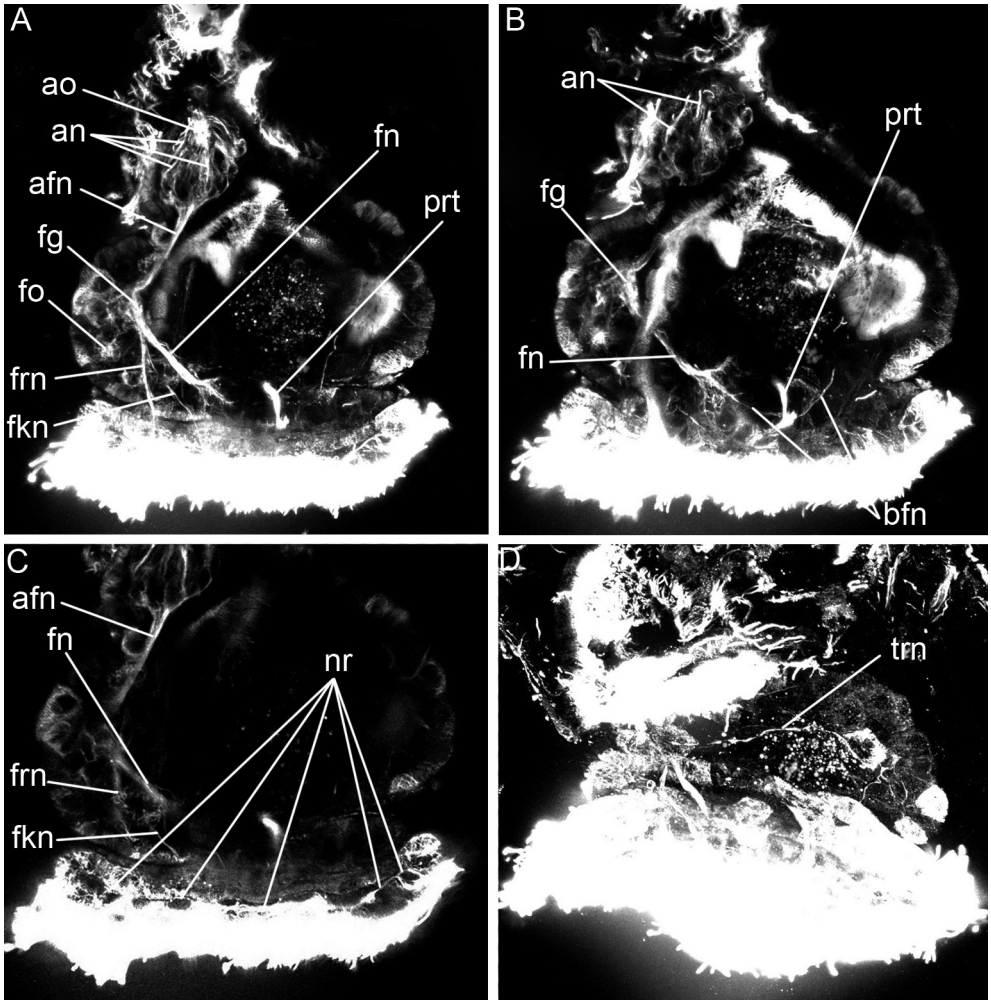

Fig. 4. Nervous system of *Barentsia gracilis* larvae, CLSM. A — lateral view on the larva showing apico-frontal connective (afn) and nerves originated from the frontal ganglion; B — lateral view on the larva showing branches of foot nerves (bfn); C — lateral view on the larva showing nerve ring of prototroch (nr); D — lateral view on the larva showing transverse nerves of episphere (trn).
Abbreviations: afn — apico-frontal connective; ao — apical organ; an — fine apical nerves; bfn — branch of foot nerve; fg — frontal ganglion; fkn – foot knob nerve; fn — foot nerve; fo — frontal organ; frn — frontal nerve; nr — nerve ring of prototroch; prt — protonephridium; trn — transverse nerve of episphere.

(Fig. 2D, E). The paired arc-shaped *pedal muscles* are located on the sides of the foot invagination (Fig. 2D, F).

Nervous system

The nervous system of entoproct larvae includes two large sensitive organs, apical and frontal, associated with apical and frontal ganglia, respectively. Fine nerve fibers run from the sensory organs to the ganglia (Figs 4A, B; 5). In case of the apical organ, at the base of the apical ganglion these fine nerve fibers (*apical nerves*) merge into a pair of *apico-frontal connectives* running to the frontal ganglion (Figs 4A; 5). Several pairs of large nerves originate from the frontal ganglion. A pair of *frontal nerves* projects from the frontal ganglion toward the mouth and contacts a *nerve ring* of *prototroch* (Figs 4A; 5). The nerve ring of prototroch runs along the prototroch (Figs 4C; 5). The *foot knob nerves* separate from the frontal nerves and extend toward the foot knob (Figs 4A; 5). Paired *foot*

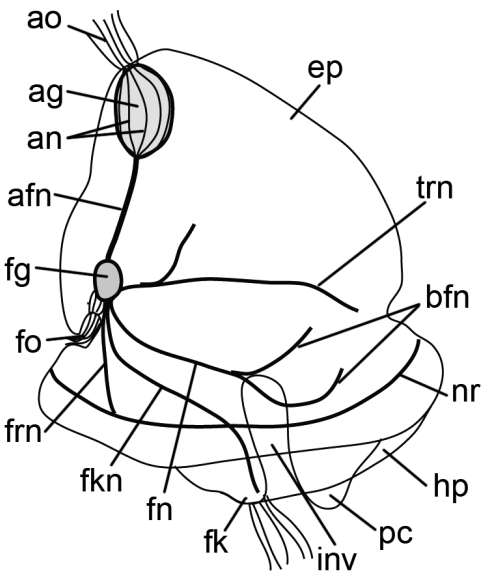

Fig. 5. Schematic diagram of the nervous system of *Barentsia gracilis* larvae.
Abbreviations: afn — apico-frontal connective; ao — apical organ; ag — apical ganglion; an — fine apical nerves; bfn — branch of foot nerve; ep — episphere; fg — frontal ganglion; fk — foot knob; fkn — foot knob nerve; fn — foot nerve; fo — frontal organ; frn — frontal nerve; hp — hyposphere; inv — foot invagination; nr — nerve ring of prototroch; pc — pedal cone; trn — transverse nerve of episphere.

nerves extend from the frontal ganglion toward the foot (Figs 4A; 5). Near the foot invagination, the foot nerves split into several nerve fibers, some of which contact the invagination of the foot, and some of which extend further to the aboral side of the larval body as *branches of foot nerve* (Figs 4B; 5). The episphere contains several pairs of fine *transverse nerves* that start from the frontal ganglion and extend to the aboral side of the body, where split into fine nerve fibers contacted the body wall (Figs 4D; 5).

Discussion

Musculature

The musculature of the larva of *B. gracilis* is complex and contains a large number of muscles running in different directions. The function of some muscles can be assumed by comparing the arrangement of muscles in a contracted and relaxed larva. The longitudinal muscles of the prototroch are involved in the retraction of the hyposphere deep into the larval body. The main constrictor of the prototroch in the contracted larva is located above the ring muscles of the prototrochal fold, and this means that the hyposphere is not just pulled up to the episphere, but is also turned inwards. Retraction of central part of hyposphere is probably provided by the dorsoventral muscles and also by lateral muscles. The oblique and frontal muscles are probably responsible for retraction of the anterior part of the hyposphere. The longitudinal muscles of the apical organ and the muscles of the frontal organ are responsible for the retraction of these organs.

Comparison of the musculature of *B. gracilis* with that of swimming-type larvae with a completely reduced foot shows that the musculature of the latter is less complex (Borisanova *et al*., 2012; Fuchs, Wanninger, 2008) (Fig. 6A). Some muscles can be found both in larvae with a completely reduced foot and in larva of *B. gracilis* with a partially reduced foot: the ring and longitudinal muscles of the apical organ, the ring muscles of the prototroch (including the main constrictor) and longitudinal muscles of the prototroch, as well as the ring musculature of the body wall. The paired longitudinal muscles described in swimming-type larvae with a completely reduced foot (frontal muscles, abfrontal muscles, lateral muscles, main retractor muscles), are difficult to homologize unambiguously with the muscles of *B. gracilis*. The main retractors described in *L. atkinsae* (Fuchs, Wanninger, 2008) and the central muscles described in *B. discreta* (Borisanova *et al*., 2012) most likely correspond to the frontal muscles of *B. gracilis*. The aboral muscles of swimming-type larvae with a completely reduced foot may correspond to the aboral muscles of *B. gracilis*. The frontal muscles of swimming-type larvae with a completely reduced foot that run from the apical organ to the prototroch near the anterior end of the body and cross each other, cannot be homologize with any of *B. gracilis* muscles. *B. gracilis* has intercrossing cross muscles but they run in a different direction, from the anterior to the aboral side of the body.

The musculature of the creeping-type larva of *L. murmanica* (Merkel *et al*., 2015) with a well-developed foot and frontal organ is more complex than that of *B. gracilis* (Fig. 6B). The larva of *L. murmanica* (as well as swimming-type larvae) has ring and longitudinal muscles of the apical organ, ring and longitudinal musculature

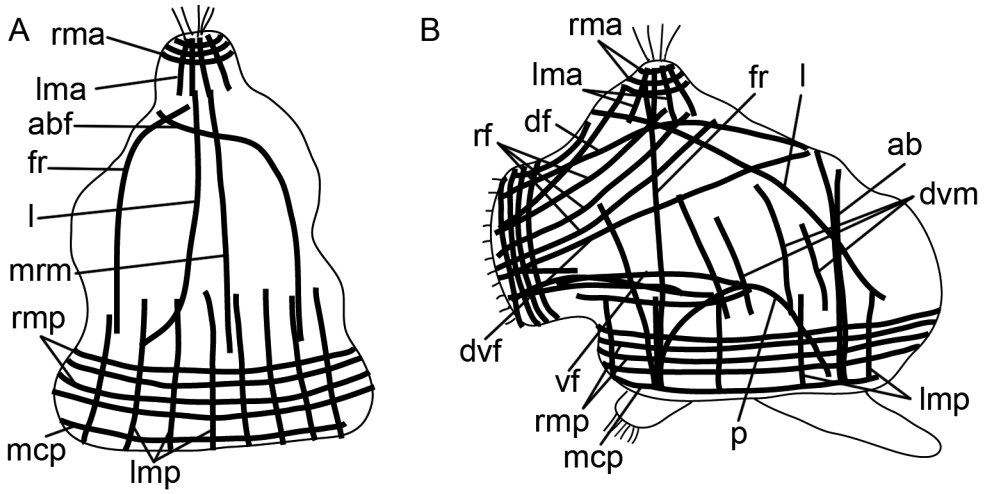

Fig. 6. Schematic diagram of the musculature of swimming-type and creeping-type entoproct larvae. A — swimming-type larva with a completely reduced foot. B — creeping-type larvae.
Abbreviations: ab — aboral muscle; abf — abfrontal muscle; df — dorsal muscle of frontal organ; dvf — dorsoventral muscle of frontal organ; dvm — dorsoventral muscle; fr — frontal muscle; l — lateral muscle; lma — longitudinal muscle of apical organ; lmp — longitudinal muscle of prototroch; mcp — main constrictor of prototroch; mrm — main retractor muscle; p — pedal muscle; rf — retractor of frontal organ; rma — ring muscle of apical organ; rmp — ring muscle of prototrochal fold; vf — ventral muscle of frontal organ.

of the prototroch, and aboral musculature. Some muscles associated with the frontal organ and foot are similar in *L. murmanica* and *B. gracilis*, although these muscles are less developed in *B. gracilis*, because both the frontal organ and the foot are partially reduced. Thus, in *L. murmanica*, several groups of paired muscles (retractors of the frontal organ, dorsal muscles of the frontal organ, dorsoventral muscles of the frontal organ and some other muscles) insert from the large frontal organ and run towards the apical organ and the upper part of the episphere. In *B. gracilis*, the frontal organ is small and only a pair of the frontal organ muscles originates from it. However, *B. gracilis* has several pairs of muscles originating from the area above the frontal organ, similar in location to the some muscles of *L. murmanica* originating from the frontal organ. For example, cross muscles of *B. gracilis* are located similarly to the branched dorsal muscles of the frontal organ of *L. murmanica*, although the latter do not cross each other. The position of the branched ventral muscles of the frontal organ of *L. murmanica* is similar to the position of the oblique muscles of *B. gracilis*. In both species the arc-shaped pedal muscles are connected to the foot, but in *L. murmanica* the left and right pedal muscles cross each other on the aboral side, while in *B. gracilis* no intercrossing of these muscles is found. In both *L. murmanica* and *B. gracilis*, paired frontal muscles extend from the anterior end of the foot to the apical organ. In both species, several pairs of dorsoventral muscles are located in the posterior half of the body. The lateral muscles of *L. murmanica* are not homologous to the lateral muscles of swimming-type larvae with a completely reduced foot, nor to the lateral muscles of the larvae of *B. gracilis*. In *L. murmanica* lateral muscles insert between apical and frontal organ and run abfrontally, ending near the hyposphere.

Nervous system

The nervous system of entoproct larvae has previously been studied using confocal microscopy methods in only two species: the swimming-type larva of *Loxosomella atkinsae* with a completely reduced foot and frontal organ (Fuchs, Wanninger, 2008) and the creeping-type larva of *L. murmanica* (Wanninger *et al*., 2007). In both cases, the serotonergic nervous system was investigated. This makes it somewhat difficult to compare with the data obtained in the present study, which used labeling with antibodies to α-tubulin. However, given that tubulin is present in all elements of the nervous system, including

serotonergic elements, some comparative analysis can still be made. The serotonergic nervous system of *L. atkinsae* includes the serotonergic cells of the apical organ, nerves running from the apical organ to the frontal neuropil on the frontal side of the larva, and nerves running from this neuropil to the nerve ring of the prototroch. All these nerve elements were found in *B. gracilis*: apico-frontal connectives linking apical and frontal ganglions and frontal nerves running from the frontal ganglion to the nerve ring of the prototroch. These nerve elements can also be identified in the creeping-type larva of *L. murmanica* (Wanninger *at al*., 2007: fig. 2c). The frontal neuropil has not been described in *L. murmanica*, but it is probably located where the bundles of nerves coming from the apical ganglion (corresponding to the apico-frontal connectives) split into separate nerves. These are nerves connecting to the anterior nerve loop, nerves inserting at the pedal nerve cords, and nerves running ventrally and inserting at the prototroch nerve ring. The latter correspond to the frontal nerves of *B. gracilis*. The paired longitudinal pedal nerves, described in *L. murmanica*, are difficult to homologize with the nerves described in *B. gracilis*. According to the authors' description (Wanninger *at al*., 2007), the pedal nerves of *L. murmanica* "pass through along the anterior–posterior axis in the mid-body region of the larva", but the foot is located in the lower part of the larva's body, so it is not certain that these nerves are, indeed, connected to the foot. The pedal nerves of *B. gracilis* run from the frontal ganglion ventrally, to the foot invagination.

Generalization of the data obtained by confocal microscopy and other methods of research (Nielsen, 1971; Nielsen, Jespersen, 1997; Haszprunar, Wanninger, 2008; Borisanova, Ivanova, 2024) allows to identify the following obligatory elements of the nervous system of entoproct larvae: apical and frontal ganglia connected by apico-frontal connectives; several pairs of nerves departing from the frontal ganglion, including the frontal nerves going to the nerve ring of the prototroch.

Acknowledgements. The author is thankful to the management and staff of Pertsov White Sea Biological Station of Lomonosov Moscow State University (WSBS MSU) for providing the opportunity to conduct the research and especially to WSBS diving team and to the staff of the center of microscopy of WSBS. The author is grateful to the Reviewer for helpful comments.

References

Borisanova A.O., Chernyshev A.V., Malakhov V.V. 2012. The structure of the muscular system in the planktonic larva of colonial Kamptozoa // Doklady Biological Sciences. Vol.442. P.31–33.

Borisanova A.O., Ivanova O.V. 2024. Ultrastructure of a swimming-type larva of *Barentsia gracilis* (Entoprocta, Coloniales) // Zoomorphology. Vol.143. P.347–366.

Fuchs J., Wanninger A. 2008. Reconstruction of the neuromuscular system of the swimming-type larva of *Loxosomella atkinsae* (Entoprocta) as inferred by fluorescence labelling and confocal microscopy // Org. Divers. Evol. Vol.8. P.325–335. https://doi.org/10.1016/j.ode.2008.05.002

Haszprunar G., Wanninger A. 2008. On the fine structure of the creeping larva of *Loxosomella murmanica*: additional evidence for a clade of Kamptozoa (Entoprocta) and Mollusca // Acta Zool. Vol.89. P.137–148. https://doi.org/10.1111/j.1463-6395.2007.00301.x

Ivanova-Kazas O.M. 1986. [The origin and phylogenetic significance of the trochophore larvae. 4. Larvae of Kamptozoa. General Ideas] // Zool. Zhurn. Vol.65. P.165–174 [in Russian, with English summary].

Merkel J., Lieb B., Wanninger A. 2015. Muscular anatomy of an entoproct creeping-type larva reveals extraordinary high complexity and potential shared characters with mollusks // BMC Evol. Biol. Vol.15. Art.130. https://doi.org/10.1186/s12862-015-0394-1

Nielsen C. 1971. Entoproct life-cycles and the Entoproct/Ectoproct relationship // Ophelia. Vol.9. P.209–341. https://doi.org/10.1080/00785326.1971.10430095

Nielsen C., Jespersen Å. 1997. Entoprocta // F.W. Harrison, E.E. Ruppert (eds.). Microscopic anatomy of invertebrates. Vol.13. New York: Wiley-Liss. P.13–43.

Sensenbaugh T. 1987. Ultrastructural Observations on the larva of *Loxosoma pectinaricola* Franzén (Entoprocta, Loxosomatidae) // Acta Zool. Vol.68. P.135–145. https://doi.org/10.1111/j.1463-6395.1987.tb00884.x

Wanninger A. 2015. Entoprocta // A. Wanninger (ed.). Evolutionary developmental biology of invertebrates 2: Lophotrochozoa (Spiralia). Springer. P.89–102. https://doi.org/10.1007/978-3-7091-1871-9_6

Wanninger A., Fuchs J., Haszprunar G. 2007. Anatomy of the serotonergic nervous system of an entoproct creeping-type larva and its phylogenetic implications // Invertebr. Biol. Vol.126. P.268–278. https://doi.org/10.1111/j.1744-7410.2007.00097.x

Responsible editors: A.V. Chernyshev, E.N. Temereva