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Structural Peculiarities of the Byssal Apparatus and Byssal Groove of the Foot in the Mediterranean Mussel (*Mytilus galloprovincialis*, Bivalvia, Mytilidae) from the Zhitkov Bay of the Sea of Japan

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Abstract—The peculiarities of morphological structure of the byssal apparatus, byssal threads, and byssal groove of the foot were studied in the commercial species of the Mediterranean mussel (*Mytilus galloprovincialis*) from the Sea of Japan. It was demonstrated that the byssal apparatus consists of a root, stem, and byssal threads that are elliptical in shape in cross-section. Each byssal thread consists of a corrugated, wide proximal part (which is located immediately behind the cuff and accounts for one-third of its length) and a relatively elastic, narrow distal part (accounts for two-thirds of the thread length), terminating with an oval attachment disk at the distal end. In each byssal thread, three types of byssal prepolymerized collagens (P, D, and NG) with a different block copolymer structure are contained at its different parts. The surface of the byssal threads is tuberous along its entire length. Two reinforcing cords are located on the attachment disk surface. The edges of the attachment disks are semitransparent. The byssal groove of the foot is arranged more primitively than in the studied Mytilidae species. It is noteworthy that the distal fossa is absent at the distal end of the byssal groove of the foot. The peculiarities of morphological structure of the byssus and attachment disks in *M. galloprovincialis* are explained by the peculiarities of the secretory organ structure.

Keywords: mytilids, byssus, byssal threads, attachment disks, scanning electron microscopy

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INTRODUCTION

The Mediterranean mussel (*Mytilus galloprovincialis* Lamarck, 1819) is a widespread circumboreal–subtropical, euryhaline species, which inhabits the upper sublittoral zone and forms the main commercial aggregations at the depths of 1–20 m (Lutaenko and Noseworthy, 2012). This species can settle on a variety of substrates, preferring sandy, silty–sandy, pebble, gravel, and coarse-sandy bottom areas. *M. galloprovincialis* also attaches successfully to the boulders, rocks, and different solid substrates. As a rule, this species inhabits mainly warm waters of temperate latitudes (Lutaenko and Kolpakov, 2016). In addition, as well as the common mussel (*Mytilus edulis* Linnaeus, 1758) and the Pacific mussel (*Mytilus trossulus* Gould, 1850), the Mediterranean mussel is an important object of cultivation in many countries of the world, since it has high organoleptic taste qualities.

The Mediterranean mussel was for the first time discovered and determined by morphological traits in the Far East region of Russia in the southern part of the Peter the Great Bay in the areas of the Sivuchya Bay, Kalevala Bay, Cape Degera, and Cape Nizmennogo in the middle of 1970s (Ivanova and Lutaenko, 1998; Lutaenko and Noseworthy, 2012; Lutaenko and Kolpakov, 2016). Over the past 10 years (from 2014 to 2024), small genetically confirmed populations of this species were detected in the Kievka Bay and Posyet Bay (Zarubino International Seaport) of the Sea of Japan, where the portion of genotypes of this species was 14 and 30–42%, respectively (Kartavtsev et al., 2014). According to the same authors (Kartavtsev et al., 2014), the portion of *M. galloprovincialis* in the Vityaz Bay and Amur Bay did not exceed 1–2%. This species of Mytilidae was introduced into our waters of the Sea of Japan by the ships entering the ports, to the bottoms of which adults of Mediterranean mussel are attached. Getting into favorable temperature conditions of 15–18°C in the waters of southern Primorye, this species reproduces successfully, the larvae are carried by currents and successfully settle in our waters of the Sea of Japan. According to data obtained from 2012 to 2024, the northern boundary of the *M. galloprovincialis* range runs along the continental coast of

the Sea of Japan to the Tikhaya Pristan Harbor of the Olga Bay and Vladimir Bay; from the island zone to the Moneron Island (southwestern part of the Sakhalin Island) (Lutaenko and Kolpakov, 2016). According to the same authors (Lutaenko and Kolpakov, 2016), the southern boundary of the *M. galloprovincialis* range runs along the continental coast of the Sea of Japan to the coast of South Korea and extends east to the coast of Japan from the southern Okinawa and Ogasawara islands to the north to the Hokkaido Island.

In order to turn into juvenile individual during the period of metamorphosis at the pediveliger stage, larvae in bivalve mollusks of the family Mytilidae settle from the water column onto the substrate surface or byssal threads of byssi in adult individuals (Selin and Vekhova, 2002) using a personal byssal apparatus. This apparatus arose evolutionarily in them as a result of neoteny and is maintained throughout the life in the environment, which is typical for the habitat of adult individuals (Yonge, 1962). Throughout their life, these bivalves can discard the byssus and, moving using the foot to a suitable habitat, form a new byssus using the foot glands (Waite, 1983, 1997; Vekhova, 2007, 2019, 2021, 2022).

During this study, the first author of the article noted that the edges of the attachment disks of the byssal threads of *M. galloprovincialis* byssus are semitransparent. This is directly associated with the peculiarities of morphological structure of the byssal groove of the foot in this species of Mytilidae. At present, there is only a single article in the scientific literature related to the study of the byssus structure in the Mediterranean mussel by a scanning electron microscopy method, in which the function of the byssal groove of the foot is only mentioned (Bairati and Vitellaro-Zuccarello, 1974).

The aim of the work was to conduct a detailed study of the structure of the byssal apparatus and byssal groove of the foot in *M. galloprovincialis* from the Zhitkov Bay of the Sea of Japan.

MATERIALS AND METHODS

Collection of Material

To study the peculiarities of morphology of the byssal apparatus, byssal threads, and byssal groove of the foot, mussels collected in the second half of May, 2023 using the diving service of the Zhirmunsky National Scientific Center of Marine Biology, Far East Branch, Russian Academy of Sciences, from a pier at the depth of 1–3 m in the Zhitkov Bay of the Sea of Japan (43°01′03.62″ N, 131°55′50.27″ E) were used. Under laboratory conditions, the shell length (mm) was measured in 4 *M. galloprovincialis* specimens using a caliper with an accuracy of ±0.1 mm, their outer and inner surfaces were photographed (Fig. 1). The shell length in the studied mussels was 72.0 ± 3.5 mm. The age of each individual was determined by the outer growth rings on the shell surface (Zolotarev, 1989). Previously, the collected individuals of *M. galloprovincialis* were kept under laboratory conditions in an aquarium with running sea water with a normal salinity of 32.0 ± 1.2‰ and temperature of 15.8 ± 0.4°C, and the process of reattachment to the substrate on plastic Petri dishes was observed for one month, as described in our previous study (Selin and Vekhova, 2004).

Morphological Studies

Before dissection, each studied individual (4 specimens) was relaxed using the injection of 1 M potassium chloride solution. Using a light microscopy (LM) method, the byssus with the byssal threads were removed; at the same time, the foot in each individual was cut off, and its parameter were studied under a binocular microscope with ×8 eyepieces and ×0.6 tube, the foot length (mm) and its width (mm) were estimated. For each individual, 30 intact byssal threads were randomly taken from different parts of the byssal stem, and the studied parameters were measured. The length of the byssal threads (mm), their width in the distal and proximal parts (μm), at the points of transition of the proximal part of the byssal thread to a distal part and transition of the distal part of the byssal thread to the attachment disk (μm) were estimated under a binocular microscope with ×8 eyepieces and a ×7 tube. The portion of the proximal part of the byssal thread of its total length (%) was calculated. The largest and the smallest diameters of the attachment disk (mm) were measured. The last two parameters are given as the arithmetic mean and standard deviation.

The peculiarities of morphological structure of the byssal threads and byssal groove of the foot were studied in 4 *M. galloprovincialis* specimens using the scanning electron microscopy (SEM) method. For this, mussels of the same age were used. For SEM, all samples were fixed in a 2.5% glutaraldehyde solution prepared in 0.2 M cacodylate buffer (pH 7.4) for 24–48 h at a temperature of 2–4°C. After this, the samples were washed in 0.1 M cacodylate buffer for 15–20 min. Then the samples were dehydrated in alcohols of increasing concentration, gradually bringing the samples to pure acetone (Mironov et al., 1994). After this, the samples were finally dried in carbon dioxide according to the critical point drying method using a critical point dryer 030 instrument (BAL-TEC), placed on the surface of aluminum stubs and coated

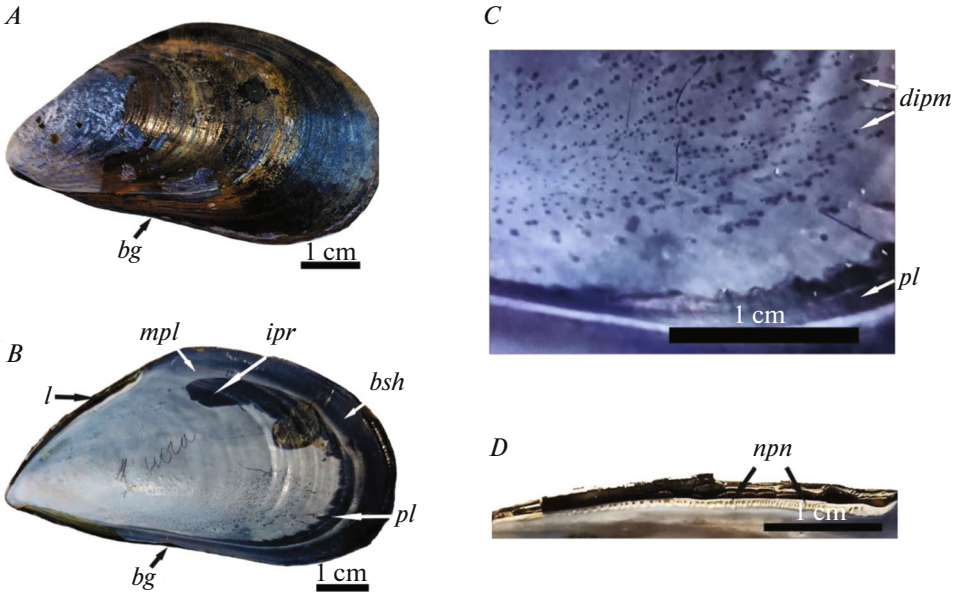

Fig. 1. Morphological traits of the shell of the Mediterranean mussel (*Mytilus galloprovincialis*) from the Zhitkov Bay, the Sea of Japan: *A*, outer surface of the shell; *B*, inner surface of the shell; *C*, enlarged fragment of the inner part of the posterior surface of the shell; *D*, enlarged porous nymph; *bg*, byssal gape; *bsh*, prismatic border along the inner edge of the shell; *l*, ligament; *ipr*, imprints of posterior retractors; *mpl*, middle pearl layer; *dipm*, dotted imprints of pallial muscles; *pl*, pallial line; *npn*, numerous pores on the nymph.

with chromium, using a Q 150T ES vacuum device for coating thin membranes. Subsequently, the peculiarities of morphology of the samples of byssal threads and byssal groove of the foot in *M. galloprovincialis* were studied on a Carl Zeiss Sigma 300 VP scanning electron microscope.

All obtained micrographs were edited using Adobe Photoshop CS6 graphical software. Using the Smartiff software, different parameters of the byssal threads and the byssal groove of the foot were measured. Statistical processing of data was performed on a personal computer using standard algorithms realized in the Microsoft Excel application software package.

COI DNA Barcoding

Four specimens of *M. galloprovincialis* from the Zhitkov Bay of the Sea of Japan were delivered to the Laboratory of Biotechnology of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences (Vladivostok, Russia) for genetic analysis. Total DNA was isolated from the pieces of mussel mantle (3–5 mm^3) according to the published protocol (Kiselev et al., 2015). Partial sequences of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene were amplified and sequenced using universal primer pairs for invertebrates: LCO1490: 5'GGT CAA CAA ATC ATA AAG ATA TTG G and HCO2198: 5'TAA ACT TCA GGG TGA CCA AAA AAT CA (Folmer et al., 1994). PCR amplification was performed in a reaction volume of 25 μL. The amplification products were used as matrices for sequencing using the same primers as for PCR and Big Dye Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems, United States) according to the manufacturer's protocol. The products of sequencing reactions were purified by ethanol precipitation at the Center for Biotechnology and Genetic Engineering of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences, and analyzed on an ABI-3130 genetic analyzer (Applied Biosystems, ABI, United States). Nucleotide sequences of the mitochondrial cytochrome *c* oxidase subunit I gene were for the first time deposited to GenBank from 4 *M. galloprovincialis* specimens from the Zhitkov Bay, the Sea of Japan: Pp869770, Pp869771, Pp869772, Pp869773. Nucleotide sequence divergences, *p*-distances, and trees were calculated using the Kimura two-parameter (K2P) nucleotide substitution model (Kimura, 1980). A neighbor-joining method was used to construct the optimal phylogenetic tree using a MEGA 11 program (Saitou and Nei, 1987). The percentage of duplicate trees, in which taxa are grouped together in a bootstrap test (1000 replicates, Felsenstein, 1985), are demonstrated near the branches.

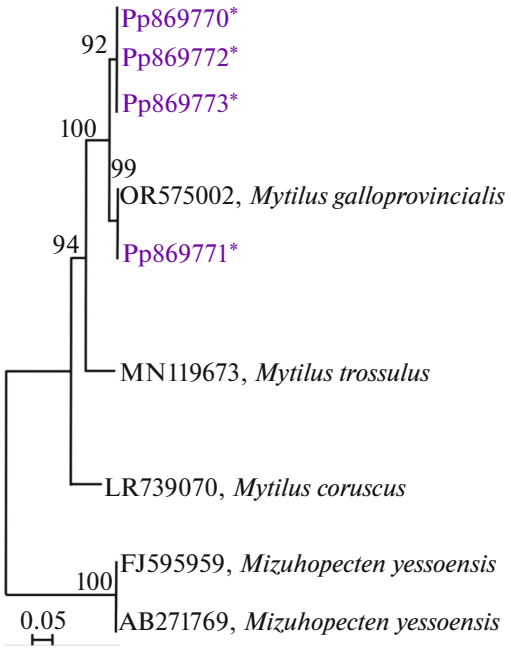

Fig. 2. Phylogenetic tree on the basis of the results of the analysis of nucleotide sequence of the mitochondrial cytochrome *c* oxidase subunit I gene in the Mediterranean mussel (*Mytilus galloprovincialis*) from the Sea of Japan. All samples (marked with an asterisk) collected in the Zhitkov Bay of the Sea of Japan belong to the same clade, have 99.6–100% identity, and belong to the same species (Mediterranean mussel, *Mytilus galloprovincialis*).

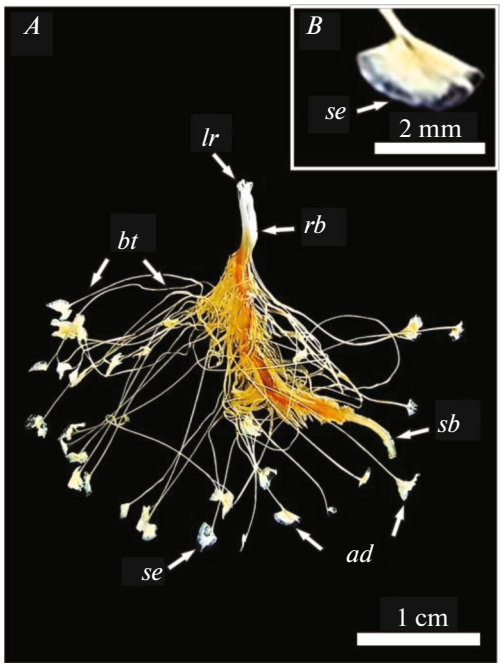

Fig. 3. Appearance of the byssus apparatus of the Mediterranean mussel (*Mytilus galloprovincialis*) with a shell length of 70.0 mm: *A*, morphological structure of the byssus; *B*, enlarged attachment disk of the byssal thread; *ad*, attachment disks; *bt*, byssal threads; *rb*, byssus root; *lr*, root lamellae; *sb*, byssus stem; *se*, semitranslucent edges of attachment disks.

RESULTS

Morphological and Molecular Analysis of Mytilus Galloprovincialis Individuals from the Zhitkov Bay, the Sea of Japan

In the collected mussel specimens, the periostracum in the anterior part of the shell is golden—brown; in the posterior part, black (Fig. 1*A*). The black border of the outer prismatic layer, devoid of internal nacreous layer, which runs along the inner edge of the shell to the ligament, is the most striking distinctive feature, which allows us to determine *M. galloprovincialis*; at the same time, muscle imprints of the posterior byssal retractors are deflected from the border (Fig. 1*B*). There is always a light middle pearl layer between them (Fig. 1*B*). In addition, according to the personal report of O.A. Scarlato, there are the dotted imprints of the mantle muscles in *M. galloprovincialis* on the shell inner surface on the ventral side at the back and at the bend of the shell (Figs. 1*B* and 1*C*). The presence of numerous pores on the nymph of the shell valves along its entire length is another trait, which allows us to determine *M. galloprovincialis* (Fig. 1*D*).

A comparative molecular analysis of the nucleotide sequence of the mitochondrial cytochrome *c* oxidase subunit I gene demonstrated that all the studied specimens are genetically stable and belong to the same bivalve mollusk species (*M. galloprovincialis*) (Fig. 2).

Structure of Byssal Apparatus

According to the results of the studies, the byssal apparatus in *M. galloprovincialis* consists of a root, stem, and byssal threads that are elliptical in shape in cross-section and terminate in oval attachment disks at the distal end (Figs. 3, 4, and 5*C*). The byssal root with a length of 5.0 ± 2.0 mm consists of numerous lamellae with a length of 3.0 ± 0.8 mm long that are deeply embedded in the tissues of the proximal part of the foot (Fig. 3*A*). The byssal stem with a length of 21.0 ± 3.0 mm is usually curved, extends ventrally from the root, and emerges from the opening of the stem (or byssus) gland located in the proximal part of the foot. The byssal stem exits the shell through the byssal gape of the ventral edge of the shell at the point of its bend (Figs. 1*A* and 1*B*). Upon closer examination, it can be seen that the stem has a lamellar structure and is surrounded on all sides by the cuffs that give rise to the byssal threads (Figs. 3 and 4). In the central part of the stem, the lamellae are tightly packed parallel to each other in a stack in a rounded core, surrounded by the cuffs with branching the byssal threads and typically located at a 90° angle relative to the bys-

sal groove of the foot. The stem core lamellae are oriented with the wide side of the ellipse toward the byssal cuffs. The byssal threads extend from the stem in two directions (toward the mussel's umbo and posterior part of the mussel shell). The stem carries only functionally active the byssal threads that are directly involved in the attachment of the mussel to the substrate (Fig. 3).

In a newly formed byssal apparatus, the root is light yellow, the root lamellae are white, the stem is light brown, and the byssal threads are usually darker in the proximal part than in distal one (Fig. 3*A*). In the proximal part, the byssal threads are beige; in distal part, light beige (Fig. 3*A*). The attachment disks have a light yellowish tone; at the same time, the edges of the attachment disks are semitransparent (Figs. 3*A* and 3*B*).

Structure of Byssal Threads

In *M. galloprovincialis*, a corrugated proximal part (which begins immediately behind the cuff and makes up 1/3 of its length) and a relatively rough, elastic distal part (2/3 of the thread' length) (which ends at the distal edge by an oval attachment disk) can be conditionally distinguished within each byssal thread (Figs. 3*A*, 3*B*, 4, 5*C*). As a rule, the byssal thread width in the proximal part is twice as large as in the distal part. Even with the naked eye, it is noticeable that the width and structure of the external surface of byssal threads differ at different parts (Fig. 3). We undertook a detailed study of byssal threads at the points of transition of the proximal part of the byssal thread to the distal part (Fig. 5*A*) and transition of the distal part of the byssal thread to the attachment disk (Figs. 5*B* and 5*C*), designating them as zone 1 and zone 2 (*z1* and *z2*), respectively. The byssal thread surface in the zones 1 and 2 is rough due to the presence of numerous rounded tubercles. The width of the transition of the distal part of the byssal thread to the attachment disk in this species is 2 times wider than the transition of the proximal part of the byssal thread to the distal part.

Proximal part of the byssal thread. The portion of the proximal part of the byssal thread is 23.0 ± 4.8% of the total length. The surface of the byssal thread proximal part is tuberous, covered with numerous transverse folds and shallow furrows oriented almost perpendicular to the longitudinal axis of the byssal thread (Fig. 5*D*). These folds make the proximal part of the byssal thread extensible. The width of the proximal part varies along the length of the byssal thread. In *M. galloprovincialis*, the largest width of the byssal thread at the proximal part is 98.5 μm; the smallest, 66.0 μm. In addition to the main transverse folds, one of the sides of the proximal part of the byssal thread has a folded surface in the form of a corrugated border (Figs. 5*D*, 5*G*, and 5*J*). The border represents closely located folds of a finer order and can be completely absent on one of the sides of the byssal thread in some specimens (Figs. 5*D*, 5*G*, and 5*J*). In *M. galloprovincialis*, the width of the corrugated border in the central part of the proximal part of the byssal thread is 7.0–14.0 μm (Fig. 5*J*). The degree of compactness of the folds changes along the proximal part of the byssal thread. In central part of the proximal part of the byssal thread, the width of the main transverse folds is 5.0–10.0 μm (Fig. 5*D*). For example, there are 3–4 transverse folds per 20.0 μm of the length of the proximal part of the byssal thread, respectively.

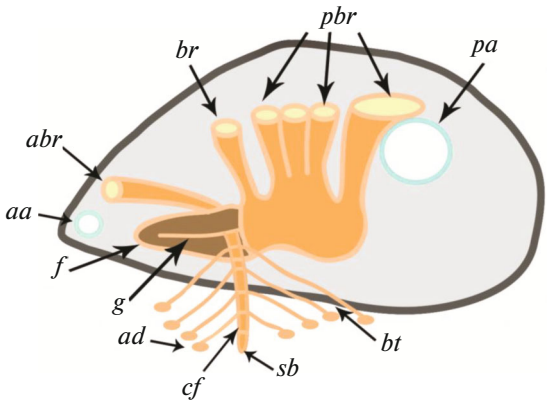

Fig. 4. Scheme of the structure of the byssal apparatus and attachment system in the Mediterranean mussel (*Mytilus galloprovincialis*) from the Sea of Japan: *aa*, anterior adductor; *pa*, posterior adductor; *abr*, anterior byssal retractor; *br*, byssal retractor; *pbr*, posterior byssal retractors; *f*, foot; *g*, byssal groove of the foot; *sb*, byssal stem; *cf*, cuffs; *bt*, byssal threads; *ad*, attachment disks.

Distal part of byssal thread. The morphology of transition zone of the proximal part of the byssal thread into the distal part combines their structural features (Fig. 5*A*). The thread width here varies in the range of 50.5–78.0 μm. The distal part of the byssal thread begins after the transition zone (*z1*) (Fig. 5*A*) and ends with the transition region of the distal part into the attachment disk (*z2*), where the byssal thread gradually expands into a plate of the attachment disk (Figs. 3*B*, 5*B*, and 5*C*). The byssal thread is flattened in cross section, has the shape of an ellipse. The byssal thread surface in the distal part is not folded, elastic, covered with numerous rounded tubercles 0.7–1.2 μm in size (Figs. 5*A*, 5*B*, 5*E*, 5*F*, 5*H*, 5*J*, and 5*K*). Along its surface, there is a clearly visible, rounded cord with a width of 5.5–12.5 μm, which occupies a lateral position on one of the sides of the byssal thread (Figs. 5*E* and 5*H*). The byssal thread section with a more powerful longitudinal cord is located in the central part of the distal section of the byssal thread. In the distal part of the byssal thread, the width varies along its length within the range of 39.0–53.0 μm, which is two times

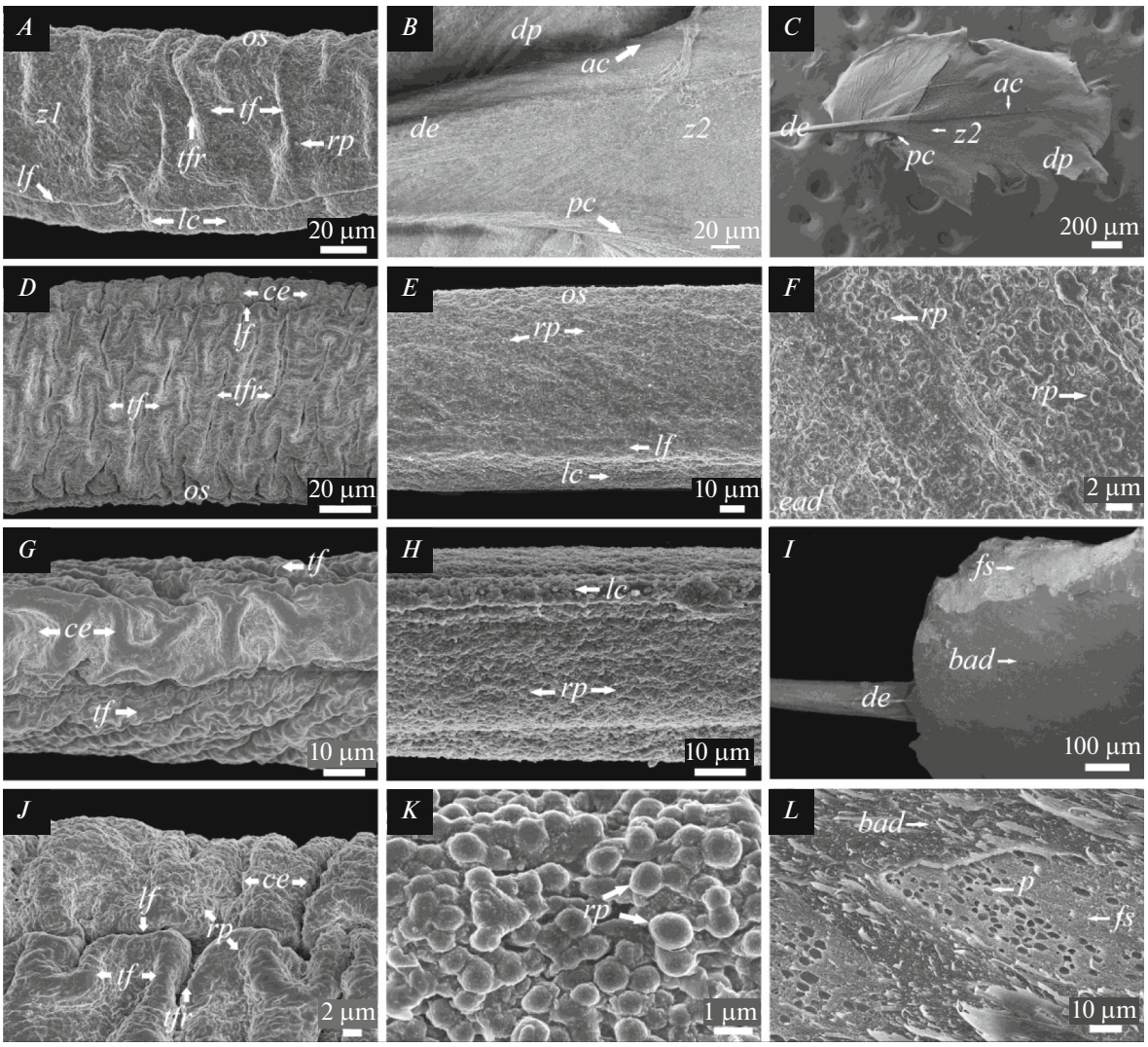

Fig. 5. Morphological structure of the byssal thread in the Mediterranean mussel (*Mytilus galloprovincialis*) from the Zhitkov Bay of the Sea of Japan (SEM): *A*, transition zone of the proximal part of the byssal thread to the distal part (*z1*); *B*, transition zone of the distal part of the byssal thread to the attachment disk (*z2*); *C*, appearance of the attachment disk; *D*, proximal part of the byssal thread, dorsal view; *E*, distal part of the byssal thread, dorsal view; *F*, enlarged fragment of the attachment disk, dorsal view; *G*, proximal part of the byssal thread, lateral view; *H*, distal part of the byssal thread, lateral view; *I*, bottom surface of the attachment disk; *J*, corrugated border of the proximal part of the byssal thread; *K*, enlarged fragment of the distal part of the byssal thread; *L*, enlarged fragment of the bottom surface of the attachment disk; *z1*, transition zone of the proximal part of the byssal thread to the distal part; *tf*, transverse fold; *tfr*, transverse groove; *os*, opposite side of the byssal thread; *rp*, rounded tubercle; *z2*, transition zone of the distal part of the byssal thread to the attachment disk; *de*, distal end of the byssal thread; *dp*, plate of the attachment disk; *ac*, anterior cord; *pc*, posterior cord; *ce*, corrugated border; *lc*, longitudinal cord; *lf*, longitudinal groove; *ead*, external surface of the attachment disk; *bad*, bottom surface of the attachment disk; *fs*, foam-like structure; *p*, pores of the bottom surface of the attachment disk.

narrower than the proximal part of the byssal thread. The thinnest part (width 39.0 μm) of the byssal thread is central; the widest part (width 78.0 μm) is located in front of the transition zone of the byssal thread from the distal part to the proximal one. The byssal thread in the transition zone of the distal region into the attachment disk is slightly flattened, with well pronounced two reinforcing cords on the surface (Figs. 5*B* and 5*C*); the width of the byssal thread here is 124.0–137.0 μm.

Attachment disk. The byssal thread at the distal edge ends with the attachment disk, which is clearly visible to the naked eye (Figs. 3*A* and 3*B*). It has the appearance of a flattened oval plate (Figs. 4 and 5*C*). The results of LM demonstrated that in *M. galloprovincialis*, the edges of the attachment disks of the byssal threads are semitransparent (Fig. 3*B*), the longitudinal axis of the byssal thread is located at an acute angle to the plane of the attachment disk (Figs. 3*B* and 5*C*). The results of SEM demonstrated that numerous

small tubercles with a size of 0.7–1.2 μm (Fig. 5*F*) and rounded reinforcing cords (they are usually no more than two) are clearly visible on the external surface of the attachment disk (Figs. 3*B*, 5*B*, and 5*C*). The anterior powerful cord extends along the attachment disk surface up to a half of its length (Fig. 5*C*). Along with it, one posterior, less pronounced thin, short cord is distinguished on the attachment disk surface (Figs. 5*B* and 5*C*). The results of SEM demonstrated that the internal structure of the attachment disk has a reticular matrix (Fig. 5*I*). The layer of the lower surface of the attachment disks is smooth, with a thickness of 1.2–2.0 μm (Figs. 5*I* and 5*L*). There is a porous structure under it, which resembles a solidified foam in appearance (Figs. 5*I* and 5*L*). The pore sizes vary in the range of 1.1–5.3 μm (Fig. 5*L*).

Structure of Byssal Groove of the Foot

According to the results of autopsy, the foot in *M. galloprovincialis* with a size of 72.0 ± 3.5 mm is usually small with a length of 5.0 ± 0.2 mm, width 3.0 ± 0.2 mm; however, due to its well-developed musculature, it can significantly change its size and, during the secretion of byssal threads, can stretch, increasing in length by 2.0–2.5 times relative to the initial foot size. As a rule, the foot has the shape of a tongue, is adapted for moving on a solid substrate; it is well pigmented and has a brown color. A system of muscular retractors is introduced into the foot tissue; they are connected to the byssal apparatus, due to which the mussel can control the tension of byssal threads and thereby reduce the wave effect on its organism (Fig. 4). A scheme of muscular attachment system, which includes a pair of anterior byssal retractors, a pair of byssal retractors, and a group of muscles consisting of four pairs of posterior byssal retractors of the foot, is presented in Fig. 4. The foot also functions as a pump, which pumps out all the secretions of the glands through the duct openings into the byssal groove of the foot during the contraction of its muscles, where they are mixed by numerous cilia (Figs. 6*M*–6*O*).

According to the results of SEM, the byssal groove of the foot in *M. galloprovincialis* is located on the ventral side of the mussel foot and extends along its central axis, approaching by its length to the foot length (Figs. 6*A*–6*C*). According to the SEM data, the foot length in *M. galloprovincialis* mussel is 13.0–13.5 mm. The length of byssal groove of the foot is 7.0–9.0 mm (Fig. 6*A*). The foot width in the central part is 3.7–4.0 mm (Figs. 6*A* and 6*B*). By appearance, byssal groove of the foot resembles a V-shaped groove covered by the folds on the side walls and on the bottom (Figs. 6*A*–6*L*). The results of SEM demonstrated that the distal end of byssal groove of the foot has no distal fossa, where the attachment disk of the byssal thread is formed (Fig. 6*C*). As a rule, the byssal groove of the foot along its entire length is not deep not wide (Fig. 6*A*). The byssal groove of the foot widen towards the proximal end and becomes deeper (Figs. 6*A* and 6*D*). At the distal end, the depth and width of byssal groove of the foot are 92.0–112.0 and 123.6–226.5 μm, respectively (Figs. 6*B* and 6*C*). In the central part, the depth and width of byssal groove of the foot are 109.0–114.0 and 228.0–236.6 μm, respectively (Fig. 6*E*). In the proximal part, the depth and width of byssal groove of the foot are 415.0–500.0 and 700.0–865.0 μm, respectively, sometimes reaching a width of even more than 1 mm (Fig. 6*D*). The folds of the walls of byssal groove of the foot are almost parallel to each other (Figs. 6*A*–6*E*). In the proximal part of byssal groove of the foot, the width of the wall folds is 34.0–58.0 μm, the width of the folds on the bottom is 43.0–58.0 μm (Figs. 6*D* and 6*G*). In the central part of byssal groove of the foot, the width of the wall folds is 50.0–67.0 μm, the width of the folds on the bottom is 35.0–55.0 μm (Figs. 6*E*, 6*H*, and 6*K*). In the distal part of byssal groove of the foot, the width of the wall folds is 87.0–130.0 μm, the width of the folds on the bottom is 90.0–103.0 μm (Figs. 6*C*, 6*F*, and 6*L*). The surface of the walls and bottom of byssal groove of the foot along its entire length is covered by clearly visible openings of the ducts of the foot glands (Figs. 6*F*, 6*G*, 6*I*–6*O*). At high magnification, it is seen that the surface of the walls and bottom of byssal groove of the foot in the proximal, central, and distal parts is covered by numerous club-shaped cilia of approximately the same length of 2.1–2.8 μm and thickness of 0.25–0.38 μm (Figs. 6*F*, 6*G*, 6*I*–6*O*).

DISCUSSION

In *M. galloprovincialis*, the shell growth and shape vary and depend largely on the environment (Elliott et al., 2008; Peharda et al., 2024), which is also typical for other representatives of the family Mytilidae (Seed, 1968, 1972, 1974; Selin and Vekhova, 2002; Vekhova, 2013). It is considered that in *M. galloprovincialis*, the presence of a border of the outer prismatic layer running along the inner edge of the shell valves to the ligament (at the same time, the imprints of posterior muscles of retractors are deflected from the border) (Fig. 1*B*), as well as the presence of numerous pores on the valve nymph (Fig. 1*D*), can be considered as typical and stable morphological species traits (Ivanova and Lutaenko, 1998; Zolotarev and Shurova, 1997). According to Zolotarev and Shurova (1997), in *M. galloprovincialis*, there is always a layer of the middle pearl layer between the prismatic border and imprints of the posterior retractors. It is also important to add that according to the personal report of O.A. Skarlato and data presented in this work, the presence of

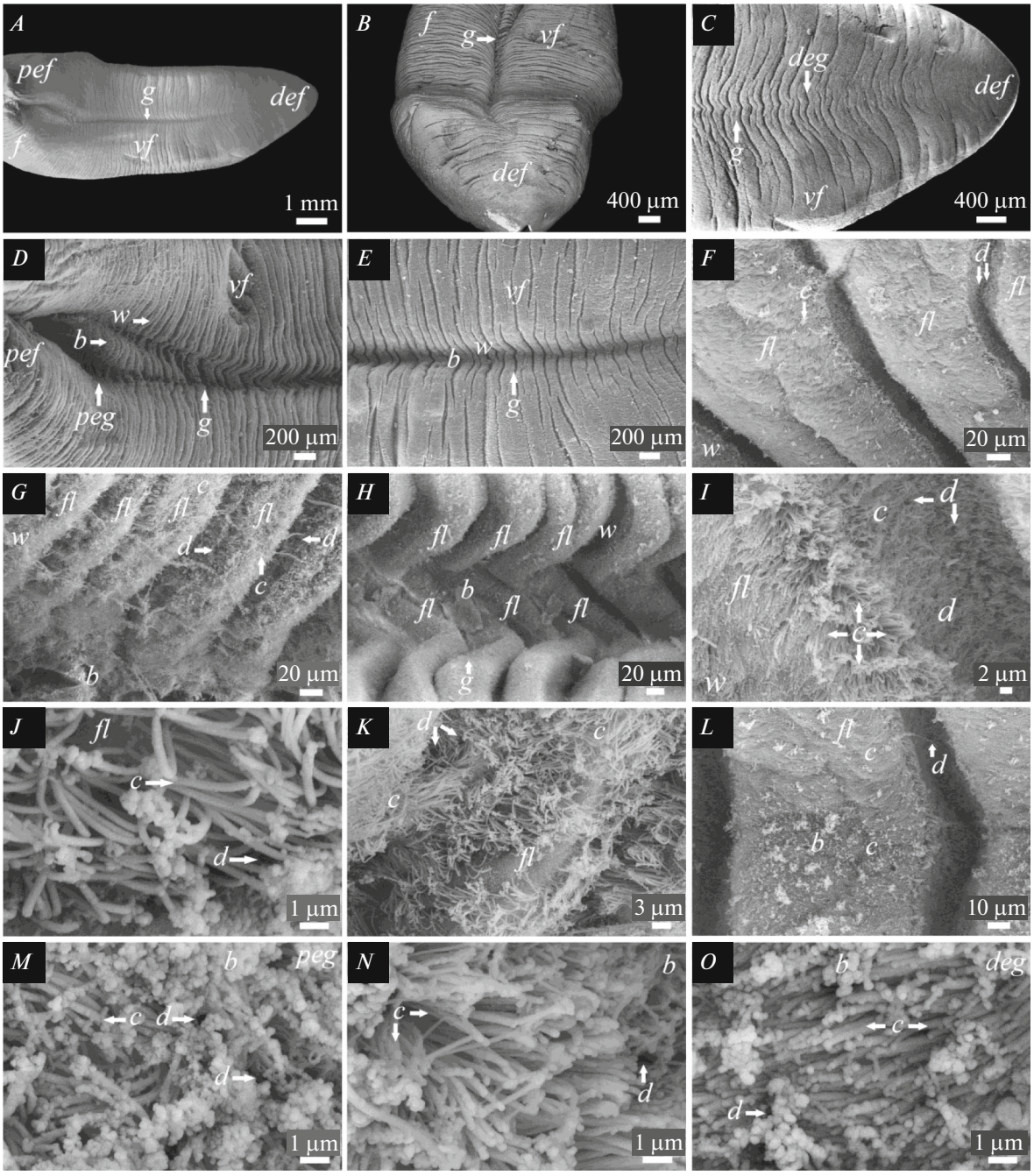

Fig. 6. Morphological structure of byssal groove of the foot in the Mediterranean mussel (*Mytilus galloprovincialis*) from the Zhitkov Bay of the Sea of Japan (SEM): *A*, ventral surface of the foot and byssal groove of the foot, general top view; *B*, distal end of the foot, frontal view; *C*, distal end of the foot and byssal groove of the foot, top view; *D*, byssal groove of the foot in the proximal part, top view; *E*, byssal groove of the foot in the central part, top view; *F*, surface of the wall of byssal groove of the foot at the distal end; *G*, surface of the wall of byssal groove of the foot at the proximal end; *H*, byssal groove of the foot in the central part, magnification; *I*, surface of the wall of byssal groove at the distal end, magnification; *J*, enlarged fragment of the wall of byssal groove of the foot on proximal end; *K*, enlarged fragment of the wall of byssal groove in the central part; *L*, the bottom of byssal groove of the foot at the distal end; *M*, enlarged fragment of the bottom of byssal groove of the foot in the proximal part; *N*, enlarged fragment of the bottom of byssal groove of the foot in the central part; *O*, enlarged fragment of the bottom of byssal groove of the foot at the distal end; *f*, foot; *vf*, ventral surface of the foot; *pef*, proximal end of the foot; *def*, distal end of the foot; *g*, byssal groove of the foot; *peg*, proximal end of byssal groove of the foot; *deg*, distal end of byssal groove of the foot; *w*, wall of the byssal groove of the foot; *fl*, folds of byssal groove of the foot; *b*, bottom of byssal groove of the foot; *c*, cilia; *d*, openings of the gland ducts in the walls and bottom of the distal end of byssal groove of the foot.

numerous dotted imprints of the mantle muscles on the inner surface of the shell valves at the back and at the site of its bending place is a characteristic distinguishing feature, which allows us to identify *M. galloprovincialis* (Figs. 1*B* and 1*C*). According to the literary data (Verdulin, 1979; Beaumont et al., 1989; Koehn, 1991; McDonald et al., 1991; Kepel' and Ozolin'sh, 1992; Zolotarev and Shurova, 1997), there are a number of other morphological traits that allow us to determine similar species of bivalves of the *Mytilus* genus complex: *M. galloprovincialis*, *M. trossulus*, and *M. edulis*. As already mentioned above, the nature of the border (emergence of the outer prismatic layer of the shell on its inner surface) is one of such distinct diagnostic features. According to Zolotarev and Shurova (1997), in another similar species (*M. trossulus*), the outer prismatic layer is continuous along the entire length in the dorsal part of the shell valves and extends to the umbo, as well as extends deep into it. In *M. edulis*, the border of the outer prismatic layer runs along the inner surface of the shell margin and is interrupted in its dorsal part, reaching only the ligament; at the same time, the imprint of the posterior retractor is indistinctly separated from the border (Zolotarev and Shurova, 1997). According to Buyanovsky (2000, 2002), the presence of pigmented radial rays when studying the shell in transmitted light is a characteristic distinguishing feature, which allows us to determine this species; sometimes the rays are clearly visible without light. The distance from the anterior end of the posterior retractor imprint to the outer prismatic layer is one more reliable trait of difference between these species; it has a maximum value in *M. galloprovincialis*, while the posterior retractor imprint in *M. trossulus* comes closely to the prismatic border, and the distance between them has a minimal value (Zolotarev and Shurova, 1997). Based on multivariate morphometric analysis, it was detected (Kepel' and Ozolin'sh, 1992) that *M. galloprovincialis* has a relatively higher and wider shell and more elongated imprints of the posterior retractor and adductor than another similar species (*M. edulis*). Only using the methods of multivariate analysis, it was possible to detect the most important traits for species identification that included the length of the anterior adductor imprint and width of the hinge plate that have a maximal value in *M. galloprovincialis* (Koehn, 1991; McDonald et al., 1991). There are a number of earlier works devoted to morphological differences between *M. edulis* and *M. galloprovincialis* (Verdulin, 1979; Beaumont et al., 1989); however, due to variability in the mussel shell shape under different environmental conditions (Seed, 1968, 1972, 1974), no significant morphological traits that allow to diagnose confidently similar species of this genus were found.

The results demonstrated that *M. galloprovincialis* has a structure of the byssus apparatus typical for Mytilidae (Figs. 3 and 4), which is completely consistent with the literature data (Brown, 1952; Tamarin and Keller, 1972; Bairati and Vitellaro-Zuccarello, 1974; Allen et al., 1976; Price, 1983; Berger et al., 1985; Eckroat and Steel, 1993; Carrington and Gosline, 2004; Vekhova, 2007, 2019, 2021). The byssus is a root deeply embedded in the tissues of stem gland or byssus gland located in the proximal part of the mussel foot. The byssus stem extends from the root outward through the byssal gape. The byssal stem is surrounded on all sides by the byssal cuffs that give rise to the proximal ends of the byssal threads. The byssal threads extend from the stem in the anteroposterior direction (Figs. 3 and 4). At the distal ends, the byssal threads terminate with oval-shaped attachment disks with the size 2.5 ± 0.4 mm with semitransparent edges typical for only *M. galloprovincialis* (Figs. 3 and 5*B*).

According to the results of scanning electron microscopy that we obtained, (1) a proximal part of the byssal thread has a very elastic, corrugated structure, which causes the extensibility of byssal threads, which smooths out the wave effect on the mussels (Figs. 5*A*, 5*D*, 5*G*, and 5*J*), while the distal part of the byssal thread is straight and elastic (Figs. 5*B*, 5*E*, 5*H*, and 5*K*), which corresponds in general to the literature data (Brown, 1952; Tamarin and Keller, 1972; Bairati and Vitellaro-Zuccarello, 1974; Tamarin, 1975; Allen et al., 1976; Berger et al., 1985; Eckroat and Steel, 1993; Vekhova, 2007, 2019, 2021); (2) the surface of the byssus thread along its entire length has a tuberous structure (Figs. 5*A*, 5*E*, 5*F*, 5*H*, 5*J*, and 5*K*), which is typical only for this species of Mytilidae. The structure of each byssus thread in *M. galloprovincialis* has a natural block copolymer structure (Qin and Waite, 1995; Coyne et al., 1997; Silverman and Roberto, 2007). The presence of byssus prepolymerized collagens (pre-collagen) of two different gradations differing in the distal and proximal parts of the byssus thread is typical for this structure: pre-collagen D with a silk central domain in the distal part of the byssus thread and pre-collagen P with elastic central domain in the proximal part. Glycine-rich pre-collagen NG is the third type of byssal thread collagen; it is evenly distributed along the entire length of the byssal thread and covers it from all sides (Qin and Waite, 1998; Waite et al., 1998; Lucas et al., 2002; Lee et al., 2011). According to Lucas et al. (2002), the presence of additional histidine amino acid residues in the central domains of all three types of byssal thread collagen is typical only for *M. galloprovincialis*.

The results of SEM demonstrated that in *M.* galloprovincialis, the external surface of the attachment disk has a tuberous surface (Fig. 5*F*), while its bottom

surface is smooth (Figs. 5*I* and 5*L*). On the outer surface of the attachment disk, two reinforcing cords are clearly distinguishable in *M. galloprovincialis* (Figs. 5*B* and 5*C*); they extend along its surface in the anterior and posterior directions, which is quite consistent with previous literature data (Vekhova, 2007, 2019, 2021). For all studied Mytilidae, the presence of the anterior strong cord extending forward to the edge of the attachment disk is necessary. According to Vekhova (2007, 2019, 2021), the presence of different number of reinforcing cords on the external surface of the attachment disks is typical for all studied species of Mytilidae. Thus, *M. trossulus* has a single anterior and two lateral reinforcing cords on the external surface of the attachment disk; the Korean mussel (*Mytilus coruscus* Gould, 1861) has up to six of them; the Gray's mussel (*Crenomytilus grayanus* (Dunker, 1853)) and the northern horsemussel (*Modiolus modiolus* (Linnaeus, 1758)) have no more than four of them; this indicates different adaptations of these species of Mytilidae to an attached lifestyle in habitats with different wave activity (Selin and Vekhova, 2002; Vekhova, 2013, 2019, 2021). According to the results of SEM, the byssal thread attachment disk in *M. galloprovincialis* has a reticular matrix (Fig. 5*I*), which is completely consistent with the literature data (see below) (Benedict and Waite, 1986; Lee et al., 2011). According to Lee et al. (2011), the attachment disk of the California mussel (*Mytilus californianus* Conrad, 1837) has a porosity of about 40% and a noticeable gradient of the pore diameter: their diameter is only 0.2 μm near the substrate and almost 3 μm where the byssal thread passes from the distal part into the attachment disk (transition zone 2). According to our data, the pore diameter in the mussel *M. galloprovincialis* near the bottom surface of the attachment disk is 1.1–5.3 μm (Fig. 5*L*), which significantly exceeds the pore diameter in *M. californianus*. In the latter species, the pores are open and are connected to each other by channels with smooth walls that are filled with a liquid substance in a natural state.

Each part of the byssal apparatus provides a strong attachment of the mussel to the substrate. It is especially important to know the structure of the byssal thread attachment disk, since namely the bottom surface of the attachment disk forms the interfacial region between its proteins and foreign substrate surface at a distance of 0.5 nm, which provides their adhesive bonding with a strength of 5 Å in a humid marine environment (Waite, 1983, 1997, 1999). At present, it is known (Lee et al., 2011) that there are 5 different polyphenolic mussel foot proteins (mfps) in the attachment disks of byssal threads of the genus *Mytilus*: mfp-2, mfp-3, mfp-4, mfp-5, and mfp-6. Among them, there are only 3 unique proteins responsible for the attachment of mussels to the substrate (mussel foot proteins mfp-3, mfp-5, and mfp-6). It is considered that mfp-3 and mfp-5 proteins represent the main adhesive glue, which interacts with the substrate surface. The mfp-3 and mfp-5 proteins interact only with each other. Mfp-6 protein mediates the association between mpf-2 and mfp-3 proteins. Mfp-2 makes up the reticular matrix of each attachment disk. One more polyphenolic protein of the mussel foot (mfp-1) is a key protein in the cuticle of byssal threads and byssus in general. Each attachment disk is completely covered with a cuticle made of mfp-1 protein and Fe^{3+} ions. The mussel foot polyphenol protein mfp-4 can mediate connections between prepolymerized collagen fibers extending from the byssal thread matrix to other proteins of the attachment disk. These and previous results clearly demonstrated that reinforcing cords on the external surface of the attachment disk and longitudinal cords running along the distal and proximal parts of byssal threads of the studied species of Mytilidae are NG precollagen fibers that strengthen the structure of the attachment disks in Mytilidae, which is consistent with literature data (Silverman and Roberto, 2007). According to the literary data (Waite, 1995; Silverman and Roberto, 2007; Lee et al., 2011), it is known that all polyphenolic proteins of mussel foot contain a large amount of 3,4-dihydroxyphenylalanine (L-DOPA) amino acid, which is oxidized to quinone under the effect of molecular oxygen.

Our results of SEM demonstrated that byssal groove of the foot in *M. galloprovincialis* is arranged more primitively than in other studied species of Mytilidae from the Sea of Japan (Vekhova, 2021, 2022). Thus, there is no distal fossa in the distal end of byssal groove of the foot (Figs. 6*A*–6*C*), where the attachment disk of the byssal thread, as is known, is formed in Mytilidae (Allen et al., 1976; Tamarin et al., 1976; Berger et al., 1985). In another studied species (*M. trossulus*), there is a narrow distal fossa with a longitudinal length along the longitudinal axis of byssal thread of 3.75–5.0 μm and transverse length of 180.0–200.0 μm at the distal end of byssal groove of the foot (Vekhova, 2021). According to Vekhova (2022), a large cup-shaped distal fossa with a longitudinal length of 128.0–138.0 μm and transverse length of 250.0–270.0 μm was found in *M. coruscus* at the distal end of byssal groove of the foot; in *C. grayanus*, this fossa is crescent-shaped with a longitudinal length of 30.0–50.0 μm and transverse length of 300.0–400.0 μm; in *M. modiolus*, it is slit-shaped with a longitudinal length of 8.5–10.0 μm and transverse length of 165.0–183.0 μm. A primitive structure of byssal groove of the foot in *M. galloprovincialis* is also indicated by the fact that among the studied species of Mytilidae, this species has the narrowest and shallowest bys-

sal groove of the foot (Figs. 6*A*–6*C*), which reaches just over 1 mm in its widest proximal part (Figs. 6*D*, 6*E*, and 6*H*). According to our data obtained in different years (Vekhova, 2021, 2022), the widest and deepest byssal groove of the foot with longitudinal powerful closing folds along its length is typical for *M. coruscus*, while closing folds are completely absent in *M. galloprovincialis*, *M. trossulus*, *C. grayanus*, and *M. modiolus*, and the width and depth of byssal groove of the foot in its central part in all studied species of Mytilidae are, respectively, 750.0–875.0 and 233.0–275.0 μm in the first species, 228.0–236.6 and 109.0–114.0 μm in the second species, 286.0–300.0 and 70.0–250.0 μm in the third species, 300.0–320.0 and 262.0–343.0 μm in the fourth species, 300.0–375.0 and 115.0–180.0 μm in the fifth species. Our results of SEM demonstrated that in *M. galloprovincialis*, the entire surface of the walls and bottom of the gutter-shaped byssal groove of the foot is densely covered with cilia with a length of 2.1–2.8 μm and thickness 0.25–0.38 μm (Figs. 6*F*, 6*G*, 6*I*, 6*J*–6*O*) that mix all secretions coming from the opening of the foot gland ducts during its contraction, which is completely consistent with the literature data (Allen et al., 1976; Berger et al., 1985; Vekhova, 2021, 2022).

The results of our study clearly demonstrated that the peculiarities of the structure of byssal groove of the foot in *M. galloprovincialis* are reflected in the peculiarities of morphological structure of byssal threads and their size. According to our data, the length of byssal threads in this mussel species is 14.5–19.1 mm, the width of byssal thread in the distal part is 0.039–0.053 mm; in the proximal part, 0.066–0.0985 mm, which is completely consistent with the literature data (Carrington and Gosline, 2004). According to the literature data (Carrington and Gosline, 2004), among the studied species of Mytilidae, *M. galloprovincialis* is characterized by the thinnest and weakest byssal threads, the strength of which is only 3 Newtons (N), while in *M. trossulus* this index is 12 N. According to our data, the attachment disk size in *M. galloprovincialis* with a shell length of 72.0 ± 3.5 mm varies and is 2.5 ± 0.4 mm. The literary data (Allen et al., 1976; Berger et al., 1985; Vekhova, 2019) indicate that in other representatives of bivalve mollusks of the family Mytilidae (such as *M. edulis*, *M. coruscus*, *C. grayanus*, and *M. modiolus*), the size of the attachment disks depends on the shell length; in the last three species, on the body size and weight and, as a rule, increases during ontogenesis. Such a wide range of variation in the size of the attachment disk of byssal threads in *M. galloprovincialis* is explained by the absence of distal fossa at the distal end of byssal groove of the mussel foot (Fig. 6*C*). Apparently, the secretions of mucoid glandular cells (secreting acidic sulfated mucopolysaccharides) and phenol gland (secreting polyphenolic proteins rich in L-DOPA amino acid) enter the distal end of the byssal groove through the ducts. In other studied species of Mytilidae, distal fossa is located at the distal end of the byssal groove, where the attachment disk is formed (Allen et al., 1976; Tamarin et al., 1976; Berger et al., 1985; Vekhova, 2021, 2022). In *M. galloprovincialis*, the secretions of these glands come in different quantities, which significantly affects the structural peculiarities of the attachment disk, namely, the presence of semitransparent edges of the attachment disks typical only for this species of Mytilidae (Fig. 3*B*) and their different size. These data are consistent with data of Pujol (1967), who demonstrated based on histochemical analysis that the attachment disks of the byssal threads in *M. edulis* consist of a mixture of mucoproteins with the prevalence of acidic sulfated mucopolysaccharides.

Thus, this and previous articles (Selin and Vekhova, 2002; Vekhova, 2007, 2019, 2021, 2022) clearly demonstrate that despite a sessile lifestyle, Mytilidae possess an extremely developed byssus, which is formed again throughout life as a result of the secretory activity of foot glands in their differently structured byssal grooves. Differences in the byssal groove structure between species are manifested in its size, presence or absence of distal fossa, as well as closing folds. All of this contributes to a successful colonization of artificial solid facilities, rocks, boulders, silt, and sand by mussels in the surf marine coastal zone. In general, this evolutionarily led to a wide distribution of bivalves of the Mytilidae family in their marine environment.

CONCLUSIONS

In *M. galloprovincialis*, byssal groove of the foot is smaller in size and more primitively structured than in other studied species of Mytilidae (Vekhova, 2021, 2022). The distal fossa is absent at the distal end of the foot; therefore, the attachment disks have peculiarities: variable diameter, semitransparent edges, and the presence of a small number of weakly expressed reinforcing cords on the disk surface strengthening the structure. Thin byssal threads with a tuberous surface are formed in narrow and shallow byssal groove of the foot. In the foot groove, all glandular secretions are mixed by numerous club-shaped cilia lining its walls and bottom. Thus, in *M. galloprovincialis*, the formation of byssal threads in the foot byssal groove occurs according to the principle of biopolymer mold-inljection followed by quinone auto-tanning (Price, 1983; Waite, 1992, 1995, 1999; Lee et al., 2011).

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

The experiments with animals were conducted in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals. Animal protocols were approved by the Biomedical Ethics Committee of the Zhirmunsky National Scientific Center of Marine Biology, Far East Branch, Russian Academy of Sciences, Vladivostok, Russia (registration number no. 3, dated April 22, 2025).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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