Invertebrate Zoology, 2025, 22(4): 565–574

First record of the cestode *Trilocularia acanthiaevulgaris* (Phyllobothriidea) in the piked dogfish *Squalus acanthias* (Elasmobranchii: Squaliformes) from the White Sea: morphological and molecular evidence

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ABSTRACT: The piked dogfish *Squalus acanthias* is a pelagic shark rarely found in the White Sea, where its biology and parasitic fauna remain largely unexplored. This study presents the first documented record of the hyperapolytic cestode *Trilocularia acanthiaevulgaris* in the White Sea population of piked dogfish. A detailed morphological description of free proglottids is provided, including novel data on their surface morphology based on the distribution and structure of microtriches. Phylogenetic analysis of SSU and LSU rDNA sequences confirmed the species identity of the cestode, showing a close affinity with previously described *T. acanthiaevulgaris* isolate. These findings expand current knowledge on shark cestode diversity in the White Sea and emphasize the need for further research on elasmobranch parasites in this geographic region.
How to cite this article: Shchenkov S.V., Denisova S.A., Gorodilova E.Yu., Sokolov S.G. 2025. First record of the cestode *Trilocularia acanthiaevulgaris* (Phyllobothriidea) in the piked dogfish *Squalus acanthias* (Elasmobranchii: Squaliformes) from the White Sea: morphological and molecular evidence // Invert. Zool. Vol.22. No.4. P.565–574. doi: 10.15298/invertzool.22.4.04

KEY WORDS: tapeworms, elasmobranchs, SEM, SSU, LSU, phylogeny.

Первая находка цестоды *Trilocularia acanthiaevulgaris* (Phyllobothriidea) в короткоперой колючей акуле *Squalus acanthias* (Elasmobranchii: Squaliformes) из Белого моря: морфологические и молекулярные данные

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РЕЗЮМЕ: *Squalus acanthias* — пелагический вид акул, крайне редкий для Белого моря, где его биология и паразитофауна остаются неизученными. Это исследование посвящено первой находке гипераполитической цестоды *Trilocularia acanthiaevulgaris* в катране (колючей акуле) из Белого моря. Представлено подробное морфологическое описание свободных проглоттид, получены данные о структуре и распределении микротрихий их тегумента. Молекулярно-филогенетический анализ последовательностей генов SSU и LSU рДНК подтвердил видовую принадлежность цестоды, продемонстрировав тесную связь с ранее обнаруженным изолятом *T. acanthiaevulgaris*. Это исследование дополняет данные о цестодах акул Белого моря и подчеркивает необходимость дальнейших исследований паразитов пластиножаберных рыб в его акватории.
Как цитировать эту статью: Shchenkov S.V., Denisova S.A., Gorodilova E.Yu., Sokolov S.G. 2025. First record of the cestode *Trilocularia acanthiaevulgaris* (Phyllobothriidea) in the piked dogfish *Squalus acanthias* (Elasmobranchii: Squaliformes) from the White Sea: morphological and molecular evidence // Invert. Zool. Vol.22 No.4. P.565–574. doi: 10.15298/invertzool.22.4.04

КЛЮЧЕВЫЕ СЛОВА: ленточные черви, пластинчатожаберные, SEM, SSU, LSU, филогения.

Introduction

The piked dogfish, *Squalus acanthias* Linnaeus, 1758, is a species of pelagic shark with a wide range, including the marine waters of the Northern and Southern Hemispheres, with the exception of the North Pacific (Ebert *et al*., 2010). This species of shark has been sporadically recorded in the White Sea, as confirmed by personal reports from fishermen and rare data from catalogues (Andriashev, 1954; Parin *et al*., 2014). The only museum specimen of *S. acanthias*, caught in 1980 in the Chupa Inlet of the Kandalaksha Gulf of the White Sea, is kept in the educational collection of the Department of Ichthyology and Hydrobiology at St. Petersburg State University (SPbU). The biology and parasites of the piked dogfish have not been studied in the White Sea.

Shark parasites are of great interest to researchers worldwide. The taxonomy of the cestodes of these fishes has been repeatedly revised at the level of high-ranking taxa. According to modern views, elasmobranchs serve as hosts for cestodes of the orders Cathetocephalidea, Diphyllidea, Lecanicephalidea, Litobothriidea, Onchoproteocephalidea, Phyllobothriidea, Rhinebothriidea, Trypanorhyncha, and the paraphyletic group of "Tetraphyllidea" relics, whose taxonomic composition requires revision (Healy *et al*., 2009; Caira *et al*., 2014, 2017). To date, only three identified species of cestodes of elasmobranchs have been found in the White Sea: *Pseudanthobothrium hanseni* Baer, 1956 (Rhinebothriidea), *Rockacestus piriei* (Williams, 1968) and *Clistobothrium* sp. (Phyllobothriidea) (Gordeev, Polyakova, 2020; Sokolov *et al*., 2024; Logvinenko *et al*., 2025).

The hyperapolytic cestode *Trilocularia acanthiaevulgaris* Olsson, 1867 (= *Trilocularia gracilis* Olsson, 1869 and *Urogonoporus armatus* Lühe, 1902) is a host-specific parasite of *Squalus* spp. (Euzet, 1952; Zhukov, 1960; Pickering, Caira, 2013) recorded from these sharks in various ocean locations (e.g., Zhukov, 1960; Alexander, 1963; Threlfall, 1969; Orlowska, 1979). The correct scientific name for this parasite has been the subject of long debate (e.g., Euzet, 1952; Ruhnke, 2011). We adhere to the name *T. acanthiaevulgaris* supported by Euzet (1952, 1994). To date, data on the morphology, including electron microscopy observations, and molecular phylogeny of *T. acanthiaevulgaris* have been obtained (e.g., Olsson, 1867; Euzet, 1952; Rees, 1953; McCullough, Fairweather, 1983, 1984; Pickering, Caira, 2013; Caira *et al*., 2014, 2021; Ruhnke *et al*., 2017). However, this species has not yet been recorded in the marine

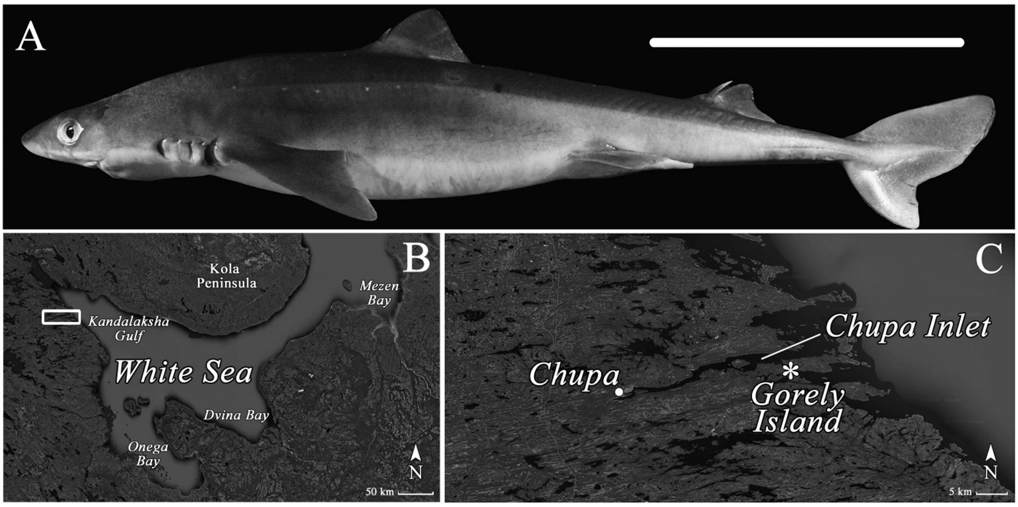

Fig. 1. A — *Squalus acanthias* — a definitive host of *Trilocularia acanthiaevulgaris* in the White Sea; B–C — a collection point near the Gorely Island in Chupa Inlet of the White Sea.
Scale bar 20 cm.

waters of the Russian Arctic. In this paper, we present the first record of *T. acanthiaevulgaris* in the White Sea piked dogfish, supported by morphological and molecular phylogenetic data.

Material and methods

A specimen of the piked dogfish was caught off the coast of Gorely Island in the Chupa Inlet of the White Sea (Fig. 1A–C) on September 17, 2024. Its digestive tract was examined for the presence of parasites using an MBS-10 (LOMO) stereomicroscope (Bychovskaja-Pavlovskaja, 1985) at the Educational and Research Station "Belomorskaia" of SPbU. Ten free mature and gravid proglottids found in the spiral valve and small intestine were collected in Petri dishes with physiological saline (0.9% sodium chloride) and then fixed in 70% ethanol for morphological examination and DNA extraction. Scolices with immature proglottids were not found.

For total preparations, parasites were stained with acetic acid carmine, dehydrated in a graded ethanol series, cleared in dimethyl phthalate, and embedded in Canada balsam (Bychovskaja-Pavlovskaja, 1985). Mounts of proglottids were observed using an Olympus BX-53 light microscope (Olympus Soft Imaging Solutions, Hamburg, Germany) at the Core Facility of the Karelian Research Centre of the Russian Academy of Sciences. The drawings were made using a camera Lucida. The whole mount is deposited in the Parasitological Collection of the Department of Invertebrate Zoology at SPbU under the No Tr_ac_1.1_151.

To study the tegumental surface of free proglottids using scanning electron microscopy (SEM) (e.g., Mccullough, Fairweather, 1983), five specimens were dehydrated in a graded ethanol series (from 70 to 96%) and ethanol–acetone mixtures. Samples were then transferred to pure acetone, critical point dried using a Leica EM CPD300 (Leica Microsystems), and coated with platinum to a thickness of 20 nm in a Jeol JEE-420D (JEOL Ltd.). Electron micrographs were obtained using a VolumeScope2 (Thermo Scientific™) scanning electron microscope at the Research Park of SPbU (Centre for Molecular and Cell Technologies). Images were processed using Adobe Photoshop CS5 (Adobe Inc.).

Total DNA was isolated from three proglottids using Proteinase K solution and Chelex-100. The partial sequence of the SSU rDNA was amplified with WormA and WormB primers according to Waeschenbach *et al.* (2007). PCR parameters were as follows: initial denaturation at 95 °C for 3 min; denaturation at 95 °C for 20 sec; annealing at 50.1 °C for 20 sec; extension at 72 °C for 2 min; final extension at 72 °C for 5 min; 35 cycles. Partial sequences of the LSU rRNA gene were amplified with LSU5 and 1500R primers (Littlewood *et al.*, 2000; Tkach *et al.*, 2003) under the following PCR parameters: initial denaturation at 95 °C for 3 min; denaturation at 95 °C for 20 sec; annealing at 56 °C for 20 sec; extension at 72 °C for 1 min 20 sec; final extension at 72 °C for 5 min; 35 cycles. All amplicons were sequenced at the Research Park of SPbU (Centre for Molecular and Cell Technologies). Both forward and reverse sequences were assembled into contigs using Chromas Pro v. 1.7.4 (Technelysium Pty Ltd). Partial sequences of the LSU rRNA gene were used for primary molecular species identifica-

Table 1. List of species, incorporated into molecular phylogenetic analysis.

Species	SSU	LSU	Host	Locality	Reference
Calliobothrium cf. *verticillatum*	KF685812	KF685753	*Mustelus canis* (Triakidae, Selachii)	USA: Old Lyme, Connecticut	Caira *et al*., 2014
Calliobothrium violae	KF685813	KF685881			
Crossobothrium laciniatum	KF685824	KF685883	*Hexanchus griseus* (Hexanchidae, Selachii)	Chile: Pacific Ocean, Puerto Montt	
Crossobothrium cf. *dohrnii*	KF685847	KF685759	*Heptranchias perlo* (Hexanchidae, Selachii)	Gulf of Mexico	
Clistobothrium montaukensis	AF286996	EF095259	*Isurus oxyrinchus* (Lamnidae, Selachii)	USA: Montauk, New York, Atlantic Ocean	Olson *et al*., 2001 / Waeschenbach *et al*., 2007
Ruhnkebothrium mattisi	KF685814	KF685889	*Sphyrna lewini* (Sphyrnidae, Selachii)	USA: Straits of Florida, Florida	Caira *et al*., 2014
Phyllobothrium cf. *lactuca*	KF685845	KF685770	*Mustelus mento* (Triakidae, Selachii)	Not specified	
Yamaguticestos cf. *squali*	KF685846	KF685897	*Squalus acanthias* (Squalidae, Selachii)	USA: Rhode Island	
Calyptrobothrium sp. 1	KF685848	KF685754	*Torpedo nobiliana* (Torpedinidae, Batoidea)		
Orygmatobothrium cf. *musteli*	KF685815	KF685768	*Mustelus mustelus* (Triakidae, Selachii)	Senegal: Mbour	
Chimaerocestos sp. 1	KF685827	KF685758	*Rhinochimaera pacifica* (Rhinochimaeridae, Chimaeroidea)	New Zealand: Chatham Rise	
Thysanocephalum crispum	KF685823	KF685902	*Galeocerdo cuvier* (Galeocerdonidae, Selachii)	USA: South Carolina	
Scyphophyllidium guariticus	KF685817	KF685888	*Paratrygon aiereba* (Potamotrygonidae, Batoidea)	Peru: Mouth of Rio Shilve, Madre de Dios	

Table 1 (continued).

Species	SSU	LSU	Host	Locality	Reference
Scyphophyllidium sp. 1	KF685821	KF685771	*Alopias pelagicus* (Alopiidae, Selachii)	Mexico: Santa Rosalia, Baja California Sur	Caira *et al*., 2014
Scyphophyllidium tyleri	KF685819	KF685890	*Chiloscyllium punctatum* (Hemiscillidae, Selachii)	Borneo: Mukah, Sarawak	
Scyphophyllidium prionacis	KF685818	KF685892	*Prionace glauca* (Carcharhinidae, Selachii)	USA: Montauk, New York	
Scyphophyllidium latipi	KF685853	KF685900	*Scoliodon macrorhynchos* (Carcharhinidae, Selachii)	Borneo: Mukah, Sarawak	
Scyphophyllidium exiguum	KF685822	KF685769	*Alopias vulpinus* (Alopiidae, Selachii)	USA: Montauk, New York	
Scyphophyllidium cf. *giganteum*	KF685854	KF685901	*Galeorhinus galeus* (Triakidae, Selachii)	New Zealand: Chatham Rise	
Trilocularia acanthiae-vulgaris (*T. gracilis*)	KF685855	KF685776	*Squalus acanthias* (Squalidae, Selachii)	USA: Rhode Island	
Trilocularia acanthiaevulgaris	PQ867140	PQ867141	*Squalus acanthias* (Squalidae, Selachii)	Russia: Chupa Inlet, White Sea	This study
Sanguilevator yearsleyi (OUTGROUP)	FJ177057	KF685762	*Lamiopsis temminckii* (Carcharhinidae, Selachii) / *Lamiopsis tephrodes* (Carcharhinidae, Selachii)	Malaysia / Borneo: Mukah, Sarawak	Healy *et al*., 2009 / Caira *et al*., 2014

tion with the standard BLAST algorithm against the GenBank NCBI "core nt" sequence collection using the "megablast" option. General alignments were first generated separately for SSU and LSU datasets using "MAFFT" algorithm (Katoh, Standley, 2013) and then concatenated in SeaView v. 5.0.5 (Gouy *et al.*, 2010). The final length of the concatenated alignment was 3470 bp. The list of sequences used in the molecular phylogenetic analysis is given in Table 1. The evolutionary model for the phylogenetic analysis was estimated using MrModeltest v. 2.4 (Nylander, 2004). The best-fitting model was GTR + G + I. Bayesian analysis was performed using MrBayes v. 3.2.7a on the CIPRES portal (Miller *et al.*, 2010) for 15,000,000 generations. Based on estimates from the built-in MrBayes tools, the first 25,000 generations were discarded for burn-in.

Results and Discussion

Free mature and gravid proglottids (n=2) are elongate, with a well-differentiated anterior attachment region (Fig. 2). The anterior attachment region is wider at the midlevel, noticeably narrowed anteriorly and moderately narrowed posteriorly, concave dorsally, and armed with numerous large spinitriches arranged in transverse rows. The total size of mature and gravid proglottids is 1148×287 μm and 2176×449 μm, respectively. The size of the anterior attachment region is 356×240 μm in mature and 429×267 μm in gravid proglottids. The testes are 18–19, oval to rounded, located in the anterior half of the main body; 42–63×40–66 μm in mature and 69–93×54–96 μm in gravid proglottids. The cirrus sac is claviform, located in the posterior part of the proglottid, and opens into the common ventral genital atrium; 81×46 μm and 156×54 μm in mature and gravid proglottids, respectively. The common genital pore is median, located near the posterior margin of the proglottid. The ovary is V-shaped, posttesticular, 189 μm long and 154 μm wide at the proximal end in the mature proglottid and 313 μm long and 492 μm wide in the gravid proglottid. The maximum width of the ovarian lobes is 63 μm in the mature and 93 μm in the gravid proglottids. The ovicapt is distinct, 7×22 μm in the mature and 18×31 μm in the gravid proglottids. The oviduct is postovarian. The Mehlis' gland is located at the level of the posterior margin of the ovary, 41×36 μm in the mature and 60×44 μm in the gravid proglottids. The vagina is thick-walled, located ventral to the cirrus sac, its subterminal portion surrounded by

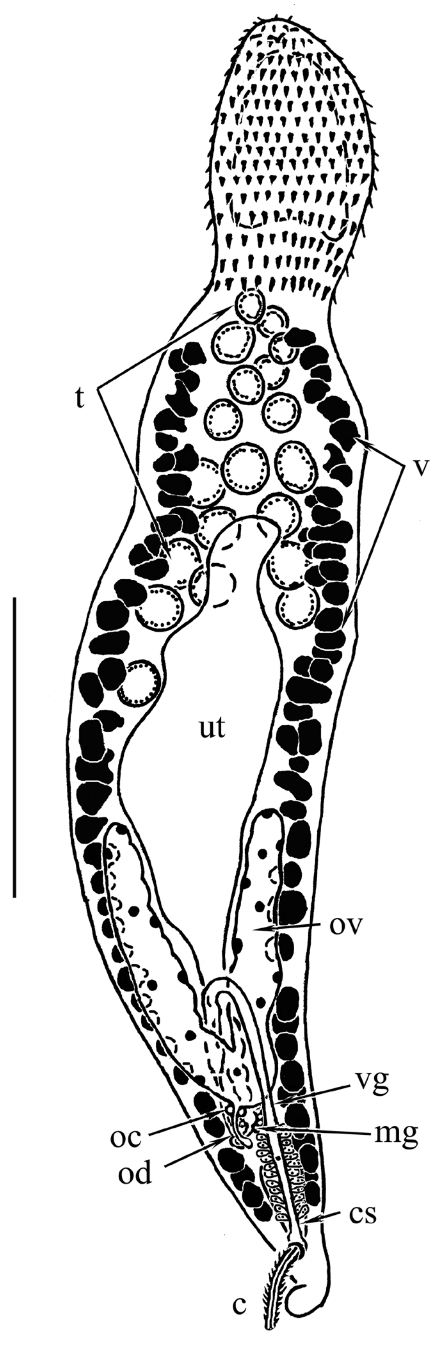

Fig. 2. Free gravid proglottid of *Trilocularia acanthiaevulgaris*, whole ventral view.
Abbreviations: c — everted cirrus; cs — cirrus sac; oc — ovicapt; od — oviduct; mg — Mehlis' gland; ov — ovary; t — testes; v — vitelline follicles; vg — vagina; ut — uterus. Scale bar 500 μm.

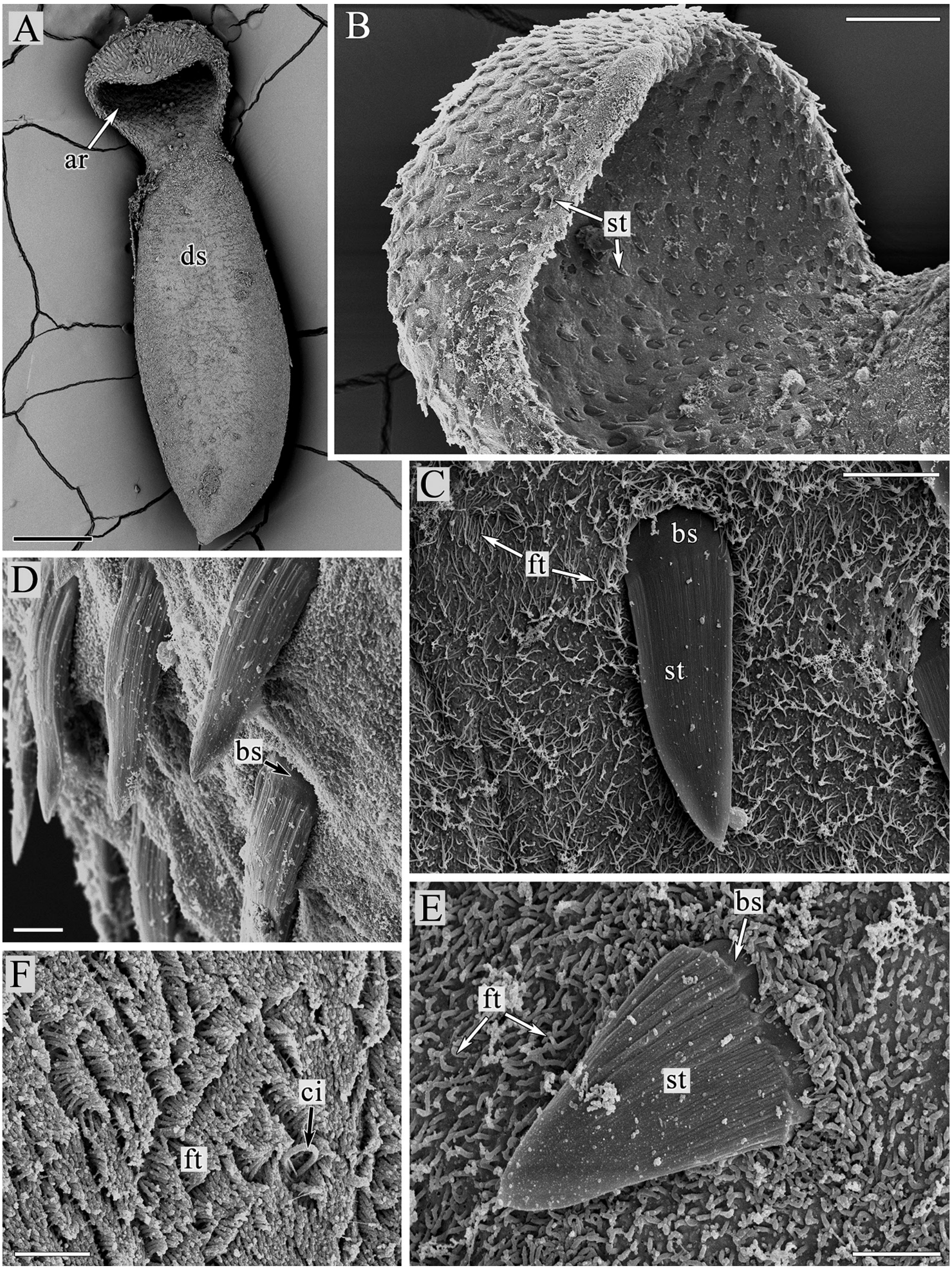

Fig. 3. Tegument morphology of free mature proglottids of *Trilocularia acanthiaevulgaris* (SEM). A — general view of the shortest proglottid examined; B — anterior attachment region; C — dorsal surface of the anterior attachment region; D — long spinitriches on the lateral surface of the anterior attachment region; E — microtriches in the proximal part of the anterior attachment region; F — filitriches on the posterior end of the proglottid.

Abbreviations: ar — anterior attachment region; bs — base of spinitriches; ci — sensory cilium; ds — dorsal surface of the proglottid; ft — filitriches; st — distal tip of spinitriches.

Scale bars: A — 100 µm; B — 50 µm; C, D — 5 µm; E, F — 2 µm.

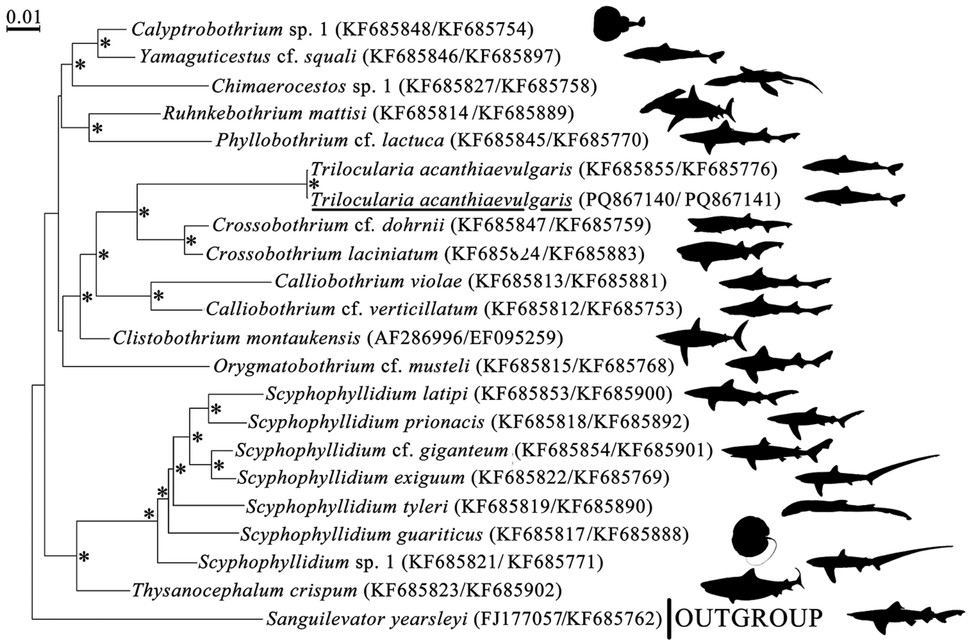

Fig. 4. Results of molecular phylogenetic analysis based on concatenated SSU rRNA and LSU rRNA gene sequences. Clades with Bayesian support more than 95% are marked with asterisk. Newly obtained sequences are underlined. GenBank NCBI numbers are given in brackets as SSU/LSU.

a dense mass of glandular cells; it opens into a common ventral genital atrium. The vitellarium is follicular; vitelline follicles are in two lateral fields, extending from just posterior to the level of the anterior testis to near the common genital pore, not interrupted by the ovary and not confluent. The uterus is median, sacculate, with (in the gravid proglottid) or without (in the mature proglottid) preoncospheres.

The length of free proglottids examined by SEM (n=5) ranged from 950 μm (Fig. 3A) to 2200 μm. The anterior attachment region has a deep dorsal concavity with a wide aperture. The anterior part of the attachment region is noticeably narrowed, measuring about 139 μm in width. The longest spinitriches (up to 15 μm) are located on the dorsal and lateral sides of the anterior attachment region (Fig. 3B–D); the size of spinitriches decreases posteriorly, and at the border of the attachment region their length does not exceed 3 μm (Fig. 3E). The spinitriches have a wide, smooth proximal base and a flattened, posteriorly-pointing distal tip with longitudinal furrows (Fig. 3C–E). The remaining tegumental surface does not bear spinitriches. Another type of microtriches is represented by small, thin filitriches, which are distributed over the entire surface of the proglottids (Fig. 3C–F). On the dorsal side of the anterior attachment region, the filitriches are about 1.17 μm long (Fig. 3C); in other areas, the filitriches are shorter (about 0.45 μm) and more densely packed (Fig. 3E–F). In addition, we found a single sensory cilium on the lateral surface of the posterior end of the proglottid (Fig. 3F).

The sequences of LSU rDNA generated in this study are almost identical to each other (percentage of similarity is 99–100%). These sequences are also very similar to a single isolate of *T. acanthiaevulgaris* available in GenBank (under the synonymous name *T. gracilis*): 100% for the SSU rRNA and 99–100% for the LSU rRNA genes. Based on high similarity, only single sequences for each gene were used further. Phylogenetic analysis based on the concatenated alignment showed that the obtained sequences clustered with those of *T. acanthiaevulgaris* available in GenBank (Fig. 4). Together, they form a sister clade to the group of *Crossobothrium* spp. In turn, the clade formed by *T. acanthiaevulgaris* and *Crossobothrium* spp. is sister to the *Calliobothrium* spp. clade. The remaining cestodes included in the analysis have a more distant affinity to *T. acanthiaevulgaris*.

The internal morphology of the free proglottids we examined corresponds to that previously described for *T. acanthiaevulgaris* (Lühe, 1902; Euzet, 1952). Free proglottids of this species differ from those of the second congener, *Trilocularia eberti* Pickering et Caira, 2012, in the morphology of the anterior attachment region: rounded to subconical or lemon-shaped and concave dorsally vs triangular, with a deep ventral concavity formed by the ventrally curved lateral margins (Lühe, 1902; Euzet, 1952; Pickering, Caira, 2012; present data). The structure of the spinitriches of the studied specimens is fully consistent with the functional role of their anterior region, providing attachment to the host intestinal mucosa (Euzet, 1952; McCullough, Fairweather, 1983; Pickering, Caira, 2012). The revealed differences in the size of spinitriches are determined by the length of the distal tip, which has also been demonstrated for the gladiate spinitriches of *T. ebertii* (Pickering, Caira, 2012). Short filitriches we observed are also characteristic of the tegument of both *T. acanthiaevulgaris* and *T. ebertii* (Mccullough, Fairweather, 1983; Pickering, Caira, 2012). In contrast, long filitriches scattered over the anterior dorsal surface have not previously been identified in proglottids of these species, but are shown for the mysorhynchus of *T. acanthiaevulgaris* (Mccullough, Fairweather 1983). In stomach and spiral valve worms, high intraspecific variation in the size and morphology of microtriches has been demonstrated, generally coinciding with the developmental stages (Pickering, Caira, 2013). In comparison, the revealed differences in size and shape of the microtriches in the specimens we studied are minor. Their tegument morphology is similar to that of *T. acanthiaevulgaris* free proglottids (McCullough, Fairweather, 1983), except that only unciliated sensory papillae have been previously described for this species (McCullough, Fairweather, 1983).

Based on previously obtained data on the suitability of the D2 region of LSU rDNA for species identification of cestodes (Brickle *et al.,* 2001), we confirm the species identity of the observed proglottids both among each other and with the previously described isolate of *T. acanthiaevulgaris*. The results of our molecular phylogenetic analysis corroborate the findings of Caira *et al*. (2014) regarding the close relationships of *T. acanthiaevulgaris* to *Crossobothrium* spp. and *Calliobothrium* spp. The genera *Trilocularia* Olsson, 1869 and *Crossobothrium* Linton, 1889 correspond to the diagnosis of Phyllobothridea (Ruhnke *et al*., 2017). At the same time, *Calliobothrium* Van Beneden, 1850 is a onchoproteocephalidean genus. Thus, the *Calliobothrium* + (*Trilocularia* + *Crossobothrium*) clade does not yet have a clear taxonomic interpretation (Caira *et al*., 2014; Ruhnke *et al*., 2017).

Compliance with ethical standards: Ethical approval was not required for this work.

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

Acknowledgments. The authors dedicate this paper to the Fiftieth Anniversary of the Research and Educational Station "Belomorskaia" of SPbU (formerly the Marine biological station of the Leningrad State University). We express our gratitude to the station staff for help with sampling. The results were obtained using the equipment of the Research Park of SPbU (Centre for Molecular and Cell Technologies). We sincerely appreciate Dr. Spencer J. Greenwood from the University of Prince Edward Island for his help in reviewing and improving the English language of this manuscript.

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Responsible editors N.M. Biserova, E.N. Temereva