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TRANS-ARCTIC DISTRIBUTION OF MARINE FISH DIGENEAN *PROGONUS MUELLERI* (DEROGENIDAE) TESTED BY MOLECULAR DATA

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In the digenean superfamily Hemiuroidea, a number of species are registered from a wide geographic range including the Arctic, Atlantic and Pacific Oceans. However, these distributions have not yet been confirmed with the molecular methods. In the present study, we performed molecular analysis of *Progonus muelleri* (Levinsen, 1881) (Derogenidae) from distant regions: the European sub-Arctic (the White, Barents and Pechora Seas) and the Pacific Northwest (the Sea of Okhotsk and the Pacific coast of the northern Kuril Islands). Two genetic lineages within *P. muelleri*, PM1 and PM2, are proved to occur in sympatry in the European sub-Arctic. We found minor differences in their maritae structure, and thus suppose they represent two pseudocryptic species. PM1 was also registered in the Pacific Northwest (PM1b) where it has differences in *cox1* gene from the European sub-Arctic lineage (PM1a). The intramolluscan life-cycle stages of *P. muelleri* from the Sea of Okhotsk are described and compared with the ones from the White Sea. We hypothesize that PM1a, PM1b and PM2 are three distinct species, but this should be further tested.

Keywords: Trematoda, Hemiuroidea, geographical range, cryptic species, life cycles

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Marine organisms with trans-Arctic distribution have been widely studied by molecular genetic methods in recent decades. Data on the genetic variability show that often instead of species with wide geographic ranges, complexes of cryptic or pseudocryptic species are common as a result of vicariance (Carr et al., 2011; Laakkonen et al., 2015, 2021; Kienberger et al., 2016; Borges et al., 2022; Chaban et al., 2023). Relevant studies on the marine parasites are few, and some species demonstrate genetic isolation between the

Pacific and Atlantic, some do have continuous distribution across the Arctic, and others do not demonstrate high genetic divergence though they have interrupted geographic range (Galaktionov et al., 2012, 2023, 2024a, 2024b). Digenetic trematodes (Digenea) are of a special interest for the studies of genetic variability on a wide geographic scale for two reasons. First, cryptic species are substantially more abundant within this group than in other parasitic helminths (Pérez-Ponce de León, Poulin, 2018). Second, the host identity and biology play an important role in their complex life cycles, and may incite speciation (Huyse et al., 2005). Among the marine digeneans with the trans-Arctic distribution, only those utilizing birds as the definitive hosts have been somewhat investigated in terms of genetic variability (Gonchar, Galaktionov, 2020, 2022; Galaktionov et al., 2023). As for the digeneans in the marine fish, there are just a few data on trans-Arctic distributions, and no intensive effort with many isolates and several genetic markers has been made.

Superfamily Hemiuroidea Looss, 1899 is a promising group for the study of cryptic species complexes, as its representatives have a wide specificity for the definitive hosts, high morphological variability and tremendous geographical distributions. This study is focused on *Progonus muelleri* (Levinsen, 1881) Looss, 1899 (family Derogenidae Nicoll, 1910) which has been documented from most regions of the Northern Hemisphere, including the Pacific, Atlantic and both Canadian and Russian Arctic (Odhner, 1905; Issaitschikov, 1933; Polyansky, 1955; Zhukov, 1963; Brinkmann, 1975; Bray, 1979). Previous studies demonstrated that specimens of *P. muelleri* from the Pacific Northwest and the European sub-Arctic do not differ in 28S rDNA (Sokolov et al., 2021; Krupenko et al., 2022), a molecular marker that is often used to delimit species of the Digenea. However, the lack of difference in 28S rDNA sequence dataset solely cannot be conclusive to state species integrity, and the analysis of variable markers like internal transcribed spacers 1 and 2 (ITS1, ITS2) and mitochondrial genes is necessary. Additionally, isolates from the White Sea form two groups divergent in 18S rDNA, 28S rDNA, ITS2 and *cox1* gene: *P. muelleri* PM1 and PM2 (Krupenko et al., 2022). To estimate if there are species-level differences within *P. muelleri*, in the present study, we performed the molecular analysis of isolates from distant regions: the European sub-Arctic (the White, Barents and Pechora Seas) and the Pacific Northwest (the Sea of Okhotsk and the Pacific coast of the northern Kuril Islands). We also described the life-cycle stages of *P. muelleri* from the first intermediate host in the Sea of Okhotsk, and compared them with the previously described ones of PM1 from the White Sea.

MATERIAL AND METHODS

Samples were collected in 2022–2024 from the European sub-Arctic seas (the White, Barents, and Pechora), and from the Pacific Northwest (the Sea of Okhotsk and the Pacific Ocean near the northern Kuril Islands) (table 1). Obtained putative life-cycle stages of *P. muelleri* (24 isolates) were fixed in 96% ethanol. Maritae were heat-killed prior to fixation. Some of the measurements (body length, oral sucker size) were taken from ethanol-fixed worms before cutting a piece for molecular analysis. Maritae and rediae were stained with acetocarmine (Sigma Aldrich, Germany), destained in 0.1 M HCl in 70% ethanol, dehydrated in a graded alcohol series, clarified in xylol, and mounted in BioMount medium (Bio Optica, Italy). Cercariae were observed alive and fixed in 2.5% glutaraldehyde in sea water for morphological descriptions. The whole mounts were studied under Leica DM 500 or Leica DM 2500 compound microscopes (Leica Microsystems, Germany) in bright field or with differential interference contrast (DIC). Photographs were taken using a Nikon DS Fi3 camera

(Nikon, Japan) or with a smartphone camera. Measurements were made in Fiji software (Schindelin et al., 2012). All measurements are in micrometers.

Table 1. Geographical locations of sampling sites

Coordinates	Site	Area	Region
66°18'N 33°38'E	Keret Archipelago	Kandalaksha Bay	White Sea
69°06'N 36°03'E	Dalniye Zelentsy	Kola Peninsula	Barents Sea
69°50'N 59°24'E	Lyamchina Bay	Vaygach Island	Pechora Sea
69°42'N 60°03'E	Varnek Bay	Vaygach Island	Pechora Sea
59°33'N 151°17'E	Ola lagoon	Taui Bay	Sea of Okhotsk
59°31'N 150°45'E	Nagaev Bay	Taui Bay	Sea of Okhotsk
59°29'N 150°55'E	Veselaya Bay	Taui Bay	Sea of Okhotsk
59°33'N 150°54'E	Gertnera Bay	Taui Bay	Sea of Okhotsk
50°02'N 155°19'E	Vasilieva Bay	Paramushir Island	Kuril Islands

The list of isolates taken for the molecular analysis is in table 2. To extract DNA, we used fragments of maritae (piece of the oral sucker) and whole rediae fixed with 96% ethanol. They were dried completely in 1.5 ml tubes, incubated in 200 µl of 5% Chelex® 100 resin (Bio-Rad, USA) with 0.2 mg/ml proteinase K (Evrogen, Russia) at 56°C for 3–4 h, then heated for 8 min at 90°C and centrifuged for 10 min at 16,000 g. The supernatant with DNA was transferred into a new tube and stored at –20°C.

We amplified partial 28S rDNA (D1–D3 domains), the complete ITS2 (with partial 5.8S and 28S rDNA), and the partial *cox1* mitochondrial gene, with primers and conditions listed in table 3. The PCR mixture contained 4 µL of ScreenMix-HS (Evrogen), 0.5 µL of each primer (10 pmol/µL), 2 µL of DNA and 13 µL of PCR-grade water (Evrogen). PCRs were run on a BioRad T100 thermal cycler (Bio-rad Laboratories Inc., USA). PCR products were stained with 0.5% ethidium bromide and visualized through electrophoresis in a 1% agarose gel. Sequencing was performed with the PCR primers on an AB3500xL genetic analyzer (Applied Biosystems, USA). Geneious Prime 2023.2.1 (https://www.geneious.com) was used to assemble sequences and to build alignments. The relevant data for comparison were obtained from GenBank (table 2). Pairwise genetic distances (as the number of base differences per site) were calculated in MEGA 11 (Tamura et al., 2021). The haplotype network for *cox1* gene sequences was constructed in PopART 1.7 (Leigh, Bryant, 2015) with the TCS network algorithm (Clement et al., 2002).

Alignments of nuclear rDNA markers were visually inspected for phylogenetically important substitutions. The phylogenetic analysis was run for the *cox1* dataset. The substitution model was determined as HKY+G in MEGA 11 (Tamura et al., 2021) for the Maximum likelihood (ML) analysis, and as TN93+G+I in bModelTest (Bouckaert, Drummond, 2017) for the Bayesian inference (BI) analysis. The ML analysis was run in PhyML 3.0 (Guindon et al., 2010) with the standard bootstrap option with 1000 replicates. The BI analysis was conducted using Monte Carlo Markov Chain (MCMC) analysis available in Bayesian Evolutionary Analysis by Sampling Trees (BEAST2) (Bouckaert et al., 2019) on XSEDE at the CIPRES Science Gateway (https://www.phylo.org). Three independent runs of MCMC were performed, each with 10,000,000 generations and sampling every 1000 generations. The trace files were checked for convergence with Tracer v1.7 (Rambaut et al., 2018). The log files were combined using LogCombiner, discarding the first 10% as burn-in. Trees were summarized with TreeAnnotator using the maximum clade credibility tree option and with node heights as mean heights.

Table 2. Derogenidae analyzed in this study

Species	Stage	Host species	Region	GenBank accession numbers			Reference
				28S	ITS2	*cox1*	
D. abba	marita	*Hippoglossoides platessoides* (Fabricius, 1780)	Svalbard, Arctic Ocean	—	—	PP384389	Bouguerche et al., 2024
D. abba	rediae and cercariae	*Euspira pallida* (Broderip & G. B. Sowerby I, 1829)	White Sea	—	—	OM807194	Krupenko et al., 2022
D. lacustris	marita	*Galaxias maculatus* (Jenyns, 1842)	Argentina	—	—	LC586092	Tsuchida et al., 2022
D. lacustris	marita	*Percichthys trucha* (Valenciennes, 1833)	Argentina	—	—	LC586093	Tsuchida et al., 2022
D. lacustris	marita	*Salvelinus fontinalis* (Mitchill, 1814)	Argentina	—	—	LC586094	Tsuchida et al., 2022
D. lacustris	marita	*Oncorhynchus mykiss* (Walbaum, 1792)	Argentina	—	—	LC586095	Tsuchida et al., 2022
D. lacustris	marita	*P. trucha*	Argentina	—	—	LC586096	Tsuchida et al., 2022
D. lacustris	marita	*G. maculatus*	Argentina	—	—	LC586097	Tsuchida et al., 2022
D. lacustris	marita	*G. maculatus*	Argentina	—	—	LC586098	Tsuchida et al., 2022
D. ruber	marita	*Chelidonichthys lastoviza* (Bonnaterre, 1788)	Western Mediterranean	—	—	OR245386	Gharbi et al., 2024
D. ruber	marita	*Ch. lastoviza*	Western Mediterranean	—	—	OR245546	Gharbi et al., 2024
D. varicus s. str.	marita	*Limanda limanda* (Linnaeus, 1758)	White Sea	—	—	OM807173	Krupenko et al., 2022
D. varicus s. str.	marita	*Gadus morhua* Linnaeus, 1758	White Sea	—	—	OM807174	Krupenko et al., 2022
D. varicus s. str.	marita	*Myoxocephalus scorpius* (Linnaeus, 1758)	White Sea	—	—	OM807175	Krupenko et al., 2022

D. varicus s. str.	marita	*Anarhichas lupus* Linnaeus, 1758	White Sea	—	—	OM807176	Krupenko et al., 2022
D. varicus s. str.	marita	*L. limanda*	White Sea	—	—	OM807177	Krupenko et al., 2022
D. varicus s. str.	marita	*Eleginus nawaga* (Walbaum, 1792)	White Sea	—	—	OM807178	Krupenko et al., 2022
D. varicus s. str.	marita	*L. limanda*	White Sea	—	—	OM807179	Krupenko et al., 2022
D. varicus s. str.	marita	*Clupea pallasii* Valenciennes, 1847	White Sea	—	—	OM807180	Krupenko et al., 2022
D. varicus s. str.	marita	*Cl. pallasii*	White Sea	—	—	OM807181	Krupenko et al., 2022
D. varicus s. str.	marita	*G. morhua*	Barents Sea	—	—	OM807182	Krupenko et al., 2022
D. varicus s. str.	marita	*Myo. scorpius*	Barents Sea	—	—	OM807183	Krupenko et al., 2022
D. varicus s. str.	marita	*Myo. scorpius*	Barents Sea	—	—	OM807184	Krupenko et al., 2022
D. varicus s. str.	rediae and cercariae	*Cryptonatica affinis* (Gmelin, 1791)	White Sea	—	—	OM807188	Krupenko et al., 2022
D. varicus s. str.	rediae and cercariae	*Cr. affinis*	White Sea	—	—	OM807189	Krupenko et al., 2022
D. varicus s. str.	rediae and cercariae	*Cr. affinis*	White Sea	—	—	OM807190	Krupenko et al., 2022
D. varicus s. str.	rediae and cercariae	*Cr. affinis*	Barents Sea	—	—	OM807191	Krupenko et al., 2022
D. varicus s. str.	rediae and cercariae	*Cr. affinis*	Barents Sea	—	—	OM807192	Krupenko et al., 2022
D. varicus s. str.	marita	*Merlangius merlangus* (Linnaeus, 1758)	North Sea	—	—	OR507183	Bouguerche et al., 2023
D. varicus s. str.	marita	*Mer. merlangus*	North Sea	—	—	OR507184	Bouguerche et al., 2023

Table 2. *Continuation*

Species	Stage	Host species	Region	GenBank accession numbers			Reference
				28S	ITS2	*cox1*	
D. varicus s. str.	marita	*Mer. merlangus*	North Sea	—	—	OR507185	Bouguerche et al., 2023
D. varicus s. str.	marita	*G. morhua*	Norway, Svalbard, Arctic Ocean	—	—	OR140779	Bouguerche et al., 2023
D. varicus s. str.	marita	*G. morhua*	Norway, Svalbard, Arctic Ocean	—	—	OR140832	Bouguerche et al., 2023
D. varicus s. str.	marita	*Mer. merlangus*	North Sea	—	—	OR140894	Bouguerche et al., 2023
D. varicus s. str.	marita	*G. morhua*	Norway, Svalbard, Arctic Ocean	—	—	OR140895	Bouguerche et al., 2023
D. varicus s. str.	marita	*G. morhua*	North Sea	—	—	OR140896	Bouguerche et al., 2023
D. varicus s. str.	marita	*Mer. merlangus*	North Sea	—	—	OR140897	Bouguerche et al., 2023
D. varicus s. str.	marita	*Mer. merlangus*	North Sea	—	—	OR140909	Bouguerche et al., 2023
P. muelleri PM1	marita	*Myo. scorpius*	White Sea	OM761979	OM762019	OM807186	Krupenko et al., 2022
P. muelleri PM1	marita	*Myo. scorpius*	White Sea	OM761980	OM762020	OM807187	Krupenko et al., 2022
P. muelleri PM1	rediae and cercariae	*Cr. affinis*	White Sea	OM761992	OM762032	OM807196	Krupenko et al., 2022
P. muelleri PM1	rediae and cercariae	*Cr. affinis*	White Sea	OM761993	OM762033	OM807197	Krupenko et al., 2022
P. muelleri PM1 isolate D19.1	rediae and cercariae	*Cr. affinis*	Barents Sea	—	—	**PQ463716**	Present study

P. muelleri PM1 isolate D19.2	rediae and cercariae	*Cr. affinis*	Barents Sea	—	—	**PQ463717**	Present study
P. muelleri PM1 isolate D19.11	marita	*Myo. scorpius*	Barents Sea	—	—	**PQ463718**	Present study
P. muelleri PM1 isolate D45.2	marita	*Myo. stelleri*	Sea of Okhotsk	**PQ568260**	**PQ567370**	**PQ463719**	Present study
P. muelleri PM1 isolate D45.3	marita	*Rhodymenichthys dolichogaster* (Pallas, 1814)	Sea of Okhotsk	—	—	**PQ463720**	Present study
P. muelleri PM1 isolate D45.4	marita	*Myo. jaok*	Sea of Okhotsk	—	—	**PQ463721**	Present study
P. muelleri PM1 isolate D45.5	marita	*Megalocottus platycephalus* (Pallas, 1814)	Sea of Okhotsk	—	—	**PQ463722**	Present study
P. muelleri PM1 isolate D45.6	marita	*Limanda aspera* (Pallas, 1814)	Sea of Okhotsk	—	—	**PQ463723**	Present study
P. muelleri PM1 isolate D45.9	rediae and cercariae	*Cryptonatica janthostoma* (Deshayes, 1839)	Sea of Okhotsk	—	—	**PQ463724**	Present study
P. muelleri PM1 isolate D45.10	rediae and cercariae	*Cr. janthostoma*	Sea of Okhotsk	—	—	**PQ463725**	Present study
P. muelleri PM1 isolate D45.11	rediae and cercariae	*Cr. janthostoma*	Sea of Okhotsk	**PQ568261**	**PQ567371**	**PQ463726**	Present study
P. muelleri PM1 isolate D45.12	rediae and cercariae	*Cr. janthostoma*	Sea of Okhotsk	—	—	**PQ463727**	Present study
P. muelleri PM1 isolate D46.3	marita	*Myo. scorpius*	Barents Sea	—	**PQ567372**	**PQ463728**	Present study
P. muelleri PM1 isolate D46.4	marita	*Myo. scorpius*	Barents Sea	—	—	**PQ463729**	Present study
P. muelleri PM1 isolate D46.5	rediae and cercariae	*Cr. affinis*	Barents Sea	—	—	**PQ463730**	Present study

Table 2. *Continuation*

Species	Stage	Host species	Region	GenBank accession numbers			Reference
				28S	ITS2	*cox1*	
P. muelleri PM1 isolate D46.7	marita	*Myo. scorpius*	Pechora Sea	—	**PQ567373**	**PQ463732**	Present study
P. muelleri PM1 isolate D48.5	marita	*Lepidopsetta bilineata* (Ayres, 1855)	Kuril Islands	—	—	**PQ463735**	Present study
P. muelleri PM1 isolate D48.6	marita	*Hippoglossus stenolepis* Schmidt, 1904	Kuril Islands	**PQ568262**	**PQ567375**	**PQ463736**	Present study
P. muelleri PM1 isolate D48.7	marita	*Myo. scorpius*	White Sea	—	—	**PQ463737**	Present study
P. muelleri PM1 isolate D48.8	metacercaria	*Caprella septentrionalis* Krøyer, 1838	Barents Sea	—	—	**PQ463738**	Present study
P. muelleri PM1 isolate D48.9	marita	*Myo. scorpius*	Barents Sea	**PQ568263**	—	**PQ463739**	Present study
P. muelleri PM2	marita	*Myo. scorpius*	White Sea	OM761978	OM762018	OM807185	Krupenko et al., 2022
P. muelleri PM2 isolate D46.6	marita	*Myo. scorpius*	Pechora Sea	—	—	**PQ463731**	Present study
P. muelleri PM2 isolate D46.8	marita	*Myo. scorpius*	Pechora Sea	—	—	**PQ463733**	Present study
P. muelleri PM2 isolate D46.9	marita	*Myoxocephalus quadricornis* (Linnaeus, 1758)	Pechora Sea	—	**PQ567374**	**PQ463734**	Present study
Allogenarchopsis problematica	redia	*Semisulcospira libertina* (A. Gould, 1859)	Japan	—	—	LC805323	Miura, Takisawa, 2024
Didymocystis wedli	marita	*Thunnus orientalis* (Temminck & Schlegel, 1844)	Japan	—	—	AB725624	Unpublished
Genarchopsis goppo	redia	*S. libertina*	Japan	—	—	LC805294	Miura, Takisawa, 2024
Thometrema patagonica	marita	*P. trucha*	Argentina	—	—	LC586100	Tsuchida et al., 2022

Newly obtained sequences are in bold.

Table 3. Primers and PCR temperature profiles used in this study

Fragment	F/R	Name	Sequence (5′–3′)	Reference	Thermocycling profile
28S rDNA	F	digl2	AAGCATATCACTAAGCGG	Tkach et al., 1999	95°C 3 min (95°C 30 s, 54°C 30 s, 72°C 2 min) ×40 72°C 10 min
	R	1500R	GCTATCCTGAGGGAAACTTCG	Olson et al., 2003	
ITS2	F	3S	GGTACCGGTGGATCACGTGGCTAGTG	Morgan, Blair, 1995	95°C 5 min (94°C 30 s, 55°C 30 s, 72°C 1 min) ×40 72°C 10 min
	R	ITS2.2	CCTGGTTAGTTTCTTTTCCTCCGC	Cribb et al., 1998	
cox1 gene	F	JB3	TTTTTTGGGCATCCTGAGGTTTAT	Bowles et al., 1993	95°C 2 min (95°C 30 s, 52°C 40 s, 72°C 1 min) ×35 72°C 10 min
	R	trem. cox1.rrnl	AATCATGATGCAAAAGGTA	Králová-Hromadová et al., 2008	

RESULTS

General account on *Progonus muelleri* occurrence

Data on inspected hosts and infection rates are provided in tables 4 and 5. In the Barents Sea, the maritae of *P. muelleri* were recovered from the European sculpin *Myoxocephalus scorpius*, metacercariae were found in the skeleton shrimps *Caprella septentrionalis*, and rediae with cercariae were obtained from the moon snail *Cryptonatica affinis*. In the White Sea, new isolates of *P. muelleri* maritae were recovered from *Myo. scorpius*. In the Pechora Sea, the maritae of *P. muelleri* were found in *Myo. scorpius* and in the fourhorn sculpin *Myo. quadricornis*.

Table 4. List of examined potential definitive hosts of *Progonus muelleri* and infection data

Region	Host order and family	Host species	*N* fish collected	*N* fish infected	Prevalence, %	Mean intensity	*N* isolates taken into molecular analysis
White Sea	**Clupeiformes**						
	Clupeidae	*Clupea pallasii*	43	0	0	—	—
	Gadiformes						
	Gadidae	*Eleginus nawaga*	46	0	0	—	—
		Gadus morhua	127	0	0	—	—
	Osmeriformes						
	Osmeridae	*Osmerus dentex*	20	0	0	—	—

Table 4. *Continuation*

Region	Host order and family	Host species	*N* fish collected	*N* fish infected	Prevalence, %	Mean intensity	*N* isolates taken into molecular analysis
	Perciformes						
	Agonidae	*Agonus cataphractus*	2	0	0	—	—
	Anarhichadidae	*Anarhichas lupus*	28	0	0	—	—
	Cottidae	*Gymnocanthus tricuspis*	1	0	0	—	—
		Myoxocephalus quadricornis	5	0	0	—	—
		Myoxocephalus scorpius	93	3	3.2	1.3	4
		Triglops murrayi	5	1	20	1	—
	Gasterosteidae	*Gasterosteus aculeatus*	5	0	0	—	—
	Zoarcidae	*Zoarces viviparus*	2	0	0	—	—
	Pleuronectiformes						
	Pleuronectidae	*Limanda limanda*	116	1	0.9	1	—
		Liopsetta glacialis	27	0	0	—	—
		Platichthys flesus	80	0	0	—	—
	Salmoniformes						
	Salmonidae	*Coregonus lavaretus*	6	0	0	—	—
		Oncorhynchus gorbuscha	5	0	0	—	—
Barents Sea	**Gadiformes**						
	Gadidae	*Gadus morhua*	25	0	0	—	—
		Melanogrammus aeglefinus	3	0	0	—	—
		Pollachius virens	2	0	0	—	—
	Perciformes						
	Cottidae	*Gymnocanthus tricuspis*	6	0	0	—	—
		Myoxocephalus scorpius	12	4	33.3	1.3	5
	Pleuronectiformes						
	Pleuronectidae	*Platichthys flesus*	1	0	0	—	—

		Pleuronectes platessa	1	0	0	—	—
	Salmoniformes						
	Salmonidae	*Salmo salar*	1	0	0	—	—
Pechora Sea	**Gadiformes**						
	Gadidae	*Eleginus nawaga*	20	0	0	—	—
	Perciformes						
	Cottidae	*Myoxocephalus scorpius*	6	3	50	1.0	3
		Myoxocephalus quadricornis	2	1	50	3	1
		Gymnocanthus tricuspis	1	0	0	—	—
	Pleuronectiformes						
	Pleuronectidae	*Liopsetta glacialis*	1	0	0	—	—
Sea of Okhotsk	**Gadiformes**						
	Gadidae	*Gadus chalcogrammus*	1	0	0	—	—
	Osmeriformes						
	Osmeridae	*Osmerus dentex*	1	0	0	—	—
	Perciformes						
	Cottidae	*Myoxocephalus stelleri*	4	3	75	5.7	1
		Myoxocephalus jaok	2	2	100	8.0	1
		Megalocottus platycephalus	2	2	100	1.0	1
		Porocottus minutus	1	0	0	—	—
	Gasterosteidae	*Pungitius pungitius*	1	0	0	—	—
	Hexagrammidae	*Hexagrammos stelleri*	2	0	0	—	—
		Hexagrammos octogrammus	1	0	0	—	—
	Pholidae	*Rhodymenichthys dolichogaster*	1	1	100	1	—
	Stichaeidae	*Alectrias alectrolophus*	4	0	0	—	—
	Pleuronectiformes						
	Pleuronectidae	*Limanda aspera*	4	4	100	5.0	1

Table 4. *Continuation*

Region	Host order and family	Host species	*N* fish collected	*N* fish infected	Prevalence, %	Mean intensity	*N* isolates taken into molecular analysis
Kuril Islands	**Salmoniformes**						
	Salmonidae	*Oncorhynchus gorbuscha*	2	0	0	—	—
		Oncorhynchus keta	1	0	0	—	—
		Oncorhynchus kisutch	3	0	0	—	—
		Oncorhynchus nerka	1	0	0	—	—
	Gadiformes						
	Gadidae	*Gadus chalcogrammus*	1	0	0	—	—
		Gadus macrocephalus	1	0	0	—	—
	Perciformes						
	Cottidae	*Hemilepidotus papilio*	1	0	0	—	—
		Myoxocephalus stelleri	1	1	100	11.0	—
	Pleuronectiformes						
	Pleuronectidae	*Hippoglossus stenolepis*	3	3	100	3.0	1
		Lepidopsetta bilineata	2	1	50	1	1

Table 5. List of examined potential first intermediate hosts of *Progonus muelleri* (Gastropoda: Naticidae) and infection data

Region	Host species	*N* specimens collected	*N* specimens infected	Prevalence, %	*N* isolates taken into molecular analysis
White Sea	*Amauropsis islandica*	44	0	0	—
	Crypronatica affinis	498	5	1.00	2
	Euspira pallida	71	0	0	—
Barents Sea	*Crypronatica affinis*	247	3	1.21	3
	Euspira pallida	32	0	0	—
Sea of Okhotsk	*Cryptonatica jantostoma*	173	11	6.36	4

In the Sea of Okhotsk, maritae of *P. muelleri* were found in the yellowfin sole *Limanda aspera*, the Steller's sculpin *Myo. stelleri*, the plain sculpin *Myo. jaok*, the belligerent sculpin *Megalocottus platycephalus*, and in the stippled gunnel *Rhodymenichthys dolichogaster*. At the Pacific coast of the northern Kuril Islands, *P. muelleri* maritae were recovered from the Pacific halibut *Hippoglossus stenolepis*, the Pacific rock sole *Lepidopsetta bilineata*, and *Myo. stelleri*. Rediae with cercariae similar to those of *P. muelleri* PM1 were recovered from the moon snail *Cr. janthostoma* from the Sea of Okhotsk.

Variation of nuclear rDNA markers

Partial 28S rDNA sequences were obtained for four new isolates: two from the Sea of Okhotsk, one from the Kuril Islands and one from the Barents Sea. They were 1128–1132 base pairs (bp) long, and completely identical to the previously published 28S rDNA sequences of PM1 (OM761979–81, OM761992–3). All PM1 sequences differed from those of PM2 (OM761978, OM761982–3) by one substitution.

Sequences containing ITS2 flanked with the partial 5.8S and 28S rDNA, 514–554 bp long, were obtained for six new isolates: one from the Barents Sea, two from the Pechora Sea, two from the Sea of Okhotsk, and one from the Kuril Islands. They split into two groups. A single sequence from the Pechora Sea was identical to the previously published ITS2 sequences of PM2 from the White Sea (OM762018, OM762022–3). The rest of the new sequences were identical to the ones of PM1 from the White Sea (OM762019–21, OM762032–33). The difference between PM1 and PM2 was in a single nucleotide. Sequences from the Sea of Okhotsk and from the Kuril Islands were obtained for the same isolates as in the 28S rDNA analysis, and they all matched the PM1 group.

Variation of mitochondrial *cox1* gene

Fragments of *cox1* mtDNA (795 bp long) were obtained for 24 new isolates of *P. muelleri*. Five sequences from Krupenko et al. (2022) were also included in the analysis. Thus, the alignment comprised 29 sequences, and it was trimmed to the shortest one, 788 bp. The *cox1*-based haplotype network is in figure 1. Two highly diverged groups were evident in the network, with a minimal intergroup distance 0.066 ± 0.009 (52 substitutions) (supplementary table 1). These groups corresponded to PM1 and PM2 from the nuclear marker analysis and from the previously published data on *cox1* (Krupenko et al., 2022). The distances within groups did not exceed 0.021 ± 0.005 (16 substitutions). PM2 comprised three haplotypes, two from the Pechora Sea, and one from the White Sea. Within PM1, we had isolates from all the sampled areas. Also, PM1 split into two subsets (PM1a and PM1b) matching the geographical origin: one subset comprised isolates from the European seas, and the other from the Pacific Northwest. The maximal genetic distances within the European subset were 0.003 ± 0.002 (2 substitutions); within the Pacific subset, the distances were higher, up to 0.010 ± 0.004 (8 substitutions). The minimal distance between the subsets was 0.014 ± 0.004 (11 substitutions).

The 11 isolates in the Pacific subset PM1b formed ten different haplotypes. In the European subset PM1a, there were only four haplotypes among 14 isolates. Three of these haplotypes were restricted to the White Sea, and one more, the dominant, combined isolates from the Barents and Pechora Seas.

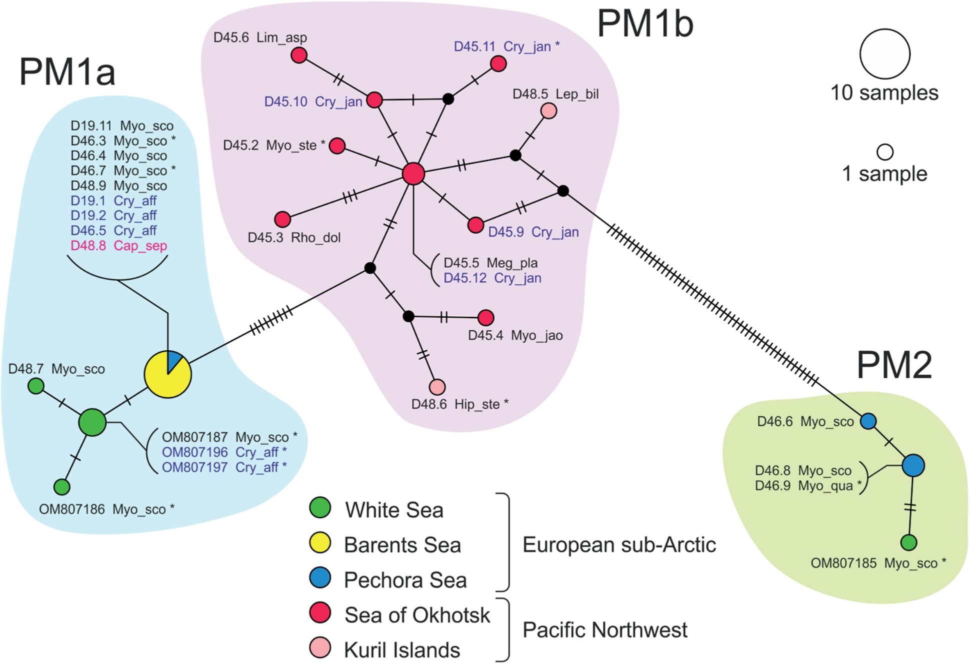

Figure 1. Haplotype network of *Progonus muelleri* isolates (N = 29) based on partial *cox1* gene sequences. Circle size represents the haplotype frequency. Black dots indicate missing haplotypes. Number of hatch marks corresponds to the number of substitutions between haplotypes. Colored background indicates three haplogroups within the *P. muelleri* species complex. Isolates taken from first intermediate hosts labeled purple, from second intermediate hosts labeled pink, and from definitive hosts labeled black. Asterisks mark the isolates for which nuclear ribosomal data are available (see table 2). Abbreviations: Cap_sep – *Caprella septentrionalis*; Cry_aff – *Cryptonatica affinis*; Cry_jan – *Cryptonatica janthostoma*; Hip_ste – *Hippoglossus stenolepis*; Lep_bil – *Lepidopsetta bilineata*; Lim_asp – *Limanda aspera*; Meg_pla – *Megalocottus platycephalus*; Myo_jao – *Myoxocephalus jaok*; Myo_qua – *Myoxocephalus quadricornis*; Myo_sco – *Myoxocephalus scorpius*; Myo_ste – *Myoxocephalus stelleri*; Rho_dol – *Rhodymenichthys dolichogaster*.

For the phylogenetic reconstruction, we removed the identical sequences from our *cox1* dataset of *P. muelleri*, and added other species from the subfamily Derogeninae: *Derogenes varicus* (Müller, 1784) Looss, 1901, *D. abba* Bouguerche, Huston, Karlsbakk, Ahmed & Holovachov, 2024, *D. ruber* Lühe, 1900, and *D. lacustris* Tsuchida, Flores, Viozzi, Rauque & Urabe, 2021. The following outgroups were selected: *Allogenarchopsis problematica* (Faust, 1924) Urabe & Shimazu, 2013, *Didymocystis wedli* Ariola, 1902, *Genarchopsis goppo* Ozaki, 1925, and *Thometrema patagonicum* (Szidat, 1956) Lunaschi & Drago, 2001. The alignment comprised 59 sequences, and after trimming it was 788 bp long. ML and BI analyses resulted in similar tree topologies, except for the relationship between *D. abba* and *D. ruber* (fig. 2A). Two groups of *P. muelleri* (PM1 and PM2) were closely related to each other with 99% (ML) and 1 (BI) support values. They formed a common branch

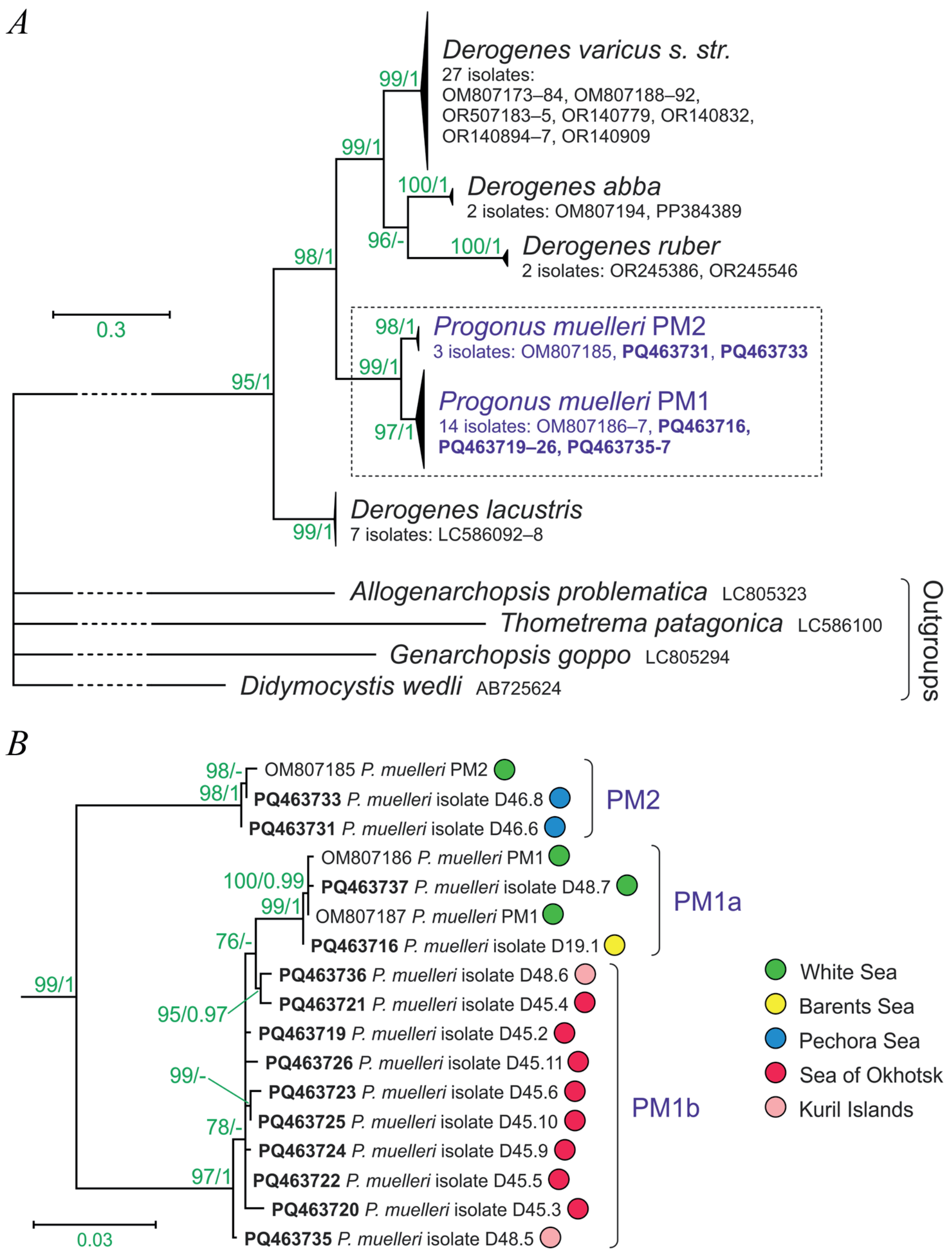

Figure 2. Phylogenetic relationships within the Derogeninae resulting from Maximum Likelihood analysis based on partial *cox1* gene sequences. *A*. Complete tree (nodes with sequence differences below 0.02 are collapsed). *B*. Expanded part of *A* (in rectangle) with *Progonus* sequences. Bootstrap support values in percent are shown at nodes, followed by posterior probabilities from the tree built for the same dataset with BI method. Support values lower than 75 (ML) and 0.9 (BI) are not shown. Scale bars show the substitution rate. Newly generated sequences are in bold.

with a clade comprising *D. varicus*, *D. abba*, and *D. ruber*, with high support values in both ML and BI analyses. *Derogenes lacustris* fell separately from the other species of the genus. All species-level taxa were well-supported. Within PM1, the isolates from the European seas (PM1a) formed a well-supported clade (fig. 2B). PM1b from the Pacific Northwest was resolved as paraphyletic. Within both PM1a and PM2, the most diverged were the isolates from the White Sea.

General considerations on morphology

Molecular data outline three groups within *Progonus muelleri*: PM1a, PM1b and PM2. The measurements of maritae for these groups are given separately in table 6, together with the measurements from Odhner (1905). Maritae of PM1a and PM1b were very similar in metrical characteristics. However, the sucker ratio was smaller in PM1b, as well as the range of egg lengths. Maritae of PM2 were generally larger than those of PM1, and in this characteristic closer to the specimens of Odhner. The sucker ratio was higher in PM2. Among the non-metrical characters, one was conspicuous: the wall of the sinus sac was substantially thinner in PM2 than in PM1, and thus the outline of this organ was barely visible (fig. 3).

Table 6. Measurements of *Progonus muelleri* maritae

Measured character	*P. muelleri* (Odhner, 1905)	PM1a (based on 8 hologenophores[1])	PM1b (based on 7 hologenophores)	PM2 (based on 5 hologenophores[2])
Body length	1500–2000	1231 (745–1827)	1222 (848–1575)	1724 (1351–2110)
Body maximum width	370–500	326 (242–471)	342 (229–471)	449 (359–610)
Forebody	N/A	559 (300–828)	523 (362–727)	714 (548–973)
Forebody to body length ratio	N/A	45 (40–48) %	43 (33–49) %	41 (39–46) %
Post-cecal region	N/A	163 (115–206)	186 (118–286)	303 (206–390)
Oral sucker	150–180 (diameter)	121 (97–147) × 131 (97–153)	136 (96–166) × 137 (98–174)	152 (104–182) × 164 (115–225)
Ventral sucker	320–400 (diameter)	241 (174–351) × 256 (176–362)	246 (172–325) × 253 (179–345)	363 (291–464) × 379 (294–464)
Sucker-length ratio	2.13–2.22 (calculated from minimal and maximal diameter values)	2.01 (1.65–2.44)	1.79 (1.39–2.11)	2.44 (2.08–2.80)
Sucker-width ratio		2.02 (1.67–2.58)	1.91 (1.53–2.38)	2.34 (2.06–2.56)
Pharynx	85	62 (49–73) × 74 (62–85)	66 (53–79) × 73 (37–91)	72 (60–96) × 91 (73–126)
Sinus sac	N/A	72 (59–86) × 85 (72–112)	76 (54–90) × 92 (65–116)	76 (64–114) × 86 (78–104)

Sinus organ length	25	32 (23–40)	28 (21–38)	37 (26–56)
Pars prostatica length	N/A	118 (65–184)	98 (61–166)	145 (116–161)
Seminal vesicle	N/A	86 (53–148) × 54 (28–62)	116 (78–179) × 57 (44–71)	154 (111–173) × 77 (65–93)
Left testis	N/A	85 (65–110) × 80 (32–113)	115 (92–146) × 104 (57–142)	139 (125–164) × 116 (103–134)
Right testis	N/A	107 (78–166) × 76 (49–123)	119 (86–142) × 94 (50–142)	139 (113–167) × 119 (95–142)
Ovary	N/A	129 (98–186) × 105 (63–177)	113 (70–149) × 92 (62–120)	141 (111–177) × 119 (78–151)
Left vitelline mass	N/A	142 (99–203) × 106 (76–173)	104 (52–142) × 80 (61–104)	136 (124–144) × 91 (80–100)
Right vitelline mass	N/A	135 (93–206) × 90 (50–129)	101 (65–131) × 83 (59–113)	136 (123–148) × 102 (94–114)
Eggs	54–60 × 25–29	53 (44–63) × 26 (22–31)	49 (41–55) × 25 (20–31)	50 (43–56) × 26 (21–30)

[1] Five new specimens and three specimens from Krupenko et al. (2022). Some measurements of hologenophores from the previous study are revised and corrected.

[2] Three new specimens and two specimens from Krupenko et al. (2022). Some measurements of hologenophores from the previous study are revised and corrected.

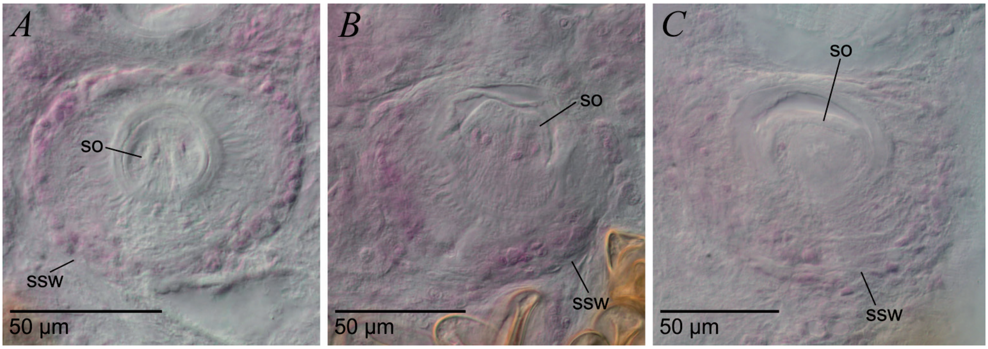

Figure 3. Sinus sac and sinus organ in maritae of PM1a (*A*), PM1b (*B*) and PM2 (*C*). Acetocarmine, DIC. Abbreviations: so – sinus organ, ssw – sinus sac wall.

Cercariae of PM1b from *Cr. janthostoma* (fig. 4A) were apparently different from those of PM1a from *Cr. affinis* (fig. 4B) previously described from the White Sea (Krupenko et al., 2022). The caudal cyst of PM1b was larger; the fin was different in shape, wider; immotile threads were shorter and more numerous (11–13 versus 7–11, often 8 in PM1a). Below we provide infection data for PM1b and describe its intramolluscan life-cycle stages.

For the prevalence and intensity values in the definitive hosts, we assume that all the *P. muelleri* maritae obtained from the Pacific Northwest belong to PM1b. We also suggest referring to the genetic lineages of *P. muelleri* defined through molecular data as '*Progonus* cf. *muelleri'* followed by a genetic group name.

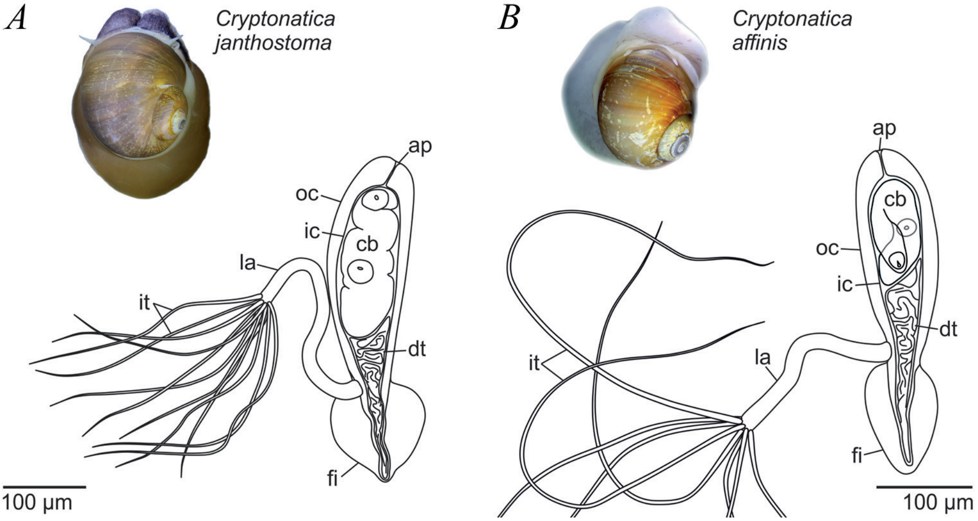

Figure 4. Comparison of cercariae of PM1b (*A*) and PM1a (*B*); host names and photographs placed along with the cercariae drawings. Abbreviations: ap – caudal cyst aperture, cb – cercaria body, dt – delivery tube, fi – fin, ic – inner cyst layer, it – immotile threads, la – locomotory appendage, oc – outer cyst layer.

Description of *Progonus* cf. *muelleri* PM1b

Family Derogenidae Nicoll, 1910

Subfamily Derogeninae Nicoll, 1910

Genus *Progonus* Looss, 1899

Localities: Taui Bay (Sea of Okhotsk); Paramushir Island (Kuril Islands).

Definitive hosts: *Limanda aspera*, *Myoxocephalus stelleri*, *Myo. jaok*, *Megalocottus platycephalus*, *Rhodymenichthys dolichogaster*, *Hippoglossus stenolepis*, *Lepidopsetta bilineata*.

Site in definitive host: stomach.

Prevalence in definitive host: 4 of 4 *Lim. aspera*, 2 of 2 *Meg. platycephalus*, 3 of 4 *Myo. stelleri*, 2 of 2 *Myo. jaok*, 1 of 1 *R. dolichogaster* (Taui Bay, Sea of Okhotsk); 2 of 2 *H. stenolepis*, 1 of 1 *Lep. bilineata*, 1 of 1 *Myo. stelleri* (Paramushir Island, Kuril Islands).

Mean intensity in definitive host: 5 in *Lim. aspera*, 1 in *Meg. platycephalus*, 5.7 in *Myo. stelleri*, 8 in *Myo. jaok*, 1 in *R. dolichogaster* (Taui Bay, Sea of Okhotsk); 2.5 in *H. stenolepis*, 1 in *Lep. bilineata*, 11 in *Myo. stelleri* (Paramushir Island, Kuril Islands).

First intermediate host: *Cryptonatica janthostoma* (Deshayes, 1839) (Caenogastropoda, Littorinimorpha, Naticidae).

Site in first intermediate host: reproductive and digestive glands.

Prevalence in first intermediate host: Gertner Bay 6.0%, N = 67; Nagaev Bay 7.7%, N = 26; Ola lagoon 1.5%, N = 65; Veselaya Bay 20.0%, N = 15.

Voucher material: Isogenophores 2024.11.13.001–003 of isolates D45.9, D45.11 and D45.12, and hologenophores 2024.11.13.004–10 of isolates D45.2, D45.3, D45.4, D45.5, D45.6, D48.5 and D48.6 are deposited in the Helminths collection of the Zoological Institute of the Russian Academy of Sciences (ZISP), section Trematoda (non-type material).

Representative DNA sequences in GenBank: PQ568260–2 (28S); PQ567370–1, PQ567375 (ITS2); PQ463719–27, PQ463735–6 (*cox1*).

Maritae structure complies with the description of Levinsen (1881) and to the redescriptions by Odhner (1905) and Bouguerche et al. (2024). The measurements based on seven hologenophores are provided in table 6. Our specimens were smaller than those of Odhner on average, and the sucker ratio was smaller. Eggs were also smaller on average than in the descriptions of Levinsen (1881) and Odhner (1905).

Rediae measurements based on 16 ethanol-fixed worms from three different host specimens. Rediae vermiform, 2262 (1322–3487) × 233 (167–303). Pharynx 54 (43–68) × 42 (35–51). Cecum 1085 (593–1640) long, 49 (32–71)% of body length. Birth pore near mouth opening. Infective cercariae found only in isolate D45.12. Rediae with infective cercariae generally bigger (2216–3487), though proportions of body and organs similar to those of smaller rediae with developing cercariae.

Infective cercariae measurements based on ten glutaraldehyde-fixed specimens. Cercariae of cystophorous type, with tail forming caudal cyst 403 (380–416) long, rounded in cross section, maximal diameter 87 (77–109). Anterior end spherical, with aperture, opposite end pointed. Cyst two-layered, with broad space between layers. Outer layer forming heart-shaped fin at pointed end, 121 (108–131) long, 105 (77–119) wide. Delivery tube and cercaria body within cyst in infective cercariae. Locomotory appendage attached near fin base, 284 (267–303) long, 19 (17–21) in diameter at base. At end of locomotory appendage, 11–13 immotile threads, 314 (283–350) long.

DISCUSSION

Criteria for species recognition are widely discussed in light of constantly emerging new molecular data. For the trematodes, Bray et al. (2022) proposed that differentiation of any two close species must be based on (1) reciprocal monophyly in the most discriminating available molecular marker, and (2) either morphological differences or distinct host distribution. Here, we tested this model of species recognition on *Progonus muelleri*, one of the fish hemiuroid trematodes with the widest geographic range covering the Arctic, Atlantic and Pacific Oceans in the Northern Hemisphere (Levinsen, 1881; Odhner, 1905; Issaitschikov, 1933; Polyansky, 1955; Zhukov, 1963; Brinkmann, 1975; Bray, 1979).

Progonus muelleri has quite a wide specificity for the definitive hosts, being recorded from over 60 fish species (summarized at WoRMS, 2024). However, it tends to occur more often in sculpins and flatfishes. The life cycle of *P. muelleri* has been described recently; it involves the naticid gastropod *Cryptonatica affinis* as the first intermediate host and caprellid amphipods as the second (Sokolov et al., 2021; Krupenko et al., 2022). Previous data also showed the possible existence of cryptic species within *P. muelleri*, lineages PM1 and PM2, living in sympatry in the White Sea (Krupenko et al., 2022). In the present study, new isolates of *P. muelleri* maritae were obtained from the Barents and Pechora Seas, and from the Pacific Northwest from several fish species. Along with this, in the Pacific Northwest, rediae and cercariae morphologically similar to those of *P. muelleri* PM1 were obtained from another first intermediate host, *Cr. janthostoma*. Through the nuclear markers (28S rDNA and ITS2), isolates from the Pacific Northwest were identical to the ones of PM1 from the European sub-Arctic. Consistent results were obtained from the analysis of *cox1* gene fragments, indicating high similarity of PM1 isolates from the European sub-Arctic and from the Pacific Northwest. Moreover, these isolates differ from each other less than those of PM1 and PM2 in sympatry. This indicates that PM1 and PM2 probably represent two different species. Notably, intermediate hosts are known only for PM1, not for PM2. Of these, one may represent *P. muelleri* sensu stricto. However, we can't tell exactly which one, as the maritae of these species demonstrate minor morphological differences, and both are similar to the type material described by Levinsen (1881) and to the more detailed redescriptions by Odhner (1905) and Bouguerche et al. (2024).

In general, sampled maritae of PM2 are bigger, and their sucker ratio is greater than in PM1, though the ranges overlap. A possible good differential characteristic is linked with the sinus sac: its wall is visibly thinner in PM2. The documented distribution of PM1 and PM2 may be a clue to the question of which one of them is *P. muelleri* sensu stricto. PM1 has been sampled in regions both with high salinity (like the south coast of the Barents Sea) and lower salinity (the White and Pechora Seas). PM2 has been sampled only in the White and Pechora Seas, not in the Barents Sea. Thus, its distribution may be restricted to the regions with the salinity below an average oceanic, possibly depending on the distribution of the first intermediate host which is yet unknown. The type locality of *P. muelleri* is the West Greenland Shelf (Levinsen, 1881), an area with normal oceanic salinity (Rysgaard et al., 2020). So PM1 is more likely to be *P. muelleri* s. str. However, as long as strong evidence is lacking, we suggest the usage of temporary names *P.* cf. *muelleri* PM1 and *P.* cf. *muelleri* PM2.

Another question is the conspecificity of the two distant lineages of PM1 from the European sub-Arctic (PM1a) and from the Pacific Northwest (PM1b). They do not differ in the analyzed nuclear markers, but demonstrate clear divergence in the *cox1* gene. It could be intraspecific and resulting from geographic remoteness enhanced by the life-cycle traits: usage of benthic crustaceans as the second intermediate hosts (instead of planktonic in the related species of *Derogenes* (Køie, 1979)) and sedentary fish (sculpins and flatfishes) as preferred definitive hosts. However, differences between PM1a and PM1b in the structure of cercariae and first intermediate host species may rather be treated as interspecific. Alternatively, these differences could be host-induced and intraspecific, if PM1 utilizes various species of the genus *Cryptonatica* as the first intermediate hosts. We suggest that the latter hypothesis is likely improbable, but to reject it more data are needed: either material from *Cr. affinis* from the Pacific Northwest for comparison, or experiments on cross-infection of the first intermediate hosts. If PM1b appears distinct from PM1a, it should be described as a new species. An uncertainty of the PM1b status is also due to our *cox1*-based phylogeny (Fig. 2): PM1b is not resolved as monophyletic, and thus does not meet the most important taxonomic criterion (Bray et al., 2022). So, isolates of *P. muelleri* should probably be tested with alternative markers, or with an extended dataset comprising more derogenids.

It is also important to point out that the circumpolar distribution of *Cr. affinis* has never been tested by the molecular methods, and we cannot be sure that *Cr. affinis* from the Pacific is the same as in the Arctic and Atlantic. Preliminary unpublished data indicate that even in the White Sea two species of "*Cr. affinis*" live in sympatry (Dr T. Neretina, personal communication). Thus, the lack of knowledge on the host cryptic diversity hinders the investigations on parasites.

Regarding the genetic variation in *cox1* gene, there are a few more details to discuss. First is the lack of shared haplotypes between the White Sea and nearby Barents and Pechora Seas both in PM1 and PM2. This suggests a restricted gene flow between these areas, and is probably linked with the low mobility of all the hosts in the life cycle (Blasco-Costa et al., 2012). Such restrictions may eventually incite speciation (Huyse et al., 2005). Second, the haplotype diversity of PM1b from the Pacific Northwest is much higher than that of PM1a in the European sub-Arctic. This indicates possible bottleneck occurrence for the PM1a, and suggests the Pacific origin of the whole PM1 lineage. The position of PM1b isolates on the *cox1*-based tree supports this conclusion. Thus, in this respect, PM1 is similar to the majority of the marine organisms in the Arctic which have a Pacific origin (Vermeij, 1991; Briggs, 2003). Further speculations on how the lineages of *P. muelleri* diverged, and is there a clear genetic gap between PM1a and PM1b, are limited by the lack of data from the Arctic seas of Siberia.

The interrelationships within the subfamily Derogeninae resolved here with the *cox1* data are similar to the previous assessment through the 28S rDNA sequences (Bouguerche et al., 2023, 2024). Notably, *D. lacustris* forms a branch separate from the other species of the genus which have sister relationships with the *P. muelleri* complex. This indicates that *D. lacustris* should be probably transferred to a separate genus, differentiated through its affinity to the freshwater environment. However, there are 24 more species of the *Derogenes* lacking any molecular data. These are needed for a well-grounded revision of the Derogeninae and a differential diagnosis of a new genus for *D. lacustris*.

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CONFLICT OF INTEREST

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

SUPPLEMENTARY MATERIAL

Supplementary table 1 is available through the following link: https://doi.org/10.13140/RG.2.2.21423.44961.

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ПРОВЕРКА ГИПОТЕЗЫ О ТРАНСАРКТИЧЕСКОМ АРЕАЛЕ ДИГЕНЕИ *PROGONUS MUELLERI* (DEROGENIDAE) С ИСПОЛЬЗОВАНИЕМ МОЛЕКУЛЯРНЫХ ДАННЫХ

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Ключевые слова: Trematoda, Hemiuroidea, географическое распространение, криптические виды, жизненные циклы

РЕЗЮМЕ

Многие представители трематод надсемейства Hemiuroidea характеризуются широким географическим распространением, включающим Северный Ледовитый, Атлантический и Тихий океаны. Однако попыток проверить молекулярными методами эти данные о распространении практически не предпринималось. В данной работе мы провели молекулярный анализ вида *Progonus muelleri* (Levinsen, 1881) (Derogenidae) из отдаленных регионов: европейской субарктики (Белое, Баренцево и Печорское моря) и северо-запада Тихого океана (Охотское море и тихоокеанское побережье Курильских островов). Показано, что два псевдокриптических вида в пределах *P. muelleri*, PM1 и PM2, встречаются в симпатрии в европейской субарктике. Они имеют незначительные различия в строении марит. PM1 также был зарегистрирован на северо-западе Тихого океана (PM1b), где он имеет четкие отличия в гене *cox1* от европейской субарктической линии (PM1a). Были описаны стадии жизненного цикла *P. muelleri* из моллюсков Охотского моря, и проведено их сравнение с таковыми из Белого моря. Мы предполагаем, что наш материал представлен тремя разными видами, однако пока недостаточно данных, чтобы сказать это наверняка, а также выяснить, какой из них представляет собой *P. muelleri sensu stricto*.