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Life cycle of the seabird digenean *Gymnophallus minor* (Gymnophallidae) in the Arctic

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Abstract

Gymnophallidae is one of the digenean families featuring bivalves as first intermediate hosts. However, the exact bivalve host species remain unknown for most members of this family. Gymnophallids have been one of the targets in our continuous efforts to reveal the diversity of digeneans in the higher north. Here, we focus on *Gymnophallus minor*, which we found in eiders from various locations in the Arctic and sub-Arctic. Sexual adults (maritae) of *G. minor* can be easily identified because they have a distinctive character: the roughly equal size of the pharynx and the ventral sucker. We also matched them, using DNA markers, with the intramolluscan stages (sporocysts, cercariae, and metacercariae) from the bivalve *Liocyma fluctuosa* collected on Spitsbergen. Taken together, we compile the first data on the life cycle of *G. minor* and discuss them in the context of other gymnophallids.

Introduction

Digeneans of the family Gymnophallidae are common parasites of seabirds. Many of them use bivalves as first and second intermediate hosts (e.g., Benito *et al.* 2023; Marchiori *et al.* 2023; Montenegro *et al.* 2021). The higher in the Arctic, the less we know about the transmission of gymnophallids. However, even limited existing data suggest that gymnophallid life cycles may occur there in diverse and flexible ways, presumably as an adaptation to the cold climate.

For example, a group of related *Parvatrema* species have developed several strategies to deal with environmental conditions in the sub-Arctic (Galaktionov *et al.* 2024). Within the second intermediate host, they reproduce parthenogenetically and, oddly enough, form cercariae – but only in some species, while other abandon this free-living stage. One more shift is from inhabiting the extrapallial space to tissue parasitism. Another case is *Gymnophallus choledochus* Odhner, 1900, which interrupts cercariae emergence in winter and switches to metacercarial development within sporocysts in the first intermediate host (Loos-Frank 1969). This obviously reduces the risks for the free-living stages in the most unfavourable seasonal conditions, and the question arises if this kind of life cycle adaptation also occurs in other gymnophallids.

Gymnophallus minor Ryzhikov, 1963, was first described from the common eider in the Gulf of Anadyr (Chukotka) (Ryzhikov 1963) and later recorded by Bishop and Threlfall (1974) in common eiders from Newfoundland and Labrador. The maritae (sexual adults) of this species are special in having an approximately equal size of the pharynx and ventral sucker, while in all other species of *Gymnophallus*, the ventral sucker is about twice as large as the pharynx. Such a clear morphological differential character facilitates the accurate identification in the field, and we have repeatedly found *G. minor* in eiders in the Arctic and sub-Arctic. These findings have now been analysed together with molecular data and recent finds of the gymnophallid intramolluscan stages in the bivalve *Liocyma fluctuosa* (A. Gould, 1841) on Svalbard. This allowed us to assess the transmission pathways of this parasite in Arctic coastal ecosystems and potential life cycle adaptations.

Material and methods

We studied the morphology in maritae of *Gymnophallus minor* from three sources: our own sampling, material shared by colleagues, and museum collections. Sampling involved obtaining wild birds in accordance with local regulations, dissection, and recovery of worms.

We identified the maritae of *G. minor* from common eiders *Somateria mollissima* (Linnaeus, 1758) in the southwest of West Spitsbergen (Bellsund Fjord; 77°30'N 14°35'E) in 1990; from common eiders in the Pechora Sea (off the Vaygach Island; 69°50'N 59°26'E) in 2010 and 2017;

and also from the king eider *Somateria spectabilis* (Linnaeus, 1758) in the Pechora Sea (Khaipudyr Bay; 68°43'N 60°3'E) in 2020. We preserved these worms in 70% ethanol, stained them with boric carmine, and whole-mounted. The mounts were deposited in the Collection of Helminths, section Trematoda, of the Zoological Institute, Russian Academy of Sciences (RAS) (ZISP, no. 3745, 3746, 3748, 3749).

Two specimens of ethanol-preserved gymnophallid maritae from the common eider collected in Ivanovskaya Bay, East Murman (Barents Sea) were kindly provided by Vadim V. Kuklin. These were as well stained with boric carmine, whole-mounted, and deposited in the ZISP collection (no. 3747).

We also studied the collection of the whole-mounted gymnophallid maritae from common eiders in Iceland, kindly provided by Karl Skírnisson, and the syntypes of *G. minor* from the trematode collection of the A. N. Severtsov Institute of Ecology and Evolution (IEE) RAS (no. 141, 863–870).

One of the two *G. minor* specimens collected from the king eider in Khaipudyr Bay (Pechora Sea) in 2020 was used for DNA extraction using Chelex 100 (BioRad, USA) (for protocol, see, for example, Krupenko *et al.* 2022).

Gymnophallid intramolluscan stages were found in the bivalve *Liocyma fluctuosa* (A. Gould, 1841) collected in September 2016 and March 2017 at tidal and subtidal sites near Ny-Ålesund (Svalbard): sites A, B, subtidal, 78°55'20"N, 11°58'30"E; site E, tidal, 78°55'35"N, 11°54'35"E. They were photographed and used for DNA extraction with a DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany). The sample codes A49, A54, B6, E1, E23, and E54 correspond to different infected *L. fluctuosa* individuals collected at sites A, B, and E.

We amplified the partial 5.8S rDNA and the complete ITS2 using the primer pair 5.8S-ITS2 and 28S-ITS2, as described in Cremonte *et al.* 2015. For the partial 28S rDNA, we used two primer pairs: digl2 and 1500R (Olson *et al.* 2003; Tkach *et al.* 1999), and C2'B and D2 (Bayssade-Dufour *et al.* 2006; Vân Le *et al.* 1993), and PCR conditions as described in Krupenko *et al.* 2020. For the partial 18S rDNA, we used two pairs of primers covering the overlapping fragments: 652 and 28, and 18S1A and 32 (Hernández-Mena *et al.* 2017). PCR products (for the parasite samples originating from the bivalves only) were cleaned using a Qiaquick PCR purification kit (Qiagen, Hilden, Germany). Sequencing was performed with the PCR primers in both directions by an automated ABI 3500xl genetic analyser (Applied Biosystems, USA) at the Research Resource Centre 'Molecular and cell technologies' (St. Petersburg University) and Eurofins Genomics (Ebersberg, Germany).

Chromatograms were inspected, analysed, edited, assembled, and aligned in Geneious Prime (https://www.geneious.com). For the comparisons, we used relevant sequences from GenBank that matched the lengths of the newly obtained ones. To estimate the phylogenetic position of our samples, we used the maximum likelihood (ML) analysis implemented as RAxML-NG v. 1.1.0 (Kozlov *et al.* 2019) in raxmlGUI 2.0 (Edler *et al.* 2021), with 'ML + transfer bootstrap + consensus' approach, random seed 317646, and 10,000 bootstrap replicates. The best substitution model was estimated prior to the analysis in the same program with ModelTest-NG (Darriba *et al.* 2020). We also performed the Bayesian inference (BI) analysis in MrBayes3.2.7a (Ronquist *et al.* 2012) with 1,000,000 iterations and the 'allcompat' option. The dataset was aimed to balance between the alignment length and the number of species: we concatenated two fragments, the partial 18S rDNA (the best substitution model TIM2+I+G) and 5.8S–ITS2–28S rDNA (GTR+G). In MrBayes, TIM2 was replaced by GTR.

Results and discussion

We recovered *G. minor* maritae from the eiders in the Barents and Pechora Sea on several occasions, but data on infection prevalence and intensity are limited. In Bellsund Fjord in 1990, one adult female *S. mollissima* was dissected and found infected, intensity ca. 70 individuals (two dissected ducklings were uninfected). Off the Vaygach Island in 2010 and 2017, five adult female *S. mollissima* were dissected, two of them infected, intensity 2–9 individuals (five dissected ducklings were uninfected). In the Khaipudyr Bay, eight adult female *S. spectabilis* were dissected, four of them infected, intensity 1–4.

The studied maritae varied in size (Table 1). We believe these variations could be introduced while handling material (i.e., the extent of the body contraction during the fixation, and the extent of coverslip pressure during mounting) or have natural origins (marita age, host- and geography-induced variation). Their morphological characters were uniform and complied with the diagnosis from the original *G. minor* species description by Ryzhikov (1963). The brief description below is based on our specimens.

Worms oval, oral sucker subterminal, about 1.5–2 times larger than ventral sucker (Table 1, Figure 1a, b). Pharynx large, roundish, roughly equal in size to ventral sucker. Seminal vesicle bipartite. Ovary pre-testicular, oval. Testes symmetrical, left testis slightly larger than right one. Vitellaria paired, follicular, located at sides and slightly posterior to ventral sucker. In young worms, uterus loops with eggs only in forebody, anteriorly to intestinal caeca. When filled with eggs, uterus loops moving posteriorly at sides of body, reaching approximately level of testes. Eggs oval, about 1.5 times longer than wide.

We detected no marked differences between the *G. minor* maritae from our samples and the syntypes from the IEE collection. Gymnophallid maritae from the common eiders from Iceland (collection of K. Skírnisson) also matched *G. minor* in their morphological characters.

Since DNA sequences were obtained from a single marita individual, the possibility of dealing with a mixture of species cannot be excluded – even though morphological data on all the examined maritae were consistent. Among trematodes, cryptic diversity is a common feature, probably found more frequently than in other helminths (Pérez-Ponce de León and Poulin, 2018). This should be kept in mind during future studies, but currently there are no contradictions to calling the species in question *G. minor* and to interpreting its life cycle the way we do below.

Gymnophallid sporocysts containing cercariae (Figure 1c) were found in the hepatopancreas of 11 out of 48 (23%) specimens of *L. fluctuosa*. These sporocysts were vermiform and moved only slowly. Some sporocysts also contained metacercariae (Figure 1c) which were similar in size to those observed in the extrapallial space of these molluscs. For molecular studies, we used material from six infected *L. fluctuosa*: sporocysts, cercariae, and metacercariae samples from B6 and E1; sporocyst samples from A54 and E54; and cercariae samples from A49 and E23. Intensity of metacercariae infection for B6 exceeded 500 individuals.

To genetically match the life cycle stages, we obtained two 5.8S–ITS2 (536 bp) and 11 28S rDNA (1256–1280 bp) sequences (submitted to GenBank under the accession numbers PQ526380–PQ526381 and PQ526368–PQ526378, respectively). The sequences

Table 1. Morphometric parameters of *Gymnophallus minor* maritae from different hosts and geographic regions

	Somateria mollissima, Spitsbergen, Bellsund. N = 13.	*Somateria mollissima*, Vaygach, Pechora Sea. N = 3.	*Somateria mollissima*, Ivanovskaya Bay, Barents Sea. N = 2.	*Somateria spectabilis*, Khaypudyr Bay, Pechora Sea. N = 4.	**Somateria mollissima*, Chukotka, Gulf of Anadyr.
Body length	303–528 (381 ± 18)	338–385 (356 ± 15)	300–370 (335 ± 35)	435–562 (501 ± 30)	368–480
Body width	177–261 (212 ± 6)	212–246 (234 ± 11)	210–215 (213 ± 3)	174–306 (241 ± 37)	190–256
Oral sucker length (OSL)	60–82 (71 ± 3)	81–94 (89 ± 4)	50–52 (51 ± 1)	71–96 (81 ± 5)	73–116
Oral sucker width (OSW)	68–92 (80 ± 2)	107–112 (110 ± 1)	63–66 (65 ± 2)	83–127 (102 ± 11)	83–112
Pharynx length (PhL)	41–49 (44 ± 1)	55–70 (64 ± 5)	39–41 (40 ± 1)	46–57 (52 ± 3)	36–59
Pharynx width (PhW)	38–53 (43 ± 1)	73–78 (76 ± 2)	43	48–78 (63 ± 8)	45–59
Ventral sucker length (VSL)	40–54 (45 ± 1)	61–72 (66 ± 3)	38–43 (41 ± 3)	53–68 (61 ± 4)	50–70
Ventral sucker width (VSW)	36–53 (47 ± 1)	61–68 (65 ± 2)	41–44 (43 ± 2)	47–69 (59 ± 6)	50–70
Left testes length	37–78 (54 ± 4)	49–62 (56 ± 7)	49–64 (57 ± 8)	44–75 (64 ± 10)	30–50
Left testes width	19–50 (31 ± 2)	38–45 (42 ± 4)	26–42 (34 ± 8)	33–52 (42 ± 5)	59–80
Right testes length	42 – 89 (59 ± 4)	48–65 (57 ± 9)	58–65 (62 ± 4)	51–79 (61 ± 9)	30–50
Right testes width	26 –35 (31 ± 1)	38–51 (45 ± 7)	37	37–52 (44 ± 4)	59–80
Ovary length	45–72 (55 ± 2)	40–67 (54 ± 14)	41–48 (45 ± 4)	56–72 (64 ± 5)	36–50
Ovary width	31–47 (39 ± 1)	41–50 (46 ± 5)	32–46 (39 ± 7)	36–46 (42 ± 3)	36–50
Egg length (EL)	18–23 (21 ± 0.2)	20–22 (21 ± 0.3)	17–22 (19 ± 0.4)	19–22 (21 ± 0.3)	20–26
Egg width (EW)	12–19 (15 ± 0.3)	15–17 (16 ± 0.2)	10–14 12 ± 0.3)	12–16 (14 ± 0.4)	12–17
OSL/VSL	1.2–1.9 (1.6 ± 0.1)	1.3–1.4 (1.4 ± 0.1)	1.2–1.4 (1.3 ± 0.1)	1.2–1.5 (1.3 ± 0.1)	–
OSW/VSW	1.4–2.2 (1.7 ± 0.1)	1.6–1.8 (1.7 ± 0.1)	1.5 (1.5 ± 0.01)	1.6–1.9 (1.7 ± 0.1)	–
VSL/PhL	0.9–1.3 (1 ± 0.03)	1–1.3 (1.1 ± 0.2)	1 (1 ± 0.04)	1–1.2 (1.1 ± 0.1)	–
VSW/PhW	0.9–1.3 (1 ± 0.04)	0.8–0.9 (0.9 ± 0.1)	1 (1 ± 0.03)	0.9–1.2 (1 ± 01)	–

N, number of measured individuals. *, data after Ryzhikov (1963).

were identical among the marita, sporocyst, cercariae, and metacercaria samples, with two nuances. First, sequences from samples A49, A54, and E1 had a single T peak instead of two distinct peaks (TT in other samples); this probably was an artefact. Second, there were three cases of clear double peaks consistently seen in both forward and reverse reads: two in 28S rDNA (marita and E54) and one in 5.8S–ITS2 (E54). We report these double peaks using IUPAC codes, as it was suggested in Blasco-Costa *et al.* (2016). In all double peak cases, one peak matched the nucleotide found in all the other sequences, and one peak differed. There are several reports of such polymorphism in trematodes – for example, in 28S rDNA (Achatz *et al.* 2019), ITS2 (Diaz *et al.* 2015; Womble *et al.* 2015), both ITS1 and ITS2 (Ahasan *et al.* 2023). Though it may indicate hybridization (Ahasan *et al.* 2023), we could not test this. Overall, we consider that the observed subtle variations do not violate the otherwise complete similarity among the sequences.

ITS2 sequences are generally conservative within species in Gymnophallidae, with a couple of modest exceptions (Galaktionov *et al.*

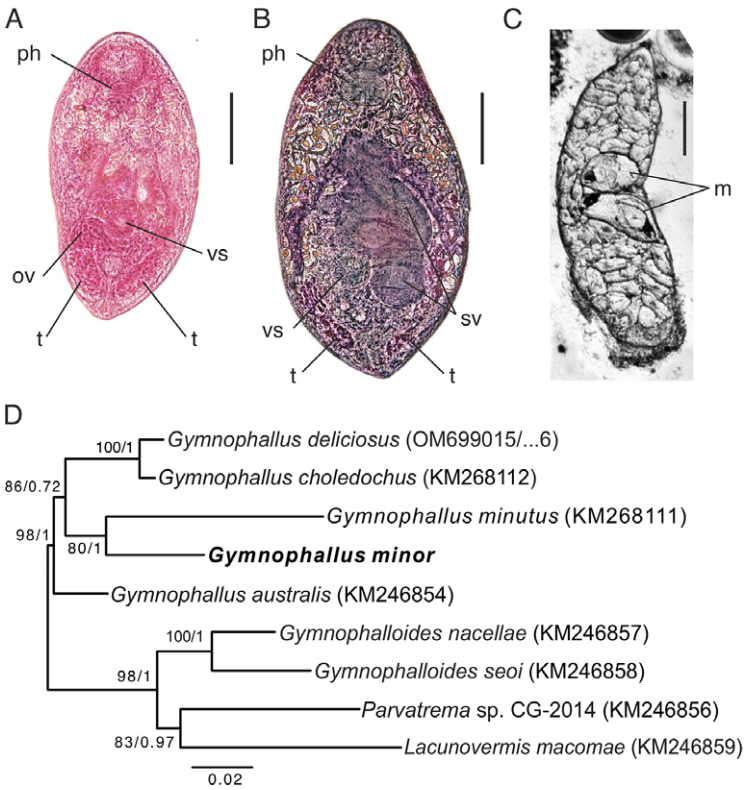

Figure 1. A–C, Representative microphotographs of life cycle stages of *Gymnophallus minor*: phase contrast view of the marita from the slide ZISP 3745 (host *Somateria mollissima*, Spitsbergen) (A); phase contrast view of the marita from the slide ZISP 3748 (host *Somateria spectabilis*, Pechora Sea) (B); live view of a sporocyst containing metacercariae along with cercarial embryos and developing cercariae (C); abbreviations: ph, pharynx; m, metacercariae; ov, ovary; t, testis; sv, seminal vesicle; vs, ventral sucker; scale bars: A, B—100 μm; C—300 μm. D, ML phylogenetic tree based on concatenated fragments of 18S and 5.8S–ITS2–28S rDNA (1,722 bp); bootstrap support values printed at nodes, followed after slash by the posterior probabilities inferred in the Bayesian analysis of the same dataset; scale bar shows substitutions per site; sequences obtained from GenBank are given with their accession numbers and originate from Shchenkov *et al.* 2022 (*G. deliciosus*) and Cremonte *et al.* 2015 (all other species).

2024) and one case with suspected cryptic diversity (Feis *et al.* 2015). The interspecific divergence in the ITS2 marker among three species of the genus *Gymnophallus* (our data for *G. minor*; GenBank data for *G. australis*, JN381028, and *G. choledochus*, JN381028) is 70 to 77 substitutions per a 550-bp alignment. Even with a single polymorphic position, our data fall within the expected intraspecific level. The same is true for the 28S rDNA data.

The DNA sequencing data therefore suggest the conspecificity of the marita, sporocyst, and metacercaria samples. Thus, the life cycle of *G. minor* was elucidated, with the bivalve *L. fluctuosa* as the first and second intermediate host, and the eider ducks *S. mollissima* and *S. spectabilis* as the definitive host species (perhaps among some other marine anatids). This conclusion is consistent with data on the spatial distribution patterns of the host species.

Most likely, *G. minor* is a circumpolar boreal–Arctic species, with the distribution range generally limited by that of its first intermediate host, *L. fluctuosa*. This bivalve is found in all Siberian seas, in the North Pacific and the North Atlantic. Eiders, the definitive hosts of *G. minor*, are also common across this range. However, *G. minor* seems not to reach the high Arctic because we have not found it at Franz Joseph Land (Galaktionov *et al.* 2021), though *L. fluctuosa* has been registered there (Golikov and Scarlato 1977). One explanation could be the low density of *L. fluctuosa* in this area (1–10 individuals/m^2; Golikov and Scarlato 1977) in comparison to southwestern Spitsbergen (an average of 185.2 or 190 individuals/m^2, depending on the sediment type; Różycki and Gruszczyński 1991). Also, the latitude does not favour transmission via the free-swimming cercariae which are sensitive to harsh environmental conditions (Galaktionov 2017). Only the life cycle of *Microphallus pseudopygmaeus* Galaktionov, 1980, without any free-living stages, is completed there (Galaktionov *et al.* 2021).

Although some conditions appear to be too cold for *G. minor* to persist, in less severe conditions, it shows considerable flexibility in the life cycle. Its sporocysts produce swimming cercariae that can facilitate transmission by spending several hours in the external environment and infecting the second intermediate host. However, our observations indicate that cercariae may also stay inside the first intermediate host and develop into metacercariae there. Finally, it was not uncommon to observe metacercariae inside the sporocysts (Figure 1c). So, we hypothesize that the life cycle may follow either the two-host or three-host scenario. In the first case, transmission is guaranteed if the definitive host eats the first intermediate host. In the second case, free-swimming cercariae enhance dispersal by encysting in other bivalves of the same or, potentially, other species. In addition to *L. fluctuosa*, gymnophallid metacercariae were found near Ny-Ålesund in *Macoma calcarea*, *Astarte* sp., *Eunucula tenuis*, *Yoldia hyperborea*, *Nuculana pernula*, and most commonly in *Mya truncata* (Mathias Wegner, unpublished). Some of them could serve as the alternative second intermediate hosts for *G. minor*, but we do not yet have evidence to support this.

This resonates with the observation of Loos-Frank (1969) that in winter at the North Sea, cercariae of *G. choledochus* do not emerge from their host *Cerastoderma edule* (Linnaeus, 1758). Instead, they develop into the metacercariae inside the sporocysts, perhaps because chances for transmission by free-swimming cercariae are

scarce in the cold season (Loos-Frank 1969). This explanation makes sense for *G. minor*, too, but applies to conditions in Ny-Ålesund not just in winter but throughout the year. Such an adaptive mechanism may be common in gymnophallids. Notably, this phenomenon does not occur in temperate regions: for example, gymnophallids in the Mediterranean seem to never harbour metacercariae within the sporocysts (Bartoli and Gibson 2007).

To complete the story, we confirmed the phylogenetic position of *G. minor* within the genus *Gymnophallus* (Figure 1d). The partial 18S rDNA sequence obtained for the marita sample was 1763-bp long (GenBank accession number PQ526379). The concatenated alignment after trimming was 1722 bp (778-bp long 18S rDNA partition and 944 bp-long 5.8S–ITS2–28S rDNA partition). The topology in the ML and BI trees was consistent, with the comparable support values (Figure 1d). Five species of *Gymnophallus* formed a well-supported monophyletic clade, with *G. minor* being the sister-species of *G. minutus*.

To sum up, we have discovered that the bivalve species *L. fluctuosa* very likely serves as first and second intermediate host of *G. minor*. Availability of alternative life-cycle scenarios, involving two or three hosts, may enhance the transmission of this parasite in extreme environmental conditions. Our data contribute to a better overall understanding of the bird parasites' circulation in Arctic ecosystems.

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Competing interest. None.

Ethical standard. The authors assert that all procedures contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals.

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