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# Diversity and Distribution of Helminths in Wild Ruminants of the Russian Arctic: Reindeer (*Rangifer tarandus*), Muskoxen (*Ovibos moschatus*), and Snow Sheep (*Ovis nivicola*)

**Olga A. Loginova [1,*], Sofya B. Rozenfeld [1], Taras P. Sipko [1], Ivan A. Mizin [2], Danila V. Panchenko [3], Kasim A. Laishev [4], Mikhail G. Bondar [5], Leonid A. Kolpashchikov [5], Aleksandr R. Gruzdev [6], Pavel S. Kulemeev [6], Dennis I. Litovka [7], Mariia N. Semerikova [7], Viktor N. Mamontov [8], Evgeniy G. Mamaev [9] and Sergei E. Spiridonov [1]**

1 A. N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, 119071 Moscow, Russia; rozenfeldbro@mail.ru (S.B.R.); sipkotp@mail.ru (T.P.S.); s_e_spiridonov@rambler.ru (S.E.S.)
2 National Park "Russian Arctic", 163000 Arkhangelsk, Russia; ivan_mizin@mail.ru
3 Institute of Biology of Karelian Research Centre of the Russian Academy of Sciences, 185910 Petrozavodsk, Russia; danja@inbox.ru
4 St. Petersburg Federal Research Center of the Russian Academy of Sciences, 199178 St. Petersburg, Russia; layshev@mail.ru
5 Joint Directorate of Taimyr Nature Reserves, 663305 Norilsk, Russia; mikisayan@yandex.ru (M.G.B.); ntnt69@yandex.ru (L.A.K.)
6 Wrangel Island State Nature Reserve, 689400 Pevek, Russia; gruzdevar@mail.ru (A.R.G.); r-k_84@mail.ru (P.S.K.)
7 Chukotka Arctic Scientific Center, 689000 Anadyr, Russia; d-litovka@yandex.ru (D.I.L.); koshornikovamn@mail.ru (M.N.S.)
8 N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, 163020 Arkhangelsk, Russia; mamont1965@list.ru
9 Commander Islands Nature and Biosphere Reserve, 684500 Nikolskoye, Russia; eumetopias@mail.ru
* Correspondence: loginova_spb@bk.ru; Tel.: +7-(950)-029-5437

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**Abstract:** The Russian Arctic supports wild sympatric ruminants and their data-deficient helminths. In this study, we: (1) collected fecal samples of wild and semiwild reindeer (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*), and snow sheep (*Ovis nivicola*) across Palearctic North territories: Arkhangelsk Oblast (including Novaya Zemlya archipelago), Karelia and Sakha Republics, Kola, Yamal, Taimyr, and Chukotka Peninsulas, Bering, Svalbard, and Wrangel Islands; (2) conducted a coprological survey (noninvasive life-time method preferable for protected animals) to obtain eggs and larvae of helminths inhabiting digestive, respiratory, nervous, and muscular systems; (3) identified helminths according to their morphology and DNA sequences; (4) estimated parasite load per host; (5) analyzed our findings. *Varestrongylus eleguneniensis* (in reindeer) was reported for the Palearctic for the first time, while *Orthostrongylus* sp. was reported both for *R. tarandus* and for the Palearctic for the first time. Capillarid-type eggs were reported for snow sheep for the first time. The question of the role of wild Arctic ruminants as vectors for rotifers was raised.

**Keywords:** helminth; *Rangifer tarandus*; *Ovibos moschatus*; *Ovis nivicola*; egg; larva; DSL; rotifer

## 1. Introduction

The relatively low biodiversity of terrestrial animal taxa is a hallmark of Polar regions [1,2], but this pattern is not obvious for the parasites of Arctic ruminants [3]. Possibly, there are geological and biological factors that influence the diversity of ruminant parasites in the Northern Palearctic. For example, the continuity of the tundra throughout the area allows animals to move freely: mountain ranges are rare and low, and large rivers are covered with ice for most of the year. In the Pleistocene, the ice sheet was located only in the west of the Palearctic [4,5], and the rest of the territory was continuously inhabited by ruminants. Human activities (including the work of herdsmen, hunters, biologists, and veterinarians) can also have an impact on parasite diversity and distribution. The presence of only three main ruminant species, reindeer (*Rangifer tarandus*) [6–10], muskox (*Ovibos moschatus*) [11,12], and snow sheep (*Ovis nivicola*) [13,14], facilitates the analysis of possible helminth exchange in the northern Palearctic. Reindeer occupy this territory fairly evenly in contrast to the more limited distribution of snow sheep. Muskoxen became extinct in the Palearctic in the Late Pleistocene (12,000 years ago) and have only recently been reintroduced from the Nearctic (1970s) [15–17], and their range is still expanding. The aim of this study is to obtain reference data for further monitoring, as this Arctic area is now undergoing active transformation due to climate warming, use of mineral resources, development of transport logistics, etc. Previous helminthological studies were carried out more than 60 years ago [18] for reindeer (mostly domestic) [19] and snow sheep [13,14], and, to the authors' knowledge, never for muskoxen in Russia. Moreover, these studies never included DNA analysis (because it was not available at the time), and their results were mostly published in Russian journals and conference proceedings, including so-called gray literature [20]. We aim to fill this gap and provide the English-speaking reader the current state of the helminth fauna of selected wild ruminants in the Russian Arctic.

## 2. Materials and Methods

### *2.1. Helminth Recovery*

Fecal sampling was done for three host species, reindeer (*R. tarandus*), muskoxen (*O. moschatus*), and snow sheep (*O. nivicola*), inhabiting the Arctic area of Russia (Figure 1, Table 1). Territory was defined according to the Conservation of Arctic Flora and Fauna (CAFF) boundary and the Russian Arctic zone boundary. Additionally, we included a site at Svalbard (Norway) due to the Svalbard Treaty recognizing right of Russia (along with many other countries) to engage in commercial activity on the islands of the Archipelago of Spitsbergen, and the actual use of this right.


**Figure 1.** Map of Palearctic indicating the sampling sites. Numbers correspond to identification numbers in Table 1.

**Table 1.** Collection data for fecal samples from reindeer, muskoxen, and snow sheep across the Northern Palearctic.

| Sample Set ID | Map Reference | Host Species | Number of Fecal Samples | Location | Coordinates (Decimal Degrees) | Date Collected |
|---|---|---|---|---|---|---|
| 1 | 1 | Wild reindeer (*Rangifer tarandus*) | 19 | Taymyr Peninsula (Krasnoyarsk Krai) | 71.10780, 98.04150 | June 2020 |
| 2 | 2 | | 3 | Novaya Zemlya, Arkhangelsk Oblast | 76.90835, 68.44880 | August 2021 |
| 3 | 2 | | 2 | Novaya Zemlya, Arkhangelsk Oblast | 76.90835, 68.44880 | July 2022 |
| 4 | 3 | | 15 | Barentsbugr, Svalbard [1] (Norway) | 78.04729, 14.28717 | August 2022 |
| 5 | 4 | | 21 | Murmansk Oblast | 68.50699, 30.03720 | September 2022 |
| 6 | 5 | | 11 | Arkhangelsk Oblast | 63.86779, 44.43266 | September 2022 |
| 7 | 6 | Semiwild reindeer (*R. tarandus*) | 50 | Yamalo-Nenets Autonomous Okrug | 66.62200, 65.71646 | August 2018 |
| 8 | 7 | | 59 | Nenets Autonomous Okrug | 67.97568, 52.91955 | October 2018 |
| 9 | 8 | | 2 | Khanty-Mansi Autonomous Okrug | 65.63307, 61.94561 | October 2019 |
| 10 | 9 | | 30 | Murmansk Oblast | 68.00424, 35.01228 | December 2020 |
| 11 | 9 | | 31 | Murmansk Oblast | 68.00424, 35.01228 | March 2021 |
| 12 | 8 | | 20 | Khanty-Mansi Autonomous Okrug | 65.63307, 61.94561 | August 2021 |
| 13 | 10 | | 42 | Bering Island [2] Kamchatka Krai | 55.26152, 165.93711 | October 2021 |
| 14 | 11 | | 7 | Republic of Karelia | 66.30072, 33.08216 | June 2022 |
| 15 | 12 | | 10 | Republic of Sakha (Yakutia) | 65.34745, 140.08864 | June 2022 |
| 16 | 13 | | 30 | Chukotka Autonomous Okrug | 65.46168, −173.47478 | June 2022 |
| 17 | 14 | | 8 | Chukotka Autonomous Okrug | 65.90614, −178.84644 | October 2022 |
| 18 | 15 | Muskoxen (*Ovibos moschatus*) | 35 | Yamalo-Nenets Autonomous Okrug | 67.58240, 66.25280 | March 2022 |
| 19 | 16 | | 24 | Wrangel Island, Chukotka Autonomous Okrug | 71.34890, −178.66722 | March 2022 |
| 20 | 17 | | 6 | Taymyr Peninsula (Krasnoyarsk Krai) | 73.10336, 95.11816 | July 2022 |
| 21 | 18 | | 25 | Taymyr Peninsula (Krasnoyarsk Krai) | 74.17696, 107.46475 | August 2022 |
| 22 | 15 | | 30 | Yamalo-Nenets Autonomous Okrug | 67.58240, 66.25280 | October 2022 |
| 23 | 19 | Snow sheep (*Ovis nivicola*) | 21 | Taymyr Peninsula (Krasnoyarsk Krai) | 68.64397, 95.66562 | July 2016 |
| 24 | 20 | | 13 | Republic of Sakha (Yakutia) | 70.51859, 129.50336 | June 2022 |
| 25 | 21 | | 5 | Taymyr Peninsula (Krasnoyarsk Krai) | 69.33130, 93.58480 | July 2022 |

[1] Non-Russian territory included due to Svalbard Treaty. [2] Site with originally domestic reindeer that eventually feralized.

Semiwild reindeer were also included in this study as representatives of *R. tarandus*. Being formally domestic animals along with cattle, sheep, and goats, they are not handled like other farm ruminants. The reindeer in question led their life as close to the natural one as it was possible. They were also migrating long distances (with their herder) and were exposed to many natural threats (weather, biting insects, and so on). Wild and semiwild reindeer are often sympatric.

Feces were collected from the ground shortly after defecation. They were stored chilled, frozen, or dried. Prior to analyses, the frozen material thawed out naturally, while the dried material had been humidified for at least 2 h. A total of 519 fecal samples were examined for the presence of helminths (at the stage of egg or larva) via complex coprological survey according to protocols of the National Standard of the Russian Federation (GOST R 54627-2011) *Ruminant animals—Methods of Laboratory Helminthological Diagnostics* [21]. Qualitative methods consisted of larvoscopy (Vajda's method), ovoscopy (flotation with Darling's solution and sedimentation in tap water), and coproculture (for nematode larvae, if possible). Briefly, Vajda's method prescribes to place 3–4 fecal pellets on a microscope slide, then to add around 1 mL of 40 °C tap water to wash out the pellets, to leave it for 30 min, to remove the pellets, and study the remaining liquid. Flotation with Darling's solution requires double centrifugation and the usage of the 1:1 mixture of glycerin and saturated sodium chloride solution, followed by supernatant microscopy. Sedimentation and coproculture were standard [22].

The quantitative method required the VIGIS chamber (analogue of the McMaster device) of the Diapar kit (VIGIS, Moscow, Russia).

Morphology of eggs and larvae obtained from feces was studied via light microscopy (LM) with the optical microscope Micmed-6 (LOMO-MA, St. Petersburg, Russia) equipped with lenses of 4× (to navigate the slide), 10×, 20×, 40×, and 100× magnifications (the latter with oil immersion). Micrographs were taken with the digital photo camera 5D Mark II (Canon, Tokyo, Japan) connected to the microscope with the C-mount adapter (LOMO-MA, Russia). Morphometry was performed based on the obtained pictures via Figi/ImageJ Version 1.2.4 RRID:SCR_003070 software (National Institutes of Health, Bethesda, MD, USA). The program was set using the microscope calibration slide (transmitted light object micrometer) OMP (LOMO-MA, Russia). We used Straight Line mode to measure eggs, and Segmented Line mode for larvae.

### *2.2. DNA Analysis*

The DNA was extracted individually from L1 or L3 by digestion with Proteinase K [23]. For species identification, a PCR was performed. To obtain a partial sequence of the internal transcribed spacer (ITS rDNA), we used the forward primer 18S (TTG ATT AGG TCC CTG CCC TTT) and the reverse primer 26S (TTT CAC TCG CCG TTA CTA AGG) [24]. The amplification conditions used were: an initial 5 min denaturation at 94 °C, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 60 s, and extension at 72 °C for 60 s, with a final elongation step at 72 °C for 5 min.

The ITS2 region of the internal transcriber spacer was amplified using the forward primer NC1 (ACG TCT GGT TCA GGG TTG TT) and the reverse primer NC2 (ATG CTT AAG TTC AGC GGG T) designed by Gasser et al. [25]. The amplification conditions used were: an initial 3 min denaturation at 95 °C, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 54 °C for 45 s, and extension at 72 °C for 60 s, with a final elongation step at 72 °C for 5 min.

For the partial sequence of the D2 and D3 domains of LSU rDNA (28S rDNA), we used the forward primer LSU391 (AGC GGA GGA AAA GAA ACT AA) [26] and the reverse primer LSU501 (TCG GAA GGA ACC AGC TAC TA) [27]. The amplification conditions used were: an initial 3 min denaturation at 95 °C, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 52 °C for 35 s, and extension at 72 °C for 60 s, with a final elongation step at 72 °C for 5 min.

Targeting the mitochondrial cytochrome c oxidase subunit I (COX1 mtDNA), we used the forward primer COI_F1 (CCT ACT ATG ATT GGT GGT TTT GGT AAT TG) and the reverse primer COI_R2 (GTA GCA GAC GTA AAA TAA GCA CG) [28]. The amplification conditions used were: an initial 5 min denaturation at 95 °C, followed by 35 cycles of denaturation at 95 °C for 45 s, annealing at 52 °C for 50 s, and extension at 72 °C for 60 s, with a final elongation step at 72 °C for 5 min.

For each run, the final elongation phase was followed by a cooling to 12 °C. Reagent-only (no DNA) reactions were used as negative controls to detect potential contamination.

The results of the PCR were visualized in a 1% agarose gel. Bands of expected molecular weight were excised, and DNA was extracted using the Wizard SV Gel and PCR Clean-Up System (Promega, Madison, WI, USA). After cleaning the PCR product with an ethanol precipitation in the presence of ammonium acetate, the samples were directly sequenced by Genotech® (Moscow, Russia). Obtained chromatograms were analyzed using Chromas 2.6.6. RRID:SCR_000598 (Technelysium Pty Ltd., Brisbane, Australia). The sequences similar to those of the studied material were searched for in GenBank using BLASTN 2.13.0+ [29,30].

## 3. Results

Eggs of trematodes, cestodes, and nematodes, as well as the first-stage larvae (L1) of nematodes, were found in reindeer feces. Third-stage larvae (L3) were obtained via coproculture in some cases. Parasites were preliminarily identified based on their morphology and morphometric data. Where possible, DNA-based identification was performed (Table 2).

**Table 2.** Species of parasitic nematodes recovered from reindeer feces and identified genetically.

| Sample Set ID | Species | GenBank [1] | Vouchers [2] |
|---|---|---|---|
| 1 | *Orthostrongylus* sp. [3] | OL700043 (for LSU)<br>OL700044 (for ITS2) | IPEE_Parasites 14284<br>IPEE_Parasites 14284 |
| 1 | *Varestrongylus eleguneniensis* [3] | OM743794 (for ITS2)<br>OL743795 (for ITS2) | IPEE_Parasites 14298<br>IPEE_Parasites 14299 |
| 10 | *Elaphostrongylus rangiferi* [4] | OQ731723 (for ITS)<br>OQ730416 (for COX1)<br>OQ746340 (for LSU) | IPEE_Parasites 14310<br>IPEE_Parasites 14310<br>IPEE_Parasites 14310 |
| 12 | *Elaphostrongylus rangiferi* [4] | OQ731722 (for ITS2) | IPEE_Parasites 14309 |
| 13 | *Ostertagia arctica* [4] | OQ726410 (for ITS2) | IPEE_Parasites 14311 |
| 13 | *Nematodirella longissimespiculata* [4] | OQ726409 (for ITS2) | IPEE_Parasites 14312 |

[1] GenBank accession numbers for sequences from the individual first larval stage (L1) or third larval stage (L3) of representative species. [2] Voucher specimens with definitive identifications and accession numbers archived in the Museum of Helminthological Collections of the Parasitology Center at the A. N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences (Moscow, Russia). [3] Possibly, *O. macrotis*. Sequence previously in GenBank as reported by Loginova et al. [31]. [4] Sequence information reported here for the first time.

Diagnostic stages of helminths obtained from reindeer feces are shown in Figure 2.

Eggs of cestodes and nematodes, as well as first-stage larvae (L1) of nematodes, were found in the feces of muskoxen and snow sheep. Parasites were preliminarily identified based on their morphology and morphometric data. Diagnostic stages of these helminths are shown in Figures 3 and 4, respectively.

The diversity and distribution of helminths found in reindeer, muskoxen, and snow sheep via coproscopy are summarized in Table 3.

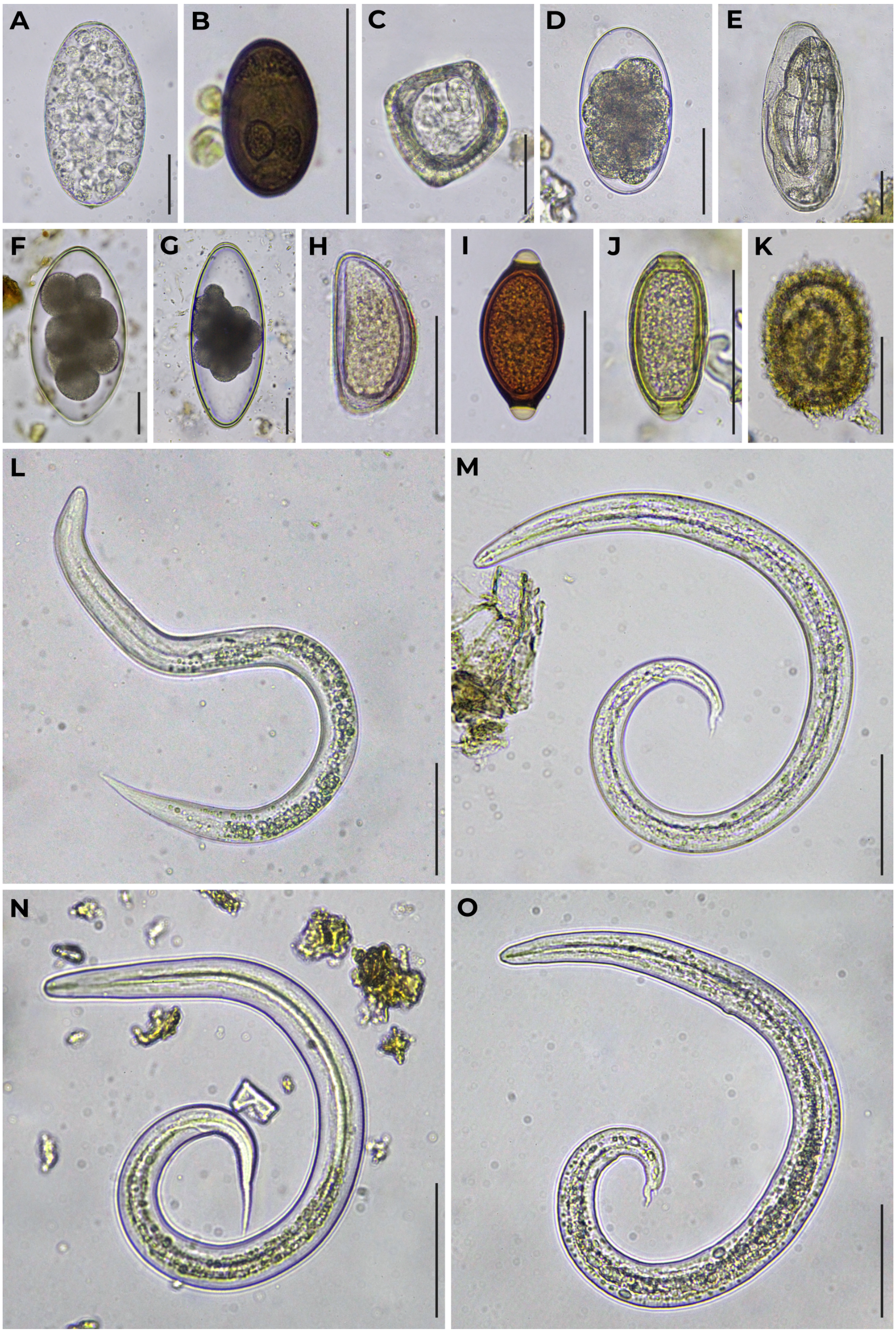


**Figure 2.** Diagnostic stages of helminths obtained from feces of reindeer (*R. tarandus*). (**A**) *Paramphistomum* sp. egg; (**B**) *Dicrocoelium* sp. egg; (**C**) *Moniezia* sp. egg; (**D**) Strongyle-type egg; (**E**) *Marshallagia* sp. egg (embryonated, dead); (**F**) *Nematodirus* sp. egg; (**G**) *Nematodirella longissimespiculata* egg; (**H**) *Skrjabinema tarandi* egg; (**I**) *Trichuris* sp. egg; (**J**) *Capillaria* sp. egg; (**K**) Possibly, *Ascaris mosgovoyi* egg (embryonated, dead); (**L**) *Dictyocaulus* sp. first-stage larva (L1); (**M**) *Elaphostrongylus rangiferi* L1; (**N**) *Orthostrongylus* sp. (possibly, *O. macrotis*) L1; (**O**) *Varestrongylus eleguneniensis* L1 (dead). Bright field microscopy, 40× objective lens magnification. Scale bar equals 50 μm.

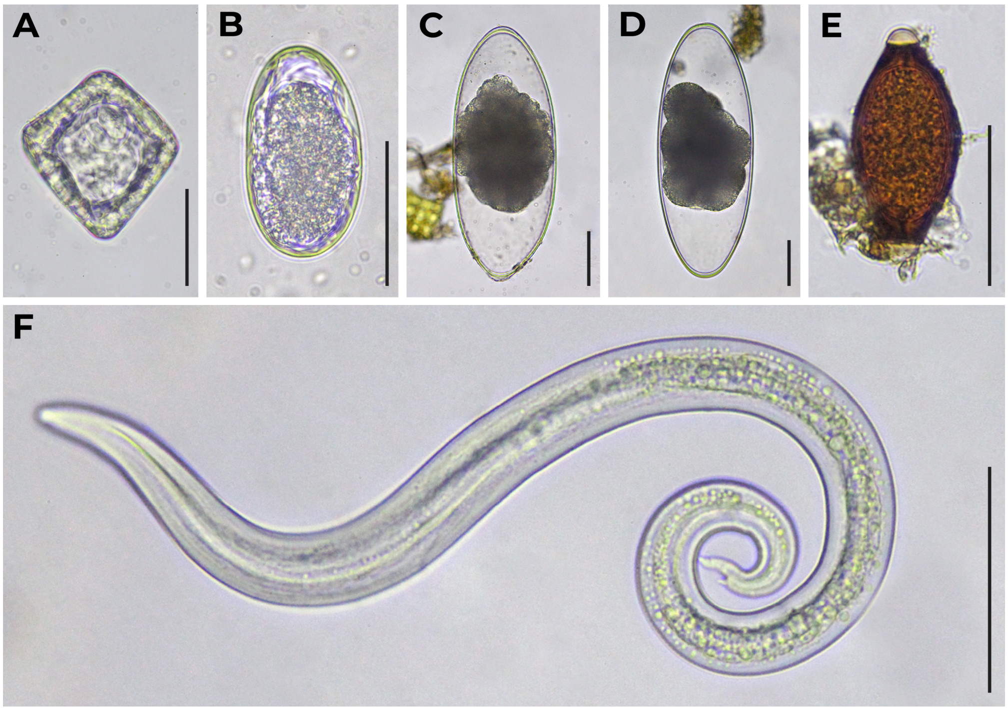


**Figure 3.** Diagnostic stages of helminths obtained from feces of muskoxen (*O. moschatus*). (**A**) *Moniezia* sp. egg; (**B**) Strongyle-type egg; (**C**) *Nematodirus* sp. egg; (**D**) *Nematodirella* sp. egg; (**E**) *Trichuris* sp. egg; (**F**) first-stage larva (L1) of the family Protostrongylidae. Bright field microscopy, 40× objective lens magnification. Scale bar equals 50 μm.

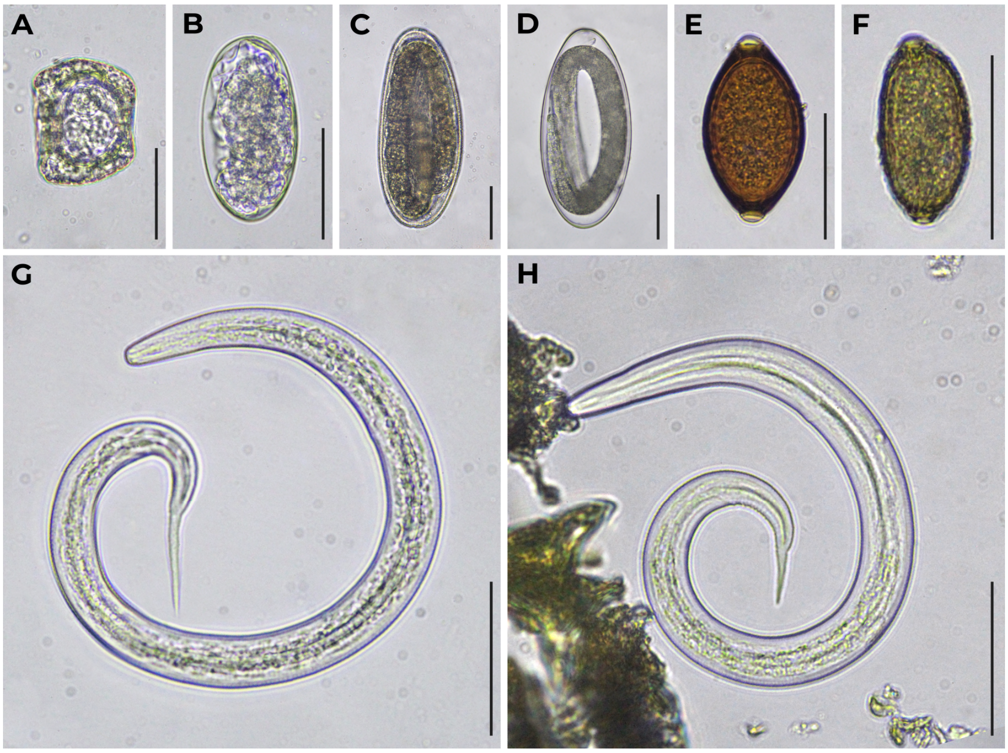


**Figure 4.** Diagnostic stages of helminths obtained from feces of snow sheep (*O. nivicola*). (**A**) *Moniezia* sp. egg; (**B**) Strongyle-type egg; (**C**) *Marshallagia* sp. egg (embryonated, dead); (**D**) *Nematodirus* sp. egg (embryonated); (**E**) *Trichuris* sp. egg; (**F**) Capillarid-type egg; (**G**) *Protostrongylus* sp. first stage larva (L1) with a longer tail spike (sample set #23); (**H**) *Protostrongylus* sp. L1 with a shorter tail spike (sample set #24). Bright field microscopy, 40× objective lens magnification. Scale bar equals 50 μm.

**Table 3.** Helminths found in the feces of reindeer, muskoxen, and snow sheep.

| | | Trematodes | | Cestodes | Nematodes | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Sample Set ID** | **Host Species** | ***Paramphistomum* sp.** | ***Dicrocoelium* sp.** | ***Moniezia* sp.** | **Strongyle-Type** | ***Marshallagia* sp.** | ***Nematodirus* sp.** | ***Nematodirella* sp.** | ***Dictyocaulus* sp.** | **Protostrongylidae** | ***Skrjabinema* sp.** | ***Trichuris* sp.** | **Capillarid-Type** | **Ascaris-Type** |
| 1 | Wild reindeer (*Rangifer tarandus*) | 9 (47%) | – | – | 15 (79%) | – | 1 (5%) | – | – | 1 (5%) [3]<br>3 (16%) [4] | – | – | – | – |
| 2 | | – | – | – | 1 (33%) | – | – | – | – | – | – | – | – | – |
| 3 | | – | – | – | 1 (50%) | – | – | – | – | – | – | – | – | – |
| 4 | | – | – | – | 11 (73%) | 1 (7%) | – | – | – | – | – | – | – | – |
| 5 | | – | – | – | 14 (67%) | – | – | – | – | 4 (19%) [5] | – | – | – | – |
| 6 | | – | – | – | 11 (100%) | – | – | – | – | – | – | 1 (9%) | – | – |
| 7 | Semiwild reindeer (*R. tarandus*) | – | – | 2 (4%) | 44 (88%) | – | 1 (2%) | – | – | 6 (12%) [5] | – | – | – | – |
| 8 | | – | 1 (2%) | 16 (27%) | 47 (80%) | – | 18 (31%) | 11 (19%) | – | 12 (21%) [5] | 2 (3%) [9] | – | – | – |
| 9 | | – | – | 1 (50%) | 2 (100%) | – | – | – | – | – | – | 1 (50%) | – | – |
| 10 | | – | – | – | 15 (50%) | – | 7 (23%) | – | – | 21 (70%) [6] | – | – | 12 (40%) [10] | – |
| 11 | | 8 (26%) | – | – | 6 (19%) | – | – | – | 1 (3%) | 16 (52%) [5] | – | – | – | – |
| 12 | | 9 (45%) | – | – | 1 (5%) | – | – | – | 1 (5%) | 6 (30%) [6] | – | – | 3 (15%) [10] | – |
| 13 | | – | – | 2 (5%) | 27 (64%) [1] | – | 4 (10%) | 5 (12%) [2] | 2 (5%) | – | – | – | 14 (33%) [10] | – |
| 14 | | – | – | – | 4 (57%) | – | – | – | – | 4 (57%) [5] | – | – | 1 (14%) [10] | – |
| 15 | | – | – | – | 4 (40%) | – | – | – | – | – | – | – | – | – |
| 16 | | – | – | 2 (7%) | 18 (60%) | – | – | – | – | – | 2 (7%) [9] | – | – | 1 (3%) [11] |
| 17 | | – | – | – | – | – | 2 (25%) | 3 (38%) | – | – | – | – | – | – |
| 18 | Muskoxen (*Ovibos moschatus*) | – | – | 2 (6%) | – | – | 1 (3%) | – | – | 19 (54%) [5] | – | 1 (3%) | – | – |
| 19 | | – | – | 4 (17%) | 3 (13%) | – | – | 1 (4%) | – | – | – | – | – | – |
| 20 | | – | – | – | 2 (33%) | – | – | – | – | – | – | – | – | – |
| 21 | | – | – | – | 6 (24%) | – | – | – | – | – | – | – | – | – |
| 22 | | – | – | 1 (3%) | 9 (30%) | – | 1 (3%) | – | – | 8 (26%) [5] | – | – | – | – |
| 23 | Snow sheep (*Ovis nivicola*) | – | – | – | – | 4 (19%) | – | – | – | 16 (76%) [7] | – | 4 (19%) | – | – |
| 24 | | – | – | 2 (15%) | – | 7 (54%) | 1 (8%) | – | – | 9 (69%) [8] | – | 5 (39%) | 1 (8%) | – |
| 25 | | – | – | – | 1 (20%) | – | – | – | – | – | – | – | – | – |

[1] Including *Ostertagia arctica*. [2] *Nematodirella longissimespiculata*. [3] *Orthostrongylus* sp. (possibly, *O. macrotis*). [4] *Varestrongylus eleguneniensis*. [5] Dorsal-spined larvae (DSL). [6] *Elaphostrongylus rangiferi*. [7] *Protostrongylus* sp. with a longer tail spike. [8] *Protostrongylus* sp. with a shorter tail spike. [9] *Skrjabinema tarandi*. [10] *Capillaria* sp. [11] Possibly, *Ascaris mosgovoyi*.

Except for one case, all the samples showed low parasitic intensity (in terms of GOST R 54627-2011). We found 1–10 eggs of trematodes per 1 g of feces, and 1–100 eggs/larvae of cestodes/nematodes per 1 g of feces. Only one sample from semiwild reindeer (#12) contained 45 eggs of *Paramphistomum* sp. per 1 g. The latter is interpreted as medium intensity (GOST R 54627-2011).

## 4. Discussion

The following trematodes were reported for *R. tarandus*: *Cotylophoron skrjabini*, *Dicrocoelium* sp., *Fasciola hepatica*, *Fascioloides magna*, *Fischoederius elongatus*, *Liorchis* sp., and *Paramphistomum* sp. [14,19,32,33] (*C. skrjabini* and *Liorchis* sp. were subsequently placed in synonymy with *Paramphistomum* sp. [34]). All of them can be detected via coproscopy. The eggs of rumen flukes *F. elongatus* and *Paramphistomum* sp. are highly similar. Their size ranges overlap: length and width of *F. elongatus* (125–135 × 65–70 µm) fit in with the criteria for *P. cervi* (114–176 × 60–90 µm) [35]. However, *F. elongatus* was reported only once for reindeer in Buryatia (Russia) [36], of which the southern boundary is 57.09183 N. Thus, we assumed that all typical-looking eggs found in wild and semiwild reindeer feces belonged to *Paramphistomum* sp. (we aim to investigate them genetically in the future). Feces were collected at different times of day, which could have affected the egg count, as a rise of egg excretion was reported for the afternoon time [37]. *D. dendriticum* (syn. *D. lanceatum*) and *D. chinensis* (cyn. *D. orientalis*) were both reported for reindeer. The dimensions of their eggs were also overlapping and host-species (host-size)-dependent [38]. Therefore, egg morphology and morphometrics allows us only genus identification. Among the cestodes available for coproscopy in reindeer, there are: *Avitellina arctica*, *Moniezia baeri*, *M. benedeni*, *M. expansa*, *M. mizkewitschi*, *M. rangiferina*, *M. taymirica*, *Thysaniezia giardi*, and possibly *Thysanosoma* sp. [14,19,32,33]. Only the eggs of *Moniezia* were detected in our study. Given that the Moniezia taxonomy requires thorough investigation (due to the recovery of cryptic species), prior to further DNA analysis, nothing can be added to our identification [39]. Nematodes are the most widespread helminths in reindeer, and the majority of them can be revealed through feces examination. Those include: gastrointestinal nematodes (GINs) (fam. Cooperiidae, Haemonchidae, Molineidae, and Trichostrongylidae), lungworms of the genus *Dictyocaulus*, representatives of Protostrongylidae, the pinworm *Skrjabinema tarandi*, the whipworm *Trichuris* sp., a few species of *Capillaria*, and *Ascaris mosgovoyi* [14,19,32,33]. GINs include *Cooperia*, *Haemonchus*, *Ostertagia*, *Trichostrongylus*, and other genera. The differential traits of their eggs are subtle and lack certain genera. Therefore, eggs of this type are called Strongyle-type eggs [22]. They were the most numerous in this study. In one case, we managed to get L3 and perform its DNA analysis. It resulted in *O. arctica* (cyn. *O. gruehneri*) detection in reindeer from the Bering Island (sample set #13). *Marshallagia* sp. eggs were recovered only in Svalbard (Norway) reindeer, which is consistent with scientific literature data reporting no findings of *Marshallagia* sp. in Russian reindeer [14,19,32,33]. Alternatively, the absence of *Marshallagia* in Russian reindeer feces can be due to its specific habitat requirements (high Arctic islands with low rainfalls) combined with seasonal egg production (highest during winter) [32,33,40]. Thus, it is desirable to sample feces from the most northern territories in the winter time, which is extremely difficult. For Svalbard reindeer, *M. marshalli* was reported [32,33,40]. Egg dimensions for this species were estimated as follows: 180–187 × 80–100 µm [41]. Meanwhile, in this study, the recovered *Marshallagia* egg (the only one found) was significantly bigger: 217 × 91 µm. Specific egg and L1 traits [42] support genus identification, but DNA analysis is highly desirable for this polymorphic helminth [43,44]. Reported *Nematodirus* species in reindeer included mostly these two: *N. skrjabini* and *N. tarandi* [19,32,33], and their synonymy is suggested. In this study, we discovered *Nematodirus* eggs of at least three morphological types; hence, further investigation of *Nematodirus* diversity in reindeer is needed and DNA analysis is essential. *Nematodirella longispiculata* and *N. longissimespiculata* are known for *R. tarandus* [19,32,33]. We identified our findings based on their morphology only up to the genus [45,46]. Three species of *Capillaria* were reported for reindeer: *C. brevipes*, *C. rangiferi*, and *Capillaria* sp., found by Kadenazii in 1963 [19]. The egg size ranges of these species overlap and their validity is questionable. Therefore, all the capillarid-type eggs in the reindeer were identified as *Capillaria* sp. Numerous findings of *Capillaria*, GINs (including *Nematodirus* and *Nematodirella*), and *Moniezia* in semiwild reindeer in contrast to the wild ones have brought up a suggestion that the physiology and tolerance of semiwild reindeer against some parasites may be genetically constrained (due to boreal conditions and the tundra-type origin of domestic animals) [33,47–50]. In fact, we have also found *Capillaria*, *Moniezia*, and *Nematodirella* only in semidomestic reindeer (Table 3). Yet, the interpretation of this fact requires accuracy to avoid survivorship bias [51]. *Capillaria*, GINs (including *Nematodirus* and *Nematodirella*), and *Moniezia* are more often found in calves than adults [19,33,49]. Fecal sampling of domestic reindeer involves many calves due to the specificity of this industry. Animals are most available during preslaughter examination. The most promising (healthy) reindeer are supposed to stay in the main herd (which can consist of a thousand animals), whereas "excessive" yearlings and weak old reindeer are supposed to be killed for meat and other products. Thus, more infected animals are fecal-sampled. In wild reindeer, the situation is usually quite reverse. Herds are also divided throughout the year (naturally) so that males are separate from females with calves. It is mostly small groups of males that are fecal-sampled alive, whereas the most weak and infected animals die themselves or become the prey of predators out of sight of researchers, and thus escape inclusion in the studies. Only sample set #1 was obtained from a group of wild reindeer including calves, and it also showed a higher parasitic load. Seasonal egg production of different parasites, as well as the sampling season, should be considered while interpreting the results [19,33]. The same holds for *Dictyocaulus* L1s that we found only in semiwild reindeer (including feralized animals from the Bering Island). DNA analyses are required to clarify the species (*D. murmanensis* and *D. eckerti* were reported [19]), especially in light of the recent discovery of new species of this genus in cervides [52,53]. Among the fam. Protostrongylidae, only *Elaphostrongylus rangiferi* was reported previously for reindeer in Russia [19]. We have found its DSL in semiwild reindeer (sample set #10 and 12) and supported our findings with DNA analyses (Table 2). Moreover, DSL were found in six other sample sets (both from wild and semiwild animals). Surprisingly, our attempt to confirm *E. rangiferi* for L1 from sample set #1 resulted in identifying *Varestrongylus eleguneniensis*—another (newly described) protostrongylid reported for *R. tarandus* in the Nearctic [54,55]. Even more surprising was a finding of non-DSL L1 of Protostrongylidae in the same sample set. DNA analysis resulted in *Orthostrongylus* sp. identification (Table 2). To date, the only species known from this genus is *O. macrotis* [56]. *Orthostrongylus* sp. has never been reported in *R. tarandus* before, nor has it been reported in the Palearctic [31,57]. *Trichuris baskakowi*, *T. globulosa*, *T. longispiculus*, *T. massino*, *T. ovis*, and *T. tarandi* were reported for reindeer [19]. Their egg ranges overlap, and the validity is questionable. Therefore, we identified our findings (both in wild and semiwild reindeer) as *Trichuris* sp. These worms were also found more frequently in young animals [33], which corresponds at least to sample set #10 (where we know that calves were present). *Skrjabinema tarandi* is a serendipitous finding during coproscopy due to the specific life cycle of this parasite [19,33]. More reliable methods include examinations of perianal deposits or cellophane (Scotch) tape tests [58]. However, it is still found from time to time [33,59]. In this study, *S. tarandi* was found only twice in semiwild reindeer (sample set #8 and #16) [60]. *Ascaris mosgovoyi* is an Ascaris-type helminth described for reindeer in 1959 [19]. It was described only via males; no pictures or descriptions of its eggs are available. That might be a reason why scientists were not reporting it (or looking for it) later on. However, an egg shown in Figure 2K is, in our opinion, *A. mosgovoyi* due to its specific traits (including larvae), size, and host. Further investigation and DNA analysis are highly desirable.

No trematodes were found in the muskoxen feces. Known cestodes reported for them and available for coprology include: *M. expansa* and *Moniezia* sp. [32]. *M. expansa* eggs tend to be triangular in shape in slides; therefore, we identify our findings as *Moniezia* sp., since they looked squarer. GINs, found in the muskoxen feces, were Strongyle-type nematodes, *Nematodirus* sp., and *Nematodirella* sp., which corresponds to the literature data. In particular, *Teladorsagia boreoarcticus* (Strongyle-type), *Nematodirella* alcidis, *N. gazelli*, *N. longissimespiculata*, as well as *Nematodirus helvetianus* and *N. tarandi*, were reported for muskoxen in North America [32]. The following protostrongylids were reported for muskoxen: *Protostrongylus stilesi*, *Umingmakstrongylus pallikuukensis*, and *V. eleguneniensis* [32]. The latter two species produce DSL. Given that all Russian muskoxen are offspring of animals (re-)introduced from North America back in the XX century [15–18], we expect that the DSL found might belong to one (or both) of these species. Taking into account *V. eleguneniensis* found in reindeer, we suggest that introduced animals could have been the source of Nearctic protostrongylids. Further thoughtful investigation (including DNA analysis and animal travel history) is needed. *Trichuris* spp. were found at a low prevalence both on the North American mainland (yet no Banks Islands) [32] and in this study.

Regarding snow sheep, the following helminths were reported for them: flatworm *Stilesia* sp., tapeworms *Moniezia benedeni*, *M. expansa*, *M. rangiferina*, *M. taymirica*, and *Moniezia* sp., GINs (including *Marshallagia mongolica*, *Nematodurus oiratianus*, *Nematodirus* sp., *Nematodirella longissimespiculata*, and *Nematodirella* sp., as well as *Ostertagia arctica Ostertagia* sp. and *Teladorsagia circumcincta*), protostrongylids (*Protostrongylus* sp. and *Spiculocaulus leuckarti*), *Skrjabinema ovis*, *S. chubuki*, *Truchuris skrjabini*, *T. ovis*, and *Trichuris* sp. [13,14]. We found *Moniezia* sp., GINs (including *Marshallagia* sp., *Nematodurus* sp., and Strongyle-type), protostrongylids (*Protostrongylus* sp.), *Truchuris* sp., and the Capillarid-type helminth (Figure 4). Notably, the *Protostrongylus* L1s were of two morphological types: the ones with a longer tail spike (from the sample set #23) and the ones with a twice-shorter tail spike (sample set #24). *Marshallagia* sp. eggs found were also (as in Svalbard reindeer) bigger than expected. Further investigation is needed.

Ranges of snow sheep in this study were independent and separated from each other and other northern ungulates. Therefore, their helminth fauna probably suggests certain autonomy. Wild reindeer from Taymyr (sample set #1) might have been sympatric to introduced muskoxen (#20, 21). Yamal muskoxen (#18, 22) might be sympatric to Yamal semiwild reindeer (these were not studied here). Muskoxen on the Wrangel Island (#19) were sympatric with introduced and ferallized semiwild reindeer. However, by 2023, those reindeer herds died out. Wild reindeer from the Murmansk Oblast (sample set #5) were not supposed to be in sympatry with domestic herds. Information regarding other populations and their sympatry with domestic and wild ungulates is fragmentary and barely reliable.

Apart from the true parasites (helminths) of the studied wild ruminants, spurious and pseudoparasites were also found. Among them were Bdelloid rotifers at their different stages (Figure A1). In dried fecal samples, they revived after adding water [61]. They could have contaminated the feces after excretion (since material was often picked up from the ground). Alternatively, rotifers were accidentally ingested and managed to survive inside the ruminants. To the authors' knowledge, Arctic ruminants have never been considered as vectors for rotifers. Given that reindeer cover long distances daily, they might play a major role in the rotifers' distribution. We welcome specialists on rotifers to collaborate.

## 5. Conclusions

The diversity of helminths in wild and semiwild reindeer, muskoxen, and snow sheep was studied using a noninvasive method (coproscopy). In *R. tarandus*, two genera of trematodes (*Paramphistomum* and *Dicrocoelium*) were found, as well as one genus of cestodes (*Moniezia*), and various nematodes: small gastrointestinal nematodes, *Marshallagia* sp., *Nematodirus* spp. (three different morphological types), *Nematodirella* sp. (including *N. longissimespiculata*), *Skrjabinema tarandi*, *Trichuris* sp., *Capillaria* spp., (possibly) *Ascaris mosgovoyi*, *Dictyocaulus* sp., *Elaphostrongylus rangiferi*, *Orthostrongylus* sp. (possibly, *O. macrotis*), and *Varestrongylus eleguneniensis*. A micrograph of what we believe to be *A. mosgovoyi* is presented for the first time. This is the first report of *V. eleguneniensis* in the Palearctic. This is also the first report of *Orthostrongylus* sp. both in relation to *R. tarandus* and to the Palearctic.

In *O. moschatus*, no trematodes, one genus of cestodes (*Moniezia*), and various nematodes (small GINs, *Nematodirus* sp., *Nematodirella* sp., *Trichuris* sp., and the DSL of Protostrongylidae) were found.

In *O. nivicola*, no trematodes, one genus of cestodes (*Moniezia*), and various nematodes (small GINs, *Marshallagia* sp., *Nematodirus* sp., *Trichuris* sp., Capillarid-type, and *Protostrongylus* spp.) were found. This is the first report of a Capillarid-type nematode (and its egg micrograph) in snow sheep.

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## Appendix A

Rotifers found in feces (including dried ones) of studied Arctic ruminants are shown in Figure A1.

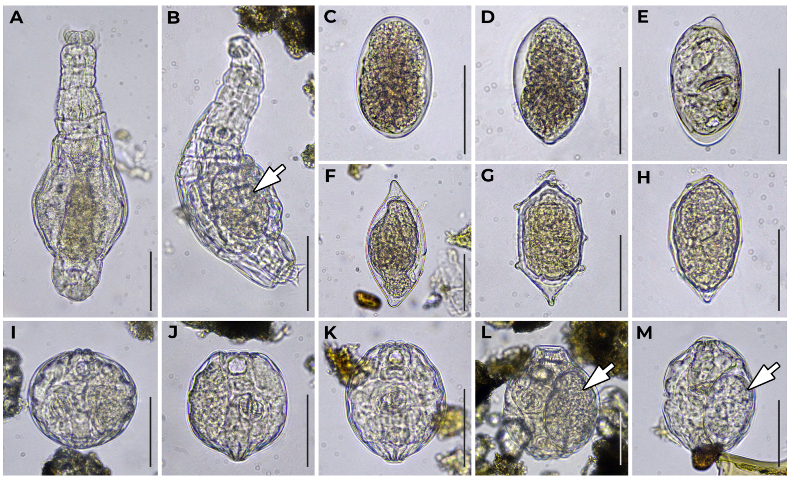


**Figure A1.** Bdelloid rotifers obtained from feces of reindeer (*R. tarandus*), muskoxen (*O. moschatus*), and snow sheep (*O. nivicola*). (**A**) Active rotifer from reindeer; (**B**) Active rotifer with an egg (arrow) from snow sheep; (**C**) Oval rotifer egg from reindeer; (**D**) Oval rotifer egg with polar protrusions from reindeer; (**E**) Oval rotifer egg with polar protrusion from muskox; (**F**) Lemon-shaped rotifer egg from reindeer; (**G**) Angular rotifer egg with 8 visible protrusions from reindeer; (**H**) Angular rotifer egg with 10 visible protrusions from reindeer; (**I**) Inert rotifer from reindeer (reviving); (**J**) Inert rotifer from snow sheep (reviving); (**K**) Inert rotifer from muskox (reviving); (**L**) Inert rotifer (reviving) with an egg (arrow) from reindeer; (**M**) Inert rotifer (reviving) with an egg (arrow) from muskox. Bright field microscopy, 40× objective lens magnification. Scale bar equals 50 µm.

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