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D-shaped Nematode Eggs in the Feces of *Rangifer tarandus*: A Story in Pictures

Olga A. Loginova

A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

Corresponding author – Olga A. Loginova, email loginova_spb@bk.ru

Abstract

D-shaped nematode eggs in the feces of *Rangifer tarandus* are expected to be oxyurid nematodes (Nemata: Oxyurida) of the genus *Skrjabinema*. The species *S. tarandi* is considered species-specific for this host. There is no consensus regarding the cross-infection of reindeer and sheep with *S. ovis* and *S. tarandi*. The drawings proposed by descriptors complicate differential diagnostics. Micrographs of *S. tarandi* eggs obtained via light microscopy and scanning electron microscopy as well as photographs of *S. ovis* eggs and drawings made on their basis are proposed to confidently distinguish between representatives of these two species, taking into account morphometric data. Thus, the egg of *S. tarandi* has a thickening on the convex side, in contrast to the egg of *S. ovis*. It is shown that because of the specific feeding habits of *R. tarandus*, D-shaped eggs of parasitic nematodes of small rodents can also be found in their feces. The latter should be considered spurious parasites.

D-образные яйца нематод в фекалиях *Rangifer tarandus*: история в картинках
Логинова Ольга Александровна

Резюме

D-образные яйца нематод в фекалиях северного оленя, как ожидается, принадлежат оксиуридным нематодам (Nemata: Oxyurida) рода *Skrjabinema*. Вид *S. tarandi* считается видоспецифичным для этого хозяина. Нет единого мнения относительно перекрестного заражения северных оленей и овец нематодами *S. ovis* и *S. tarandi*. Рисунки, предложенные видоописателями, затрудняют дифференциальную диагностику. Предложены изображения яиц *S. tarandi*, полученные при световой и сканирующей электронной микроскопии, а также снимки яиц *S. ovis* (световая микроскопия) и выполненные на их основе рисунки, позволяющие уверенно различать представителей этих двух видов с учётом морфометрических данных. Так, яйцо *S. tarandi* имеет вздутие на выпуклой стороне, в отличие от яйца *S. ovis*. Показано, что из-за специфических пищевых привычек северных оленей в их фекалиях могут встречаться D-образные яйца нематод-паразитов мелких грызунов. Последних следует считать ложными паразитами.

Keywords: D-shaped egg, crescent-shaped, orange section, *Rangifer tarandus*, reindeer, caribou, *Skrjabinema*, *S. tarandi*, *S. ovis*, Oxyuridae, pinworm

Among different helminths that have been reported from reindeer/caribou (*Rangifer tarandus* L.), D-shaped eggs are known to be produced only by pinworms—nematodes of

the genus *Skrjabinema* within the family Oxyuridae (see Mizkewitsch, 1967; Kutz et al., 2019). *Skrjabin* and *Mizkewitsch* (1930) described the *Rangifer*-specific species *S.*

tarandi in the Palearctic. Later, Swales (1934) described *S. oreamni* from the mountain goat (*Oreamnos americanus*) in the Nearctic and placed *S. tarandi* in synonymy with *S. ovis*. Thus, *S. oreamni* was considered to be a species that infects both mountain goat and caribou; however, Skrjabin and his colleagues did not accept that idea (Skrjabin et al., 1960). Schad (1959) then suggested that Swales (1934) had studied heterogeneous material (a sample containing individuals of two different species), and consequently *S. oreamni* from the mountain goat should be considered synonymous with *S. ovis*, whereas *S. oreamni* from caribou should be synonymous with *S. tarandi*. Neiland (1972) mentioned *S. oreamni* in his report on caribou disease in Alaska as a helminth commonly found in caribou examined in the early 1950s (with reference to his personal communication with R.L. Rausch) and apparently rarely encountered in surveys conducted from 1970 to 1971.

Skrjabinema tarandi is not considered pathogenic (Oksanen, 1999, with reference to Soulsby, 1982), but it is difficult to attribute any pathogenesis that may be caused by *S. tarandi* since it is unlikely that a host would have no other parasites. Skrjabinemiasis is rarely diagnosed during the lifetime of semiwild or domestic reindeer (not to mention the wild ones) because of the specific nature of this industry: animals migrate long distances with their herder throughout the year. They are not accustomed to regular handling via veterinary checks and in particular to examinations of perianal deposits via cellophane Scotch-tape tests—which are the reliable diagnostic methods for pinworms in these animals (Greiner, 2014). Only relatively healthy animals that can withstand a long journey actually get to the veterinary control points before slaughter. Little is known about the parasitic abundance of reindeer that died on the way, and thus almost nothing is known about the impact on the health of *R. tarandus* by *S. tarandi*.

Even though *S. tarandi* has been known since 1930, information regarding the life cycle of these pinworms remains remarkably incomplete. Skrjabin and Mizkewitsch (1967) suggested that the life cycle is similar to that of *S. ovis* (see Skrjabin and Mizkewitsch, 1930; Skrjabin et al., 1960). That is, the life cycle of *S. tarandi* is direct, with one host, and closed, which is an ecological term coined by Paramonov (1962), referring to the fact that eggs do not hatch in the external environment and hatch only after being ingested by a reindeer (Schultz and Gvozdev, 1970). Kutz et al. (2019) wrote (evidently in error) that *Skrjabinema* eggs hatch as first-stage larvae (juveniles) in the environment. If *S. tarandi* is a typical zooparasitic pinworm, then females might migrate from intestines to the perianal area of the host to deposit eggs (Mizkewitsch, 1967; Greiner, 2014). This migration bothers a host, which

results in restless behavior. For reindeer it might include scratching, grooming, and shaking (Kynkäänniemi et al., 2014). Restless behavior takes time that otherwise might be spent for grazing and fat accumulation. That is, such behavior affects the body condition of reindeer (Kutz et al., 2012; Witter et al., 2012; Raponi et al., 2018). Overlapped with harassment by blood-feeding flies (mosquitoes, deer flies, and black flies), infection with pinworms may decrease an animal's chances for reproduction and survival, as a reduction of weight and organism stores diminishes the recruitment to the reindeer population (Colman et al., 2003; Kutz et al., 2012; Witter et al., 2012; Raponi et al., 2018; Benedict and Barboza, 2022). Therefore, there are knowledge gaps regarding *S. tarandi* actual life cycle and pathogenicity.

Some uncertainty seeps through the publications about *S. ovis* in ruminants (mostly domestic) and reindeer in particular. Thus, in discussing endoparasite treatment of *R. tarandus*, Oksanen (1999) presents a light micrograph of what is certainly an egg of *S. tarandi* yet labels it *Skrjabinema* sp. in the figure legend and gives the description of the egg only at the genus level, such as “markedly asymmetrical, rather like an orange section,” providing size ranges that appear to combine the morphometry of both *S. tarandi* and *S. ovis*. Verocai et al. (2020) offer a light micrograph of what appears to be exactly an egg of *S. ovis* labeled as “*Skrjabinema* sp. egg” for pinworms of small ruminants and so does Sabatini et al. (2023). Meanwhile, the question about possible exchange and sharing of the species *S. tarandi* and *S. ovis* between reindeer and small ruminants still has no answer. Some researchers assume there is potential for parasite cross-transmission, as indicated by the following reports: *Ostertagia gruehneri* transmitted from reindeer to sheep (Manninen et al., 2014) and *Nematodirus battus* transmitted from sheep to reindeer (Robertsen, 2020; Utaaker et al., 2023). Others indicate no transmission (Bye, 1987) or even take host specificity (narrow host range) of nematodes for granted and use the idea as a means to reduce anthelmintic usage in the control of gastrointestinal nematodes in cervids and bovids (Tapia-Escarate et al., 2021). We do not know if sympatry of sheep and reindeer is good, bad, or neutral in terms of ecological fitting (Janzen, 1985) (also known as host-switching) of species of *Skrjabinema*. There were (and still are) difficulties in distinguishing species of *Skrjabinema* found in reindeer, whether they are adults or only the eggs (Fruetel and Lankester, 1989; Robertsen, 2020). Up to 24 February 2023, only 20 *Skrjabinema*-related sequences were available in the NCBI GenBank, and none are from parasites of *R. tarandus* (<https://www.ncbi.nlm.nih.gov/nuccore/?term=Skrjabinema>).

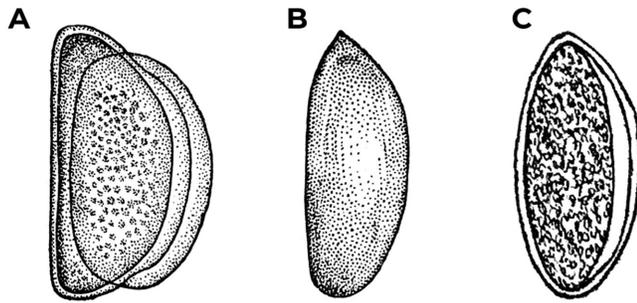


Figure 1. Drawings of *Skrjabinema* eggs. **A.** *S. tarandi* (after Mizkewitsch, 1967). **B.** *S. ovis* (after Skrjabin et al., 1960). **C.** *S. ovis* (after Polyakov, 1953).

Because of the lack of a connection between morphology and molecular characteristics of *Skrjabinema* eggs and the adult nematodes, the study of the eggs remains a starting point for any further investigation. *Skrjabinema tarandi* eggs are usually found serendipitously during routine fecal tests, and morphological comparisons of eggs can then serve as reliable criteria for differential diagnostics of adult females of *S. tarandi* vs. *S. ovis*. Clear, unambiguous descriptions of egg morphology are essential, preferably with digital images, so interpretation of the morphological characteristics of the egg does not have to be estimated; this is clearly demonstrated by the fact that drawings of *Skrjabinema* eggs are relatively useless for identification (Fig. 1).

The aim of this study is to offer diagnostic images of the eggs of pinworms from *Rangifer*.

Material and Methods

Egg sources

Studies of *S. tarandi* eggs were made from material derived partly from the feces of reindeer and partly from dissections of female pinworms.

Eggs of *S. tarandi* were found during a coprological survey for helminths of *R. tarandus* in the Palearctic started by the author in 2018. This study uses several technical methods, including macroscopic examination of feces, larvoscopy (Vajda's method), ovoscopy (flotation with Darling's solution and sedimentation in tap water), and coproculture (if needed). Eggs of *S. tarandi* were recovered from feces of semiwild reindeer from the following areas: Nenets Autonomous Okrug (Russia) in 2018 (2 eggs in 1 fecal sample, 35 samples total), wild reindeer from Arkhangelsk Region (Russia) in 2022 (1 egg, 21 samples total), and semi-wild reindeer from Chukotka Autonomous Okrug (Russia) in 2022 (2 eggs, 1 per sample, 30 samples total). Feces were picked up immediately after defecation and remained naturally moist.

All the eggs found were recovered using Vajda's method (Latypov, 2019), which includes placing 3–4 fecal pellets on a microscope slide, adding around 1 ml of 40°C tap water to wash out the pellets, removing the pellets 30 min later, and studying the remaining water. This method was developed to isolate nematode larvae; even so, eggs of helminths can occasionally be found.

Eggs of *S. ovis* found in the feces of sheep from the Rostov region (Russia) in 2022 using flotation were included in this study for comparison. This method requires using Darling's solution, which is a 1:1 mixture of saturated sodium chloride solution and glycerin (Latypov, 2019).

A D-shaped egg, different from both *S. tarandi* and *S. ovis* was found in feces of wild reindeer from the Arkhangelsk region in 2022 (1 egg, 11 samples total) using sedimentation. This specimen was also included in this study.

Twelve females of *S. tarandi* were collected on 16 October 1968 from the large intestine of *R. tarandus* in Chukotka Peninsula (Russia) by N.S. Nazarova. This material had been stored in formalin in a vial (#186695) at the Helminthological Museum (Moscow, Russia). Ten females were used in this study for egg examination. No less than 10 eggs were studied from each nematode.

Microscopy

Eggs found in feces were placed on a clean microscope slide with a drop of tap water and covered with a coverslip. The morphological characteristics were studied via light microscopy (LM) with an optical microscope Micmed-6 (LOMO-MA, Russia) equipped with phase contrast and dark field optics FATEK M 6-7 (LOMO-MA, Russia) under bright field, dark field, and phase contrast illumination using objective lenses with 4×, 10×, 20×, 40×, and 100× magnifications (the latter with oil immersion). Images were made using a digital photo camera 5D Mark II (Canon, Japan) connected to the microscope with a C-mount adapter (LOMO-MA, Russia). Morphometry was based on the micrographs using Fiji/ImageJ Version 1.2.4 RRID:SCR_003070 software (National Institutes of Health, USA) in straight line mode. The program was set using a microscope calibration slide (transmitted light stage micrometer) OMP (LOMO-MA, Russia).

Eggs derived from females of *S. tarandi* were studied using using a Nature STV-120M compact portable microscope (Kenko, China). Eggs were placed on a glass slide without any media or coverslip. Pictures were taken via camera of the smartphone Xperia XA2 DS (Sony, Japan).

Females were taken out of a vial, placed on a wafer, and manually sliced with a blade. Scanning electron microscopy (SEM) was performed using a Tabletop Microscope TM4000Plus (Hitachi, Japan) at low-voltage mode. No conductive coating was applied.

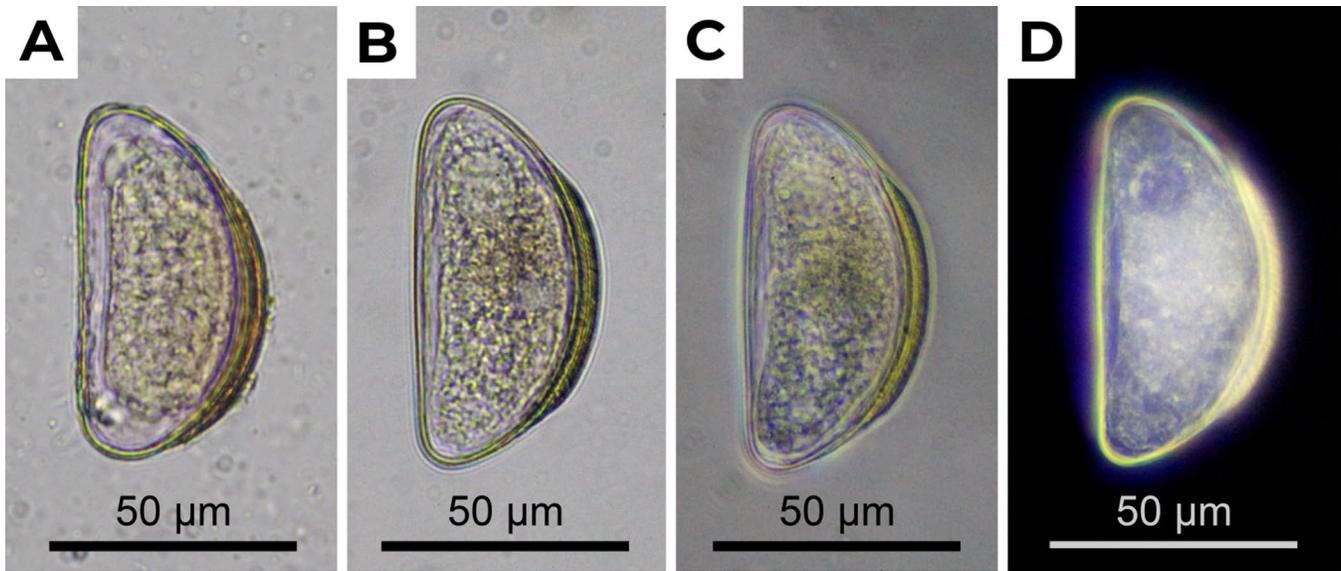


Figure 2. Light micrograph images of *S. tarandi* eggs taken at 400× magnification. **A.** Egg recovered from feces (bright field illumination). **B.** Egg dissected from female (bright field illumination). **C.** Egg dissected from female (phase contrast illumination). **D.** Egg dissected from female (dark field illumination). Eggs are in tap water on a slide under a coverslip.

Results and Discussion

Eggs of zooparasitic pinworm nematodes recovered from feces of *Rangifer* and those obtained directly from the uterus of female pinworms variously may or may not differ in size, shape, and proportions (Tetley, 1935, 1941). Therefore, it was a priority to discover how similar the eggs of *S. tarandi* obtained from feces and those dissected from females were to understand how reliable and interconvertible their images would be. Measurements of eggs from the feces ($n = 5$) were 68.6 (66–70) μm long by 35.6 (32–38) μm in maximum width. Eggs dissected from females ($n = 100$) were 72 (68–77) μm long and 35.3 (33–40) μm wide. The estimated size limits reported by Skrjabin and Mizkewitsch (1930) were 70–76 \times 36–46 μm . That is, grossly, all the eggs studied regardless of their origin met the criteria 0.07 \times 0.04 mm. The ratio of their length to width also remained constant and was around 1.9. Images of eggs obtained from feces and from females are presented in Figure 2.

Eggs of *S. tarandi* of different origin look quite alike. A diagnostically important feature of those D-shaped eggs is a thickening of the lobe of the capital D (Fig. 2). Skrjabin and Mizkewitsch described it as “heavy double-contoured bulging” (Skrjabin and Mizkewitsch, 1930). What can be seen by means of LM is that this structure does have a higher density than other parts of the eggshell, as it looks

darker under bright field illumination and lighter under dark field illumination. Also, fine diagonal striation of this structure can be spotted.

SEM provides a better look at the details of this structure as well as the general morphology of the *S. tarandi* egg (Fig. 3).

The eggshell seems heterogeneous, at least in its thickness in different parts of the eggs of *S. tarandi*. It is thickest (around 3 μm) at the bulge of the egg (right edge of the lobe of the capital D) and is thinnest (around 0.7 μm) on the opposite side (the lateral side of the stem of the capital D). All three zones can be distinguished in Figure 3C: the thinnest zone (on the left) looks the darkest, and the thickest (on the right) looks the lightest. The striation previously mentioned is probably caused by the tubular structure of the egg membrane. However, the distinct border of the thickening (“heavy double-contoured bulging”) is hardly seen.

Ornate eggs are widely presented among oxyurids. Thus, eggs of oxyurids that parasitize invertebrates can bear circular crests, longitudinal ridges, or excrescences also called bosses. These structures are sometimes referred to as lenses or resembling a lens (Shah et al., 2011; Carreno, 2018). Thickenings of *S. tarandi* eggs illuminated from above and captured without any media or coverslip do resemble lenses to some extent; however, this resemblance is not too prominent (Fig. 4).

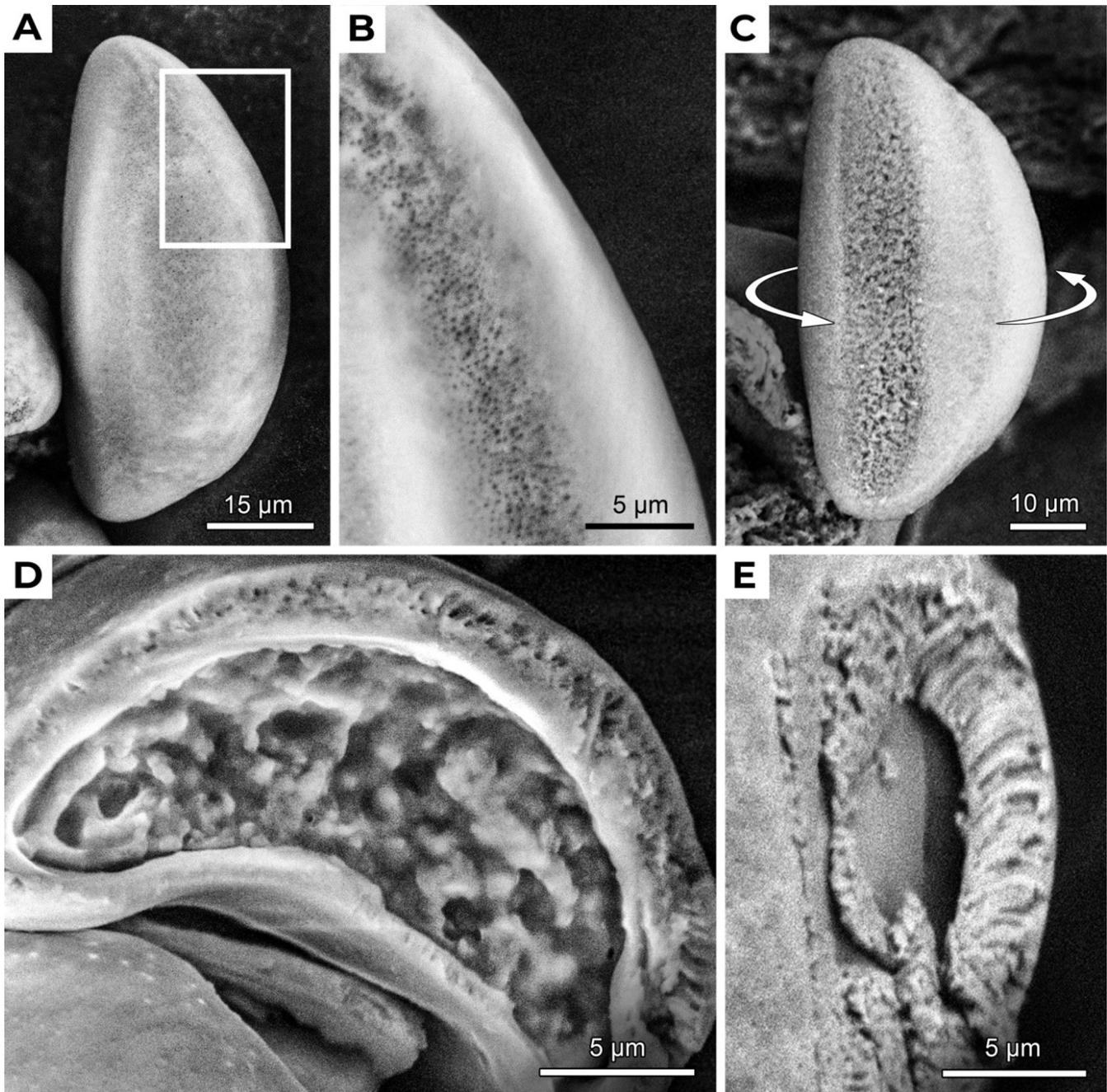


Figure 3. SEM micrographs of *S. tarandi* eggs dissected from females. **A.** Lateral view of an egg in D-shaped position. **B.** Magnified fragment of the previous image marked with rectangle, focused narrowly on the surface (speckled strip). **C.** General view of an egg slightly rotated clockwise around its longitudinal axis, so that a lateral side of the stem of the capital D can be seen. **D.** Cross-section of an egg. **E.** Magnified fragment of an egg bulge (part of the egg membrane is cut off).

The thickenings of *S. tarandi* eggs are visible at most magnifications with a light microscope (Fig. 5). Even at the level of detail provided by a 10× lens (100× total magnification), this structure can be seen. Fine striation is best visible via oil immersion (Fig. 5, E and J). The surface view of the thickening on the egg is reminiscent of the mantle of a slug.

It is difficult to offer any suggestions regarding a function of the thickening of the *S. tarandi* egg, given that some D-shaped (“crescent-shaped”) eggs of entomoparasitic oxyurids are nonornate (like *Leidyneema* sp.), but some species within the genus *Skrjabinema* are also nonornate. Thus, eggs of *S. ovis* are D-shaped but lack any thickenings (Fig. 6, A and D).

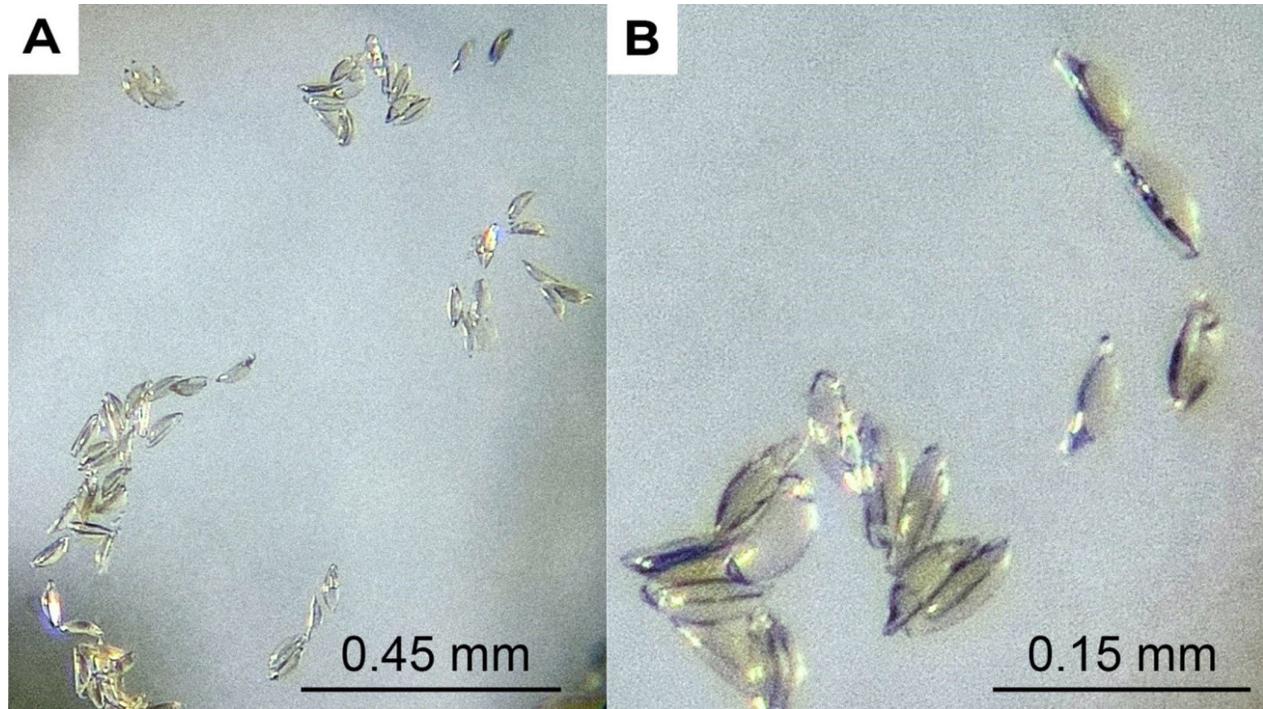


Figure 4. Light micrographs of *S. tarandi* eggs from females obtained via compact portable microscope. **A.** General view of the eggs placed on the glass slide without any media or coverslip and illuminated from above. **B.** Same as A but a magnified fragment.

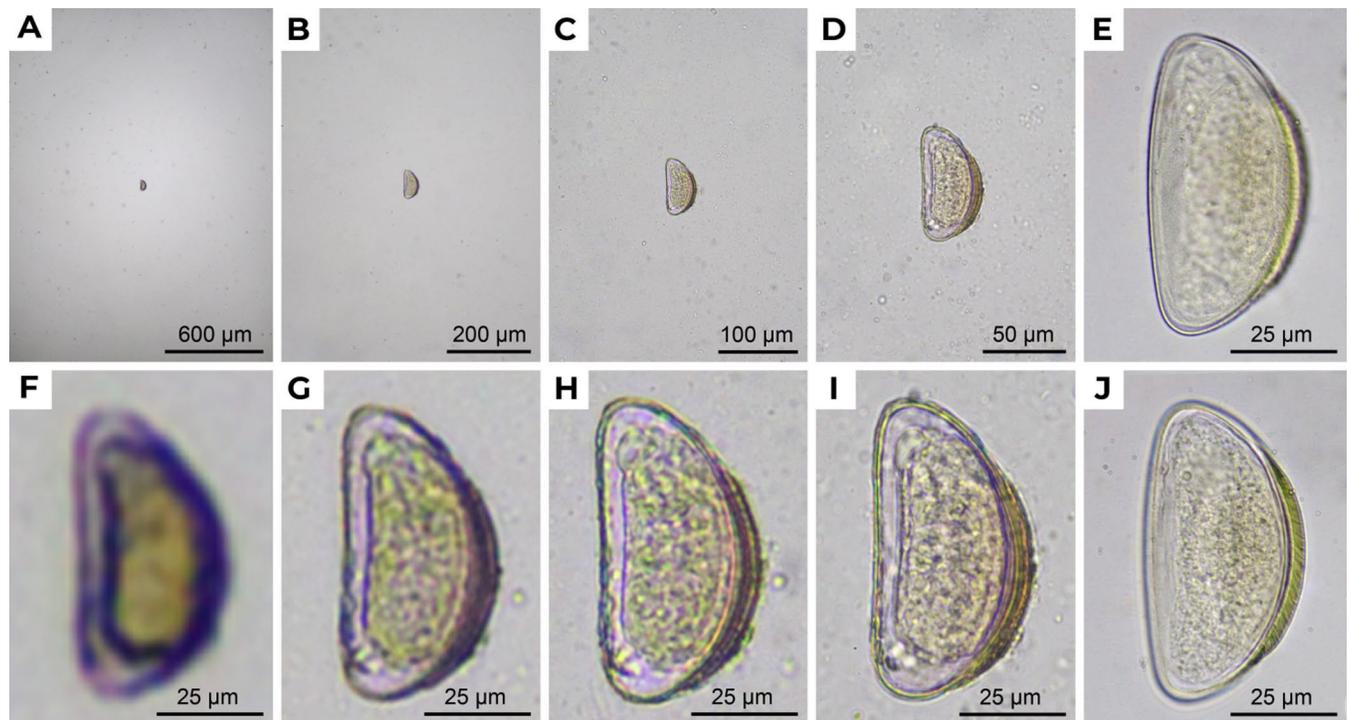


Figure 5. Light micrographs of *S. tarandi* eggs at different magnifications. **A.** Egg captured at 40×. **F.** Same as A, magnified. **B.** Egg captured at 100×. **G.** Same as B, magnified. **C.** Egg captured at 200×. **H.** Same as C, magnified. **D.** Egg captured at 400×. **I.** Same as D, magnified. **E.** Egg at 1000× (oil immersion), surface view. **J.** Same as E, optical section. **A–D, F–I.** Fecal egg. **E and J.** Egg dissectioned from female. **F–J.** Eggs in the same scale. Eggs are in tap water under coverslip. (Note that because of pressure on the coverslip by the objective lens using oil immersion the LM egg appears wider.)

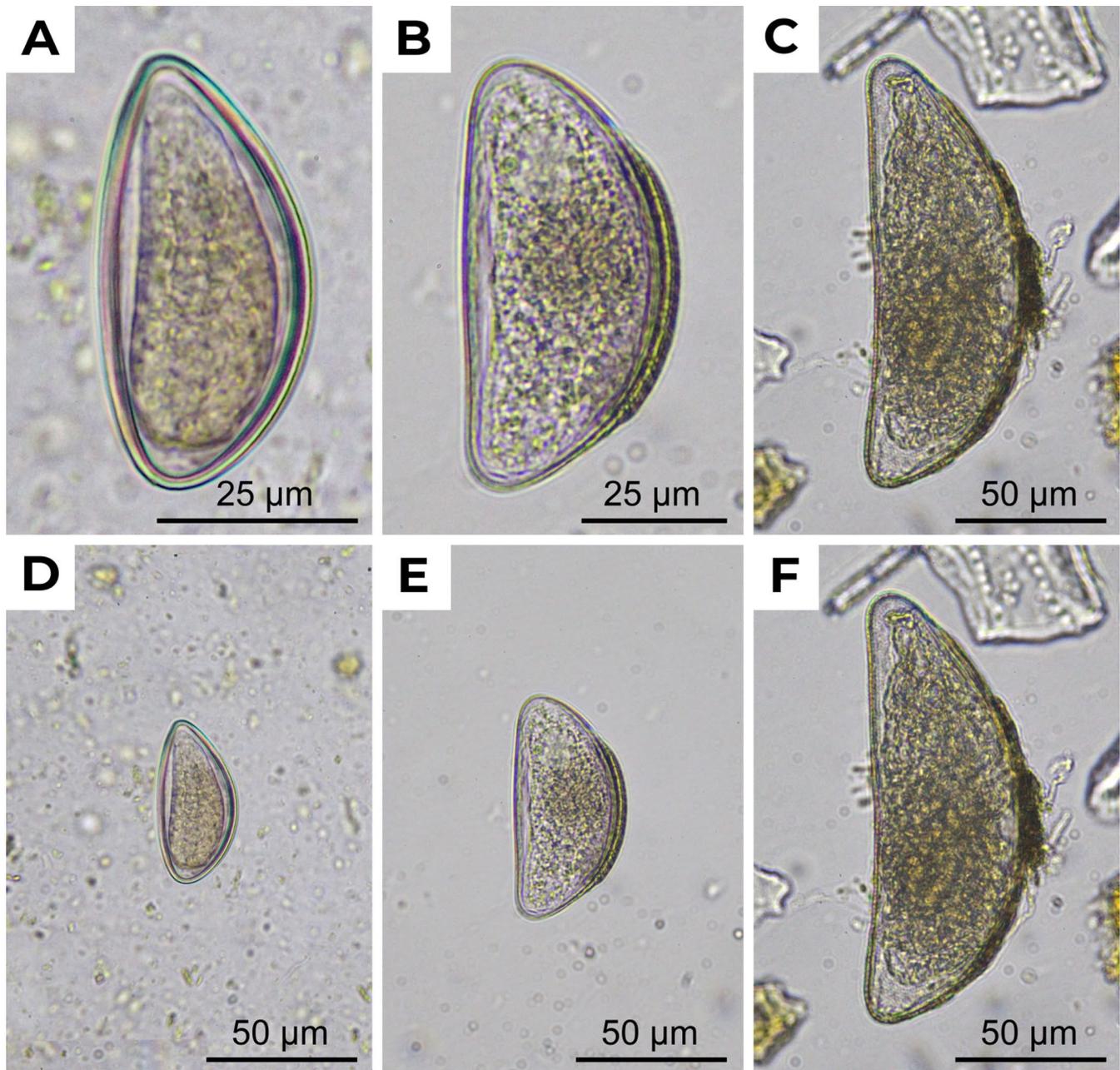


Figure 6. Light micrographs of D-shaped eggs in ruminant feces. **A, D.** Egg of *S. ovis* obtained from the sheep feces via flotation (egg is in Darling's solution under coverslip). **B, E.** Egg of *S. tarandi* obtained from reindeer feces via larvoscopy (egg is in tap water under coverslip). **C, F.** D-shaped egg obtained from reindeer feces via sedimentation (egg is in tap water under coverslip); all pictures were taken at 400 \times . **A, B.** Magnified images. **D–F.** Eggs in the same scale.

Recent findings (Fig. 6, C and F) showed that eggs of *S. tarandi* are not the only D-shaped oxyurids that might be discovered in the feces of reindeer. This egg also appears to have a thickened area, but it is twice as large ($143 \times 55 \mu\text{m}$), and the ratio of its length to its width is 2.6 in contrast to the 1.9 of *S. tarandi*. These morphological and morphometric data meet the criteria for the eggs of *Syphacia*

(an oxyurid nematode of small rodents)—for example, *S. obvelata*, *S. stroma*, or others. Information regarding the size of the egg of *S. obvelata* from the scientific literature varies: $115 \times 35 \mu\text{m}$ (Skrjabin et al., 1960) vs. $111\text{--}153 \times 33\text{--}55 \mu\text{m}$ (Baker, 2006). Thus, for the reindeer that were studied, *Syphacia* would be a spurious parasite (true parasitic organism but with a different host). How did this egg

get into the feces? It could have contaminated feces after their excretion (they were picked up from the ground). Alternatively, reindeer could ingest it because its food habits include predation and coprophagy (Turkin and Satunin, 1900; Semenov-Tyan-Shansky, 1977; Smith, 2006). Apart from true parasites with D-shaped eggs such as *Skrjabinema*, spurious parasites such as *Syphacia* with D-shaped eggs and pseudoparasites (nonparasitic objects) that are also D-shaped might also be found in reindeer feces. For example, pollen of wild garlic (*Allium ursinum*) has grains that are smaller, measuring only $30 \times 17 \mu\text{m}$, and absent an embryo (Halbritter et al., 2018).

Eggs of *S. tarandi* can be easily distinguished from the eggs of *S. ovis* based on morphometrics as well as morphology. Eggs of *S. tarandi* are $70\text{--}76 \times 36\text{--}46 \mu\text{m}$ (Skrjabin and Mizkewitsch, 1930) and $66\text{--}77 \times 32\text{--}40 \mu\text{m}$ (this study), while the eggs of *S. ovis* are $55\text{--}63 \times 34 \mu\text{m}$ (Skrjabin, 1915), $50\text{--}60 \times 30 \mu\text{m}$ (Ivashkin et al., 1989), and $53\text{--}60 \times 25\text{--}32 \mu\text{m}$ (Melnychuk and Reshetylo, 2020). Finally, it is clear that the eggs of *S. tarandi* are notably larger than the eggs of *S. ovis* (Fig. 6). Morphologically, eggs of *S. tarandi* have a thickening at the bulging side (which can be seen as a dark crescent during LM) that the eggs of *S. ovis* lack (Fig. 6) (Oksanen, 1999; Al-Dabagh, 2014). These two criteria can help to distinguish two *Skrjabinema* species both during fecal tests and during examination of adult females.

Drawings of *S. tarandi* eggs by Mizkewitsch (1967) do indicate the thickening but put excessive visual emphasis on it. A drawing of an *S. ovis* egg by Skrjabin et al. (1960), with all due respect to the scientist, has a few disadvantages: in the drawing, the egg seems opaque, it tapers prominently at one end, and it is too thin (length-to-width

ratio is 2.7 instead of 2). An explanation for these features might be that Skrjabin obtained females from sheep that had died from *Variola ovium* infection (Skrjabin, 1915). To facilitate differentiation of *S. tarandi* and *S. ovis* eggs, Figure 7 is offered as an aid in identification.

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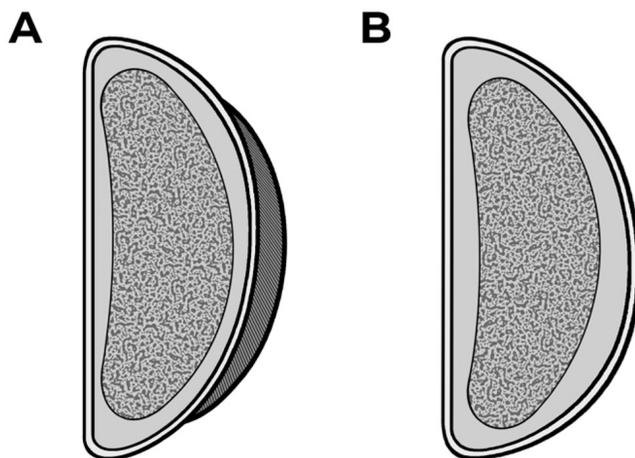


Figure 7. Original drawings of D-shaped eggs in ruminant feces as they appear with light microscopy. **A.** Egg of *S. tarandi*. **B.** Egg of *S. ovis*.

References

- Al-Dabagh, S.M.K.; Al-Amery, A.M.A.; Al-Ani, D.A.M. 2014. Prevalence study of gastrointestinal Nematodes in goats in Baghdad province-Iraq. *Al-Anbar Journal of Veterinary Sciences* 7: 29–38.
- Baker, D.G. 2006. Parasitic diseases. In: *The Laboratory Rat*. 2nd ed. D.G. Baker (ed.). Chester, Academic Press. 454–467 p.
- Benedict, B.M.; Barboza, P.S. 2022. Adverse effects of Diptera flies on northern ungulates: *Rangifer*, *Alces*, and *Bison*. *Mammal Review* 52: 425–437.
- Bye, K. 1987. Abomasal nematodes from three Norwegian wild reindeer populations. *Canadian Journal of Zoology* 65: 677–680.

- Carreno, R.A. 2018. Pinworms (Nematoda: Thelastomatoidea) from insects collected in Mississippi, USA, with description of a new species of *Protrellus* Cobb, 1920 from the cockroach *Ischnoptera deropeltiformis* Brunner von Wattenwyl, 1865 (Blattaria: Ectobiidae). *Zootaxa* 4531: 567–577.
- Colman, J.E.; Pedersen, C.; Hjermann, D.Ø.; Holand, Ø.; Moe, S.R.; Reimers, E. 2003. Do wild reindeer exhibit grazing compensation during insect harassment? *Journal of Wildlife Management* 67: 11–19.
- Fruetel, M.; Lankester, M.W. 1989. Gastrointestinal helminths of woodland and barren ground caribou (*Rangifer tarandus*) in Canada, with keys to species. *Canadian Journal of Zoology* 67: 2253–2269.
- Greiner, E.C. 2014. Laboratory diagnostics of parasitic diseases. In: *Equine Infectious Diseases*. 2nd ed. D.C. Sellon and M.T. Long (eds.). Amsterdam, Netherlands, Elsevier. 449–456 p.
- Halbritter, H.; Ulrich, S.; Grímsson, F.; Weber, M.; Zetter R.; Hesse, M.; et al. 2018. *Illustrated Pollen Terminology*. Cham, Switzerland, Springer Open. 483 pp.
- Ivashkin, V.M.; Oripov, A.O.; Sonin, M.D. 1989. [The key to helminths of small ruminants]. Nauka, Moscow. 254 pp. (in Russian)
- Janzen, D.H. (1985). On ecological fitting. *Oikos* 45: 308–310.
- Kutz, S.J.; Ducrocq, J.; Verocai, G.G.; Hoar, B.M.; Colwell, D.D.; Beckmen, K.B.; et al. 2012. Parasites in ungulates of Arctic North America and Greenland: a view of contemporary diversity, ecology, and impact in a world under change. *Advances in Parasitology* 79: 99–25.
- Kutz, S.J.; Laaksonen, S.; Asbakk, K.; Nilssen, A. C. 2019. Parasitic infections and diseases. In: *Reindeer and Caribou: Health and Disease*. M. Tryland and S.J. Kutz (eds.). Boca Raton, CRC Press (Taylor and Francis Group). 177–235 p.
- Kynkäänniemi, S.-M.; Kettu, M.; Kortet, R.; Härkönen, L.; Kaitala, A.; Paakkonen, T.; et al. 2014. Acute impacts of the deer ked (*Lipoptena cervi*) infestation on reindeer (*Rangifer tarandus tarandus*) behaviour. *Parasitology Research* 113: 1489–1497.
- Latypov, D.G.; Timerbayeva, R.R.; Kirillov, E.G. 2019. [Parasitology and invasive diseases of ruminants]. St. Petersburg, Russia, Lan'. 474 pp. (in Russian)
- Manninen, S.M.; Thamsborg, S.M.; Laaksonen, S.; Oksanen, A. 2014. The reindeer abomasal nematode (*Ostertagia gruehneri*) is naturally transmitted to sheep when sharing pastures. *Parasitology Research* 113: 4033–4038.
- Melnichuk, V.V.; Reshetylo, O.I. 2020. Morphological characteristic of *Skrjabinema ovis* (Nematoda, Oxyuridae) obtained from domestic sheep. *Regulatory Mechanisms in Biosystems* 11: 378–383.
- Mizkewitsch, V. Yu. 1967. [Reindeer helminths and the diseases they cause]. Leningrad, Kolos. 308 pp. (in Russian)
- Neiland, K.A. 1972. Caribou disease studies. Alaska Department of Fish and Game, Division of Game, Juneau, Alaska.
- Oksanen, A. 1999. Endectocide treatment of the reindeer. *Rangifer* 19: 7–50.
- Polyakov, P.A. 1953. [Lifetime differential diagnostics of strongylatosis of the digestive tract of ruminants based on morphology of invasive larvae]. Moscow, All-Union Institute of Helminthology. 207 pp. (in Russian)
- Paramonov, A.A. 1962. [Fundamentals of Phytohelminthology]. Moscow, Publishing house of the Academy of Sciences of the USSR. 480 pp. (in Russian)
- Raponi, M.; Beresford, D.V.; Schaefer, J.A.; Thompson, I.D.; Wiebe, P.A.; Rodgers, A.R.; Fryxell, J.M. 2018. Biting flies and activity of caribou in the boreal forest. *Journal of Wildlife Management* 82: 833–839.
- Robertson, P.A. 2020. Gastrointestinal parasites in sympatric reindeer (*Rangifer tarandus*) and sheep (*Ovis aries*). Trondheim, Inland Norway University of Applied Sciences. 70 pp.
- Sabatini, G.A.; de Almeida Borges, F.; Claerebout, E.; Gianechini, L.S.; Höglund, J.; Kaplan, R.M.; et al. 2023. Practical guide to the diagnostics of ruminant gastrointestinal nematodes, liver fluke and lungworm infection: interpretation and usability of results. *Parasites & Vectors* 16: 58.
- Schad, G.A. 1959. A revision of the North American species of the genus *Skrjabinema* (Nematoda: Oxyuroidea). *Proceedings of the Helminthological Society of Washington* 26: 138–147.
- Schultz, R.S.; Gvozdev, E.V. 1970. [Fundamentals of General Helminthology]. Moscow, Nauka. 492 pp. (in Russian)
- Semenov-Tyan-Shansky, O.I. 1977. [Reindeer]. Moscow, Nauka. 94 pp. (in Russian)
- Shah, M.M.; Mohilal, N.; Pramodini, M.; Bina, L.; Hemananda, Th. 2011. Nematode parasites of invertebrates from Manipur, North East India (diagnosis, keys and illustration). *Zootaxa* 3107: 1–37.
- Skrjabin, K.I. 1915. [*Oxyuris ovis* nov. sp.—a new parasite of sheep]. *Archives of Veterinary Sciences* 7: 695–699. (in Russian)
- Skrjabin, K.I.; Mizkewitsch, W. 1930. *Skrjabinema tarandi* n. sp. eine Oxyuride des Nordischen Rentieres. *Deutsche tierärztliche Wochenschrift* 38: 183–185. (in German)
- Skrjabin, K.I.; Shikhobalova, N.P.; Lagodovskaya, E.A. 1960. [Fundamentals of Nematology. Vol. 8, Oxyurata, part 1]. Moscow, Publishing house of the Academy of Sciences of the USSR. 558 pp. (in Russian)
- Smith, T. 2006. Carnivorous herbivores. In: *The Real Rudolph: A Natural History of the Reindeer*. United Kingdom, Sutton Publishing. p. 49.
- Soulsby, E.J.L. 1982. *Helminths, Arthropods and Protozoa of Domestic Animals*. 7th ed. London, Bailliere Tindall. 809 pp.

- Swales, W.E. 1934. *Skrjabinema oreamni* sp. nov. a nematode parasite of *Oreamnos americanus* and *Rangifer* sp. in Canada. Canadian Journal of Research 10: 527–531.
- Tapia-Escárate, D.; Mackintosh, C.; Scott, I.; Lopez-Villalobos, N.; Wilson, P.; Pomroy, W. 2021. Evaluation of cross-grazing deer with sheep or cattle, as means to reduce anthelmintic usage to control gastrointestinal and pulmonary nematodes in farmed red deer (*Cervus elaphus*) in New Zealand. Veterinary Parasitology 298: 109534.
- Tetley, J.H. 1935. Ecological studies on *Nematodirus* species in sheep in Manawatu District, New Zealand. Journal of Helminthology 13: 41–58.
- Tetley, J.H. 1941. *Haemonchus contortus* eggs: comparison of those *in utero* with those recovered from feces, and a statistical method for identifying *H. contortus* eggs in mixed infections. Journal of Parasitology 27: 453–463.
- Turkin, N.V.; Satunin, K.A. 1900. [Animals of Russia]. Moscow, Kushnerev & Co. 118 pp. (in Russian)
- Utaaker, K.S.; Ytrehus, B.; Davey, M.L.; Fossøy, F.; Davidson, R.K.; Miller, A.L.; et al. 2023. Parasite spillover from domestic sheep to wild reindeer—the role of salt licks. Pathogens 12: 186.
- Verocai, G.G.; Chaudhry, U.N.; Lejeune, M. 2020. Diagnostic methods for detecting internal parasites of livestock. Veterinary Clinics: Food Animal Practice 36: 125–143.
- Witter, L.A.; Johnson, C.J.; Croft, B.; Gunn, A.; Gillingham, M.P. 2012. Behavioural trade-offs in response to external stimuli: time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. Journal of Animal Ecology 81: 284–295.