

Research Paper

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Larval spirurids in a supralittoral amphipod in the north-east of Russia and the identification of the intermediate host of *Antechiniella septentrionalis* (Spirurida: Acuariidae), parasitic in a tundra vole

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Abstract

The supralittoral amphipod *Traskorchestia ditmari* (Derzhavin, 1923) was identified as the intermediate host for *Antechiniella septentrionalis* Ivanova, Dokuchaev & Spiridonov, 2019, a parasite of the tundra vole *Microtus oeconomus* and *Skrjabinocerca* sp. (both Spirurida: Acuariidae) in Magadan Oblast in north-eastern Russia. Joint infection by both larval spirurids was not observed. The infective stage of *A. septentrionalis* was the encysted larvae, while larvae of *Skrjabinocerca* sp. were free in the amphipod's coelom. The identity of *A. septentrionalis* was confirmed using *cox1* mtDNA gene analysis, performed on adult stages from a tundra vole and on larvae from amphipods. Possible transmission routes of *A. septentrionalis* are discussed.

Introduction

A tundra vole *Microtus oeconomus* heavily infected with spirurid nematodes was found in Magadan Oblast in the north-east of Russia (Dokuchaev and Atrashkevich, 2015), followed by the description of a new member of the *Antechiniella* Quentin & Beveridge, 1986 (Spirurida, Acuariidae). It was the first finding of a representative of the genus outside Australia. Large numbers of adult and late juvenile stages of *Antechiniella septentrionalis* Ivanova, Dokuchaev & Spiridonov, 2019 were observed in the duodenum of its definitive host. The remainder of the nematode life cycle was unknown, but the assumption was made that amphipod crustaceans may play a role in the transmission of the nematode (Ivanova *et al.*, 2019). Amphipods have been reported to be suitable intermediate hosts for representatives of the Habronematoidea (Fagerholm & Butterworth, 1988) and many Acuarioidea, such as *Cosmocephalus obvelatus* (Creplin, 1825), *Paracuaria adunca* (Creplin, 1846), *Skrjabinocerca* spp., *Skrjabinoclava morrisoni* Wong & Anderson, 1987, *Streptocara crassicauda* (Creplin, 1829) (Skrjabin *et al.*, 1965; Bartlett *et al.*, 1989; Anderson, 2000), *Cheilospirura hamulosa* (Diesing, 1851) (Cram, 1931; Alicata, 1938) and *Echinuria uncinata* (Rudolphi, 1819) (Kotelnikov, 1961; Misiura, 1970; Austin & Welch, 1972).

An arthropod must be included in the food web of the host if it is to act as the intermediate host for a spirurid parasite. However, the tundra vole is believed to be strictly vegetarian and arthropods do not constitute a part of its normal diet (Yudin *et al.*, 1976; Batzli & Lesieutre, 1991). Even so, we screened amphipods from the habitats of the infected tundra voles for the presence of spirurid larvae, assuming that infected amphipods can be consumed accidentally. We assumed that amphipods would make better intermediate hosts for the parasite of a tundra vole than other arthropods found in soil traps, which were mainly from the Coleoptera, considering that the tundra vole does not have predatory feeding habits. Dokuchaev & Atrashkevich (2015) have speculated that some species of talitrid amphipods could act as an intermediate host for *A. septentrionalis*. *Traskorchestia ditmari* (Derzhavin, 1923) is a supralittoral talitrid amphipod, and is the most abundant arthropod species on the seashores of the Magadan region, Russia, from May to October. It is often found near the tundra vole's feeding sites and aggregation of faeces. This talitrid is well adapted to the severe climatic condition of the area where it thrives, as demonstrated by its high densities. The cold resistance of this amphipod allows it to tolerate temperatures as low as -35°C , at which 50% of amphipods survive (Berman *et al.*, 1990). However, many aspects of its biology are not known, e.g. the number of broods per year. The species obviously plays an important role in the degradation of plant and other organic detritus in the maritime marshes. The distribution range of *T. ditmari* includes the Kamchatka peninsula, the south of Sakhalin island, the South Kuril Islands

Table 1. Parasite prevalence and abundance of *Antechiniella septentrionalis* in *Traskorchestia ditmari*.

Date of collection	Number of amphipods examined	Number of amphipods infected	Prevalence (%) ^a	Nematode larvae (number)	Abundance ^b	Range (if present)
8.05.2016	7	1	14.3	16	2.3	16
13.07.2017	30	18	60	98	3.3	1–13
24.09.2017	10	5	50	20	2.0	1–10
20.05.2018	44	25	56.8	95	2.2	1–15
20.05.2018	10	8	80	50	5.0	1–17
26.06.2018	2	1	50	5	2.5	5
14.08.2018	20	2	10	2	0.5	1
14.08.2018	16	3	18.8	24	1.5	2–19
Total	139	63	45.3	310	2.2	1–19

^aPrevalence: per cent of individual testing positive for the presence of the parasite.

^bAbundance: the mean number of larvae per host calculated over all samples (infected + uninfected).

and the shores of the Okhotsk Sea. It penetrates up to 2 km ashore, where it is found on floodplains (Regel, 2005). To our knowledge, *T. ditmari* has never been reported as an intermediate host for parasitic nematodes in invertebrates. A survey of *T. ditmari* in the Ola marshes in the northern part of the Sea of Okhotsk, which is inhabited by infected tundra voles, was carried out and the results are presented in the Results section.

Material and methods

Amphipods *T. ditmari* were collected from May to September from the maritime marshes at Ola Bay, Magadan Oblast, Russia. Animals were dissected in the laboratory and both cysts with nematodes and non-encysted nematodes were collected and preserved in ethanol. Cysts extracted from live amphipods were partially dissected before fixation and the nematodes were removed. The remainder were recovered from preserved capsules.

Morphological and molecular studies were performed as described in Ivanova et al. (2019). Scanning electron microscope (SEM) images were taken on a Tescan CamScan MV 2300, Brno, Czech Republic.

Results

In total, 63 out of 139 amphipods examined were found to be infected. Out of 63 infected amphipods, three contained a single active, non-encysted juvenile each, while the remaining 60 contained from one to 19 (mean 2.2) cysts, each with a single juvenile. Based on morphology, juveniles without cysts were identified as *Skrjabinocerca* sp., whereas encysted ones were identified as *A. septentrionalis*. The identity of the latter was confirmed using the *cox1* mtDNA gene: the *cox1* mtDNA sequences were obtained for two juveniles recovered from two individuals of the amphipod hosts. A secure reading of approximately 400 bp was obtained for both specimens, which were found to be identical to one another and completely coincided with the corresponding sequence of gravid females from the rodents.

Infective larva of *A. septentrionalis* Ivanova, Dokuchaev & Spiridonov, 2019 from *T. ditmari*

Infected amphipods were prevalent in May and at the end of September (table 1). The minimum infestation was observed in

August, which could be due to the prevalence of young, and not yet infected, amphipods in the population at this season. The older amphipods had greater parasite loads. The lowest value of abundance was observed in August. Heavily infected amphipods were collected at each sampling occasion.

Cysts were whitish globular formations measuring 1–2 mm in diameter, with transparent but moderately thick walls; often with shortest appendages at one pole (pedunculate). Each cyst contained one tightly coiled, inactive larva (fig. 1). The larvae differed in length and were represented by second-stage larvae moulting into the third stage (body length 730–1080 µm) and third-stage larvae (1200–1682 µm long). Such traits as a folded and partially loose cuticle and a tightly folded oesophagus were regarded as indications of the ongoing process of moulting. Otherwise, the morphology of both groups of larvae was similar.

Description

Body tightly coiled, robust, not dilated in the anterior region but tapering to both ends (fig. 2n). Cuticle thickened, annuli up to 5 µm wide (fig. 2g). Paired pseudolabia each terminating in a single tooth. Cephalic papillae and amphids inconspicuous (fig. 3a, b). Cordons crescentic, with smooth surface, or slightly wrinkled surface, lacking formed cuticular plates and divided by a median groove; recurved but not anastomosing, with a perfectly symmetrical arrangement (fig. 3a, b). Buccal cavity strongly cuticularized (fig. 2a–e). Pharynx elongate, deirids simple, at level of buccal cavity and muscular oesophagus junction (fig. 2f). Nerve ring surrounding first quarter of the muscular oesophagus. Excretory pore posterior to the mid-length of muscular oesophagus. Cardia well developed. Genital primordium observed in two specimens only, 120–130 µm long. Tail c. 2.5–3 anal diameter long, bluntly conical, always curved on dorsal side (figs 3d and 2h–m). Tail tip with 1–3 tiny cuticular projections (fig. 2h, j, m). Phasmids subterminal, pore-like (fig. 3c).

Moulting second-stage larva ($n = 4$). Length = 831 (730–920) µm; maximum diameter = 45 (40–50) µm; anal diameter = 27 (25–28) µm; cordon length = 7 (6–8) µm; buccal cavity length ($n = 1$) = 77 µm; buccal cavity width ($n = 1$) = 4 µm; muscular oesophagus length ($n = 1$) = 89 µm; muscular oesophagus width ($n = 1$) = 14 µm; glandular oesophagus length ($n = 1$) = 320 µm; glandular oesophagus width ($n = 1$) = 31 µm; nerve ring ($n = 1$) = 93 µm; excretory pore ($n = 1$) = 117 µm; tail length ($n = 4$) = 50 (42–60) µm.



Fig. 1. Cysts with larvae of *Antechiniella septentrionalis* Ivanova, Dokuchaev & Spiridonov, 2019 found in the body cavity of *Traskorchestia ditmari*. All scale bars are in μm .

Infective third-stage larva ($n = 11$). Length = 1413 (1200–1682) μm ; maximum diameter = 44 (39–50) μm ; anal diameter = 27 (23–32) μm ; cordon length = 7.4 (6–8) μm ; buccal cavity length = 78 (52–108) μm ; buccal cavity width = 2.8 (4–2) μm ; muscular oesophagus length = 95 (70–107) μm ; muscular oesophagus width = 12 (10–15) μm ; glandular oesophagus length = 424 (300–515) μm ; glandular oesophagus width = 28 (22–37) μm ; distance from apex to deirid = 103 (65–170) μm ; nerve ring = 116 (78–185) μm ; excretory pore = 138 (113–166) μm ; tail length = 64 (55–84) μm ; genital primordium length ($n = 2$) = 120–130 μm .

Remarks

In general, the morphology of the *A. septentrionalis* larvae collected from the amphipods is similar to that of the adult nematodes from tundra voles. Although the arrangement of the cephalic cordons in the larvae resembles that in the adult stages, the intricate structure of cordon surface is absent in the larvae examined in the study.

Currently, descriptions of the third-stage infective larvae are available for a few genera of Acuariidae (Cram, 1931; Quentin *et al.*, 1972; Rietschel, 1973; Quentin & Seureau, 1983). Moravec *et al.* (2003), referring to Anderson (2000), noted that ‘it is believed that cordons are absent from the acuariid third-stage larvae and appear only in conspecific fourth stage larvae’ because of the lack of SEM data in previous studies. In their study, Moravec *et al.* (2003) observed cordons in the third-stage larvae of Acuariidae from a New Zealand crab.

The ability to form a capsule or a cyst to protect an infective juvenile is recognized in members of different families of Spirurida and genera of Acuariidae. For example, acuariids *C. hamulosa* and *Cheilospirura spinosa* Cram, 1927 were shown to form cysts inside their experimental intermediate hosts (grasshoppers), while juveniles of *Dispharynx spiralis* Molin, 1858 were found free in their isopod hosts (Cram, 1931). Pedunculate cysts, similar in shape to those observed in the present study, were reported in the Physalopteroidea (Bain *et al.*, 2014). In the wild, infective juveniles form capsules in different intermediate hosts. To our knowledge, there is no evidence that the ability to form cysts depends on the kind of the intermediate host. In experiments carried out by Cram (1931), larvae of the same species formed cysts or not according to their species in different, though taxonomically related, intermediate hosts. Cram (1931) also noted that non-encysted larvae were active and free-moving while encysted ones were coiled and inactive.

Systematics

Family: Acuariidae Railliet, Henry & Sisoff, 1912

Skrjabinocerca Shikhobalova, 1930

Skrjabinocerca sp. third-stage larvae ($n = 2$)

Description

Length = 3385–3730 μm ; maximum diameter 100–125 μm ; tail length = 105–147 μm ; de Man indices: $a = 29.8$ – 34.5 ; $b = 2.6$ – 2.2 ; $c = 25.4$ – 32.3 ; $c' = 3$. Body not dilated at anterior, stocky in appearance, barely tapering towards rounded head end (figs 4a

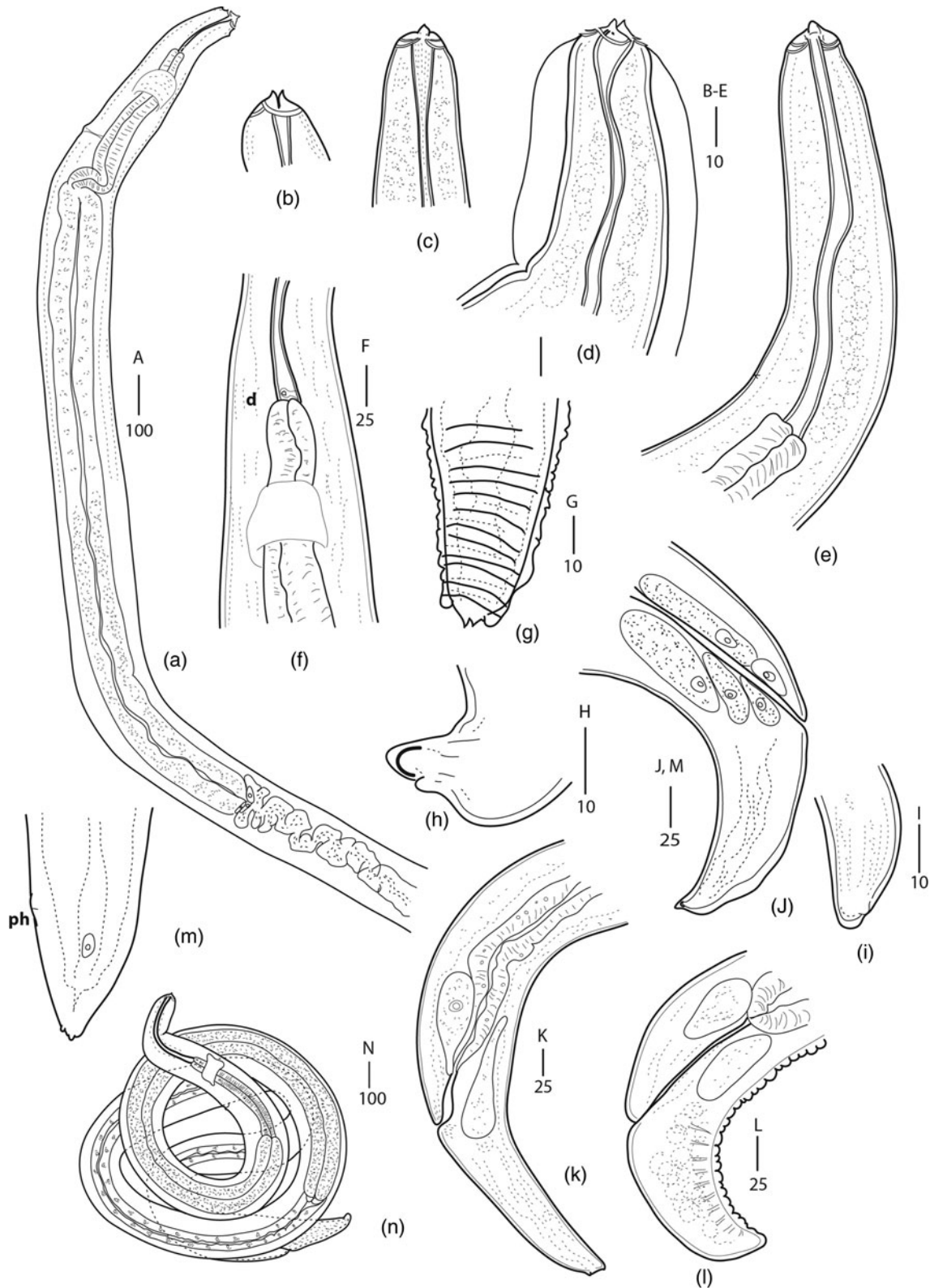


Fig. 2. Larva of *Antechiniella septentrionalis* Ivanova, Dokuchaev & Spiridonov, 2019 from *Traskorchestia ditmari*. (a) Anterior end; (b–e) anterior extremity; (f) region of junction of stoma and muscular oesophagus; (g–i, m) tail tip; (j–l) tail; (n) entire coiled juvenile. Abbreviations: d, deirid; ph, phasmid. All scale bars are in μm .

and 5a). Cephalic extremity with two large lateral pseudolabia, each ending with short terminal tooth, four papillae and two pore-like amphids situated on pseudolabia (figs. 4c, d and 5c). Cuticle $1\ \mu\text{m}$ thick, annulated and longitudinally striated.

Lateral alae well developed, wing-like, up to $15\ \mu\text{m}$ wide at mid-body, with marked transversal striations, originating posterior to amphids and ending prior to anus (fig. 5c, d, h). Cuticular cordons prominent, $154\text{--}196\ \mu\text{m}$ long, starting between pseudolabia

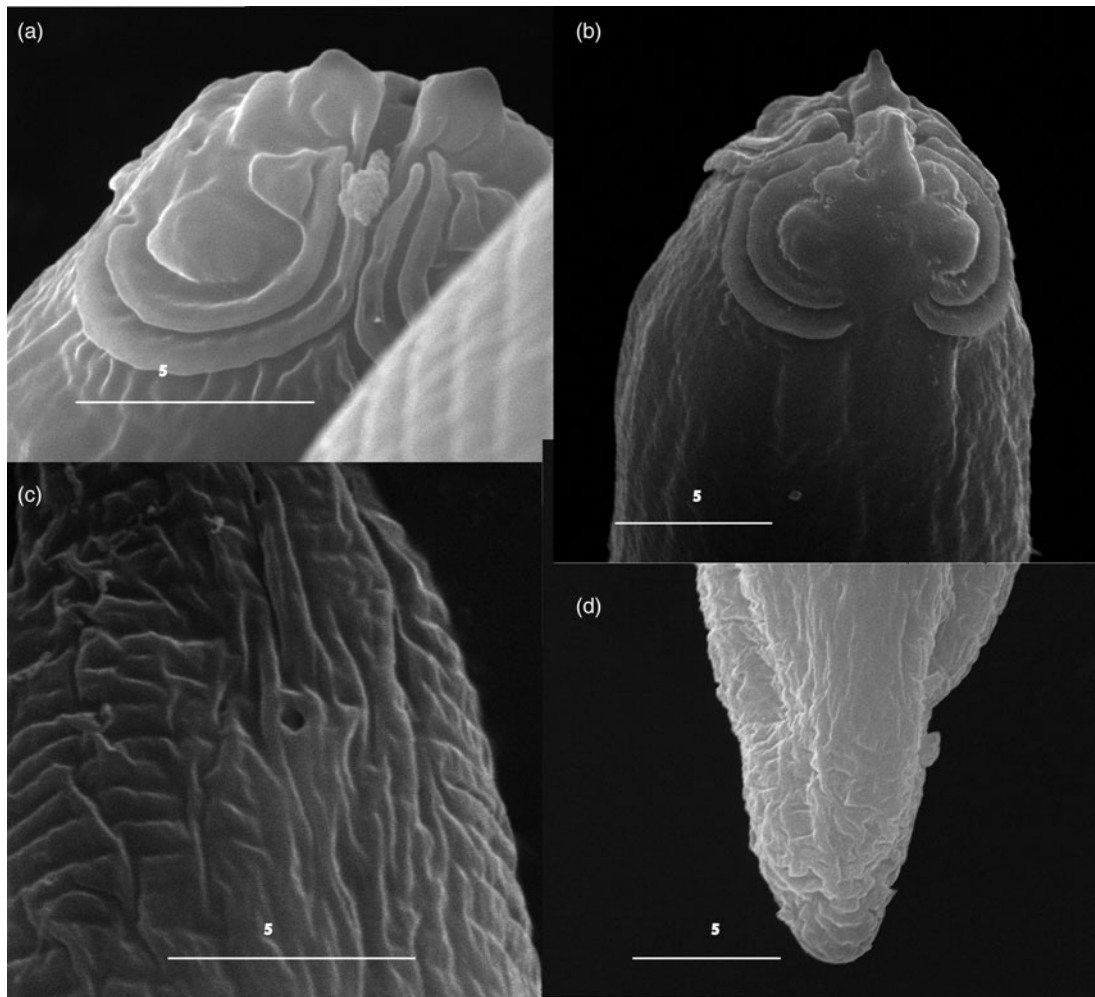


Fig. 3. Larva of *Antechiniella septentrionalis* Ivanova, Dokuchaev & Spiridonov, 2019 from *Traskorchestia ditmari*. SEM images. (a, b) Anterior extremity; (b) phasmid; (c, d) posterior extremity. All scale bars are in μm .

and extending as straight, non-recurrent, non-anastomosing cords terminating slightly posterior to nerve ring; each cordon *c.* 2 μm wide, consisting of one row of transversally orientated plates attached to longitudinal band from one side; no median groove present (figs 4b and 5c, g). Deirids simple, conical (fig. 5g) (digitiform in one larva; see fig. 4b), prominent, 15–17 μm long, situated on lateral ala at level of mid-length of muscular oesophagus or just posterior to free cordon ends at 165–200 μm from apex. Postdeirids prominent, diamond-shaped, 20–24 μm long; the first situated 1900–2150 μm posterior to cardia and another 300–340 μm further posteriad (fig. 5b, f). Oral opening apical, flattened dorsoventrally. Buccal capsule narrow, moderately thickened, 72–83 μm long and 4–5 μm wide (fig. 5c–e). Muscular oesophagus 198–243 μm long and 27–29 μm wide. Glandular oesophagus 1200–1260 μm long and 55–78 μm wide. Entire oesophagus length 1430–1530 μm . Cardia prominent, 15–17 μm long. Nerve ring situated 117–142 μm from apex, surrounding muscular oesophagus in its anterior third. Excretory pore situated slightly posterior to nerve ring or 135–167 μm from apex (fig. 5d, e). Genital primordium 180–200 μm long. Rectal glands present. Large pedunculate papilla *c.* 12 μm in diameter present just posterior to anus (fig. 5h–j). Tail straight, short, gradually tapering and ending in bluntly rounded tip

with three small protuberances (fig. 5k). Phasmids subterminal, small, papilliform (fig. 5k).

Taxonomical remarks

The species found was identified as a representative of *Skrjabinocerca* Shikhobalova, 1930 due to the characteristic shape of the cordons (straight, long, non-recurrent) and the presence of lateral alae. The genus *Skrjabinocerca* comprises five species, i.e. *S. prima* Shikhobalova, 1930, *S. americana* Wong & Anderson, 1993, *S. europaea* Wong & Anderson, 1993, *S. bennetti* Bartlett & Anderson, 1996 and *S. canutus* Diaz, Cremonte, Navone & Laurenti, 2005 (Shikhobalova, 1930; Wong & Anderson, 1993; Bartlett & Anderson, 1996; Diaz *et al.*, 2005), all parasitic in birds. Although the identification of acuariids is normally based on the morphology of the adult stages, the available descriptions of larval stages including the corresponding third stage of two species of *Skrjabinocerca* (Bartlett *et al.*, 1989; Diaz *et al.*, 2005) led us to believe that larvae from our material represented members of the *Skrjabinocerca*. Bartlett *et al.* (1989) had described the infective larva of *S. prima* from an experimentally infected freshwater amphipod *Hyalella azteca*. Larvae from naturally infected *T. ditmari* most closely resembled that from material in Bartlett *et al.* (1989), except for a few differences:

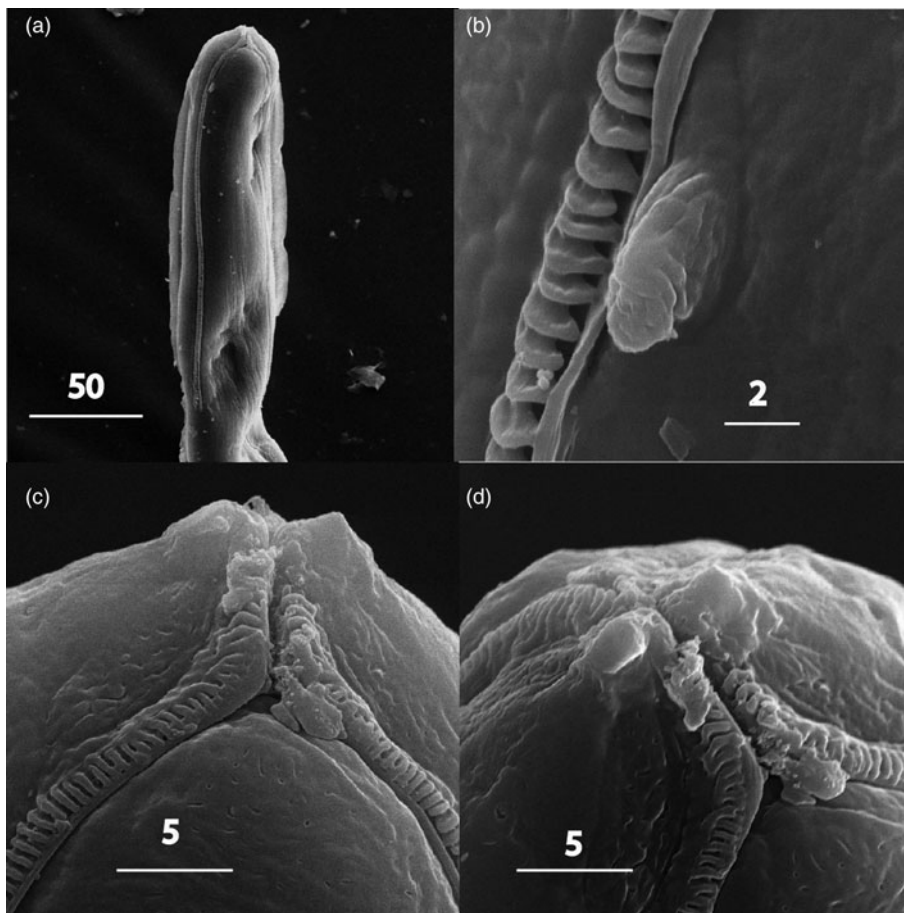


Fig. 4. Larva of *Skrjabinocerca* sp. from *Traskorchestia ditmari*. SEM images. (a) Anterior end; (b) deirid; (c, d) anterior extremity. All scale bars are in μm.

those in our study were larger (c. 3.5 mm vs. 2.1 and 2.4, males and females, respectively) but with less advanced genital primordia (c. 200 vs. 403 and 1009, males and females, respectively) and a different tail shape without any constrictions at its length. The anterior end morphology, shape and position of deirids and post-deirids, characteristic shape of lateral alae and presence of pedunculate post-anal papilla were almost the same as in the species from our material.

It should be noted that Tsimbalyuk & Kulikov (1966) reported a semi-terrestrial amphipod *Orchestia* (= *Traskorchestia*) *ochotensis* as an intermediate host for *S. prima* in the Bering Sea region. In addition, Diaz et al. (2005) described *S. canutus* from the definitive host, the bird *Calidris canutus rufa*, giving the description of the third-stage larva from the bird's oesophagus. The comparison of these larvae with our material also confirms the close relations between them.

No molecular data are yet available for members of the *Skrjabinocerca*.

Discussion

The study showed that in the north-east of Russia, *T. ditmari* acts as an intermediate host for at least two species of spirurid nematodes (*Skrjabinocerca* sp., supposedly a parasite of birds, and *A. septentrionalis*, the parasite of a mammal). Joint infection by these two species was not observed. It is likely that the high population density of *T. ditmari* and its ready availability makes it a suitable intermediate host for a number of spirurid parasites of

different vertebrate animals inhabiting the area of *T. ditmari* distribution. Host specificity toward an intermediate host species is not tight in the Spirurida (Anderson, 2000; Bain et al., 2014). It has been shown that *E. uncinata* can develop in amphipods, ostracods, conchostracans and cladocerans (cf. Anderson, 2000) in the wild and in experiments, and *Spirocerca lupi* Railliet & Henry, 1911 can use five species of dung beetles as intermediate hosts under experimental conditions (Mukaratirwa et al., 2010). In earlier experimental studies on other arthropod species, similar results were obtained (Cram, 1931; Anderson, 2000).

However, as the infection of *A. septentrionalis* has been so far found only in regions where *T. ditmari* is distributed (Yi-Fan et al., 2014), it looks likely that the transmission of *A. septentrionalis* is based solely on this amphipod species. The definitive host, the tundra vole, is regarded as one of 'key herbivorous species of subarctic tundra ecosystems' (Soininen et al., 2013) and, therefore, it cannot be expected to consume infected arthropods. Soininen et al. (2013) studied the diets of arctic rodents, including *M. oeconomus*, and found the rodents' diet to be highly diverse. The DNA barcoding used in this study was for the seed plant content only and, therefore, could not detect meat consumption, but flexibility in feeding habits was noted. It has been observed (Landry, 1970; Samuels, 2009) that nearly all rodents will opportunistically consume meat. Although we did not find evidence indicating such habits in the tundra vole, we cannot exclude such a possibility. We do not know whether, or how often, tundra voles consume arthropods as meat in subarctic ecosystems deliberately or if its consumption bears an accidental

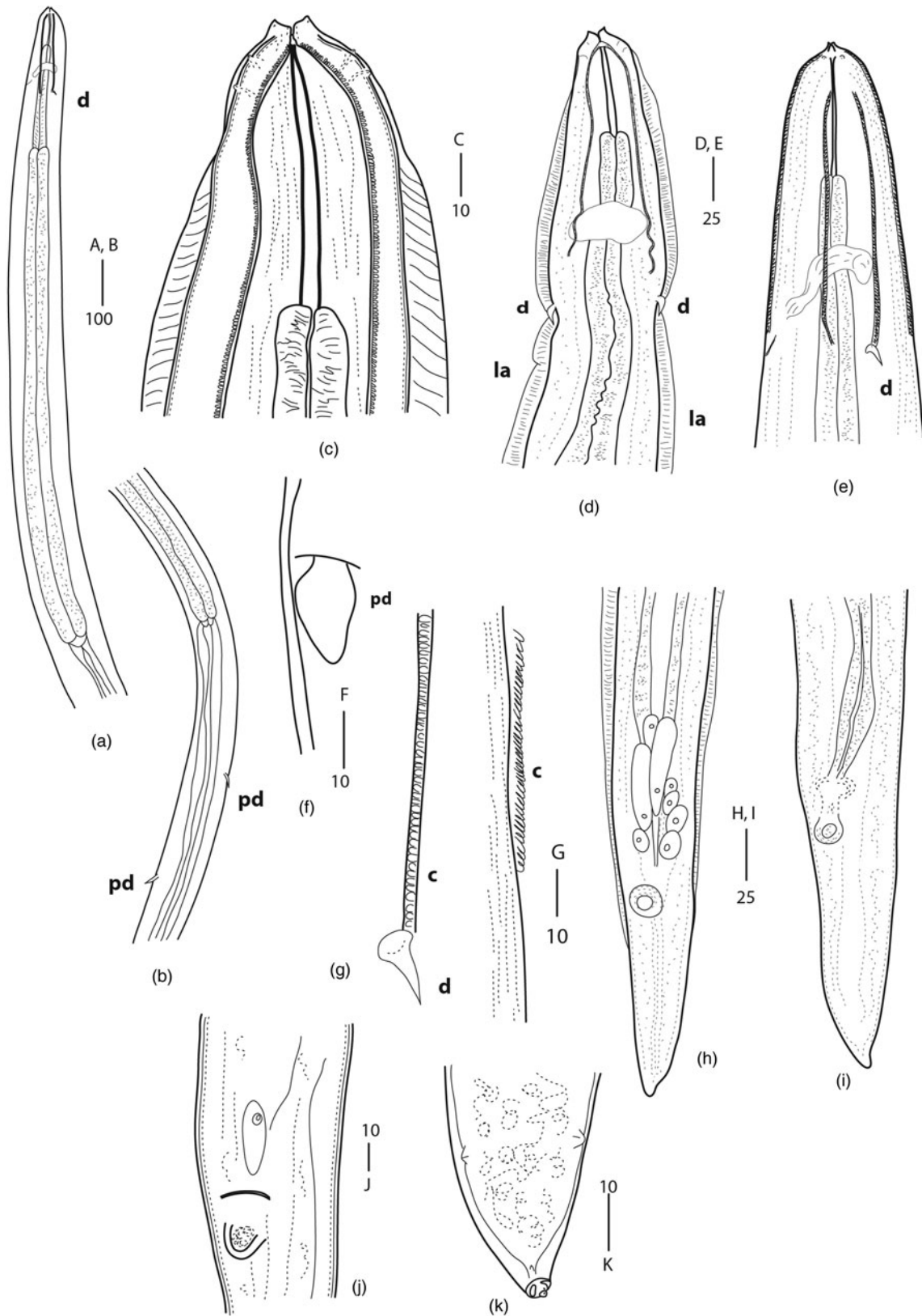


Fig. 5. Larva of *Skrjabinocerca* sp. from *Traskorchestia ditmari*. (a) Anterior body region; (b) mid-body region; (c, d) anterior extremity, ventral; (e) anterior extremity, lateral; (f) postdeirid; (g) posterior end of cordon and deirid, sublateral; (h, i) tail, subventral; (j) anus region, subventral; (k) tail tip, ventral. Abbreviations: d, deirid; c, cordon; la, lateral ala; pd, postdeirid. All scale bars are in μm .

character. Several scenarios or combinations leading to the transmission of an intestinal parasite such as *A. septentrionalis* can be observed: (1) tundra voles, although they do not collect amphipods for winter storage, eat them willingly during summer; (2) tundra voles eat amphipods accidentally with plant food; and (3) coprophagy, practiced by the majority of herbivorous rodents such as the microtines (Cranford & Johnson, 1983), may also take place and facilitate the ingestion of infected amphipods feeding on the same site. Alternately, for the amphipods, the aggregations of the host's faeces is the easiest place to get infected by *A. septentrionalis* by swallowing its eggs. The possibility of the transmission of infection from a recently dead infected amphipod should also be considered, as an encysted nematode larva is able to survive for some time after the death of its amphipod host. Nematodes belonging to various taxa that are parasitic in invertebrates such as insects, earthworms, diplopods, etc. are able to survive a short period of time in their hosts after the host's death, even without being protected by a cyst (our observation). Thus, ingestion of a recently dead amphipod with an encysted juvenile inside will bring about infection. The high parameters of infection found in amphipods may reflect the random character of the invasion intermission because of the non-predatory habits of tundra voles. A high number of cysts per host can have an impact on an amphipod, hindering its motility and facilitating its transmission to the definitive host, in a similar manner to that found in infected tenebrionids, as shown by Schutgens et al. (2013).

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Conflicts of interest. None.

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