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Neoskrjabinolepis paradoxa n. sp. from shrews on Sakhalin Island, Russia, with an amended diagnosis of Neoskrjabinolepis Spassky, 1947 (Cestoda: Cyclophyllidea: Hymenolepididae), a key, and a review on geographical distribution of the species

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Abstract

A taxonomic review was performed on cestodes of the genus *Neoskrjabinolepis* Spassky, 1947 that parasitize different species of *Sorex* shrews in different regions of the northern Palearctic and in the Nearctic (Alaska, USA). Information on Palearctic *Neoskrjabinolepis* cestodes published in various articles is summarized. An overview of the geographical distribution of the *Neoskrjabinolepis* species is also presented. Currently, the genus includes 17 species. In the European part of the Palearctic, four species of the genus are registered; in the Asian part, 13 species; and on the American continent (Seward Peninsula, Alaska, USA), two species. Descriptions, illustrations, and differential diagnoses are given for a new species of *Neoskrjabinolepis*, i.e. *N. paradoxa* n. sp., which was found in shrews *Sorex unguiculatus* Dobson and *S. caecutiens* Laxmann on Sakhalin Island. A unique feature of the new species is irregularly alternating genital pores in the uterus series in the strobila. Amended new differential features (positioning of the uterus relative to osmoregulatory canals and alternation of genital pores) of genus diagnosis and an identification key for *Neoskrjabinolepis* spp. are presented.

Introduction

Cestodes of the genus *Neoskrjabinolepis* Spassky, 1947 are characterized by high species richness and widespread occurrence in the Holarctic, as evidenced by their finds in various species of shrews *Sorex* (Mammalia: Soricidae) during faunal studies in various regions of Eurasia (from the Pyrenees to Chukotka and the Japanese islands) and North America (Alaska) (Zarnowski 1955; Prokopič 1958; Schaldybin 1964; Arzamasov *et al.* 1969; Jourdane 1971; Vaucher 1971; Prokopič & Matsaberidze 1972; Prokopič *et al.* 1974; Eltyshev 1975; Genov 1984; Roots 1992; Novikov 1995; Hanzelová & Ryšavý 1996; Tkach & Zhumabekova 1996; Sawada 1999; Anikanova *et al.* 2001, 2002; Irzhavsky & Gulyaev 2002; Binkiene 2006; Binkiene *et al.* 2011; Kornienko 2012; Kornienko & Dokuchaev 2012, 2023; Haukisalmi 2015; Kirillov *et al.* 2018; Kornienko *et al.* 2022c).

For more than a century, the history of the genus *Neoskrjabinolepis* has been accompanied by persistent discussion about its species composition. Some researchers have believed that the genus includes two species: *Neoskrjabinolepis schaldybini* Spassky, 1947 and *N. singularis* (Cholodkovsky, 1912) Spassky, 1954 (Spassky 1954; Spassky & Andreyko 1970; Vaucher 1971; Eltyshev 1975; Genov 1984). Other researchers have recognized only one species, *N. singularis*, with a transpalearctic range (Kobuley 1953; Zarnowski 1955; Kisielewska 1958; Procopič 1956; 1959; Pojmańska 1957; Rybicka 1959; Schaldybin 1964). Kornienko *et al.* (2006), using a set of new morphological features, came to a conclusion about the validity of both species of the genus, as confirmed later by molecular data (Binkiene & Kontrimavichus 2007). Over the past 20 years, more than 10 species of the genus *Neoskrjabinolepis* have been described, which, until the present study, has included 16 species of cestodes (Kornienko *et al.* 2022b).

In helminthological material from shrews of Sakhalin Island, a cestode was found that we attributed to the genus *Neoskrjabinolepis.* By the end of the last century, there had been only one study by Japanese authors on helminths of insectivores of Sakhalin (Sawada & Kobayashi 1993). It listed only three species of cestodes, one of which was identified as *Neoskrjabinolepis singularis* (Cholodkovsky, 1912) Spassky, 1954. Currently, in Sakhalin shrews, five species of the genus *Neoskrjabinolepis* are registered—*N. kedrovensis* Kornienko, Gulyaev & Melnikova, 2007; *N. kunashiriensis* Kornienko & Gulyaev, 2011; *N. nadtochijae* Kornienko, Gulyaev & Melnikova, 2006; *N. nana* Kornienko & Gulyaev, 2011; and *N. nuda* Kornienko, Gulyaev, Melnikova & Georgiev, 2008—with three species (*N. kunashiriensis*, *N. nana*, and *N. nuda*) being Sakhalin–Kunashir endemics (Kornienko *et al.* 2008; Kornienko & Gulyaev 2011). The cestode we found differs from already known representatives by the presence of several characteristics, including a unique feature (alternation of genital pores in proglottids), suggesting that this cestode is a new taxon.

The widespread occurrence of the genus in the Palearctic and the substantial increase in its species diversity (from two to 17 species) necessitate a taxonomic revision of the genus *Neoskrjabinolepis* with clarification of species affiliation of previously found cestodes. In addition, the inclusion of new morphological features of the genus makes it necessary to expand the existing set of morphological criteria (Kornienko *et al.* 2006, 2007) and make additions to genus diagnosis (Kornienko *et al.* 2008).

The aim of this work was a taxonomic revision of the genus *Neoskrjabinolepis*, clarification of genus diagnosis on the basis of new diagnostic traits, and an update of the genus identification key as well as a description of a new species from shrews of Sakhalin Island.

Materials and methods

From June–September 2005, cestodes were collected from shrews at two localities on Sakhalin Island: Sokol Biological Station (SBS) and suburbs of the town of Poronaysk. Cestodes were collected from two species of *Sorex*: *S. unguiculatus* Dobson (95 specimens) and *S. caecutiens* Laxmann (22 specimens).

Host specimens were dissected immediately after their death. Live cestodes were isolated and relaxed in water, then fixed in 70% ethanol. For morphological analysis, six specimens were stained with Ehrlich's hematoxylin, differentiated in a 3% aqueous solution of ferric ammonium sulphate 12-hydrate, dehydrated in an ethanol series, cleared in clove oil, and mounted in Canada balsam. Four specimens were mounted in Berlese's medium to facilitate the examination of the rostellar hooks and copulatory apparatus.

Type specimens were deposited in collections of the Zoological Museum at the Institute of Systematics and Ecology of Animals (ISEA), Novosibirsk, and the Natural History Museum, Geneva, Switzerland (MHNG).

Measurements are given in micrometers (μm) except where otherwise stated. Metrical and meristic data are presented as a range (min–max) followed by the mean and the number of the measurements taken (n) in parentheses. Levels of infection were assessed using the following parameters (Fedorov 1986): P, prevalence (percentage of individuals of a host population infected with a certain helminth species); I, the intensity range (the minimum and maximum number of cestodes of a certain species in infected individuals in the host population). The terminology used in the description of different stages of proglottid development is according to Mas-Coma & Puchades (1991).

Results

Neoskrjabinolepis (Neoskrjabinolepidoides) paradoxa n. sp.

Type host: *Sorex unguiculatus* Dobson, 1890 (Eulipotyphla: Soricidae).

Type locality: Sokol Biological Station (SBS), Sakhalin Island, Russia (N 47°14′ E 142°46′).

Site: Intestine.

Type material: Holotype: on the slide ISEA No. 18.11.5.1 ex *Sorex unguiculatus*, intestine, 4 September 2005 (Dissection No. 229); the holotype specimen (placed on the right) and another cestode specimen belonging to the same species were mounted on one slide in Canada balsam. Paratypes: MHNG INVE 91138 ex *Sorex unguiculatus*, SBS, 4 September 2005, with the same collection data as in the holotype, a specimen stained and mounted in Canada balsam; ISEA No. 18.11.5.3 ex *S. unguiculatus* (Dissection No. 229), SBS, 4 September 2005, with the same collection data as in the holotype, two specimens stained and mounted in Canada balsam; ISEA No. 18.11.5.4 ex *S. unguiculatus* (Dissection No. 229), SBS, 4 September 2005, with the same collection data as in the holotype, a specimen stained and mounted in Canada balsam; ISEA No. 18.11.5.5 ex *S. caecutiens* (Dissection No. 44), Poronaysk, 8 July 2005, with the same collection data as in the holotype, three scolices and three fragments of strobila in Berlese's medium; ISEA No. 18.11.5.6 ex *S. unguiculatus* (Dissection No. 92), SBS, 24 June 2005, with the same collection data as in the holotype, one scolex and one fragment of strobila in Berlese's medium.

Another host: Sorex caecutiens Laxmann 1788

Another locality: suburbs of the town of Poronaysk, Sakhalin Island, Russia (N 49°13′ E 143°06′).

Prevalence and intensity: 2.1% and 2–10 (av. 0.13) *in S. unguiculatus*; 4.5% and 5 in *S. caecutiens.*

Etymology: The specific name *paradoxa* refers to the unusual (irregular) alternation of genital pores, which is unique among its congeners.

Description (based on seven strobila with one series of pregravid proglottids and three strobila with two pregravid proglottids; Figures 1a-f): body small, slender, 6.0–7.0 mm (6.6, n = 6) long; strobila flat, consisting of 250–280 proglottids; maximum width 320–340 (330, n = 6) at level of proglottids with young uterus. Strobilation serial (group of simultaneously laid down segments then develops synchronously), pregravid or gravid strobila usually consisting of four series of proglottids. First series consists of juvenile or premature proglottids; second section consists of hermaphroditic mature proglottids; third series consists of postmature or pregravid proglottids; fourth series consists of pregravid or gravid proglottids; each series consists of ca. 50–70 proglottids. Strobilar portions containing juvenile, premature, or mature proglottids without external segmentation; proglottids externally distinct at level of postmature part of strobila.

Scolex 270–350 (320, n = 6) wide, distinctly wider than neck (Figure 1a). Suckers round, 120–130 × 110–130 (122 × 116, n = 6), with well-developed musculature. Rostellar apparatus complex. Rhynchus short, 65–82 long, 100–120 wide (72 × 114, n = 6). Rostellum sac-like, 91–120 × 92–120 (107 × 100, n = 6); its walls consist of external layer of longitudinal muscular fibers and internal layer of circular muscular bundles. Rostellar hooks 10 in number, arranged in single row, 42–45 (43, n = 10) long, with characteristic pincer-like shape; axis of blade almost parallel to axis of guard; blade almost three times length of handle, curved medially; handle causes large epiphyseal thickening. End of guard deflected away from blade (Figure 1b). When rostellar apparatus retracts, rostellar hooks with blades directed anteriorly. Rostellar pouch voluminous, 210–250 × 180–200 (230 × 190, n = 6), extending beyond level of posterior margins of suckers. Neck 180–200 (193, n = 6) wide.

Proglottids acraspedote, transversely elongate. Mature proglottids 20–33 × 240–330 (25 x 300, n = 10) (Figure 1c) [because external segmentation appears only at level of postmature proglottids, length of mature proglottids is measured as distance between genital atria of adjacent proglottids], with length/width ratio 1:10; lateral fields 50–60

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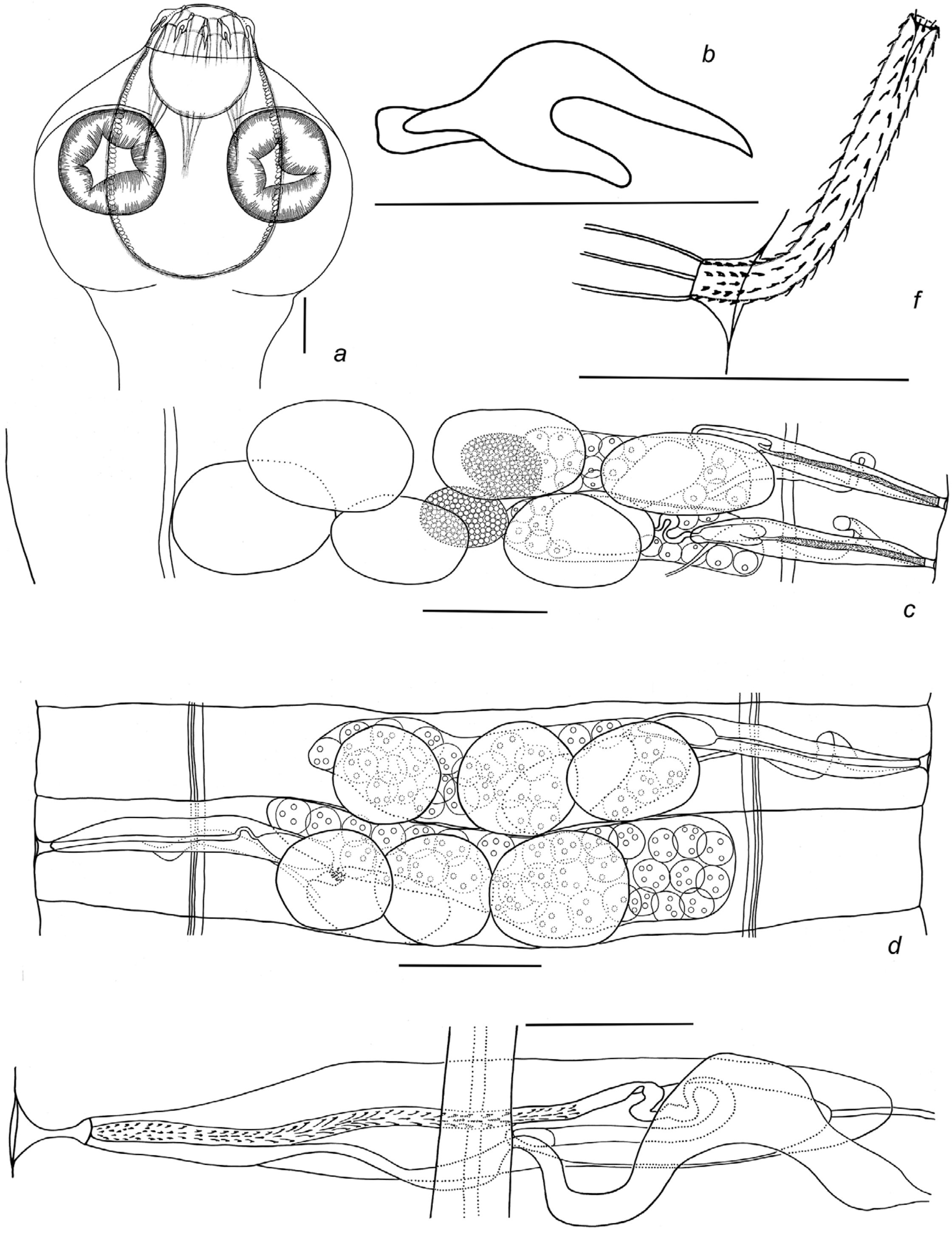

Figure 1 *N.* (*Neoskrjabinolepidoides*) *paradoxa* n. sp.: a, Scolex; b, Rostellar hook; c, Mature proglottids; d, Postmature proglottids; e, Cirrus sac; f, Cirrus. Scale bars: a, 100 µm; b, 45 µm; c & d, 50 µm; e, 20 µm; f, 30 µm.

(55, n = 10) wide; gonads densely situated in median field. Pregravid proglottids 54–77 × 320–340 (69 × 330, n = 8), with length/width ratio ca. 1:5–6. Osmoregulatory canals two pairs, without transverse anastomoses; ventral canals 5–7 wide; dorsal canals 1–3 wide. A special feature of this species is the irregularly alternating genital pores in postmature (3) (Figure 1d) and pregravid (4) series of strobila. In series of hermaphroditic mature proglottids, genital pores are most often located unilaterally; however, in several strobila of type series, irregularly alternating genital pores were also found in series of hermaphroditic mature proglottids. Genital atrium simple, 6–7 deep, 3–4 in diameter.

Testes three, oval or elliptical, 30–60 × 42–70 (46 × 52, n = 10), arranged in transverse row, two antiporal and one poral relative to midline of proglottid or one antiporal and two poral relative to midline of proglottid (Figure 1c). Diameter of testes greater than proglottid length and, consequently, dense dorsal testicular field formed in

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mature region of strobila (pattern described as "neoskrjabinolepid-type of organization," see Gulyaev & Kornienko 2009). Degenerating testes persist in postmature proglottids. Cirrus sac elongate, thin-walled, cigar-shaped (Figure 7), 91–110 × 10–12 (99 × 11, n = 10), passes into median field but does not reach far median line of proglottid (Figures 1c, d). Cirrus short, cylindrical, 60–65 (63, n = 7) long; armed with different types of spines; its basal part covered with numerous small rosethorn-shaped spines; middle part armed with fine, needle-shaped spines, whose size decreases in distal direction (Figure 1e, f). Internal seminal vesicle small, 24–38 × 7–13 (29 × 9, n = 10), occupying not more than a third of cirrus sac length even when filled. External seminal vesicle 34–49 × 21–32 (40 × 29, n = 10), connected to cirrus sac by long narrow duct.

Vitellarium subspherical, 21–39 × 20–36 (29 × 25, n = 6), situated antiporally to ovary. Ovary transversely elongate, compact, 11–27 × 88–110 (19 × 99, n = 10), in poral half of median field; overlaps cirrus sac, external seminal vesicle and testes ventrally (Figure 1c). Vagina thin-walled, passes ventrally to cirrus sac, forming coil after entering median field (Figure 1e). Conductive part of vagina gradually enlarges and passes into small, sac-like seminal receptacle.

Uterus not extending into lateral fields. Uterine wall thin, membranous throughout morphogenesis of uterus. Number of eggs in uterus 45–60 (54, n = 8).

ZooBank registration: To comply with the regulations set out in Article 8.5 of the amended version of the International Code of Zoological Nomenclature (ICZN, 2012), details of the new species were submitted to ZooBank. The Life Science Identifier for *Neoskrjabinolepis paradoxa* n. sp. is urn:lsid:-zoobank.org: pub:69-AF891D-7638-4F2D-8FC5-85EDA846D406.

Remarks

N. paradoxa n. sp. is characterized by a serial strobilar development and therefore belongs to the subgenus *Neoskrjabinolepis* (*Neoskrjabinolepidoides*) Kornienko, Gulyaev & Melnikova, 2006, which currently includes 10 species: *N. singularis* (Cholodkowsky, 1912); *N. nadtochijae* Kornienko, Gulyaev & Melnikova, 2006; *N. corticirrosa* Kornienko, Gulyaev & Melnikova, 2007; *N. kedrovensis* Kornienko, Gulyaev & Melnikova, 2007; *N. nuda* Kornienko, Gulyaev, Melnikova & Georgiev, 2008; *N. merkushevae* Kornienko & Binkiene, 2008; *N. gvosdevi* Kornienko, Erzhanov & Gulyaev, 2010; *N. kunashiriensis* Kornienko & Gulyaev, 2011; *N. nana* Kornienko & Gulyaev, 2011; and *N. hobergi* Kornienko & Dokuchaev, 2012.

Two species, *N. singularis* and *N. merkushevae*, from the European part of the Palearctic Region and from the south of West Siberian, have been recorded (Kornienko *et al.* 2006; Kornienko & Binkiene 2008). The remaining eight species from the shrews of the Asiatic part of the Palearctic (mainly in the Far East) have been described (Kornienko *et al.* 2006, 2007; Kornienko & Gulyaev 2011; Kornienko & Dokuchaev 2012), with the exception of *N. gvosdevi.* This species has not been recorded outside the Kazakh Uplands and is considered endemic to Kazakhstan.

The new species has a unique feature that radically distinguishes it from all existing species in the genus, namely, the irregular alternation of the genital pores. Nonetheless, this arrangement of genital pores was noted only in the series of postmature proglottids. Therefore, the absence of a such series in the strobila may complicate the identification of cestodes of this species. In this case, the new species can be distinguished from all of these based on the length and shape of the rostellar hooks, the armament and size of the cirrus, the structure of the male copulatory apparatus, and the number of eggs per uterus.

N. paradoxa is most similar to *N. gvosdevi* and *N. nadtochijae.* These species have similar length and shape of their rostellar hooks: 42–45 μm in *N. paradoxa* vs. 40–44 μm in *N. gvosdevi* and 40–45 μm in *N. nadtochijae.* The cirrus of *N. paradoxa* is intermediate in length (60–65 μm) between *N. gvosdevi* (45–50 μm) and *N. nadtochijae* (71–74 μm). Nevertheless, the armament of cirri is different among these species. The median region of the cirrus of *N. paradoxa* is armed with fine, needle-shaped spines decreasing in the distal direction; in contrast, the cirri of *N. gvosdevi* and *N. nadtochijae* are armed with fine needle-shaped spines and sabre-shaped spines along the entire length, respectively. In addition, the new species differs from *N. gvosdevi* and *N. nadtochijae* by the size of the cirrus sac and the number of eggs within the uterus. The cirrus sac of *N. paradoxa* (91–110 μm in length) passes deeply into the median field but does not reach the median line of a proglottid; in contrast, the cirrus sac of *N. gvosdevi* (62–82 μm in length) slightly crosses poral osmoregulatory canals. In terms of the size of the cirrus sac, *N. nadtochijae* has a longer cirrus sac (160–180 μm in length) than *N. paradoxa* does. The numbers of eggs per uterus differ between *N. paradoxa*, *N. gvosdevi*, and *N. nadtochijae*, i.e. 45–64, 9–18, and 20–46, respectively.

Species *N. paradoxa* and *N. nuda* have the same length (42–45 and 40–44 μm, respectively) but different shapes of rostellar hooks. Additionally, the new species differs from *N. nuda* by the length (60–65 and 95–100 μm, respectively) and armament of the cirrus and by the number of eggs per gravid uterus (45–60 and 15–22, respectively).

N. paradoxa differs from all the other species of the subgenus *Neoskrjabinolepidoides* by having shorter rostellar hooks: 42–45 vs. 48–53 μm in *N. corticirrosa*, 56–65 μm in *N. singularis*, 53–59 μm in *N. kunashiriensis*, and 63–66 μm in *N. hobergi.* These species have short cirri but differ from each other in cirral armament and in the number of eggs per gravid uterus: 45–60 in *N. paradoxa*, 10–20 in *N. corticirrosa*, 7–13 in N. *kunashiriensis*, 34–43 in *N. singularis*, and 12–16 in *N. hobergi.*

The new species has longer rostellar hooks than do *N. nana*, *N. kedrovensis*, *N. merkushevae*: 37–39, 36–38, and 35–37 μm, respectively. Compared to *N. nana* and *N. kedrovensis*, which have a long cirrus (85–90 and 90–110 μm, respectively), that of *N. paradoxa* is short (60–65 μm). The cirrus of *N. merkushevae* is even shorter (35–40 μm). The armament of the cirrus varies greatly among these species.

Based on the above-mentioned differences, we recognize the investigated specimens as a new species. The name *Neoskrjabinolepis paradoxa* was published for the first time by Zubova *et al.* (2008a) in conference proceedings. Because the name was not accompanied by a description, this publication does not meet the availability criteria of the International Commission on Zoological Nomenclature (ICZN 1999) (Chapter 4, Article 13) and is considered a *nomen nudum.* According to the ICZN, this name is now proposed as available for the same concept, together with the first description of the species.

The main differential criteria of the genus *Neoskrjabinolepis* included in the modified genus diagnosis (Kornienko *et al.* 2008) are the type of strobilation, the shape and size of rostellar hooks, the size of the cirrus sac and its position relative to poral osmoregulatory canals, the size and armament of the cirrus, the number of eggs in uterine proglottid, and positioning of the uterus located in the median field of a proglottid, not beyond osmoregulatory canals. Later, in the American species *N. hobergi* found in *Sorex tundrensis* Merriam from the Seward Peninsula (Alaska, USA), a different positioning of the uterus in the proglottid was discovered: having different degrees of maturity (postmature and gravid proglottids), with the uterus crossing osmoregulatory canals and reaching lateral areas of the proglottid (Kornienko & Dokuchaev 2012).

One of the features included in the latest diagnosis of the family Hymenolepididae is unilateral positioning of genital pores, with rare cases of alternations (Czaplinski & Vaucher 1994). For the genus *Neoskrjabinolepis*, the unilateral positioning of genital pores is characteristic, and consequently this feature was not even mentioned in the genus diagnosis. Nonetheless, for the new species *N. paradoxa*, irregular alternation of genital pores was found in the uterus series in the strobila, whereas in a series containing mature proglottids, the positioning of genital pores is usually unilateral. Thus, because new morphological features were found (possible irregular alternation of genital pores and penetration of the uterus into lateral fields of the proglottids), we believe that it is necessary to add them to the existing genus diagnosis.

Neoskrjabinolepis Spassky, 1947

Genus diagnosis [adapted from ref. (Kornienko *et al.* 2008)]. Cestodes of small body size, consisting of numerous acraspedote proglottids. Anterior portion of strobila (to level of postmature proglottids) without external segmentation. Both gradual and serial patterns of strobilar development occur. Mature proglottids considerably wider than long; gravid proglottids almost as long as wide or longer than wide. Scolex relatively large, having complex rostellar apparatus with invaginable rostellum. Rostellar hooks 10 in number, pincer-shaped, with epiphyseal thickening of handle. Male and female genital systems with simultaneous development. Genital pores unilateral, rarely alternating. Testes three, arranged in transverse row situated dorsally to female gonads. Cirrus sac short or long, from just crossing poral osmoregulatory canals to reaching median line of proglottid. Cirrus armed with spines, often of various shapes. Vitellarium compact, rounded, situated in antiporal half of median field. Ovary oval, transversely elongate, poral to vitellarium. Uterus sac-like, situated in median field during its entire development or rarely extends laterally beyond osmoregulatory canals. Gravid proglottid with strong persisting walls, functioning as oophore and enabling group dispersion of eggs. Parasites of shrews of genus *Sorex* (Eulipotyphla: Soricidae) in Palearctic and Nearctic Regions. Type species: *N. schaldybini* Spassky, 1947.

Below we propose a key representing the current taxonomic concept of the genus *Neoskrjabinolepis*, and it includes all known so far species.

The identification key to the species of the genus *Neoskrjabinolepis*

1a. Strobilar development gradual …[subgenus *Neoskrjabinolepis* (*Neoskrjabinolepis*)]	2
1b. Strobilar development serial …[subgenus *Neoskrjabinolepis* (*Neoskrjabinolepidoides*)]	7
2a. Fully-everted cirrus short, cylindrical	3
2b. Fully-everted cirrus long, whip-shaped	4
3a. Fully-everted cirrus 40–42 μm long, its parabasal region armed with several large, claw-shaped spines; middle and distal regions of cirrus armed with sparsely distributed, sabre-shaped spines. Rostellar hooks 38–43 μm long	*N. schaldybini*
3b. Fully-everted cirrus 45–50 μm long, its median region armed with thin, sabre-shaped spines, with size decreasing in distal direction; distal region of cirrus unarmed. Rostellar hooks 52–55 μm long	*N. plagis*
4a. Fully-everted cirrus > 100 μm	5
4b. Fully-everted cirrus < 100 μm	6
5a. Fully-everted cirrus 120–125 μm long, armed with small, relatively scarce spines whose size decreases in distal direction, becoming indistinct on distalmost region of cirrus. Rostellar hooks 41–45 μm long; axes of blade and guard form acute angle. Eggs per proglottid 16–20 in number	*N. longicirrosa*
5b. Fully-everted cirrus 100–110 μm long, armed with small, dense spines along its entire length. Rostellar hooks 45–49 μm long; axes of blade and guard almost parallel. Eggs per proglottid 35–47 in number	*N. pilosa*
6a. Fully-everted cirrus 85–100 μm long. The cirrus-sac does not reach median line of proglottid. The vagina has no muscular sphincter. Rostellar hooks 38–42 μm long. Eggs per proglottid 55–70 in number	*N. fertilis*
6b. Fully-everted cirrus 80–100 μm long. The cirrus-sac reaches the midline of the proglottid. The vagina has muscular sphincter. Rostellar hooks 37–40 μm long. Eggs per proglottid 40–50 in number	*N. yanchevi*
7a. Fully-everted cirrus long, whip-shaped	8
7b. Fully-everted cirrus short, cylindrical	10
8a. Fully-everted cirrus > 90 μm	9
8b. Cirrus 85–90 μm long. Rostellar hooks 37–39 μm long. Eggs per proglottid 12–16 in number	*N. nana*
9a. Fully-everted cirrus 90–110 μm long; its distal region with scarce, sabre-shaped spines. Rostellar hooks 36–38 μm long	*N. kedrovensis*
9b. Fully-everted cirrus 95–100 μm long; its distal region smooth. Rostellar hooks 40–44 μm long	*N. nuda*
10a. Rostellar hooks ≤60 μm	11
10b. Rostellar hooks ≥59 μm	12
11a. Rostellar hooks 60–65 μm long. Uterus extends not into lateral fields of postmature and gravid proglottids. Eggs per proglottid 35–43 in number	*N. singularis*
11b. Rostellar hooks 63–66 μm long. Uterus extends into lateral fields of postmature and gravid proglottids. Eggs per proglottid 36–45 in number	*N. hobergi*

(*Continued*)

(*Continued*)

12a. Eggs per proglottid < 20 in number	13
12b. Eggs per proglottid > 20 in number	16
13a. Cirrus > 50 μm long	14
13b. Cirrus < 50 μm long	15
14a. Rostellar hooks 53–59 μm long. Cirrus 55–65 μm long, parabasal region smooth, middle region with several longer saber-shaped spines, distal region with needle-shaped spines, decreasing towards the cirrus apex. Eggs per proglottid 7–13 in number	*N. kunashiriensis*
14b. Rostellar hooks 48–53 μm long. Cirrus 60–65 μm long, armed in parabasal region with several small claw-shaped spines; remainder with scarce, sabre-shaped spines. Eggs per proglottid 10–20 in number	*N. corticirrosa*
15a. Rostellar hooks 35–37 μm long. Cirrus 35–40 μm long. Eggs per proglottid 12–16 in number	*N. merkushevae*
15b. Rostellar hooks 40–44 μm long. Cirrus 45–50 μm long. Eggs per proglottid 9–18 in number	*N. gvosdevi*
16a. Rostellar hooks 40–45 μm long. Cirrus 71–74 μm long. Eggs per proglottid 20–46 in number	*N. nadtochijae*
16b. Rostellar hooks 42–45 μm long. Cirrus 60–65 μm long. Eggs per proglottid 45–64 in number	*N. paradoxa* n.sp.

Discussion

Clarification of the differential species features of this genus allowed us to show that the genus *Neoskrjabinolepis* is a taxon having very high species richness among the Hymenolepididae of mammals. Furthermore, it became possible to clarify species affiliation of this genus's cestodes found by other authors in various regions of the Palearctic. Studies by most authors either represent faunistic summaries on helminths of shrews from different parts of the Palearctic without inclusion of any morphological traits of the found cestodes or contain data that do not match diagnoses of modern species; this state of affairs casts doubt on the correctness of their identification (Arzamasov *et al.* 1969; Eltyshev 1975; Anikanova *et al.* 2001, 2002; Irzhavsky & Gulyaev 2002; Haukisalmi 2015; Kirillov *et al.* 2018; Nikonorova *et al.* 2019). Publications containing not only information about finds of *Neoskrjabinolepis* species in various hosts but also morphometric features (e.g. rostellar hook sizes and cirrus or cirrus sac lengths) enabled us to rectify species affiliation of the found cestodes, as reflected in Table 1.

Currently, the genus *Neoskrjabinolepis* contains 17 species (see Table 1) (Kornienko *et al.* 2022b). Sixteen species parasitize Palearctic shrews (Kornienko *et al.* 2007, 2008, 2010, 2022b; Kornienko & Binkienė 2008; Kornienko & Gulyaev 2011). Two species from Nearctic shrews of Alaska (*N. hobergi* and *N. fertilis*) have been described (Kornienko & Dokuchaev 2012).

Four species from European shrews are currently known: *N. schaldybini*, *N. singularis*, *N. merkushevae*, and *N. yanchevi* (Kornienko *et al.* 2022b). Representatives of the genus have been repeatedly registered in Poland (Zarnowski 1955; Pojmanska 1957; Rybicka 1959). In *S. araneus* and *S. minutus*, Zarnowski (1955) found *N. singularis* with rostellar-hook lengths of 55–57 and 36–39 μm, respectively. That author attributed such a wide range of hook lengths to the size of the scolex. Rybicka (1959) associated differences in sizes of the hooks of two forms of *Hymenolepis singularis* (= *Neoskrjabinolepis singularis*) with parasitizing of different shrew species. According to her, the length of hooks in cestodes from *S. minutus* is 35–40 μm, and this parameter in cestodes from *S. araneus* is 58–60 μm. Nonetheless, because the validity of both species has already been proven (Kornienko et al. 2006), we believe that Rybicka and Zarnowski found both species of the genus. In *S. araneus* and *S. minutus*, Pojmanska (1957) detected *N. singularis* with rostellar hooks 37–40 μm long. That author's figures show a mature proglottid with an evaginated long cirrus and a uterine proglottid containing a small number of eggs (no more than 20). Most likely, however, not all eggs are shown in the drawing of the uterine proglottid, because usually, eggs fill the uterus tightly. We can hypothesize that the cestode found by that author belongs to the species *N. yanchevi*, characterized by a long cirrus and considerable hook length (Kornienko *et al.* 2022b). Unfortunately, all processed slides of the genus *Neoskrjabinolepis* from the Polish helminthologists' collection are thought to be lost (Pojmańska *et al.* 2012); therefore, it is impossible to use them to clarify species affiliation of the aforementioned specimens. While re-describing the species *N. singularis* from *S. araneus* of Hungary, Kobulej (1953) specified the length of the hooks, the location of the cirrus sac relative to poral osmoregulatory canals, and the armament of the cirrus, all of which corresponded to the species *N. schaldybini*.

In *S. araneus* and *S. minutus* from Mordovia, Schaldybin (1964) discovered a cestode, identified it as *N. schaldybini*, and listed among differential features the serial type of strobila, rostellar hooks 39–52 μm long, and the cirrus sac 50–55 μm long. Most likely, the description is based on fragments of some strobilae, which may match *N. schaldybini*, *N. merkushevae*, and *N. yanchevi*. Nevertheless, it is possible that among the found cestodes, there is a new species. Because cestodes with hooks larger than 43 μm are not known among European representatives of the genus, except for *N. singularis*, with rostellar hooks 60-65 μm long.

Eleven species of *Neoskrjabinolepis* have been found in Asian Palearctic shrews (Kornienko et al. 2006, 2007, 2008, 2010; Kornienko & Gulyaev 2011; Kornienko 2012). On the territory of Kazakhstan, aside from *N. schaldybini* and *N. singularis*, Tkach & Zhumabekova (1996) recorded *Neoskrjabinolepis* sp. differing in the length of hooks (48–50 μm) and hypothesized that they discovered a new species. Based on this trait, we can theorize that these may be *N. corticirrosa* or *N. pilosa*, which occur in adjacent territories (Altai Mountains) (Kornienko *et al.* 2007).

In shrews (*S. caecutiens* and *S. isodon*) of the Russian Far East (Magadan Oblast), Novikov (1995) detected the cestode *N. singularis* with rostellar hooks 41–52 μm long. Nonetheless, these hook sizes match *N. longicirrosa*, *N. fertilis*, *N. nadtochijae*, and *N. corticirrosa*. In shrews from Magadan Oblast (unpublished data), we have found all these species except for *N. fertilis*. All the above species have been registered in adjacent territories (Republic

Table 1. The list of the species of *Neoskrjabinolepis* Spassky, 1947, their hosts, and their geographical range

Species	Hosts	Geographical region and source
		with gradual strobilation
Neoskrjabinolepis schaldybini Spassky, 1947 (Type species)	*Sorex araneus* L., 1758	**Europe**: Belarus (Arzamasov *et al.* 1969; Merkusheva & Bobkova 1981), Bulgaria (Genov 1984), Latvia, Estonia (Binkiene *et al.* 2011), Lithuania (Binkiene 2006; Binkiene *et al.* 2011), Switzerland (Vaucher 1971), Moldova (Spassky & Andreyko 1970), Hungary (Kobuley 1953), Germany (Vaucher 1971), Finland (Vaucher 1971; Haukisalmi 1989, 2015), France (Jourdane 1971; Vaucher 1971), Netherlands (Vaucher 1971), Belgium (Vaucher 1971), Sweden (Vaucher 1971), Norway (Vaucher 1971), Poland (Zarnowski 1955; Rybicka 1959; Vaucher 1971), Czechoslovakia (Prokopic 1959; Vaucher 1971; Murai & Mészáros 1984; Hanzelova & Ryshavy 1996), Romania (Skolka *et al.* 2004); Ukraine (Tkach 1993); United Kingdom (Sharpe 1964; Lewis 1968, 1987; Vaucher 1971; Roots 1992), Spain (Mas-Coma & Gallego 1977),Russian Federation: Karelia (Anikanova *et al.* 2001, 2002; Nikanorova *et al.* 2019), Komi (Yushkov 1995), Samarskaja oblast' (Kirillov *et al.* 2018), Mordovia (Schaldybin 1964) **Asia**: Russian Federation: West Siberia (Kornienko *et al.* 2006; Sheykina & Zhigileva 2018), Zabaykalye (Eltyshev 1975)
	Sorex sp.*	**Asia**: Russian Federation: West Siberia* (Spassky 1947)
	S. asper Thomas, 1914	**Asia**: Kazakhstan (Bekenov *et al.* 1985; Tkach & Zhumabekova 1996)
	S. minutus L., 1766	**Europe**: Belarus (Shimalov 2012); Bulgaria (Genov 1984), Lithuania (Binkiene 2006); Finland (Haukisalmi 1989, 2015), France (Jourdane 1971), Moldova (Spassky & Andreyko 1970), Russian Federation: Karelia (Anikanova *et al.* 2002); Komi (Yushkov 1995), Mordovia (Schaldybin 1964), Samarskaja oblast' (Kirillov *et al.* 2018) **Asia**: Kazakhstan (Bekenov *et al.* 1985; Tkach & Zhumabekova 1996)
	S. alpinus Schinz, 1837	**Europe:** Czechoslovakia (Murai & Mészáros 1984)
	S. isodon Turov, 1924	**Europe**: Finland (Haukisalmi 1989, 2015), Russian Federation: Karelia (Anikanova *et al.* 2002); Komi (Yushkov 1995) **Asia**: Russian Federation: West Siberia (Kornienko *et al.* 2006)
	S. caecutiens Laxmann, 1788	**Europe**: Finland (Haukisalmi 1989, 2015), Russian Federation: Karelia (Anikanova *et al.* 2002), Komi (Yushkov 1995) **Asia**: Russian Federation: West Siberia (Kornienko *et al.* 2006); Zabaykalye (Eltyshev 1975)
	S. roboratus Hollister, 1913	**Asia**: Russian Federation: West Siberia (Kornienko *et al.* 2006)
	S. minutissimus Zimmermann 1780	**Asia**: Russian Federation: Zabaykalye (Eltyshev 1975)
	S. tundrensis Merriam, 1900	**Europe**: Russian Federation: Komi (Yushkov 1995) **Asia**: Kazakhstan (Tkach & Zhumabekova 1996)
	S. satunini Ognev, 1922	**Asia**: Russian Federation: North Caucasus (Irzhavsky & Gulyaev 2002; Irzhavsky & Ketenchiev 2011; Kornienko *et al.* 2022a)
	S. volnuchini Ognev, 1922	**Asia**: Russian Federation: North Caucasus (Irzhavsky & Gulyaev 2002; Irzhavsky & Ketenchiev 2011; Kornienko *et al.* 2022a)
	S. raddei Satunin, 1895	**Asia**: Russian Federation: North Caucasus (Irzhavsky & Gulyaev 2002; Irzhavsky & Ketenchiev 2011; Kornienko *et al.* 2022a)
N. fertilis Kornienko & Dokuchaev, 2012	*S. tundrensis**	North America: Alaska (USA), Seward Peninsula*(Kornienko & Dokuchaev 2012) **Asia:** Russian Federation: East Siberia: Republic of Sakha (Yakutia) (Kornienko *et al.* 2018); Far East: Chukotka (Kornienko & Dokuchaev 2012)
	S. caecutiens	**Asia:** Russian Federation: East Siberia: Republic of Sakha (Yakutia) (Kornienko *et al.* 2018)
N. longicirrosa Kornienko, Gulyaev & Melnikova, 2006	*S. araneus**	**Asia**: Russian Federation: West Siberia (Altay Mts*) (Kornienko *et al.* 2006)
	S. minutus	**Asia**: Russian Federation: West Siberia (Altay Mts) (Kornienko *et al.* 2006)
	S. isodon	**Asia**: Russian Federation: West Siberia (Altay Mts) (Kornienko *et al.* 2006); East Siberia: Republic of Sakha (Yakutia) (Kornienko *et al.* 2018); Far East: Kamchatka Peninsula, Paramushir Island (Kornienko & Dokuchaev 2023); Bolshoi Shantar Island (Kornienko *et al.* 2014); Magadan oblast' (**present date)**
	S. caecutiens	**Asia:** Russian Federation: West Siberia (Altay Mts) (Kornienko *et al.* 2006); East Siberia: Republic of Sakha (Yakutia) (Kornienko *et al.* 2018); Far East: Kamchatka Peninsula, Paramushir Island (Kornienko & Dokuchaev 2023); Bolshoi Shantar Island (Kornienko *et al.* 2014); Magadan oblast' (**present date)**
	S. daphaenodon Thomas, 1907	**Asia:** Russian Federation: Far East: Kamchatka Peninsula (Kornienko & Dokuchaev 2023)
N. pilosa Kornienko, Gulyaev & Melnikova, 2007	*S. araneus**	**Asia:** Russian Federation: West Siberia (Altay Mts*) (Kornienko *et al.* 2007)
	S. isodon	**Asia:** Russian Federation: West Siberia (Altay Mts) (Kornienko *et al.* 2007)
N. plagis Kornienko, Gulyaev & Melnikova, 2007	*S. caecutiens**	**Asia:** Russian Federation: East Siberia: Republic of Sakha (Yakutia) (Kornienko *et al.* 2018); Far East: Chukotka* (Kornienko *et al.* 2007)

(*Continued*)

Table 1. (*Continued*)

Species	Hosts	Geographical region and source
N. yanchevi Kornienko, Vasileva & Georgiev, 2022	*S araneus**	**Europe:** Bulgaria*(Kornienko *et al.* 2022b), Poland (Pojmanska 1957), Russian Federation: Arkhangelskaya Oblast' (Kornienko *et al.* 2022b), Komi (**present data**)
	with serial strobilation	
N. singularis (Cholodkovsky, 1912) Spassky, 1954 (Type species)	*S. araneus*	**Europe**: Belarus (Shimalov 2001, 2007, 2012); Bulgaria (Prokopič & Genov 1974; Prokopič *et al.* 1974; Yanchev 1974; Yanchev & Karapchanski 1974; Yanchev & Stoykova-Hadzhinikolova 1980), Lithuania (Binkiene 2006), Poland (Zarnowski 1955; Soltys 1952; Rybicka 1959; Vaucher 1971), Moldova (Spassky & Andreyko 1970), France (Vaucher 1971), Switzerland (Vaucher 1971), Netherlands (Vaucher 1971), Germany (Vaucher 1971), Denmark (Vaucher 1971), Norway (Vaucher 1971), Sweden (Vaucher 1971), Finland (Vaucher 1971; Haukisalmi 1989, 2015), Czechoslovakia (Prokopič 1958; Jankovská *et al.* 2005); Russian Federation: Karelia (Nikanorova *et al.* 2019) **Asia**: Georgia (Prokopič & Matsaberidze 1972); Russian Federation: West Siberia (Kornienko *et al.* 2006; Sheykina & Zhigileva 2018)
	Sorex sp.*	**Europe**: Russian Federation: Novgorod* (Cholodkovsky 1912)
	S. asper	**Asia**: Kazakhstan (Tkach & Zhumabekova 1996)
	S. isodon	**Asia**: Russian Federation: West Siberia (Altay Mts) (Kornienko *et al.* 2006)
	S. caecutiens	**Europe**: Finland (Haukisalmi 1989, 2015) **Asia**: Russian Federation: West Siberia (Kornienko *et al.* 2006; Sheykina & Zhigileva 2018)
	S. minutus	**Europe**: Belarus (Shimalov 2007, 2012); Bulgaria (Prokopič *et al.* 1974), Czechoslovakia (Prokopič 1958;) Poland (Soltys 1952) **Asia**: Russian Federation: West Siberia (Altay Mts) (Fedorov 1975; Kornienko *et al.* 2006)
	S. tundrensis	**Asia**: Kazakhstan (Tkach & Zhumabekova 1996)
N. corticirrosa Kornienko, Gulyaev & Melnikova, 2007	*S. caecutiens**	**Asia**: Russian Federation: West Siberia (Altay Mts) (**present data**); East Siberia: Republic of Sakha (Yakutia) (Kornienko *et al.* 2018); Far East: Chukotka*, Kamchatka Peninsula (Kornienko & Dokuchaev 2023); Bolshoi Shantar Island (Kornienko *et al.* 2014); Priamurye (Kornienko *et al.* 2007)
	S. tundrensis	**Asia**: Russian Federation: West Siberia (Altay Mts) (**present data**); East Siberia: Republic of Sakha (Yakutia) (Kornienko *et al.* 2018); Far East: Chukotka*, Kamchatka Peninsula; Priamurye (Kornienko *et al.* 2007)
	S. isodon	**Asia**: Russian Federation: Far East: Bolshoi Shantar Island (Kornienko *et al.* 2014)
N. gvosdevi Kornienko, Erzhanov & Gulyaev, 2010	*S. tundrensis**	**Asia**: Kazakhstan: Pavlodar Prov.* (Kornienko *et al.* 2010)
N. hobergi Kornienko & Dokuchaev, 2012	*S. tundrensis**	North America: Alaska (USA), Seward Peninsula* (Kornienko & Dokuchaev 2012)
N. kedrovensis Kornienko, Gulyaev & Melnikova, 2007	*S. unguiculatus**	**Asia**: Russian Federation: Far East: Primorye* (Kornienko *et al.* 2007); Sakhalin Island (Zubova *et al.* 2008a); Japan, Hokkaido Island (Sato *et al.* 1988; Zubova *et al.* 2008b)
	S. isodon	**Asia**: Russian Federation: Far East: Primorye, Kamchatka Peninsula (Kornienko *et al.* 2007); Paramushir Island (Kornienko & Dokuchaev 2023)
	S. caecutiens	**Asia**: Russian Federation: Far East: Primorye, Kamchatka Peninsula (Kornienko *et al.* 2007; Kornienko & Dokuchaev 2023); Paramushir Island (Kornienko & Dokuchaev 2023); Bolshoi Shantar Island (Kornienko *et al.* 2014); Magadan oblast' (**present date);** Japan, Hokkaido Island (Sato *et al.* 1988; Zubova *et al.* 2008b)
	S. daphaenodon	**Asia**: Russian Federation, Far East, Kamchatka Peninsula (Kornienko & Dokuchaev 2023)
	S. shinto shinto Thomas, 1905	**Asia**: Japan, Honshu Island (Sawada & Koyasu 1990; Sawada *et al.* 1992; Sawada & Harada 1993), Sado Island (Sawada & Koyasu 1991)
N. kunashiriensis Kornienko & Gulyaev, 2011	*S. unguiculatus**	**Asia**: Russian Federation: Far East: Kunashir Island*, Sakhalin Island, Japan, Hokkaido Island (Sato *et al.* 1988; Kornienko & Gulyaev 2011)
	S. gracillimus	**Asia**: Russian Federation: Far East, Kunashir Island* (Kornienko & Gulyaev 2011); Japan, Hokkaido Island (Sato *et al.* 1988)
	S. shinto shinto	**Asia**: Japan, Honshu Island (Sawada & Harada 1993)
	S. shinto sadonis Yoshiyuki, Imaizumi, 1986	**Asia**: Japan, Sado Island (Sawada & Koyasu 1991)
N. merkushevae Kornienko & Binkiene, 2008	*S. minutus**	**Europe**: Brest Region, Belarus*, Lithuania (Kornienko & Binkiene 2008), Latvia (Binkiene *et al.* 2011); Russian Federation: Crimea (Kornienko 2021) **Asia**: Russian Federation: West Siberia (Altay Mts) (Kornienko & Binkiene 2008), North Caucasus (Kornienko *et al.* 2022a)
	S araneus	**Europe**: Belarus, Lithuania (Kornienko & Binkiene 2008) **Asia**: Russian Federation: West Siberia (Altay Mts) (Kornienko & Binkiene 2008)
	S. raddei	**Asia**: Russian Federation: North Caucasus (Kornienko *et al.* 2022a)

(*Continued*)

Table 1. (*Continued*)

Species	Hosts	Geographical region and source
	S. satunini	**Asia**: Russian Federation: North Caucasus (Kornienko *et al.* 2022a)
	S. volnuchini	**Asia**: Russian Federation: North Caucasus (Kornienko *et al.* 2022a)
N. nadtochijae Kornienko, Gulyaev & Melnikova, 2006	*S. isodon**	**Asia**: Russian Federation: Far East: Priamurye* (Kornienko *et al.* 2006); Kamchatka Peninsula, Paramushir Island (Kornienko & Dokuchaev 2023)
	S. caecutiens	**Asia**: Russian Federation: Far East: Primorye; Priamurye (Kornienko *et al.* 2006); Kamchatka Peninsula, Paramushir Island (Kornienko & Dokuchaev 2023); Kunashir Island (Kornienko *et al.* 2008); Magadan oblast' (**present date)**
	S. unguiculatus	**Asia**: Russian Federation: Far East: Primorye; Priamurye (Kornienko *et al.* 2006); Sakhalin Island, Kunashir Island (Kornienko *et al.* 2008); Japan, Hokkaido Island (Zubova *et al.* 2008b)
	S. tundrensis	**Asia**: Russian Federation, East Siberia, Republic of Sakha (Yakutia) (Kornienko *et al.* 2018)
	S. daphaenodon	**Asia**: Russian Federation, East Siberia, Republic of Sakha (Yakutia) (Kornienko *et al.* 2018)
	S. shinto shinto	**Asia**: Japan, Honshu Island (Sawada & Harada 1993)
N. nana Kornienko & Gulyaev, 2011	*S. gracillimus**	**Asia**: Russian Federation: Far East: Kunashir Islands*, Sakhalin Island (Kornienko & Gulyaev 2011)
	S. minutissimus	**Asia**: Russian Federation: Far East, Kunashir Island (Kornienko & Gulyaev 2011)
N. nuda Kornienko, Gulyaev, Melnikova & Georgiev, 2008	*S. unguiculatus** Dobson, 1890	**Asia**: Russian Federation: Far East: Sakhalin Island*, Kunashir Island (Kornienko *et al.* 2008); Japan, Hokkaido Island (Sato *et al.* 1988; Zubova *et al.* 2008b)
	S. gracillimus Thomas 1907	**Asia**: Russian Federation: Far East: Sakhalin Island, Kunashir Island (Kornienko *et al.* 2008); Japan, Hokkaido Island (Sato *et al.* 1988)
	S. isodon	**Asia**: Russian Federation: Far East, Sakhalin Island (Kornienko *et al.* 2008)
	S. caecutiens	**Asia**: Russian Federation: Far East, Sakhalin Island (Kornienko *et al.* 2008); Japan, Hokkaido Island (Sato *et al.* 1988)
N. paradoxa n.sp.	*S. unguiculatus** *S. caecutiens*	**Asia**: Russian Federation: Far East, Sakhalin Island*

*Type host and locality

of Sakha [Yakutia]) (Kornienko & Dokuchaev 2015; Kornienko *et al.* 2018). Because, aside from hook length, Novikov did not specify other parameters of the found cestodes, we believe that he could have encountered all of the above species.

While recognizing the existence of a single species—*N. singularis*—in the genus, Karpenko recorded this species in the shrews of Priamurye (Karpenko 2004). Because that author did not specify morphological features of the found cestode, it is impossible to determine its species identity. Furthermore, according to our current data and published evidence, *N. singularis* and *N. schaldybini* have not been found east of Transbaikalia (Eltyshev 1975; Kornienko et al. 2006, 2022b).

On the Japanese islands, these two species of cestodes have been recorded repeatedly (Sato *et al.* 1988; Sawada & Koyasu 1990, 1991; Sawada *et al.* 1992; Sawada & Harada 1993). The illustrated material in the form of drawings and photographs used by Japanese parasitologists for describing the cestodes has made it possible in several cases to clarify the systematic position of the cestodes that they have found. Sato *et al.* (1988) reported finding cestodes *N. schaldybini*, *N. singularis*, and *Neoskrjabinolepis* sp. in shrews *S. unguiculatus*, *S. gracillimus* Thomas, 1907, and *S. caecutiens saevus* on the Japanese island of Hokkaido. According to their illustrated description, the cestodes they encountered correspond to *N. nuda*, *N. kedrovensis*, and *N. kunashiriensis*. Moreover, we also found the latter species on Hokkaido Island (Kornienko & Gulyaev 2011). The species *N. kedrovensis* was also detected in the material collected from the shrew *S. caecutiens saevus* of Hokkaido (Sawada *et al.* 1992). Those authors presented illustrations of rostellar hooks and a uterine proglottid. *N. singularis* is also listed among the specimens collected by Sawada & Koyasu (1990, 1991) from shrews *S. hosonoi* Imaizumi, 1954; *S. shinto* Thomas, 1905; and *S. shinto sadonis* of Honshu and Sado islands. Nevertheless, the presented photographs of hooks and their length match the species *N. kedrovensis*, whereas the short cirrus sac corresponds to *N. kunashiriensis.* Most likely, those authors presented photographs of fragments belonging to different species. In another article by Japanese authors, the length of rostellar hooks of *N. singularis* (43–51 μm) from *S. shinto* of the Honshu Islands (Sawada & Harada, 1993) most likely also represents several species of the genus: *N. nadtochijae*, *N. kedrovensis*, and *N. kunashiriensis.* The illustration of rostellar hooks matches the species *N. nadtochijae*, whereas the illustrations of mature proglottids with a long cirrus sac and long armed cirrus correspond to *N. kedrovensis.* Thus, we believe that shrew cestode fauna of the Japanese islands includes the following species: *N. kedrovensis*, *N. kunashiriensis*, *N. nadtochijae*, and *N. nuda.*

The rich taxonomic diversity of the genus was initially based on morphological features. The first molecular genetic data obtained for the genus confirmed the validity of the two species *N. singularis* and *N. schaldybini* (Binkiene & Kontrimavichus 2007). The study of genetic variability of *Neoskrjabinolepis* cestodes and reconstruction of phylogenetic relationships between species of the genus by means of the gene of 28S ribosomal RNA and mitochondrial gene *NAD1* suggests a high genetic diversity of the genus, validating some species of the genus (*N. nadtochijae*, *N. nuda*, *N. kunashiriensis*, *N. kedrovensis*, and *N. corticirrosa*) as well as to revealing heterogeneity of individual species (*N. schaldybini* and *N. merkushevae*), suggesting that they are a species complex (Kornienko *et al.* 2022c).

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Obviously, more than one taxon is covered by these species names, and this issue requires further research.

Conclusion

The genus *Neoskrjabinolepis* is characterized by high species richness based on morphological diversity. Recent studies show that representatives of the genus occur in shrews of various species in various regions of Eurasia (from the Pyrenees to the Japanese Islands) and in Alaska, implying its Holarctic occurrence. In Europe, four species of the genus have been recorded to date, and we registered three of them (*N. schaldybini*, *N. singularis*, and *N. merkushevae*) in the Asian part of the Palearctic (Altai Mountains) (Kornienko et al. 2006; Kornienko & Binkienė 2008; Kornienko 2021). On the American continent (Seward Peninsula, Alaska, USA), two species have been found—*N. hobergi* and *N. fertilis*—which could have entered North America from Chukotka together with *S. tundrensis* during the course of Late Pleistocene faunal exchanges (during the existence of the "Bering Land Bridge") (Bannikova *et al.* 2010; Kornienko & Dokuchaev 2012). Geographic ranges of most species (12), constituting ~70% of the species diversity, are located in the Asian part of the Palearctic. At the same time, species diversity of *Neoskrjabinolepis* from northern regions of the Palearctic, Eastern Siberia, Central Asia, and the Caucasus mountains remains poorly investigated.

The rich taxonomic diversity of the genus—exclusively based on morphological features—was later confirmed by molecular genetic data, which also point to high genetic diversity of the genus. The previously obtained molecular genetic data make the genus *Neoskrjabinolepis* a convenient model taxon for studies on its phylogeography and phylogeny.

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Competing interest. The authors declare no conflict of interest.

Ethical standard. The authors carefully reviewed the ethical standards of the journal and hereby certify that the procedures used with the investigated species comply fully with those standards. The authors assert that all procedures and methods contributing to this work and used in the current study comply with the ethical standards of the relevant national and institutional guides with laws of the Russian Federation and were approved by the ethics committee of the ISEA, Novosibirsk, Russia.

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