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Distribution of the cestode *Urocystis prolifer* Villot, 1880 (Cyclophyllidea: Hymenolepididae) in the Palaearctic and new data on its postembryonic development

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Research Paper

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Abstract

Urocystis prolifer Villot, 1880 is an intestinal parasite of *Sorex* spp. In the Palaearctic. There are significant differences in the descriptions of both adults and stages of ontogenesis of *U. prolifer* as described by various authors. The experimental infection of intermediate hosts with cestodes has been conducted. An overview of the geographical distribution, infestation of the definitive hosts and the development of the metacestode stages of *U. prolifer* are presented. The cestode is characterized by an extensive geographic area in the Palaearctic, wide host specificity and very high rates of infection of its definitive host. *Urocystis prolifer* has been recorded mostly in the taiga and forest zones of Palaearctic. Fourteen species of *Sorex* were registered as the definitive host. Redescription of *U. prolifer* and an amended generic diagnosis are provided. A complete description of the ontogeny from oncosphere to fully developed metacestode is given. Features of development of the metacestode are an asexual larval reproduction, the absence of the anterior and posterior obturator valve in the cyst of the fully developed urocyst, as well as excretory bodies.

Introduction

Urocystis prolifer Villot, 1880 (Cyclophyllidea: Hymenolepididae) is one of the smallest cestodes parasitizing shrews of the genus *Sorex*. It has attracted particular attention due to its wide distribution in the Palaearctic and high rates of infection in definitive hosts (Vaucher, 1971; Genov, 1984; Binkiene, 2006; Binkiene *et al*., 2011; Shimalov, 2012). The high abundance of *U. prolifer* is associated with a peculiarity of its ontogenesis – the asexual reproduction of larvae by budding in the intermediate host.

Villot (1880) discovered a polycephalic larva in the diplopod *Glomeris lumbatus*, which was named *U. prolifer* Villot, 1880. The adult form of this cestode was described considerably later. Moreover, different authors have described the cestode under various names (Stammer, 1955; Zarnowski, 1955; Rybicka, 1958; Baer & Della Santa, 1960; Kisielewska, 1960). Spassky & Andrejko (2004) and Vaucher (1971) considered the forms described by all previous authors to be the same species, *Hymenolepis prolifer*, and believed that the main diagnostic character, the number of rostellar hooks (80–190), is widely varying in this species. The name *U. prolifer* Villot, 1880 was adopted for this form in the recent taxonomic surveys (Czaplinski & Vaucher, 1994; Georgiev *et al*., 2006; Mariaux *et al*., 2017).

Despite the long history of studies on this species, its status as the only member of the genus, wide distribution in the Palaearctic and the detailed descriptions of adults (Zarnowski, 1955; Rybicka, 1958), there are significant differences in the data provided by various authors, including differences in the number of testes, proglottides in the strobila and rostellar hooks (table 1). Several articles have presented information on the stages of its metacestode development (Villot, 1880; Joyeux, 1922; Kisielewska, 1960).

The aims of the present work were to study the distribution of *U. prolifer* in the Palaearctic and to identify its geographical range as well as to redescribe the adult stage, provide an amended generic diagnosis and a detailed description of the metacestode development.

Materials and methods

New collections and specimens examined

The adult specimens of *U. prolifer* used in the present study were collected in 1990–2018 from different regions of Russia, detailed in the following.

Rostov Oblast' (27 specimens): Sholokhovsky District, the vicinity of the Stanitsa Vyoshenskaya in 2018 (49°37′N, 41°43′E; seven specimens of *Sorex araneus* Linnaeus, 1758

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Table 1. Comparison of the main taxonomic characters of gravid strobila of *Urocystis prolifer*.

Source Parasite name used	Number of proglottides	Number of testes	Number of hooks	Length of cirrus sac	Size of strobila	Number of eggs
Zarnowski (1955) *Pseudodiorchis multispinosa*	18–20	2	123–130	34–38 reaching middle of proglottis	350–600 × 100–120	7–8
Genov (1984) *Pseudodiorchis prolifer*	28–42	3	158–180	32–49	641–829 × 128–227	Few
Vaucher (1971) *Hymenolepis prolifer*	–	3	190	28–45	400–1100 × 130–200	Few
Baer & Della Santa (1960) *Hymenolepis prolifer*	–	3	160–180	45	270–548 × 90–137	–
Rybicka (1958) *Pseudodiorchis kampinosi*	36–52	2	80–120	45–53 58–67 reaching middle of proglottis	670–900 × 120–175	15–20
Sato *et al.* (1988) *Pseudodiorchis prolifer*	About 42	2	120	46 × 11	672 × 148	–
Sadovskaja (1965) *Echinoproboscilepis kedrovensis*	98	3	–	33 × 6	1100 × 49	10–12
Spassky & Andrejko (2004) *Urocystis prolifer*	30–40	–	80–100	–	670–900 × 40–110	10–15
Present study	35–50	2	120–130	55–60 Cirrus sac not reaching middle of proglottis	1200–1550 × 150–175	12–20

and one specimens of *Sorex minutus* Linnaeus, 1766), the vicinity of the town Belaya Kalitva in 2015 (48°10′N, 40°47′E; 12 specimens of *S. araneus* and seven specimens of *S. minutus*).

North Caucasus (172 specimens): Republic of Adygeya, Maykopsky District, the vicinity of the village Nikel in 2014–2015 (44°10′N, 40°09′E; 31 specimens of *Sorex raddei* Satunin, 1895, 31 specimens of *Sorex volnuchini* Ognev, 1922 and 21 specimens of *Sorex satunini* Ognev, 1922); the Karachay–Cherkess Republic, Teberda Nature Reserve in 2016 (43°21′N, 41°42′E; 31 specimens of *S. raddei*, six specimens of *S. volnuchini* and 14 specimens of *S. satunini*); the Republic of North Ossetia–Alania, Tseysky Nature Reserve in 2017 (43°11′N, 44°14′E; 16 specimens of *S. volnuchini* and 22 specimens of *S. satunini*).

Eastern Siberia (107 specimens): Krasnoyarsk Kraj, the vicinity of the village Tanzibey in 2009 (53°08′N, 92°56′E; one specimen of *Sorex isodon* Turov, 1924, five specimens of *S. minutus* and 21 specimens of *S. araneus*); Republic of Buryatia, Baikal Nature Reserve in 1990 (51°20′N, 105°09′E; 18 specimens of *S. minutus*, 29 specimens of *S. isodon*, 15 specimens of *S. araneus* and 18 specimens of *Sorex caecutiens* Laxmann, 1785).

Western Siberia (234 specimens): Altai Republic, Turochakskiy District, the vicinity of the village Artybash in 2015–2018 (51°47′N, 87°18′E; 151 specimens of *S. araneus*, 16 specimens of *S. caecutiens*, 35 specimen of *S. isodon*, one specimen of *Sorex minutissimus*, 21 specimens of *S. minutus* and ten specimens of *Sorex tundrensis* Merriam, 1900).

Far East: Primorsky Kraj (201 specimens): Kedrovaya Pad Nature Reserve in 2002 (43°06′N, 131°30′E; 50 specimens of *S. caecutiens*, 48 specimens of *S. isodon*, ten specimens of *Sorex unguiculatus* Dobson, 1890, one specimens of *Sorex gracillimus* Thomas, 1907 and 24 specimens of *Sorex* sp.); Lazovski Nature Reserve in 2003 (43°14′N, 133°24′E; 23 specimens of *S. unguiculatus* and 45 specimens of *S. caecutiens*); Khabarovsk Kraj (573 specimens): Bolshekhekhtsirsky Nature Reserve in 2003 (48°12′N, 134°51′E; 42 specimens of *S. caecutiens*, nine specimens of *S. unguiculatus*, 14 specimens of *S. isodon*, two specimens of *S. gracillimus* and one specimen of *S. minutus*); Solnechny District, the vicinity of the village Berezovka in 2004 (51°39′N, 135°40′E; 21 specimens of *Sorex daphaenodon* Thomas, 1907, eight specimens of *S. unguiculatus*, 430 specimens of *S. caecutiens*, five specimens of *S. minutissimus* Zimmermann, 1780, nine specimens of *S. gracillimus*, 29 specimens of *S. isodon* and three specimens of *Sorex roboratus* Hollister, 1913); Kamchatka Kraj, the vicinity of the town Yelizovo in 2002 (53° 11′N, 158°23′E; 13 specimens of *S. caecutiens*, 11 specimens of *S. isodon* and one specimen of *S. daphaenodon*).

Islands of the Far East (352 specimens): Sakhalin Island, Poronayskiy Nature Reserve in 2005 (48°55′N, 144°30′E; 130 specimens of *S. unguiculatus*, 16 specimens of *S. caecutiens*, nine specimens of *S. minutissimus*, ten specimens of *S. gracillimus*, five specimens of *S. isodon*, 17 specimens of *Sorex* sp.), the vicinity of the town Yuzhno-Sakhalinsk in 2006–2007 (46°57′N, 142°44′E; 42 specimens of *S. unguiculatus*, three specimens of *S. caecutiens*, one specimen of *S. minutissimus* and 11 specimens of *S. gracillimus*); Kunashir Island, Kurils Nature Reserve in 2006 (44°05′N, 145°59′E; 103 specimens of *S. unguiculatus*, one specimen of *S. caecutiens* and 15 specimens of *S. gracillimus*).

In addition, the analysis included shrews caught in Japan, Hokkaido Island (69 specimens), the vicinity of the city Tomakomai in 2005 (43°30′N, 143°00′E; 41 specimens of *S. unguiculatus*, 17 specimens of *S. caecutiens* and 11 specimens of *S. gracillimus*).

The levels of infection were assessed using the following indicators (Fedorov, 1986): P, prevalence (percentage of individuals of host population infected with a certain helminth species) and its standard error (±SE); I, intensity range (the minimum and maximum number of cestodes of a certain species in infected individuals in the host population); MI, mean intensity (average

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number of cestodes of a certain species per one infected individual of the host population); MA, mean abundance (average number of cestodes of a certain species per one studied individual of the host population).

For examination of the metacestode development, a stock culture of millipedes *Julus ghilarovi* Gulička, 1963 was obtained from the upper layer of soil and litter and kept in the laboratory in the Institute of Systematics and Ecology of Animals, Novosibirsk, Russia (ISEA) since 2018. The millipedes were kept at room temperature (20–25°C) in cages filled with an upper layer of soil, birch and aspen litter.

Adult specimens of *U. prolifer* were collected from the small intestines of *S. araneus* in the summer of 2019 in the vicinity of the village Artybash, Turochakskiy District, Altai Republic, Russia. Host specimens were dissected immediately after death. The collected worms were rinsed quickly in mammalian Ringer's balanced salt solution at room temperature. Some cestodes were fixed in 70% ethanol and then stained with Ehrlich's haematoxylin, differentiated in a 3% aqueous solution of ferric ammonium sulphate 12-hydrate, dehydrated in an ascending ethanol series, cleared in clove oil and mounted in Canada balsam. Some scoleces were mounted in Berlese's medium to facilitate the observation of rostellar hooks. Slides of mounted specimens were studied using standard light and phase-contrast microscopy.

The specimens of *U. prolifer* from the present study (slide numbers 18.15.1–18.15.13) have been deposited in the collection of ISEA, Novosibirsk, Russia.

For the experimental infection, approximately 300–350 millipedes were used. Prior to infection, the millipedes were not fed for two days. A fully developed strobila of *U. prolifer* with gravid proglottides was placed on a substrate in a cage with millipedes. Infected millipedes were maintained at 20–22°C. The dissection of millipedes was carried out in physiological saline (0.7–0.9%), with 10–12 specimens dissected per day. The examination of millipedes started on the ninth post-infection day (DPI). Measurements and photomicrographs of live metacestodes were obtained using a standard Ringer solution for poikilothermic organisms, an Axiolab phase-contrast microscope and an MC-80 microphotocamera. Measurements were in micrometres (µm) unless otherwise stated. The terminology used to describe the stages of hymenolepidid metacestode development in this paper follows that proposed by Skrjabin & Mathevossian (1942) and Chervy (2002).

Results

Adult stage

Urocystis prolifer Villot, 1880

Synonyms: *Hymenolepis prolifer* Villot, 1880, *Hymenolepis curiosa* Stammer, 1955, *Pseudodiorchis multispinosa* Žarnowski, 1955, *Pseudodiorchis kampinosi* Rybicka, 1958, *Echinoproboscilepis kedroviensis* Sadovskaja, 1965, *Coronacanthus parvihamata* Sawada & Harada, 1990.

Redescription

(Based on specimens from intestines of *S. araneus* from Artybash village, Turochakskiy District, Altai Republic, Russia; figs 1 and 2.) Small-sized tapeworm (fig. 1). Gravid specimens 1.2–1.5 mm (1.4 mm, $n = 11$) long. Strobila flat, consisting of 35–50 (38, $n = 11$) proglottides: 6–9 juveniles (with primordia of male gonads), 6–9 with mature testes (with primordia of female gonads), 6–9 with hermaphroditic (with testes and female gonads), 8–15 postmature and 2–4 gravid. Strobilation gradual. Proglottides acraspedote, transversely elongate, in process of maturation increase somewhat in length (fig. 2a). Development and maturation of strobila follows pattern of typical protandry: primordia and maturation of male gonads appearing before primordia and maturation of female gonads. Female gonads appear in proglottides with mature testes and an almost formed male copulative apparatus. In the first female proglottis, only rudiment of the aporal testis remaining, internal seminal vesicle and seminal receptacle empty. Cirrus sac persisting in pregravid and gravid proglottides. In the last two female proglottides, young vesicular uterus distinct.

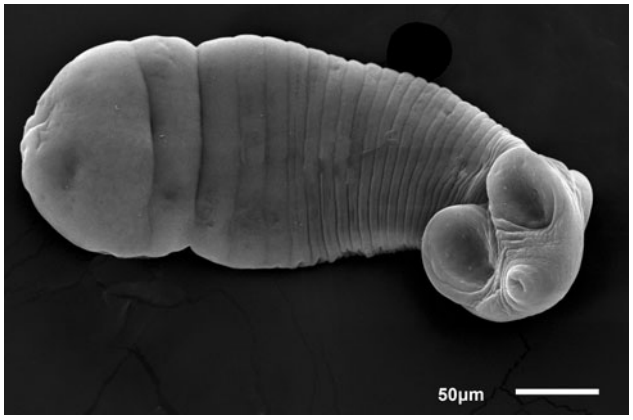

Fig. 1. General view of *Urocystis prolifer* Villot, 1880.

Scolex small, conical, 150–170 × 160–180 (161 × 167, $n = 11$), with rostrum (fig. 2a). Suckers subspherical, 80–83 × 80–84, with well-developed musculature, widely spaced and shifted to corners of scolex. Rostellar apparatus complex. Rhynchus small, 58–68 long, 55–57 wide, with well-developed own musculature consisting of circular and retractor muscle system. Rhynchus retractors extending from its top, divided into two bundles: one fixed at top of rostellar pouch, second at its equator. Surface of rhynchus corrugated (fig. 2b).

Rostellum subspherical, 30–35 × 35–40 (32 × 38, $n = 8$), with invagination, deeply immersed in rostellar pouch. Rostellar hooks 120–130 in number, very small, arranged in single row, 4–6 (5, $n = 25$) long (fig. 2c). Each hook associated with muscle bundle. Muscle fibres from several rostellar hooks merge, thus forming 14–16 retractors. Rostellar pouch voluminous, 80–83 × 100–140 (81 × 128, $n = 8$), reaching posterior margins of suckers. Ten bundles of retractor muscles extending from bottom of rostellar pouch and passing into thin layer of longitudinal musculature of strobila in neck region. Basal part of rostellar pouch filled with glandular matrix (fig. 2b). Neck clearly distinct from scolex.

Two pairs of osmoregulatory canals without transverse anastomoses. Ventral osmoregulatory canals 5–7 (5, $n = 8$) in diameter, dorsal canals 2–3 (3, $n = 8$) in diameter. Genital pores unilateral, dextral, opened in middle or somewhat anterior to middle of proglottis margin. Genital atrium simple, cylindrical, 8–16 deep (14, $n = 8$), surrounded by large glandular cells.

Male mature proglottides 15–20 × 135–150 (15 × 142, $n = 11$). Testes two, 15–18 × 20–28 (16 × 26, $n = 11$), oval, in one row, one poral and one antiporal, situated symmetrically in median field of proglottis (fig. 3a). Testes of neighbouring male proglottides adjacent. Cirrus sac cigar-shaped, elongate, thin-walled,

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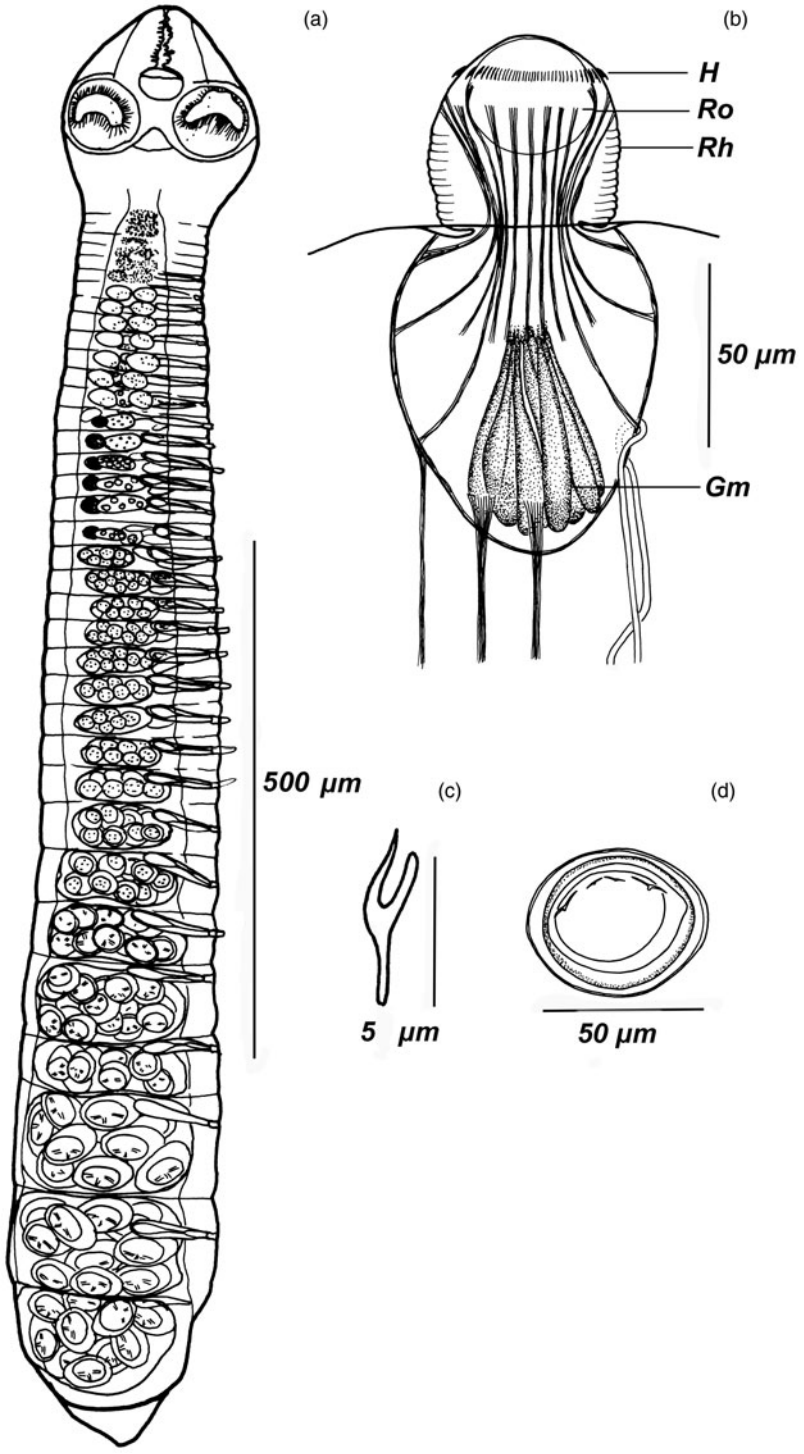

Fig. 2. *Urocystis prolifer*: (a) whole strobila; (b) rostellar apparatus complex; (c) hook; (d) egg. Abbreviations: Ro, rostellum; Rh, rhynchus; H, hooks; Gm, glandular matrix.

13–15 × 55–62 (13 × 57, $n = 11$), crossing poral osmoregulatory canals; not reaching midline of proglottis (fig. 3a). Cirrus short, 20–22 (22, $n = 11$), armed with small spines, covering only its proximal part (fig. 3b). Internal seminal vesicle ovoid, elongated, 10–12 × 15–25 (10 × 26, $n = 11$). External seminal vesicle 15–18 × 23–25 (16 × 26, $n = 11$), connected to cirrus sac by long and curved duct.

Hermaphroditic mature proglottides 15–20 × 150–175 (16 × 168, $n = 11$). Ovary sacciform, transversely elongate, 15–19 × 58–63 (16 × 61, $n = 11$), in centre of proglottis. Vitellarium compact, subspherical, 11–13 × 15–18 (11 × 16, $n = 11$), aporal and dorsal to ovary. Vagina thin-walled, opening ventral to cirrus sac. Copulatory part of vagina 25–28 (26, $n = 11$). Seminal receptacle pear-shaped, large, 15–16 × 25–26 (16 × 26, $n = 11$) (fig. 3a).

Young uterus vesicular. Gravid uterus sac-like, occupying entire median field, does not cross osmoregulatory canals (fig. 2a), containing 12–20 (13, $n = 10$) eggs. Eggs large, 45–48 × 56–60 (46 × 56, $n = 11$), with a sclerotized outer embryonic membrane (fig. 2d). Embryonated eggs lie freely in uterine cavity, not contacting closely with uterine epithelium, scattered one by one through breaks in uterine wall.

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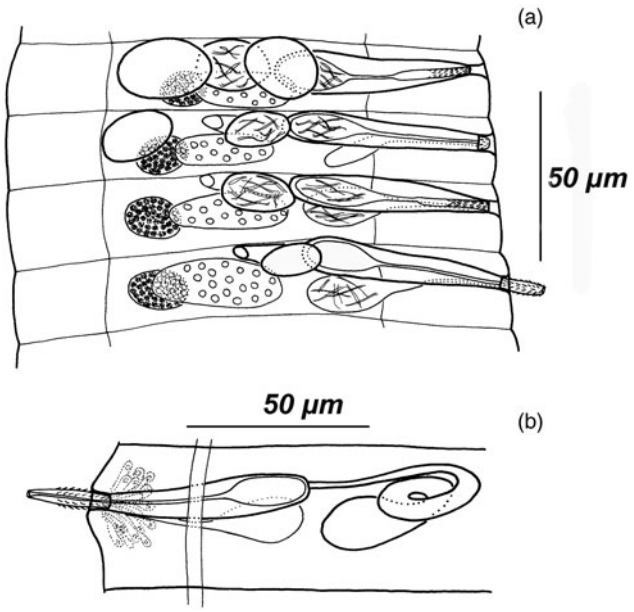

Fig. 3. *Urocystis prolifer*: (a) strobila fragment with male and female mature proglottids; (b) copulatory apparatus.

Amended generic diagnosis (modified after Czaplinski & Vaucher, 1994). Proglottides much broader than long. Scolex with retractile, armed rostellum. Hooks numerous (more than 100), very small. Testes two or three, in transverse row, more or less overlapping female gonads. Ovary sacciform, transverse, in centre of proglottis. Vitellarium compact, subspherical, aporal to ovary. Cirrus sac not reaching middle of proglottis. Cirrus armed with small spines. Uterus sacciform, containing few eggs. Type-species *U. prolifer* Villot, 1880.

Distribution of the species in the Palaearctic

The monotypic genus *Urocystis* is included in many checklists of helminths of shrews from the western to eastern areas of the Palaearctic. The species has been recorded mostly in the taiga and forest zones (in temperate broadleaf deciduous and mixed forests) (fig. 4) (Vaucher, 1971; Prokopič & Matsaberidze, 1972; Genov, 1984; Sato *et al.*, 1988; Anikanova *et al.*, 2001; Kornienko, 2001; Irzhavsky & Gulyaev, 2002; Dokuchaev *et al.*, 2003; Ribas *et al.*, 2003; Skolka *et al.*, 2004; Binkiene, 2006; Kornienko *et al.*, 2008; Zubova *et al.*, 2008a, b; Binkiene *et al.*, 2011). Despite Vaucher's statement that *U. prolifer* is absent from Scandinavia (Vaucher, 1971), there are records of it in southern Finland (on the coast of the Gulf of Finland) (Haukisalmi *et al.*, 2010; Haukisalmi, 2015). In addition, we have found this species in Sweden and Finland (Västernorrland County, Sweden, 62°45′N, 17°52′E; northern Savo, Finland 62° 53′N, 27°40′E). According to our data and data in the literature, this species has not been recorded in the tundra and arid zones and some forest zone regions of the Palaearctic (north-east of the East European Plain, Russian Far East (Chukotka Peninsula), eastern Siberia (Yakutia and Tuva), south of the Lesser Caucasus (Armenia) and northern Kazakhstan) (Yushkov, 1995; Movsessian *et al.*, 2006; Kirillov *et al.*, 2017; Kornienko *et al.*, 2018; Sheykina & Zhigileva, 2018). The lack of records in these regions is likely due to the absence of intermediate hosts of the cestode (diplopods). Novikov (1995) found three specimens of *U. prolifer* in *S. isodon* caught in the Selemdzha River basin (Magadan Oblast, Russian Far East). However, the coordinates of the cestodes (60°18′N) provided by the author do not correspond to the location of this river. The site of this record requires clarification.

The cestode *U. prolifer* is characterized by not only an extensive geographical range but also wide host specificity. Definitive hosts of *U. prolifer* include *S. araneus*, *S. isodon*, *S. minutus*, *S. caecutiens*, *S. gracillimus*, *S. daphaenodon*, *S. roboratus*, *S. satunini*, *S. raddei*, *S. volnuchini*, *S. minutissimus*, *S. tundrensis*, *S. unguiculatus* and *Sorex shinto* Thomas, 1905.

The characteristics of cestode infection (prevalence, abundance and intensity) vary significantly among different species of shrews in different parts of the Palaearctic. In a study of *S. araneus* in Bulgaria, no more than 5% of the shrews were infected by this tapeworm (Genov, 1984). In a study in the territory of Belarus, only 2% of the studied common shrews were found to host *U. prolifer* (Shimalov, 2012). In a study in Lithuania, approximately 20% of the examined common and pygmy shrews were infected with *U. prolifer* (Binkiene, 2006). In our investigations in the European part of Russia and West and East Siberia, approximately a third of the studied shrews were infected with *U. prolifer*; in mainland and insular part of the Russian Far East, the prevalence of the cestode is lower. Despite the large regional variation in the prevalence of infection with this cestode, the intensity of infection is high across the study regions (table 2). There is some difference in infection levels between different species of shrews. In the Caucasus, *S. raddei* has the highest infection rate with *U. prolifer*. In Siberia (both western and eastern), all shrews species (except tundra shrew in the western, and pygmy shrew in eastern Siberia) have high level of infection with *U. prolifer*: the prevalence, abundance and intensity. At the same time, *S. caecutiens* has the highest infection rate with *U. prolifer* in all of the researched regions (table 2). About 30% of the common shrews from the European part of Russia and Siberia are infected with cestode. The prevalence of *U. prolifer* in *S. minutus* is low: single specimens of pygmy shrew are infected. In mainland and insular part of the Far East, the prevalence of *U. prolifer* is no higher than 20%. The lowest infection with *U. prolifer* is detected in *S. daphaenodon*, *S. gracillimus* and *S. minutissimus*. Some specimens of *S. roboratus*, *S. minutissimus* and *S. minutus* caught in the Khabarovsk Kraj are not infected with *U. prolifer*. Among the Japanese shrews, only the long-clawed shrew is infected with *U. prolifer* (table 2).

Larvogenesis of cysticercoid of U. prolifer in millipedes J. ghilarovi

Megalospheres lying in the body cavity of millipedes were found on the ninth DPI. The megalosphere is a morula-like structure covered with a thin fibrillar membrane (fig. 5a), reaching 52 in diameter.

In the following six days (10th–16th DPI), larvae were at the stage of elongation. From the megalosphere, a saccular maternal individual (blastomere) is formed (fig. 5b) with a primary lacuna, which increases in proportion to the growth of the larva and reaches 57 in length. The length of the elongated larva is 71–75.

On the 22nd DPI, metacestodes at stages of budding of primary blastogens were found. The maternal individual begins to bud off primary blastogens (fig. 5c), and a saccular colony of

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Fig. 4. Localities of *Urocystis prolifer* in the Palaearctic. Own data are indicated by circles, literature data by triangles (see chapter "Distribution of the species in the Palaearctic").

larvae appears (fig. 5d). The maximum colony length is 800 and the width ranges from 38 to 100. Each colony contains several dozen spherical and elongated larvae with transverse constrictions. Young blastogens of the colony do not have primary lacuna. During the period of growth and formation of the primary lacuna, daughter buds detach from the wall of the maternal individual (fig. 5e, f) and are capable of a new cycle of budding (fig. 6a). Blastogens with a primary lacuna reach 11–17 in diameter (fig. 5e).

The stage of budding of secondary blastogens was found on 24th–25th DPI. This blastogen has narrow tail-like outgrowth connecting it to the maternal individual during the early stages of morphogenesis (fig. 6b). Subsequently, the secondary blastogen detaches from the maternal individual and develops separately.

On the 26th–28th DPI, metacestodes were at the stage of elongation and early morphogenesis of the scolex. At this stage, the larva measures 38–40 in width by 54–56 in length, and the size of the primordium of the scolex is 17–18 × 16–18 (fig. 6b). Subsequently, suckers are formed and rostellar hooks start their development on the rhynchus (fig. 6c). The scolexogenesis of secondary blastogens can occur in unseparated (fig. 6d) and separated individuals (fig. 6c). Thus, at least two asexual larval generations are observed in the ontogeny of *U. prolifer*. Characteristic features of this stage of larvogenesis are the absence of the primary lacuna and cercomer and the small size of the rudiments of the strobila and cysts (fig. 6c, d). There is no formation of excretory atrium.

At the stage of late morphogenesis of the scolex (29th–30th DPI), the measurements of larvae increase to 69–71 × 69–75; suckers are 25–33 × 24–28 (fig. 6e). Rhynchus, 25–30 wide in 24–26 long, is retracted before the encysting of the larva (fig. 6e). Encystation occurs without invagination of the scolex; the primordium of the cyst actively advances on the scolex. The two-layered cyst wall of the encysted larva is very thin and mobile. The cyst of the definitive urocyst lacks anterior and posterior obturator valves (fig. 6f). In addition, excretory bodies are completely absent (a unique feature among metacestodes).

The fully developed cysticercoids measure 54–80 × 46–75 (fig. 6f).

Discussion

Our study and the analysis of the data by previous authors (see above) allow us to clarify the morphological characteristics of *U. prolifer*, and to provide a generic diagnosis of *Urocystis* and the geographical range of this cestode species. Despite the inclusion of the genus *Urocystis* in many checklists of helminths from shrews in different regions of the Palaearctic, we believe that the northern boundary of the geographical range of *U. prolifer* is no higher than the 62nd parallel north and that the southern boundary is no lower than the 42nd parallel north.

The cestode *U. prolifer* is characterized by an extensive geographical range, wide host specificity and high characteristics of infection (prevalence, abundance and intensity). The high infection levels of *U. prolifer* are due to the generalized diet and high abundance of some species of shrews (Haukisalmi, 1989; Binkiene, 2006).

The characteristics of larval development and intermediate hosts are known for only a sixth of the 70 species of tapeworms from *Sorex*: *Ditestolepis* Cholodkowsky, 1906, *Mathevolepis* Spassky, 1948, *Staphylocystis* Villot, 1877, *Lineolepis* Spassky, 1959, *Vigisolepis* Mathevosyan, 1945, *Neoskrjabinolepis* Spassky, 1947, *Monocercus* Villot, 1882 and *Urocystis* Villot, 1880 (e.g.

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Table 2. Infection in shrews of the genus *Sorex* with *Urocystis prolifer*.

Localization	Shrew species	P ± SE	MA	I	MI
Rostov Oblast'	Total infection	**29.6 ± 8.9**	**55.6**	**10–1000**	**187.5**
	Sorex araneus	36.8 ± 11.0	26.3	10–20	71.4
	S. minutus	1 of 8	125	1000	1000
North Caucasus		**31.4 ± 3.5**	**186.1**	**10–10 000**	**592.9**
	S. raddei	70.9 ± 5.8	422.3	15–10 000	595.1
	S. satunini	8.8 ± 3.7	11.9	10–600	136.0
	S. volnuchini	9.4 ± 4.0	97.2	10–5000	1030.0
Western Siberia		**29.3 ± 2.9**	**132.2**	**1–5000**	**451.2**
	S. araneus	21.9 ± 3.4	155.4	2–5000	710.9
	S. caecutiens	68.8 ± 11.6	73.4	1–600	106.7
	S. isodon	42.9 ± 8.4	154.7	10–1600	361.0
	S. minutus	28.6 ± 9.8	33	5–300	115.5
	S. tundrensis	5 of 10	84.1	6–350	168.2
Eastern Siberia		**26.2 ± 4.2**	**44.4**	**5–1000**	**169.7**
	S. araneus	19.4 ± 6.6	19.2	40–250	98.6
	S. caecutiens	61.1 ± 11.5	185	10–1000	302.7
	S. isodon	30.0 ± 8.4	23.7	5–300	78.9
	S. minutus	4.3 ± 4.3	1.0	22	22.0
Far East (Primorsky Kraj)		**19.2 ± 2.7**	**54.2**	**1–2000**	**282.9**
	S. caecutiens	20.0 ± 4.1	81.3	1–2000	406.6
	S. isodon	18.8 ± 5.6	49.3	4–1000	262.8
	S. unguiculatus	18.2 ± 6.7	5.0	1–100	27.7
	S. gracillimus	1 of 1	200	200	200
Far East (Khabarovsk Kraj)		**12.3 ± 1.4**	**13.5**	**1–2000**	**110.1**
	S. caecutiens	21.5 ± 1.9	57.2	1–100	50.1
	S. isodon	11.6 ± 6.4	6.8	5–100	58.6
	S. unguiculatus	17.6 ± 9.2	176.5	1–2000	1000
	S. gracillimus	4 of 9	3.7	1–30	8.3
	S. daphaenodon	9.5 ± 6.4	0.8	2–15	8.5
Far East (Kamchatka Kraj)		**8.0 ± 5.4**	**2.72**	**21–47**	**34**
	S. isodon	1 of 11	4.3	47	47
	S. caecutiens	1 of 13	1.6	21	21
Islands of the Far East		**23.1 ± 2.2**	**16.8**	**1–1200**	**72.7**
	S. caecutiens	40.0 ± 10.9	7.25	3–145	18.1
	S. unguiculatus	19.2 ± 2.4	16.2	1–1200	84.1
	S. gracillimus	11.1 ± 5.2	31.9	30–50	286.8
	S. minutissimus	1 of 10	0.3	3	3.0
Hokkaido Island		**4.3 ± 2.5**	**2.1**	**5–100**	**49.3**
	S. unguiculatus	4.3 ± 2.5	2.1	5–100	49.3

P, prevalence; SE, standard error; MA, mean abundance; I, intensity range; MI, mean intensity.

Joyeux, 1922; Kisielewska, 2017, 1959, 1960; Rawson & Rigby, 1960; Ryšavý & Prokopič, 1965; Quentin & Beaucournu, 1966; Prokopic, 1968a, b; Procopič *et al.*, 1970; Obushenkov & Rudzhanskaite, 1984; Ryšavý, 1989; Gulyaev & Kornienko, 1998; Lefebvre *et al.*, 2009a, b; Gulyaev *et al.*, 2010; Kornienko & Ishigenova, 2012; Ishigenova & Kornienko, 2013).

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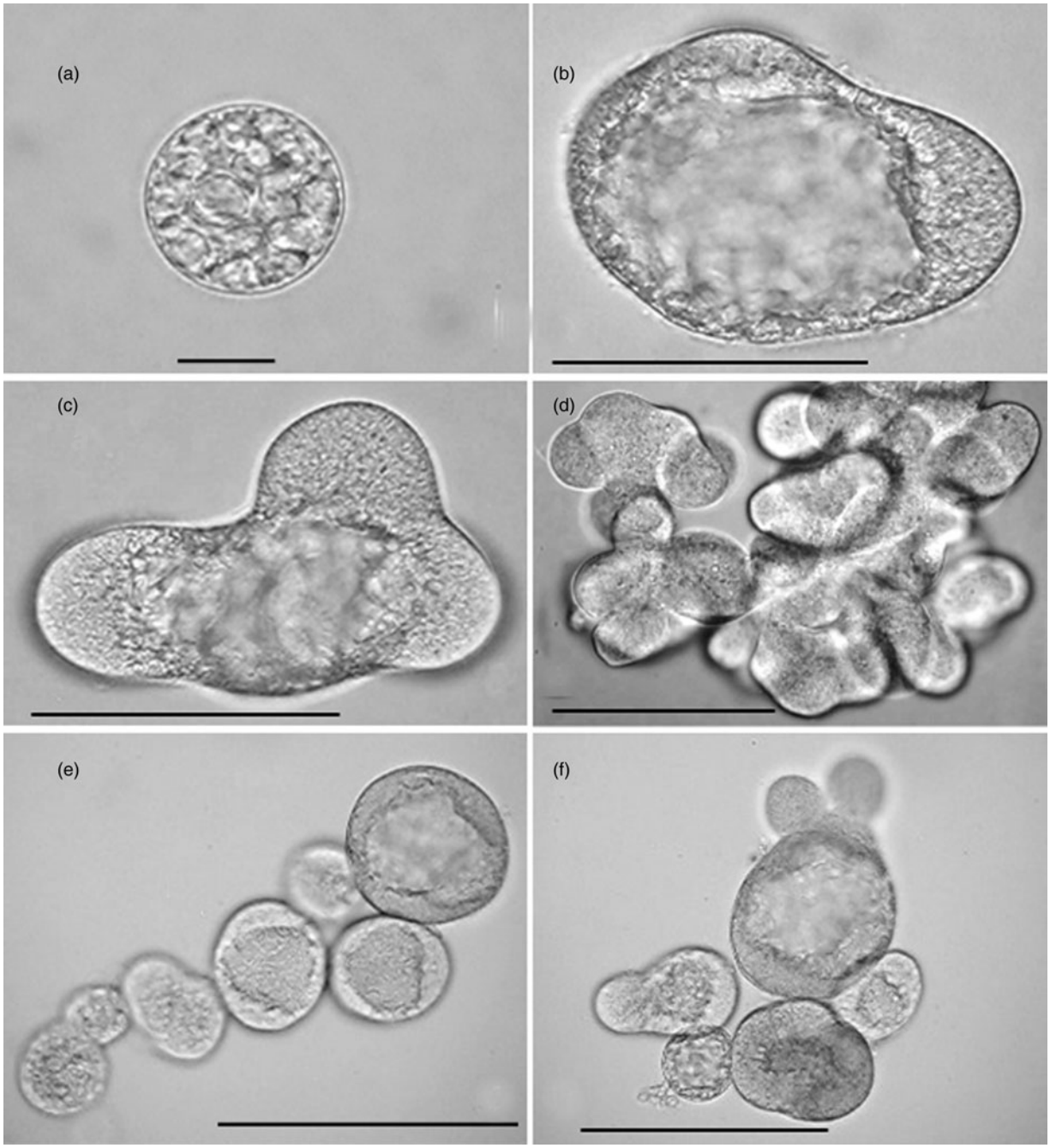

Fig. 5. Postembryonic development of *Urocystis prolifer*: (a) megalosphere; (b) elongation and differentiation; (c) the formation of primary blastogens, leading to the formation of a saccular colony (d); (e, f) formation of a primary lacuna in secondary blastogens. Scale bars: (a) 20 μm; (b, c) 50 μm; (d–f) 30 μm.

Several studies have examined the structure of the fully developed larva of *U. prolifer* or the stages of larval development (Villot, 1880; Joyeux, 1922; Stammer, 1955; Baer & Della Santa, 1960; Kisielewska, 1960; Ishigenova, 2009). According to the literature, the intermediate hosts of *U. prolifer* are the millipedes (Diplopoda) *Glomeris limbata* Lutz, *Glomeris conspersa* Koch and *Craspedosoma alemanicum* Verhoeff (Stammer, 1955; Villot, 1880; Baer & Della Santa, 1960). We performed an experimental infection of millipedes *J. ghilarovi* Gulička, 1963 (Julida: Julidae). Millipedes are common terrestrial invertebrates, and most are slow-moving detritivores that inhabit the upper layer of soil and litter. Millipedes may accidentally ingest eggs of *U. prolifer* with decaying leaves and become intermediate hosts. The shrews willingly eat infected millipedes, as evidenced by the high prevalence of the cestode in shrews (table 2).

According to previous authors, the larva of *U. prolifer* is a polycephalic cysticercoid that is produced by budding (blastogenesis) and detaches from the maternal tissue. The process of cysticercoid budding (asexual larval reproduction) was first mentioned by Jones & Alicata (1935), who indicated that fully developed larvae of *Hymenolepis* (=*Staphylepis*) *cantaniana* resemble mycelium from which cysticercoids bud and reproduce. Wardle & McLeod (1952) termed this type of cysticercoid 'urocyst'. Subsequently, Chervy (2002) modified the nomenclature of the stages of larval

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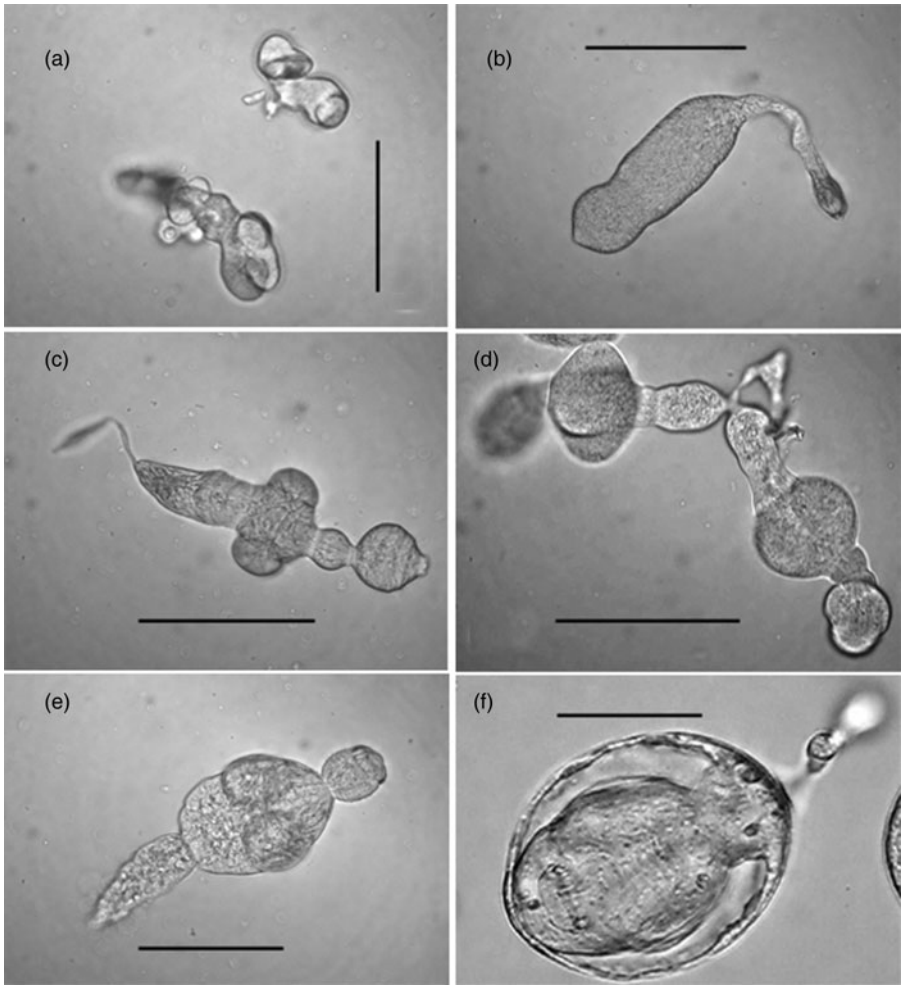

Fig. 6. Postembryonic development of *Urocystis prolifer*: (a) secondary blastogens; (b) detached secondary blastogen at the stage of early morphogenesis of the scolex; (c) formation of suckers and rostellar apparatus; (d) morphogenesis of the scolex in undetached secondary blastogens; (e) late morphogenesis of the scolex and primordium of rostellar hooks; (f) fully developed urocyst. Scale bars: (a–f) 40 μm.

development and the larvae of different taxonomic groups of cestodes. This author suggested that cysticercoids similar to *U. prolifer* be called urocysticercoid or urocyst.

The cysticercoid of *U. prolifer* developed by blastogenesis occurs over the entire surface of the maternal tissue. Within the intermediate host, a colony of metacestodes forms, consisting of individuals of different generations: the maternal saccular larva (blastomeres), which arise by sexual reproduction, and daughter cysticercoids (blastogens), formed by asexual larval reproduction. The body cavity of infected millipedes becomes filled with single larvae and groups of colonial larvae of various shapes: from morula-like solitary individuals to budding ones (fig. 5). The urocyst is a multilobed parenchymatous mass, from which cysticercoids develop; the cysticercoid has a long pedicel and separates before the completion of its development.

Some cestode species in which blastogenesis is observed (e.g. *Polycercus paradoxa* (Rudolphi, 1802) (Gulyaev, 2000) have a small number of proglottides in the strobila, and the small size of the uterus limits their fecundity. Similar traits are apparent in the adults of *U. prolifer* (see above). These traits likely result in slow rates of ontogeny and the maturation of invasive eggs (Gulyaev & Kornienko, 2009). Invasive eggs have a sclerotized outer embryonic membrane (Korneva *et al.*, 2012), which probably enables the eggs to persist in the litter for an extended period. The intermediate hosts, eating invasive eggs, become infected with the larvae of *U. prolifer*, each of which gives rise to a clone. Asexual reproduction of the cestode in the intermediate host, through several cycles of budding, results in a large number (table 2) of cysticercoids in the host. Each oncosphere of *U. prolifer* forms numerous and the smallest among the members of Cyclophyllidea cysticercoids. A shrew that has eaten even a small number of intermediate hosts containing larvae becomes infected with multiple cestodes, which leads to a high infection intensity and, thus, high densities of micropopulations of these cestodes. The infection intensity of *U. prolifer* ranges from 1 to 10,000 individuals per infected shrew (table 2).

The large number of *U. prolifer* larvae that enter the intestines of one definitive host from several intermediate hosts provides a high probability of cross-fertilization between adults, which may increase the level of heterozygosity of the parasite population (Ishigenova, 2009).

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Ethical standards. 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 contributing to this work comply with the ethical standards of the relevant national and institutional guides on the care and use of laboratory animals in accordance with the legislation of the Russian Federation. The methods used in the current study were approved by the ethics committee of the Institute of Systematics and Ecology of Animals, Novosibirsk, Russia.

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