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ORIGINAL PAPER

The second rhizocephalan species, *Lernaeodiscus kasyanovi* sp. nov. (Cirripedia: Rhizocephala: Peltogastridae), parasitizing the porcellanid crab *Pachycheles stevensii* Stimpson, 1858 (Decapoda: Anomura: Porcellanidae), from Russian waters of the Sea of Japan

Olga M. Korn[1] · Darya D. Golubinskaya[1] · David J. Rees[2] · Henrik Glenner[2,3] · Jens T. Høeg[4]

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Abstract

Molecular and morphological methods are used to describe the rhizocephalan *Lernaeodiscus kasyanovi* sp. nov. from Russian waters of the Sea of Japan, the second of two *Lernaeodiscus* species parasitizing the porcellanid crab *Pachycheles stevensii* Stimpson, 1858. *Lernaeodiscus kasyanovi* sp. nov. differs from the other species found on this host, *Lernaeodiscus rybakovi* Korn et al., 2020a, by molecular markers, by a smaller size, a lighter color, by the shape of receptacles, by the presence of marginal lobes in mature specimens, and by the retinacula type on the internal cuticle. *Lernaeodiscus kasyanovi* sp. nov. is the sister taxon to *Lernaeodiscus porcellanae* in the monophyletic genus *Lernaeodiscus*. *Lernaeodiscus kasyanovi* is rather rare compared to *L. rybakovi*, their prevalence on the porcellanid crab *P. stevensii* does not exceed 2%. It is the second example of two rhizocephalan species infesting the same brachyuran species in Peter the Great Bay.

Keywords Rhizocephalan barnacles · Two-species infestation · Morphology · DNA analysis · Northwestern Sea of Japan

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✉ Olga M. Korn
olgamkorn@mail.ru

Darya D. Golubinskaya
dddemchyk@mail.ru

David J. Rees
David.Rees@uib.no

Henrik Glenner
henrik.glenner@uib.no

Jens T. Høeg
jthoeg@bio.ku.dk

[1] A.V. Zhirmunsky National Scientific Center of Marine Biology, FEB RAS, Vladivostok, Russia

[2] Department of Biological Sciences, University of Bergen, Bergen, Norway

[3] Center for Macroecology, Evolution and Climate, Globe Institute, University of Copenhagen, Copenhagen, Denmark

[4] Marine Biology Section, Department of Biology, University of Copenhagen, Copenhagen, Denmark

Introduction

The fan-shaped porcellanid crab *Pachycheles stevensii* Stimpson, 1858 (Decapoda: Anomura: Porcellanidae), occurs in the Sea of Japan, from Peter the Great Bay (Russia) to Hokkaido and Honshu (Japan). It is found from shoreline to 30 m depth on stony substrates, in druses of bivalve mollusks and on mussel banks, where it forms large aggregations (Marin 2013). The rhizocephalan parasite *Lernaeodiscus rybakovi* Korn et al., 2020a was recently described from numerous specimens of *P. stevensii* collected from 2005 to 2018 in Russian waters of the Sea of Japan (Korn et al. 2020a). The prevalence on *P. stevensii* in the investigated area reached 9%. In the same locality, we collected in 2018 two specimens of *P. stevensii* infested by a rhizocephalan, which differs from *L. rybakovi* in numerous morphological features. This parasite was much less prevalent (ca. 2%), with ten parasites in total being collected for 3 years. Here, we describe these specimens as a new species based on available morphological and molecular data from all species in the genus *Lernaeodiscus* Müller, 1862.

Material and methods

Sampling

Specimens of *Pachycheles stevensii* infested with *Lernaeodiscus kasyanovi* sp. nov. were collected by SCUBA diving at a depth of 1.5–3 m. These specimens were found in Vostok Bay, in Amursky and Ussuriysky bays (Peter the Great Bay, Sea of Japan). The type material was fixed in 96% ethanol. The holotype and one paratype, each with a rhizocephalan externa undetached, were deposited at the Museum of the National Scientific Center of Marine Biology (MIMB), Vladivostok, Russia. Two voucher specimens after DNA extraction were deposited as paratypes at the Museum of the University of Bergen (ZMBN), Bergen, Norway.

Molecular techniques

DNA extraction, gene amplification, sequencing handling, and molecular analyses were performed as in Korn et al.'s study (2020a). Sequence data for all samples have been submitted to GenBank (NCBI, http://www.ncbi.nlm.nih.gov/) under the accession numbers MW916318 (16S), MW916319 (18S), MW916320 (28S), and MW916508 (COI).

Investigation of the externa

The externae of the rhizocephalans were detached from the hosts and drawn; the width (greatest distance between lateral margins) was measured. The carapace width (greatest distance between lateral margins) and the sex of the host crabs were also determined.

Three externae (one mature and two immature) were fixed in Bouin solution, dehydrated through a gradient ethanol-xylene series, and embedded in paraffin. Transverse and longitudinal sections, 6-µm thick, were stained with Ehrlich hematoxylin and examined with a Carl Zeiss Axio Imager Z.2 light microscope furnished with a digital camera.

For SEM preparation, the cuticle of three externae was dehydrated in an alcohol series and acetone, critically point-dried in CO_2, and sputtered with chromium. It was observed with a Zeiss Sigma 300 VP microscope (National Scientific Center of Marine Biology FEB RAS, Vladivostok).

All morphological terminology follows Øksnebjerg (2000). All papers for taxon authorities for parasites not hosts are provided in the reference list.

Results

Phylogenetic analyses

The genetic distances between *Lernaeodiscus kasyanovi* sp. nov. and the three other *Lernaeodiscus* species for which molecular data are available reveal a remarkably large divergence in four genetic markers (Table 1, p-distances of the two mitochondrial genes 16S and CO1 and the nuclear genes 28S and 18S). In the fastest evolving marker, 16S, the p-distances ranged from 24% between *L. kasyanovi* sp. nov. and *L. porcellanae* Müller, 1862, and 30.6% between *L. kasyanovi* sp. nov. and *Lernaeodiscus ingolfi* Boschma, 1928, confirming *L. kasyanovi* as a new species, well-separated from all other *Lernaeodiscus* for which molecular data are available.

The phylogenetic analysis in Korn et al. (2020a) was based on 19 rhizocephalan species, four thoracican outgroup species, and the four genetic makers mentioned above. By adding *L. kasyanovi* sp. nov. to this dataset and conducting a maximum likelihood and Bayesian inference analyses, solid support (100% boots trap and 1 pp) was found for a sistergroup relationship between *L. kasyanovi* sp. nov. and *L. porcellanae* in a monophyletic *Lernaeodiscus*. *Lernaeodiscus rybakovi* and *L. ingolfi* formed another sistergroup pair within the genus (Fig. S1 in the online Supplementary information).

Taxonomy

Superorder Rhizocephala Müller, 1862
Family Peltogastridae Lilljeborg, 1861; amended by Høeg et al. (2020)
Genus *Lernaeodiscus* Müller, 1862
Lernaeodiscus kasyanovi sp. nov.
http://zoobank.org/5CCEE4A6-A6F5-43DD-9544-D4921A991BF9

Table 1 Pairwise distances (16S / CO1 / 28S / 18S) between species of the genus *Lernaeodiscus*

	L. porcellanae	*L. rybakovi*	*L. kasyanovi* sp. nov.
L. porcellanae			
L. rybakovi	0.322 / 0.231 / 0.081 / 0.026		
L. kasyanovi sp. nov.	0.289 / 0.239 / 0.105 / 0.042	0.234 / 0.225 / 0.111 / 0.047	
L. ingolfi	0.306 / 0.254 / 0.094 / 0.042	0.274 / 0.236 / 0.098 / 0.045	0.241 / 0.195 / 0.061 / 0.041

Material examined

Holotype: one specimen (5.5 mm, with embryos), on *Pachycheles stevensii* (female, 7.7 mm width), depth 1.5 m, Amursky Bay, Sea of Japan, 2.12.2020 (catalogue number 40953, MIMB).

Paratypes:

One specimen (4.6 mm width, without embryos), on *P. stevensii* (female, 10.4 mm width), depth 1.5 m, Amursky Bay, Sea of Japan, 19.08.2020 (catalogue number 40954, MIMB);

One specimen (8.5 mm width, with embryos), on *P. stevensii* (female, 11.5 mm width), depth 3 m, Vostok Bay, Sea of Japan, 10.07.2018 (catalogue number 139866, ZMBN);

One specimen (8.0 mm width, without embryos), on *P. stevensii* (female, 9.0 mm width), depth 3 m, Vostok Bay, Sea of Japan, 8.07.2019 (catalogue number 139867, ZMBN).

Additional material examined:

One specimen (5.6 mm width, without embryos), on *P. stevensii* (female, 14.0 mm width), depth 1.5 m, Amursky Bay, Sea of Japan, 16.12.2019 (used for cuticle investigation); one specimen (3.5 mm width, without embryos), on *P. stevensii* (female, 8.2 mm width), depth 3 m, Ussuriysky Bay, Sea of Japan, 13.03.2020 (used for cuticle investigation); one specimen (5.0 mm width, with embryos), on *P. stevensii* (female, 7.8 mm width), depth 1.5 m, Amursky Bay, Sea of Japan, 19.08.2020 (used for cuticle investigation);

One specimen (6.6 mm width, with embryos), on *P. stevensii* (male/female, 11.3 mm width), depth 3 m, Ussuriysky Bay, Sea of Japan, 24.07.2020 (used for histology); one specimen (5.6 mm width, without embryos), on *P. stevensii* (female, 14 mm width), depth 3 m, Ussuriysky Bay, Sea of Japan, 16.12.19 (used for histology); one specimen (4.5 mm width, without embryos), on *P. stevensii* (male/female, 11.8 mm width), depth 1.5 m, Amursky Bay, Sea of Japan, 19.08.2020 (used for histology).

Diagnosis

Externa of medium size, white, yellowish or slightly reddish, bilobed, flattened dorsoventrally and bilaterally symmetrical. Mature externa with distinct bilobed marginal lobes. Mantle opening and stalk placed in median plane and directed dorsally. Mantle opening lacks protruding crenulated lip. Stalk short, narrow. External cuticle lacks papillae or excrescences. Internal cuticle with smooth finger-likeretinacula. Dorsal mesentery broad and extending along dorsal surface of visceral sac from stalk to mantle opening. Ventral mesentery much narrower and shorter than dorsal one. Simple colleteric glands placed symmetrically about median plane in lateral position. Paired receptacles placed dorsally in posterior part of visceral sac, symmetrical relative to median plane. Receptacle ducts strongly coiled within the receptacle sacs.

Type locality

Amursky Bay, Peter the Great Bay, the Sea of Japan, Russia

Host

Lernaeodiscus kasyanovi sp. nov. was found on ten specimens of the fan-shaped porcellanid crab *Pachycheles stevensii*. The prevalence of infestation in the crab population did not exceed 2%. The carapace width of the infested crabs ranged from 7.7 to 14.0 mm. Eight infested crabs were females (with three pleopods on abdominal segments 3–5). Two crabs had an addition pleopod on the second abdominal segment, which probably indicates a change in the morphology of the crab due to parasitism. Most *P. stevensii* specimens had their externa attached on the ventral surface of the second abdominal segment, but it could also be found on the third abdominal segment.

We only sampled the host crabs in Peter the Great Bay above 3 m depth. The host crab *Pachycheles stevensii* also occurs along Japanese islands from Hokkaido to Honshu, down to 30 m depth (Marin 2013), but we have no data on the true geographical distribution and depth range of the new parasite.

Etymology

The name of a new species is given in honor of Prof. Vladimir Kasyanov (1940–2005), the director of the Institute of Marine Biology FEB RAS, who died in a car accident.

Description

Externa always single and attached on ventral surface of second (rarely third) abdominal segment of host crab. Parasite of medium size (3.5–8.5 mm), white, yellowish, or slightly reddish. Externa bilobed, flattened dorsoventrally, and bilaterally symmetrical. Mature externa with approximately six bilobed marginal lobes (lappet-like extensions of mantle) filled with embryos (Figs. 1a, 2a). Lobes proximally constricted and distally expanded. Marginal lobes of immature externae less pronounced (Figs. 1b, 2c). Mantle opening and stalk placed in median plane and directed dorsally. Mantle opening rhomboid, not surrounded by protruding crenulated lip. Stalk short, narrow. Cuticle surrounding stalk with number of concentric molting lines.

External mantle cuticle with distinct cellular structure but lacks papillae or excrescences (Fig. 3a). Higher magnification showed that surface heavily wrinkled (Fig. 3b).

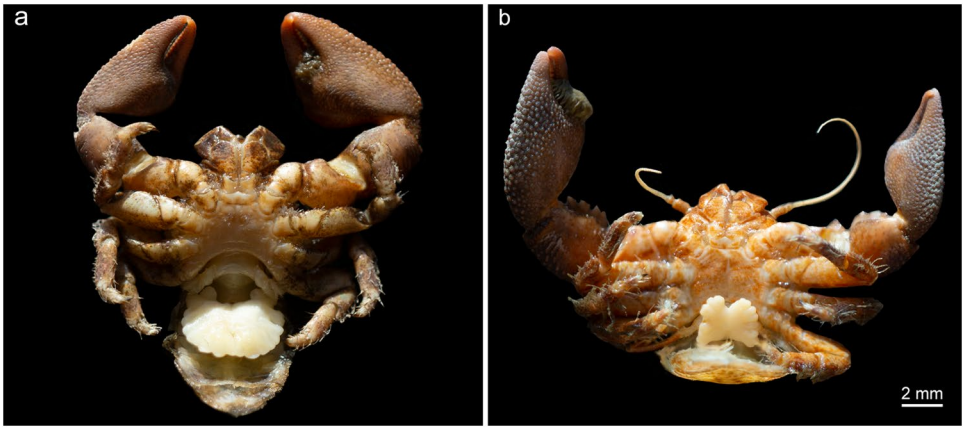

Fig. 1 *Pachycheles stevensii* infested by *Lernaeodiscus kasyanovi* sp. nov. with mature externa (**a**) and with immature externa (**b**)

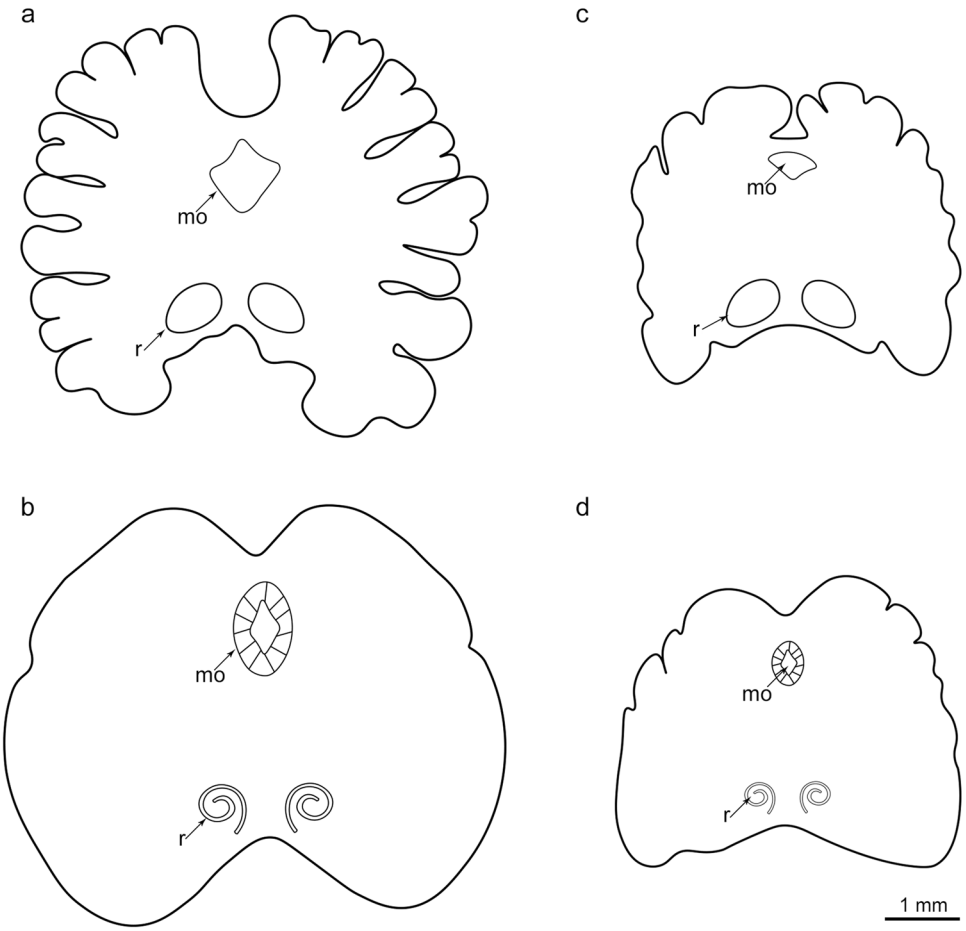

Fig. 2 Schematic drawings of the mature externae of *Lernaeodiscus kasyanovi* sp. nov. (**a**), *L. rybakovi* (**b**), and immature externae of *Lernaeodiscus kasyanovi* sp. nov. (**c**), *L. rybakovi* (**d**). mo, mantle opening; r, receptacle

Internal mantle cuticle also wrinkled (Fig. 3c) and covered with numerous smooth finger-like retinacula (from single to group of seven arising from common base) (Fig. 3d–e). Retinacula often placed in shallow depressions. Internal cuticle and retinacula covered with layer of secretion and bacteria.

Visceral sac placed dorsally in posterior part of mantle cavity. Dorsal mesentery broad and extends along almost whole dorsal surface of visceral sac from stalk to mantle opening. Ventral mesentery much narrower and shorter than dorsal one. Bilobed ovary occupies most of visceral sac and contains oocytes at various stages of development following reproductive cycle (Figs. 4a, 5a). Paired colleteric glands oval (190 × 125 µm), simple (undivided) and placed symmetrically about median plane (Fig. 4a). They found in lateral position, slightly dorsally, approximately halfway between stalk and mantle opening (Fig. 5a). Ovigerous

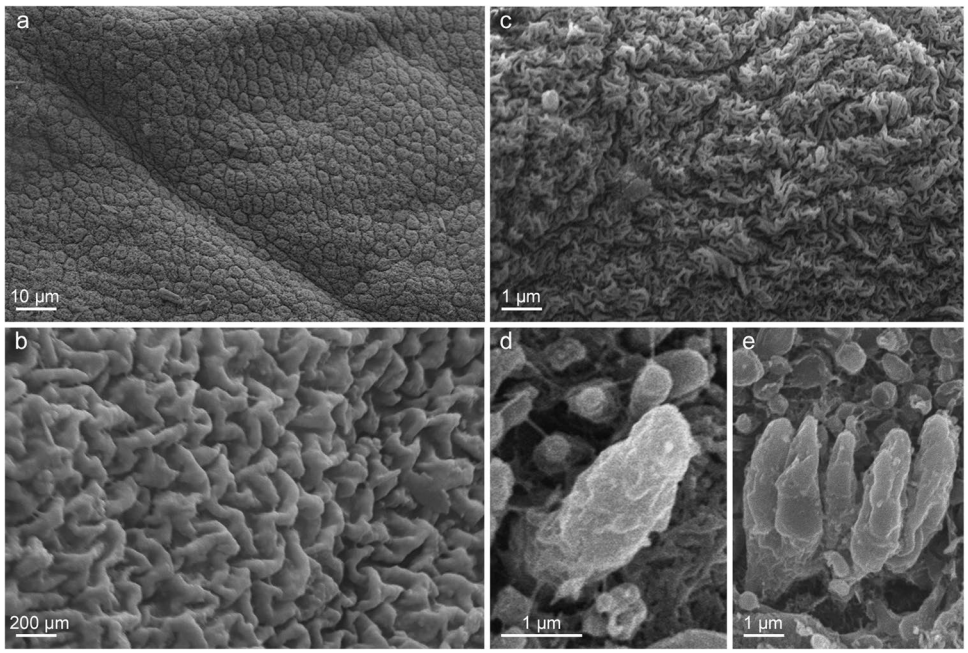

Fig. 3 SEM showing cuticle structure of the externa of *Lernaeodiscus kasyanovi* sp. nov. **a**, **b** External cuticle; **c** internal cuticle; **d**, **e** groups of retinacula

externae with developing embryos in mantle cavity found in July and August (Fig. 4b).

Paired receptacles, which hosts implanted dwarf males, are placed dorsally in posterior part of visceral sac, on "bridge" between ovarian lobes (Fig. 4c). They are almost symmetrical relative to median plane (Fig. 5b). The organ consists of the receptacle sac surrounding strongly coiled receptacle duct; in a single longitudinal section, a duct can appear up to eight times and with diameters ranging from 77 to 176 µm (Fig. 4c–f). Spermatogenic cells, representing implanted dwarf males, are found in central part of receptacle, and can be at different stages of development, again depending on stage of the reproductive cycle (Fig. 4d, f). The sinuous receptacle ducts turn first to dorsal and then to ventral surface and open into the mantle cavity on the sides of ventral mesentery. Ducts approximately equal in diameter to receptacles themselves (Figs. 4d, f, 5c).

Discussion

In Russian waters of the Sea of Japan, we have now found the crab *Pachycheles stevensii* to be infested by two rhizocephalan species of the genus *Lernaeodiscus*: *L. rybakovi* Korn et al., 2020a and *L. kasyanovi* sp. nov. It is quite common that crab species can be infested by several different species of rhizocephalans, but it is rare that the same host can carry two or more such species within the same local area, so we here review a few such examples. In Shimoda (Japan), two rhizocephalan species, *Triangulus cornutus* (Boschma, 1935) and *Lernaeodiscus okadai* Boschma, 1935, parasitize on one porcellanid crab *Petrolisthes japonicus* (De Haan, 1849), while the latter being less common (Boschma 1935). Three species, *Sacculina confragosa* Boschma, 1933, *Sacculina imberbis* Shiino, 1943, and *Parasacculina yatsui* (Boschma, 1936), were found to parasitize a single host crab, *Pachygrapsus crassipes* Randall, 1840, in a single restricted locality in eastern Japan (Tsuchida et al. 2006). Similar three-species infestation of two hermit crabs, *Pagurus nigrivittatus* Komai, 2003 and *Pagurus filholi* (de Man, 1887), by *Peltogaster lineata* Shiino, 1943, *Peltogaster postica* Yoshida et al., 2011, and *Peltogasterella gracilis* (Boschma, 1927) in a single locality were found along the Pacific coast of mainland Japan. The host preference of rhizocephalans shifted from one hermit crab species to the other along the four collection sites (Yoshida et al. 2014). *Peltogaster lineata* and *P. postica* are often sympatrically distributed and parasitize the same host species (*P. nigrivittatus* or *P. filholi*), but they never occur together on the same host specimen. Høeg and Lützen (1985) reported that the hermit crab *Pagurus bernhardus* (Linnaeus, 1758) was infested by both *Clistosaccus paguri* Lilljeborg, 1861, and *Peltogaster paguri* Rathke, 1842, on the west coast of Sweden. In the same locality, *Pagurus cuanensis* Bell, 1845, was infested by both *Peltogasterella sulcata* (Lilljeborg, 1859), *Peltogaster curvata* Kossmann, 1874, and a second, possibly new, species of *Peltogaster*.

In none of the cases above, including our *P. stevensii* material, did a crab specimen ever carry more than a single rhizocephalan species. In contrast, we have found that a population of the spider crab *Pugettia* aff. *ferox* Ohtsuchi & Kawamura, 2019 from Russian waters of the Sea of Japan is not only infested by two sympatric rhizocephalans, *Sacculina pilosella* Van Kampen & Boschma,

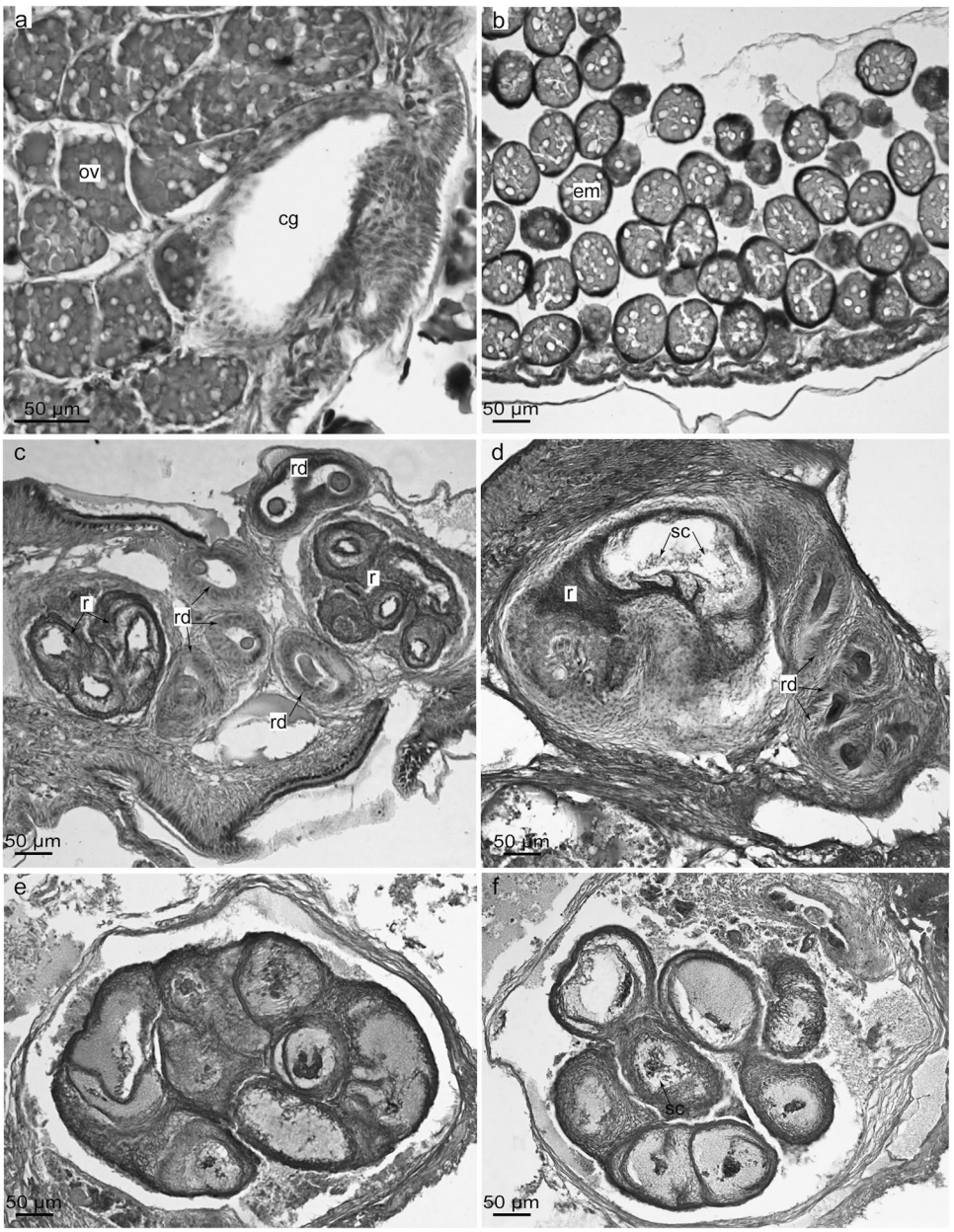

Fig. 4 Transverse and longitudinal sections of the externa of *Lernaeodiscus kasyanovi* sp. nov. **a** Ovary and colleteric gland; **b** embryos; **c**, **d** receptacles and receptacle ducts (transverse section); **e, f** receptacles (longitudinal section). cg, colleteric glands; em, embryos, ov, ovary; r, receptacle; rd, receptacle duct; sc, spermatogenic cells

1925 and *Sacculina pugettiae* Shiino, 1943, but both parasites can occur simultaneously on the same host specimen.

Until recently, the genus *Lernaeodiscus* (Rhizocephala: Peltogastridae) included eight species: *L. ingolfi*; *L. okadai*; *L. porcellanae*; *Lernaeodiscus pusillus* Boschma, 1950; *Lernaeodiscus schmitti* Reinhard, 1950; *Lernaeodiscus squamiferae* Pérez, 1922; *Lernaeodiscus tableta* Boyko & Harvey, 2000; and *Lernaeodiscus triangularis* Lützen, 1985 (WoRMS 2021). The main morphological features *Lernaeodiscus kasyanovi* sp. nov. agree well with all characters of the genus *Lernaeodiscus* as summarized by Høeg and Lützen (1985), Boyko and Harvey (2000), and Øksnebjerg (2000).

Despite the fact that *L. rybakovi* and *L. kasyanovi* sp. nov. parasitize the same host and are found sympatrically, the two species show distinct morphological differences. The externa of *L. kasyanovi* sp. nov. is somewhat smaller (3.5–8.5 mm vs 4–13 mm in *L. rybakovi*). The mantle opening of *L. kasyanovi* sp. nov. is larger, and the crenulated lip is less pronounced than in *L. rybakovi*. The receptacles are spiral-shaped forming two turns in *L. rybakovi*, whereas they are strongly coiled within the receptacle sacs in *L. kasyanovi* sp. nov. Several characters also differ between mature and immature specimens of both species. The mature externa is red–orange in *L. rybakovi*, while it is light colored (white or yellowish) in *L. kasyanovi* sp. nov. The immature externa

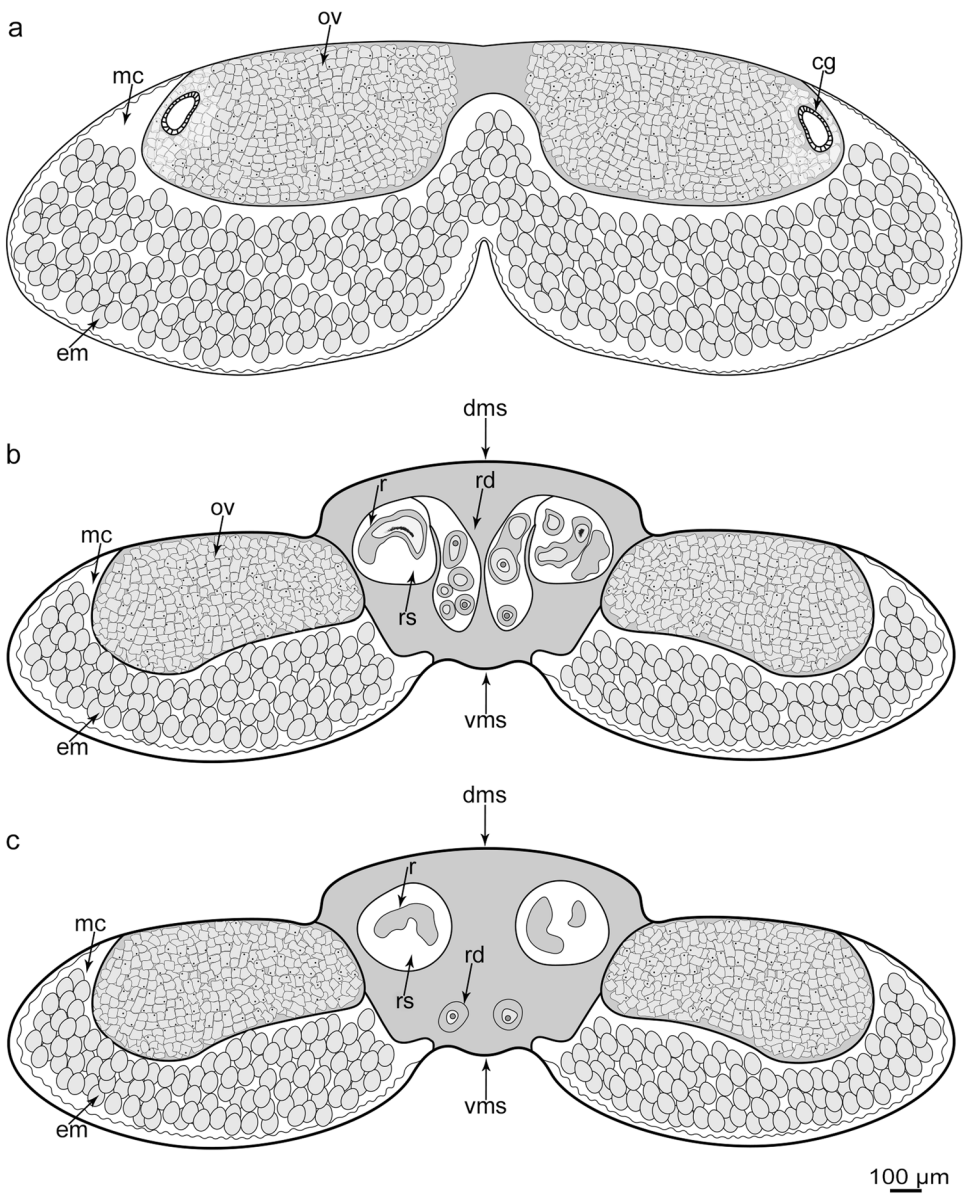

Fig. 5 Diagram illustrating the position of principal organs (transverse sections) in the externa of *Lernaeodiscus kasyanovi* sp. nov. **a** At the level of colleteric glands (approximately half-way between the stalk and the mantle opening); **b** at the level of receptacles (approximately 1/3 way from the stalk); **c** at the level of receptacle ducts (closer to the stalk). cg, colleteric glands; dms, dorsal mesentery; em, embryos; r, receptacle; rd, receptacle duct; mc, mantle cavity; ov, ovary; rs, receptacle sac; vms, ventral mesentery

is red in *L. rybakovi* (even in virginal specimens), while it is only slightly reddish in *L. kasyanovi* sp. nov. The mature externa of *L. kasyanovi* sp. nov. has distinct marginal lobes that are lacking in mature externa of *L. rybakovi*. Immature externae of both species lack distinct lobes (Fig. 2).

The breeding season of most rhizocephalans in the northwestern part of the Sea of Japan is confined to the summer months (Korn et al. 2004, 2020a, b), and in agreement with this, the populations of both *Lernaeodiscus* species consist of immature externae most of the year. During this period, *L. rybakovi* and *L. kasyanovi* sp. nov. can be distinguished by color, by the shape of the receptacles, and by the structure of the mantle opening. Mature externae *L. kasyanovi* sp. nov. are always well-distinguished by the presence of distinct marginal lobes.

Retinacula are cuticular excrescences on the internal wall of the mantle that may function as holdfasts for the brooded mass of embryos (Rybakov and Høeg 2002). Until recently, it was considered that the internal cuticle of *Lernaeodiscus* species lacks retinacula (Boschma 1928, 1935, 1969; Boyko and Harvey 2000). The presence of retinacula in *L. rybakovi* and *L. kasyanovi* sp. nov. suggests that this character may be more widespread among rhizocephalans, but has escaped notice because they can be easily missed when using only light microscopy. The retinacula of the lamp-brush type in *L. rybakovi* sp. nov. and the finger-like retinacula in *L. kasyanovi* sp. nov. further indicate that these structures allow a clear separation of two sympatric rhizocephalans. We therefore follow Rybakov and Høeg (2002) and recommend that all future species descriptions

of rhizocephalans include SEM studies of the inner mantle wall.

The presence or absence of marginal lobes also seems to be a reliable character to distinguish the species of *Lernaeodiscus*; marginal lobes are mentioned only in *L. porcellanae*, *L. tableta*, and *L. pusillus*, but *L. kasyanovi* sp. nov. differs from these rhizocephalans in other characters. Distinct marginal lobes are always present in *L. porcellanae* (Müller 1862; Reinhard 1950; Boschma 1969; Boyko and Harvey 2000). The investigation of thousands of externae of *L. porcellanae* never revealed any without distinct lobes (Korn et al. 2020a). Separation of *L. porcellanae* from *L. kasyanovi* sp. nov. is clearly assured by the molecular data and also by the greater size (up to 11 mm width). *Lernaeodiscus tableta* and *L. pusillus* both have extremely small mature externae, never exceeding 2 mm in width, and this separates them from all the remaining species of the genus. In addition, *L. tableta* is characterized by microscopic elongate papillae (excrescences) on the external cuticle (Boyko and Harvey 2000), while the external cuticle in *L. kasyanovi* is smooth. The marginal lobes in *L. pusillus* are inconspicuous (Boschma 1950). The remaining *Lernaeodiscus* species (*L. schmitti*, *L. squamiferae*, *L. triangularis*, *L. okadai*, and *L. ingolfi*) have trapeziform or triangular externae without distinct lobes (Boschma 1928, 1935; Shiino 1943; Reinhard 1950; Høeg and Lützen 1985; Lützen 1985; Boyko and Harvey 2000; Øksnebjerg 2000).

The presence of distinct marginal lobes is seemingly connected with the stage of development of the externa, so their use as a diagnostic character should be confined to mature externae. In both *L. kasyanovi* sp. nov. and *L. porcellanae* (see Høeg and Ritchie 1985), mature and immature externae differ greatly in this regard. Another example is *L. okadai*; although Boschma (1935) first described this species as having no marginal lobes, he later found that lobes may be distinct in mature specimens (Boschma 1950).

Colleteric glands of the oviducts secrete a substance that serves to keep the egg mass together (see Lange 2002). In most *Lernaeodiscus* species, the colleteric glands are small, nearly globular, undivided, and differ only by their position in the visceral sac, and those in *L. kasyanovi* sp. nov. do not present any new features. In contrast, the variation of receptacle structure among *Lernaeodiscus* species can serve as a taxonomic character. The strongly coiled receptacle ducts of *L. kasyanovi* sp. nov. are probably similar those of *L. pusillus.* Receptacle shape allows an easy separation of the two sympatric species, *L. rybakovi* and *L. kasyanovi* sp. nov., even without any preparation as they can be clearly seen on both live and preserved externae through the thin mantle tissue.

Conclusions

Our most significant finding may be the sympatric presence of two congeneric rhizocephalans on the same host species. Next to nothing is known about either species' evolution within Rhizocephala or potential interspecific competition for the presence on the same host species. The numerous cases of crustaceans potentially being infested by two or more rhizocephalan species but the scarcity of such situations occurring sympatrically might suggest that rhizocephalans do compete for their hosts. Furthermore, known variations in prevalence might even suggest that the outcome for single rhizocephalan species depends both on the host species and the geographic locality (see Høeg and Lützen 1995). At a more general level, this concerns the exciting question on how rhizocephalans evolve onto new host species and how they achieve the often very extensive control over both morphology and a range of biological functions of the infested crab.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12526-021-01211-x.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on request.

Author contribution OMK and DDG studied morphological characters. DAR and HG performed the molecular analysis. OMK and JTH wrote the manuscript. DDG performed all illustrations. All authors read and approved the manuscript.

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