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# The first record of the parasite *Peltogaster lineata* (Rhizocephala: Peltogastridae) on the hermit crab *Pagurus middendorffii* (Anomura: Paguridae)

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**Marine Record**

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**Abstract**

In Peter the Great Bay (Russian waters of the Sea of Japan), rhizocephalan barnacle *Peltogaster lineata* Shiino, 1943, a common parasite of the hermit crab *Pagurus brachiomastus* (Thallwitz, 1891), was founded for the first time on the hermit crab *Pagurus middendorffii* Brandt, 1851 (Anomura: Paguridae). Taxonomical identification of the parasite was made using morphological and molecular methods. *Pagurus middendorffii* is the sixth host of *P. lineata.*

## Introduction

*Pagurus middendorffii* Brandt, 1851 (Anomura: Paguridae) is a hermit crab inhabiting coastal waters in the Pacific Ocean from Olyutorsky Bay to the northern Honshu (Japan) and Korea, and from the Aleutian Islands to Vancouver (Canada) (Kim and Kwon, 1988; Nagasawa *et al.*, 1996; Marin, 2013). This species is distributed up to 50 m depth, on sandy and silty-sandy bottoms, and may occur in the intertidal baths. In 1971–1975 and 1987, *P. middendorffii* was the dominant species in the whole Peter the Great Bay of the Sea of Japan (Volvenko, 1995). In different parts of Vostok Bay (inner gulf of Peter the Great Bay), the proportion of this species varied from 33 to 100% (Pogrebov and Kashenko, 1976) or was 45.6% (Volvenko, 1995) of the total abundance of all coastal hermit crabs. However, in 2014–2015, its density decreased significantly to 1.3% of the total abundance of hermit crabs (Selin *et al.*, 2016).

*Pagurus middendorffii* is the host of parasitic isopods of the family Bopyridae including *Athelges japonicus* Shiino, 1958 (Shiino, 1958), *A. takanoshimensis* Ishii, 1914 (Kim and Kwon, 1988), *Erimitione lata* (Shiino, 1958) (Shiino, 1958), and also the colonial parasitic barnacle *Peltogasterella gracilis* (Boschma, 1927) (Rhizocephala: Peltogasterellidae) (Nagasawa *et al.*, 1996). In 2014–2015, 35.4% of *P. middendorffii* specimens from Vostok Bay were infested by isopods and rhizocephalans: 20.83% by *P. gracilis* (Figure 1A, B), 14.58% by *A. takanoshimensis*, and rarely by *E. lata*. Some hermit crabs carried *P. gracilis* + *A. takanoshimensis* or *E. lata* + *A. takanoshimensis* simultaneously (Kornienko *et al.*, 2018). It is possible that the high infestation of the *P. middendorffii* population and parasitic castration of the hosts was the reason for the large decline in abundance of this hermit crab in Peter the Great Bay (Selin *et al.*, 2016).

Until now, the only rhizocephalans recorded on *P. middendorffii* was *P. gracilis* (McDermott *et al.*, 2010; Kornienko *et al.*, 2018). In 2021, we found a *P. middendorffii* specimen with a single (not colonial) rhizocephalan in Vostok Bay. This parasite was similar to *Peltogaster lineata* Shiino, 1943 recorded earlier on the hermit crab *Pagurus brachiomastus* (Thallwitz, 1891) in this locality (Golubinskaya *et al.*, 2021a). In 2023, two more hermit crabs with this parasite were found. In the present work, these rhizocephalans are identified using morphological and molecular methods.

## Material and methods

Specimens of *P. middendorffii* infested by rhizocephalans (Figure 1C, D) were collected by SCUBA diving in Vostok Bay (42°53′N, 132°43′E) at a depth of 0.5–1 m, in September 2021 and 2023. These hermit crabs were deposited at the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology, FEB RAS, Vladivostok (MIMB).

### *Material examined*

One specimen (6.1/2.7 mm, with embryos without eyes), on *P. middendorffii* (male, 3.4 mm, depth 0.5 m, Vostok Bay, 5.09.2021) (catalogue number, MIMB 48412).


**Figure 1.** Host crab, *Pagurus middendorffii*, infested by *Peltogasterella gracilis* (A, B) and *Peltogaster lineata* (C, D).

One specimen (5.0/1.8 mm, with embryos without eyes), on *P. middendorffii* (female, 4.1 mm, depth 1.0 m, Vostok Bay, 11.09.2023) (catalogue number, MIMB 48413); a part of the cuticle was used for SEM.

One specimen (6.3/2.0 mm, with embryos without eyes), on *P. middendorffii* (female, 4.0 mm, depth 1.0 m, Vostok Bay, 11.09.2023); was used for histology.

## Molecular techniques

Two specimens of the rhizocephalan parasite and one specimen of *P. middendorffii* were fixed in 96% ethanol and subjected to molecular analysis. Total genomic DNA was extracted from the externae and from the tissue of crab chela using a chelating resin Chelex 100 (Bio-Rad, USA, CA) according to the protocol described by HwangBo *et al.* (2010). The gene fragments of COI and 16S rDNA sequences were retrieved as in Golubinskaya *et al.*'s (2021a) study.

All sample PCR products were sequenced for both heavy and light strands, in order to improve accuracy, and aligned using MUSCLE (Edgar, 2004) implemented in MEGA v.11.0.8 (Tamura *et al.*, 2021). Additional data for outgroup and ingroup taxa were taken from GenBank (NCBI, https://www.ncbi.nlm.nih.gov/). Phylogenetic trees were built for the genus *Peltogaster* (Figures 2 and 3) and for the genus *Pagurus* (Figures S1 and S2). Accession numbers for all taxa were included in alignments and phylogenetic analyses can be found in Table S2. The best-fit model of nucleotide substitution for the data sets was identified using ModelFinder (Kalyaanamoorthy *et al.*, 2017) on the IQ-TREE webserver (http://www.iqtree.org/) (Trifinopoulos

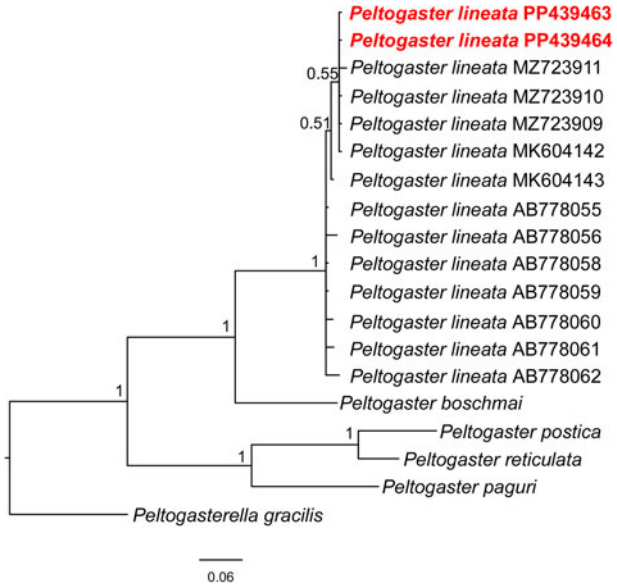


**Figure 2.** Bayesian phylogenetic tree for the COI dataset. The phylogeny shows the position of samples from this study within a monophyletic *Peltogaster lineata*. Nodal support is indicated in the form of Bayesian posterior probabilities (pp).

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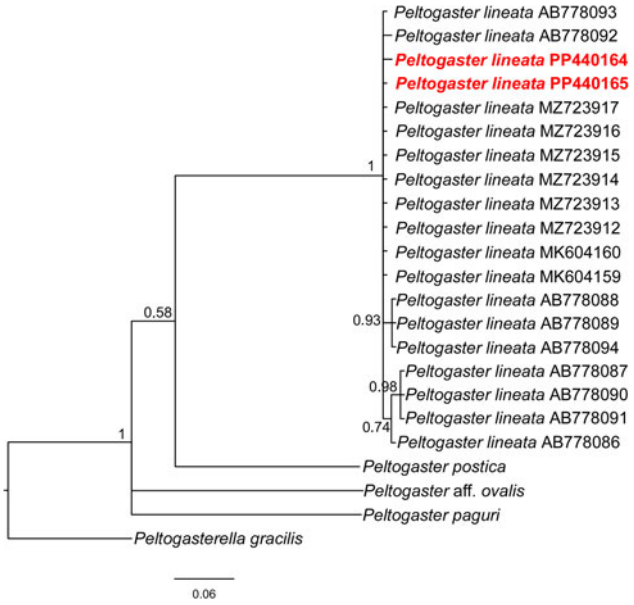


**Figure 3.** Bayesian phylogenetic tree for the 16S dataset. The phylogeny shows the position of samples from this study within a monophyletic *Peltogaster lineata*. Nodal support is indicated in the form of Bayesian posterior probabilities (pp).

*et al.*, 2016). For the parasite specimens, TIM3 + F + I + G4 model was selected as the best for COI, and TPM3u + F + G4 model for 16S. For the host specimen, TVM + F + I + G4 model was chosen for COI and K3Pu + F + I + G4 model for 16S.

For Bayesian analysis, we used the closest appropriate models. Bayesian trees were constructed using MrBayes 3.2.7a (Ronquist *et al.*, 2012) implemented in CIPRES Science Gateway (http://www.phylo.org/) (Miller *et al.*, 2010) with the following parameters: 10,000,000 generations, with four parallel chains and sample frequencies set to 500 in two separate runs. Based on the convergence of likelihood scores, 25% of the sampled trees were discarded as burn-in. All results trees were visualized using FigTree v. 1.4.4 (Rambaut, 2012). The pairwise genetic distances were calculated using MEGA v.11.0.8 (Tamura *et al.*, 2021). Intra- and interspecific nucleotide variability of the analysed species was based on the Kimura 2-parameter model (K2P) (Kimura, 1980) for COI sequences and uncorrected genetic distances were calculated for 16S sequences.

All resulting sequences were submitted to the National Center for Biotechnology Information (GenBank, NCBI, https://www.ncbi.nlm.nih.gov/) nucleotide database. The following are the accession numbers for *P. lineata:* COI, PP439463–PP439464, 16S, PP440164–PP440165 (Table 1 and Table S1). The accession numbers for *P. middendorffii* are: COI, PP439465, 16S, PP440166.

### Morphological investigation of the externa

An infested specimen of *P. middendorffii* was photographed alive. Microscopic examination of rhizocephalan was conducted under MBS-10 stereomicroscope and Olympus CX41 microscope. The following measurements of the parasite externae were made: length (distance between anterior and posterior ends) and width at the level of the stalk. The length of the anterior calcified part of the carapace (shield length) of the host hermit crab was also measured. Sex of the host was determined based on the presence of four unpaired pleopods in females and three unpaired pleopods in males (Tudge *et al.*, 2012). The location of the rhizocephalan externa on each host crab was noted.

One mature externa of the rhizocephalan was fixed in Bouin solution, dehydrated through a gradient ethanol-xylene series and embedded in paraffin. Transverse sections, 6 µm thick, were stained with Ehrlich haematoxylin (Kiernan, 2015). Material was examined with a Zeiss Axio Imager Z.2 light microscope furnished with a digital camera. For SEM, the mantle of one externa was dehydrated through an ethanol series and acetone, critical point dried in CO2, and sputtered with chromium. It was observed with a Zeiss Sigma 300 VP microscope.

## Results

### Molecular analysis

For host, the length sequences were 543 bp for COI and 458 bp for 16S and after alignment and trimming to the same length the final data set was 479 and 334 bp, respectively. All sequences belonging to *P. middendorffii* form the same clade with low value of genetic distances between them. For COI, genetic distance between our (PP439465) and other sequences was 1.27 ± 0.51% (mean ± standard error), and intraspecific distance was 0.42 ± 0.3%. Here and further, intraspecific genetic distances were calculated without including own data. For 16S, these values were 0.04 ± 0.04% between our (PP439466) and other sequences with intraspecific distance 0.09 ± 0.08%. Thus, the identity of the hosts sample as *P. middendorffii* was confirmed by molecular analysis (Figures S1 and S2).

For parasite, the sequence length for our data was 574 ± 674 bp for COI and 449 ± 464 bp for 16S. However, sequences from GenBank (NCBI) were included in current analysis that contains incompletely overlapping fragments because of using the different primer pairs for analysed gene fragments. The final data set after alignment and trimming to the same length was 385 and 263 bp, respectively. Phylogenetic trees for both COI and 16S rDNA showed that sequences retrieved for this research form a single monophyletic clade with other sequences of *P. lineata* (which were obtained from different research and from different crab hosts) (Figures 2 and 3, Table 1 and Table S1). Genetic distances between our data and the data obtained from GenBank (NCBI) were 0.83 ± 0.29% for COI and 0.44 ± 0.2% for 16S with the following value of intraspecific distances 1.03 ± 0.28% and 0.43 ± 0.21% for COI and 16S, respectively. Thus, the comparison of pairwise genetic distances also indicated the absence of significant differences between analysed sequences of *P. lineata* for both fragments (Tables S2 and S3). So, the molecular analysis with the use of the markers COI and 16S showed that our rhizocephalans found parasitizing the hermit crab *P. middendorffii* belong to *P. lineata*.

### Taxonomy

Superorder Rhizocephala Müller, 1862
Family Peltogastridae Lilljeborg, 1861; amended by Høeg *et al.* (2020)
Genus *Peltogaster* Rathke, 1842
*Peltogaster lineata* Shiino, 1943
*Peltogaster lineatus* – Shiino, 1943:23–24, fig. 16.
*Peltogaster lineata* – Yoshida *et al.*, 2014: 471, 473, figs. 2C–E, 3B; Jung *et al.*, 2019: 7–8, figs. 2A, 5A; Golubinskaya *et al.*, 2021a.

### Short description of the externa

We found one male and two females of *P. middendorffii* each bearing single externa of *P. lineata.* Each externa was attached near the second pleopod of the host. The shield length of infested hermit crabs ranged from 3.4 to 4.1 mm. The mature externae with embryos without eyes were pale, oval and slightly curved. The size of the externae ranged from 5.0 to 6.3 mm in length and from 1.8 to 2.7 mm in width. The anterior end was broad and bilobed, with the mantle opening placed subterminally on

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**Table 1.** Genbank accession details for *Peltogaster lineata* used in phylogenetic analyses

| Species | COI | 16S | Host | Collection site | Cite |
|---|---|---|---|---|---|
| *Peltogaster lineata* | PP439463–PP439464 | PP440164–PP440165 | *Pagurus middendorffii* | Vostok Bay, Peter the Great Bay, Russia | This study |
| *Peltogaster lineata* | AB778055–AB778056 | AB778086–AB778087 | *Pagurus filholi* | Shirahama, Wakayama, Japan | Yoshida *et al.* (2014) |
| *Peltogaster lineata* | | AB778088–AB778089 | *Pagurus maculosus* | Shimoda, Shizuoka, Japan | Yoshida *et al.* (2014) |
| *Peltogaster lineata* | AB778058–AB778059 | AB778090–AB778091 | *Pagurus nigrivittatus* | Shimoda, Shizuoka, Japan | Yoshida *et al.* (2014) |
| *Peltogaster lineata* | AB778060 | AB778092 | *Pagurus nigrivittatus* | Shirahama, Wakayama, Japan | Yoshida *et al.* (2014) |
| *Peltogaster lineata* | AB778061 | AB778093 | *Pagurus nigrivittatus* | Misaki, Kanagawa, Japan | Yoshida *et al.* (2014) |
| *Peltogaster lineata* | AB778062 | AB778094 | *Pagurus nigrivittatus* | Okinoshima, Chiba, Japan | Yoshida *et al.* (2014) |
| *Peltogaster lineata* | MK604142 | MK604159 | *Pagurus brachiomastus* | Yangyang, Korea | Jung *et al.* (2019) |
| *Peltogaster lineata* | MK604143 | MK604160 | *Pagurus filholi* | Busan, Korea | Jung *et al.* (2019) |
| *Peltogaster lineata* | MZ723909–MZ723911 | MZ723912–MZ723917 | *Pagurus brachiomastus* | Vostok Bay, Peter the Great Bay, Russia | Golubinskaya *et al.* (2021a) |

the side facing of the host. The mantle opening was U-shaped, slightly elevated and inserted between the two slightly projecting subequal lobes. The conspicuous fusiform shield covered near 1/4 of the externa. A very short stalk was located on the midpoint of the body axis.

A visceral sac with large developing oocytes extended dorsally along most of the externa (Figure 4A). The mantle cavity was closely filled with embryos with a diameter from 110 to 130 µm. The mantle was ca. 50 µm in thickness (Figure 4B). The colleteric glands were short strongly flattened tubes with a size ranging from 293 × 37 to 443 × 72 µm, placed within the shield level (Figure 4A, C). They gradually passed into thin posterior parts, with a diameter 67–79 µm. Short tubular receptacles, with a diameter of 65–118 µm, were placed inside the visceral sac within the shield level (Figure 4D). The receptacles gradually passed into receptacle ducts with a diameter of 31–63 µm (Figure 4E). The posterior (distal) parts of the receptacle ducts were coiled and opened on the lateral surfaces of the visceral mass.

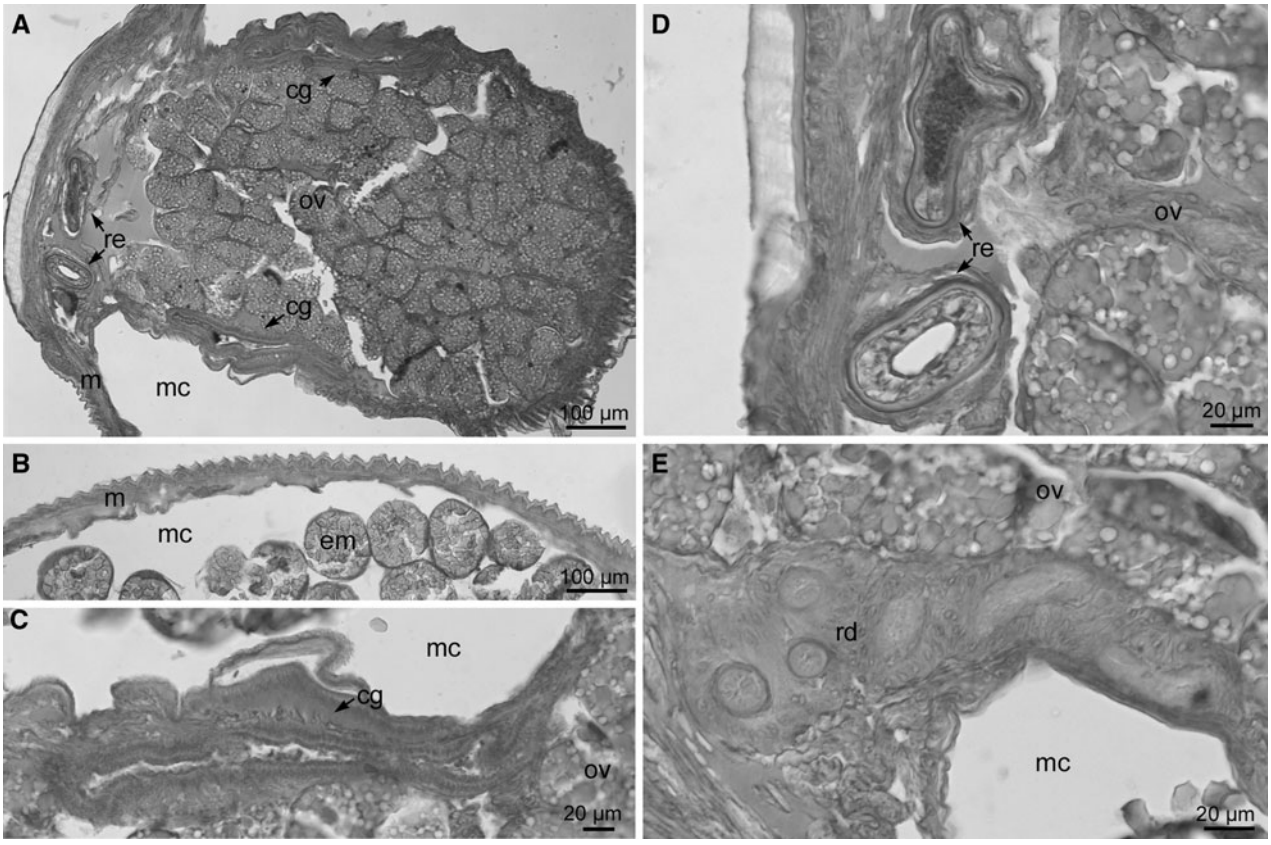


**Figure 4.** Histology of the externa *Peltogaster lineata*. Transverse section of the whole externa (A); mantle (B); strongly flattened colleteric gland (C); receptacles (D); coiled receptacle duct (E). cg, colleteric gland; em, embryon; m, mantle; mc, mantle cavity; ov, ovary; rd, receptacle duct; re, receptacles.

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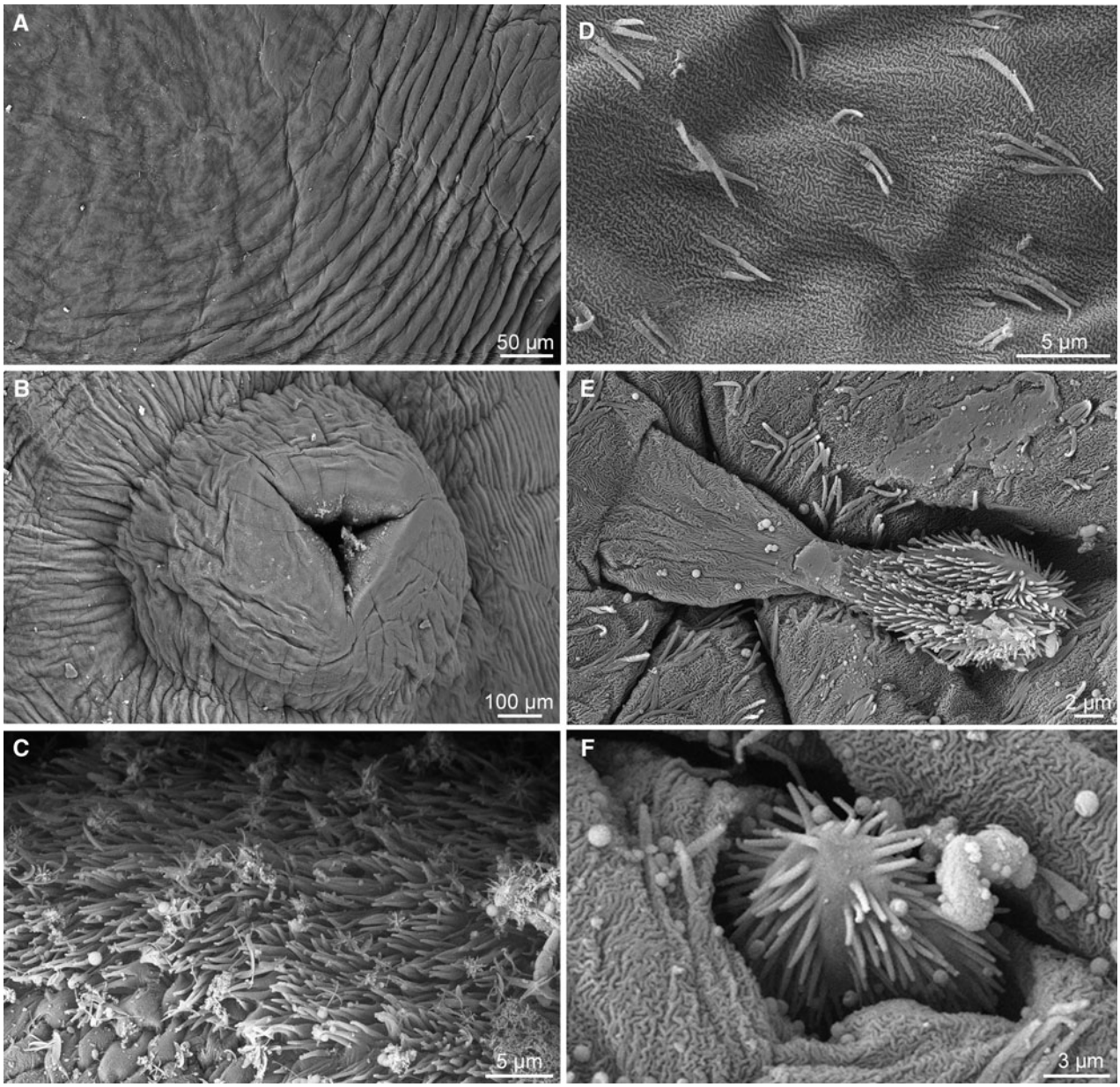


**Figure 5.** SEM showing cuticle structure of the externa of *Peltogaster lineata*. Smooth external cuticle (A); mantle opening (B); numerous spines densely covering mantle opening (C); wrinkled internal cuticle covered with papillae ('hairs') (D); clavate barbed retinaculum (E, F).

The external cuticle was smooth, without papillae or excrescences (Figure 5A). The mantle opening was surrounded by lips densely covered with numerous spines (Figure 5B, C). The internal cuticle was wrinkled and covered with sparse papillae ('hairs') (Figure 5D). Numerous clavate barbed retinacula of 12–14 µm in length occurred singly, some of them were placed in depressions (Figure 5E, F).

## Discussion

The morphological investigation showed the great similarity between rhizocephalans parasitizing *P. brachiomastus* and *P. middendorffii*. They are similar in external shape, coloration and position on the host. Their cuticles are also nearly identical. At the same time, these species differ in two anatomical characters. The mantle of the parasite from *P. middendorffii* is considerably thinner than that from *P. brachiomastus* (50 *vs* 100 µm). Moreover, its colleteric glands are strongly flattened and reach greater diameter (443 *vs* 239 µm) (Golubinskaya *et al.*, 2021a). These differences may be due to the large number of developing eggs in the mantle cavity, which could cause the stretching of the mantle and flattening of the oviducal glands. The molecular analysis herein confirmed that the rhizocephalans found on *P. middendorffii* as well as on hermit crabs *Pagurus filholi* (de Man, 1887), *P. nigrivittatus* Komai, 2003 and *P. maculosus* Komai & Imafuku, 1996 were all *P. lineata*.

In rhizocephalans, multi-species infestation of a single host is not rare; however, previously, it was believed that different parasites are rarely found sympatrically. In 2006, three species, *Sacculina confragosa* Boschma, 1933, *S. imberbis* Shiino, 1843 and *Parasacculina yatsui* (Boschma, 1936), were found parasitizing a single host crab, *Pachygrapsus crassipes* Randall, 1840, in a restricted locality (Tsuchida *et al.*, 2006). Last years, we observed two examples of parasitism with two sympatric rhizocephalans on the same host in Peter the Great Bay. Two congeneric species, *Lernaeodiscus rybakovi* Korn, Golubinskaya, Rees, Glenner & Høeg, 2020 and *L. kasyanovi* Korn, Golubinskaya, Rees, Glenner & Høeg, 2021, infest the anomuran crab *Pachycheles stevensii* Stimpson, 1858 (Korn *et al.*, 2020, 2021). The parasitization of the spider crab *Pugettia* aff. *ferox* Ohtsuchi & Kawamura by

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two sacculinids, *Sacculina pugettiae* Shiino, 1943 and *Parasacculina pilosella* (Van Kampen et Boschma, 1925), from different genera and families, is an example not only of sympatric multi-species infestation, but the first finding of two different parasites on a single crab specimen (Golubinskaya *et al.*, 2021b). *Pagurus middendorffii* is another crab infested by two parasites, *Peltogasterella gracilis* and *P. lineata*, from different rhizocephalan families in the same locality.

*Peltogaster lineata* parasitizes numerous crab species. In Seto, this species occurs on *Pagurus japonicus* (Shiino, 1943). Yoshida *et al.* (2014) did not find *P. japonicus* infested by *P. lineata* along the Pacific coast of Honshu, but revealed three new hosts for this rhizocephalan: *P. filholi*, *P. nigrivittatus* and *P. maculosus*. In Japan, the main host of *P. lineata* was *P. nigrivittatus*; its prevalence reached 70%, followed by *P. filholi* at 20%, and *P. maculosus* as only 10% of the examined material. The fifth host of *P. lineata*, *P. brachiomastus*, was found in Korea; the prevalence of *P. filholi* and *P. brachiomastus* was 50% each (Jung *et al.*, 2019). In Russian waters, *P. lineata* was so far found only on *P. brachiomastus* (Golubinskaya *et al.*, 2021a). *Pagurus middendorffii* is the sixth known host of *P. lineata*. The host preference of *P. lineata* changes from *P. filholi* + *P. nigrivittatus* + *P. maculosus* in Japan to *P. filholi* + *P. brachiomastus* in Korea (Yoshida *et al.*, 2014; Jung *et al.*, 2019), and to *P. brachiomastus* + *P. middendorffii* in Russia.

**Supplementary material.** The supplementary material for this article can be found at https://doi.org/10.1017/S0025315424000511

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

**Author contributions.** N. A. A. collected the material. O. M. K. and D. D. G. studied morphological characters. O. M. K. wrote the manuscript. D. D. G. performed all illustrations. S. N. S. performed the molecular analysis. All authors read and approved the manuscript.

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**Competing interest.** None.

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

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