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ORIGINAL PAPERS

Molecular Identity of *Laonice cirrata* (Sars, 1851) (Annelida, Spionidae) and Description of a New *Laonice* species from the Northwest Pacific[1]

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Abstract—Originally described from the northern Norway, *Laonice cirrata* (M. Sars, 1851) has been considered cosmopolitan and widely distributed in the North Pacific. To clarify the taxonomic status of the Pacific worms, we obtained the genetic characteristics of *L. cirrata* from Grøtsund Fjord, near Tromsø, one of the sites where Michael Sars collected worms to describe this species. The phylogenetic analysis of sequences of five gene fragments (mitochondrial *COI* and *16S* rDNA, nuclear *18S* rDNA and *28S* rDNA, and *Histone 3*) showed significant difference between the Norwegian worms and worms from the north-western part of the Sea of Japan (Russia) earlier identified by morphology as *L. cirrata*. Common inhabitants of shallow waters in the Sea of Japan, these worms are assigned to the new species *Laonice kasyanovi* sp. nov. Both Northeast Atlantic and the Northwest Pacific populations exhibit high and overlapping variability of the diagnostic morphological characters of adults, and thus the two species can be considered as siblings. The distribution of these two species in the North Pacific remains uncertain and can only be elucidated by molecular data. Adults and one larva from the White Sea were also sequenced and found to be genetically identical to *L. cirrata* from Norway. The trochophores of *L. cirrata* are described and illustrated. They are characterized by two circles of large vesicles in the thick egg membrane and have been incorrectly referred to *Aonides* by previous authors.

Keywords: polychaete, marine biodiversity, systematics, sibling species, genetics, biological invasions

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INTRODUCTION

In the 19th and first half of the 20th century, annelids were considered to have high morphological variability and high ecological plasticity. As a result of this belief, many species were, and still are, considered widespread if not cosmopolitan [1]. It is noteworthy that the concept of "cosmopolitism" prevails particularly among older-named species, the brief original descriptions of which often contain only general characters that in hindsight may correspond to similar species throughout the world.

Fifteen widespread or cosmopolitan species have been reported in one of the largest polychaete families, Spionidae Grube, 1850 [2]. All of them were originally briefly described in the nineteenth century or earlier, largely from European waters. A number of spionid taxa, previously considered cosmopolitan, have been resolved as distinct, and usually provincially restricted, species [2–5]. In some cases, wide distributions have been confirmed, but these are now regarded as secondarily derived due to human-mediated dispersal by various vectors and routes [6, 7]. However, most

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"cosmopolitans" still await careful examination by taxonomists. One of these species, *Laonice cirrata* (M. Sars, 1851), is considered in the present study.

The annelid *Nerine cirrata* from northern Norway was originally described in the order Dorsibranchiata Cuvier, 1816 by Michael Sars [8]. In the 19th century, annelid family and genus concepts were unstable, and *L. cirrata* M. Sars, 1851 was assigned to six different genera by various authors (see [9]: 220). Malmgren [10] placed this species in the family Spionidae Grube, 1850 and established a new genus for it, *Laonice* Malmgren, 1867. This genus is one of the most speciose in the Spionidae, currently comprising 49 described species throughout the world from the intertidal to abyssal depths [11]. Identification of *Laonice* worms is often a challenge due to 1) the presence of sibling and cryptic species, 2) high ontogenetic and individual morphological variability, and 3) fragmented and low-quality material usually available for identification (adults are very fragile and break easily when preserved) [12]. Molecular data widely used in taxonomic studies are available for a small number of *Laonice* species and mainly include sequences of the mitochondrial cytochrome c oxidase subunit I (*COI*) and/or *16S* gene fragments (e.g., [13–16]).

The original description, here translated, of *N. cirrata* by Sars ([8]: 208) was brief and not illustrated: "Like other spionids, it has two long palps and a thread-like occipital antenna on the dorsal posterior part of the head. It differs from *N. foliosa* by the long thread-like pointed branchiae arranged on 40–41 anterior chaetigers only, and that the branchiae are well separated from the notopodial postchaetal lamellae." Worms from all over the world fit these characters, and it was thus not surprising that *L. cirrata* has been sometimes considered circumpolar and cosmopolitan [17, 18]. After the original description, *L. cirrata* was "redescribed" by different authors from distant localities. These descriptions "showed" high morphological and ecological variability of this species, but, in fact, have served to obfuscate the unique characteristics of genuine *L. cirrata* as anchored by Norwegian populations (below). Sequences named "*L. cirrata*" from distant populations available in GenBank do not help to clarify the issue and have often been obtained from not only other species but also members of non-spionid families (e.g., [19]).

In the Pacific Ocean, *L. cirrata* was first recorded in the Sea of Japan (Russia) by Zachs [20]. Later, along the Asian coast, this species was recorded in Japan [21], Vietnam [22], China [23], and Korea [24, 25]. Along the American coast, it was recorded from the Bering Sea south to Mexico [18, 26–28]. Such a wide distribution of one species has been questioned by some authors [17]. A morphological study of specimens from South America did not confirm the presence of *L. cirrata* on this subcontinent [12]. Molecular analysis of mitochondrial *COI* gene data suggested the presence of a worldwide complex of cryptic species hidden under the name *L. cirrata* [14]. However, most reports have never been verified by modern tools and analyses.

The purpose of the present study was to review reports of *Laonice* from the Northwest Pacific Ocean and provide a taxonomic revision of these worms based on old and new material. As the main references for this revision, we collected and sequenced *L. cirrata* from the Grøtsund Fjord, near Tromsø (Norway), one of the places where M. Sars collected worms to describe *N. cirrata*, and sequenced specimens of *L.* "*cirrata*" from Peter the Great Bay, Sea of Japan, Russia.

MATERIALS AND METHODS

Field Sampling, Laboratory Study and Museum Deposits

Collections were made from shallow water habitats in the Norwegian Sea (Norway), the White Sea (Russia), the Sea of Japan (Russia), and the East Sea (South Korea). Sediments were collected using grab and SCUBA equipment, sieved in the field on a 500-μm mesh sieve, and the residue was taken for further examination in the laboratory. Live *Laonice* were removed from the residue, relaxed in an isotonic solution of magnesium chloride, and examined using compound light microscopes. After examination, specimens were fixed in 10% formalin solution, then rinsed in fresh water and transferred to 70% ethanol. Fragments of some specimens were directly preserved in 95% ethanol and genetically examined by Sikorski et al. [16] and in the present study. Formalin-fixed specimens were stained with a 70% ethanol solution of methylene green (for details see [29]) and then examined and photographed using a Zeiss Stemi 305 microscope equipped with an AmScope MU633-BI digital camera. Some formalin-fixed specimens were critical point-dried in carbon dioxide, coated with gold palladium, and viewed with an LEO 440 scanning electron microscope (SEM) equipped with a digital camera at the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., USA.

Vertical plankton tows (from a depth of about 100 meters) were made with a 100-μm mesh plankton net in the Kandalaksha Bay (White Sea) in September 2016 and September 2019. Live *Laonice* larvae were photographed using a LOMO Micmed-1 compound microscope equipped with Canon 550D digital camera. After photographing, one trochophore (collected on September 8, 2016; Figs. 3c, 3d) was preserved in 95% ethanol and then entirely used for sequencing *COI*. One larva was fixed in 4% formalin solution, dehydrated in a series of ethanol-acetone mixtures with an increase in acetone concentration to 100% acetone, coated with gold palladium, and viewed with

Table 1. Taxa, sampling location data, museum registration numbers of voucher specimens and GenBank accession numbers of sequences used in the analysis. New sequences are given in **bold**

Gr*	Species	Locality	Date	Voucher	GenBank accession number ** ***				
					COI	*16S*	*18S*	*28S*	*Histone 3*
0	***Laonice sinica***	East Sea, South Korea	10 Dec 2010	ID 19949	**OR029446**	**OQ998702–03**	**OQ998673–74**	**OQ998730–31**	
1	*L. cirrata*	Grøtsund Fjord, Tromsø, Norway	12 Sep 2018	ID 21165, 23751	MT606421 (LC-09 worm-1)[1]	**OQ998684**	**OQ998665**	**OQ998711**	**OQ994993**
1	*L. cirrata*	Grøtsund Fjord, Tromsø, Norway	12 Sep 2018	ID 21165, 23752	MT606420 (LC-10 worm-2)[1]	**OQ998683**	**OQ998664**	**OQ998710**	**OQ994992**
2	*L. cirrata*	Barents Sea, Norway	19 Aug 2013	ID 19662		**OQ998680**	**OQ998661**	**OQ998708**	**OQ994990**
2	*L. cirrata*	Barents Sea, Norway	5 Aug 2013	ID 19663		**OQ998681**	**OQ998662**	**OQ998709**	**OQ994991**
2	*L. cirrata*	Barents Sea, Norway	7 Aug 2013	ID 19664		**OQ998682**	**OQ998663**	**OQ998707**	**OQ994989**
3	*L. cirrata*	off Iceland	Aug 2013	ID 25741	MG234460–61[2]				
3	*L. cirrata*	off Iceland	Aug 2013	ID 25742	MG234459[2]				
3	*L. cirrata*	off Iceland	Aug 2013	ID 25743	MG234455[2]				
4	*L. cirrata*	White Sea, Russia	19 Sep 2011	ID 17052		**OQ998678**		**OQ998706**	**OQ994988**
4	*L. cirrata*	White Sea, Russia	13 Sep 2011	ID 17394		**OQ998679**			
4	*L. cirrata*	White Sea, Russia	17 Sep 2011	ID 18340; WS 1459	**KM998733**	**OQ998677**	**KM998753**	**OQ998704**	**OQ994987**
4	*L. cirrata*	White Sea, Russia	21 Jul 2011	ID 18341; WS 925	**KM998732**	**OQ998676**	**KM998752**	**OQ998705**	**OQ994986**
4	*L. cirrata*	White Sea, Russia	8 Sep 2016		**OR029444**				
5	*L. kasyanovi* sp. nov.	Sea of Japan, Russia	19 Oct 2011	ID 17259; WS 2231–2235	**KM998734–38**	**OQ998685–89**	**KM998754–58**	**OQ998712–16**	**OQ994994–98**
5	*L. kasyanovi* sp. nov.	Sea of Japan, Russia	13 Jul 2013	ID 18037; MIMB 42772	**OR030112**	**OQ998690–92**	**OQ998666**	**OQ998717–19**	**OQ994999–OQ995001**
6	*L.* cf. *kasyanovi*	East Sea, Geoje Is., South Korea	31 Oct 2013	ID 18250; MIMB 44697	**OR030113**	**OQ998693**	**OQ998667**	**OQ998720**	**OQ995002**
7	*L.* cf. *kasyanovi*	Onagawa Bay, Honshu, Japan	20 Dec 2011	ID 24466		LC595685[3]	LC545855[3]		
7	*L.* cf. *kasyanovi*	Onagawa Bay, Honshu, Japan	27 Sep 2011	ID 25744		LC595686[3]	LC545856[3]		
8	*L. bahusiensis*	Sandefjord, Norway	29 May 2011	ID 20328; MIMB 40460	MT379948[1]	**OQ998698**	**OQ998671**	**OQ998728**	**OQ995008**
9	*L. grimaldii*	Gulf of Lion, France	24 Jun 2014	ID 18622; MIMB 39037	MT379942[1]	**OQ998694**	**OQ998668**	**OQ998721–24**	**OQ995003–05**
10	*L. irinae*	Bay of Morlaix, France	8 Sep 2016	ID 20113; MIMB 39044	MT379928–29[1]	**OQ998695–97**	**OQ998669–70**	**OQ998725–27**	**OQ995006–07**
11	*L. mediterranea*	Adriatic Sea, Croatia	18 May 2011	ID 21577	MT379949[1]	**OQ998699**			**OQ995009**
11	*L. mediterranea*	Adriatic Sea, Croatia	29 Jun 2011	ID 21580	MT379950[1]	**OQ998700**			**OQ995010**
11	*L. mediterranea*	Tuscany, Italy	26 Jul 2018	ID 21889	**OR029445**	**OQ998701**	**OQ998672**	**OQ998729**	**OQ995011**

* Geographic groups of individuals designated to calculate pairwise average distances between them (see Supplementary Table ESM6).
** Two last digits are shown for the second and other numbers in successive series.
*** One sequence number corresponds to one examined individual. Reported by: [1]Sikorski et al. [16]; [2]Bogantes et al. [14]; [3]Abe & Sato-Okoshi [66].

a Hitachi S-405A scanning electron microscope equipped with a digital camera at the White Sea Biological Station of the Lomonosov Moscow State University, Russia.

Formalin-fixed specimens were deposited in the polychaete collections of the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology (MIMB), Vladivostok, Russia; Zoological Institute, St Petersburg (ZISP), Russia; Senckenberg Museum, Frankfurt am Main (SMF), Germany; and the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. Brief information (museum acronyms and registration numbers) about new material and museum samples examined during this study and complete information about the type specimens is given in the Results preceding species descriptions; the number of specimens in a sample is given in parentheses after the museum abbreviation and registration number. Complete information about all samples mentioned in this study is given in Supplementary Tables ESM1–ESM4. Tables also include material reported by other authors which was not examined in the present study (noted in the Comments as "Reported by ..."). A complete list of the museums and other collections (and their acronyms) holding the examined or reported samples is additionally given in Supplementary Table ESM5. Information about samples used for molecular analysis is given in Table 1 and Supplementary Table ESM6.

To link newly obtained sequences and those provided in earlier studies with the material reported herein, unique numbers (VIR ID) from the VIR's database are given to samples in Tables ESM1–ESM4 and ESM6. These numbers precede collecting locations names on the tree resulted from phylogenetic analysis of molecular data (Fig. 1). When more than one specimen of the same species sample was used in the analysis, the individual numbers follow the VIR ID numbers separated by a dot, for example, 18037.1 Russia, Sea of Japan.

When no coordinates were provided for sampling sites in old studies, we collected them from the Google Earth map according to the original descriptions of the locations. Sampling locations reported in the present study are plotted on maps using QGIS 3.28 software and the geodata provided by the OpenStreetMap Project (https://osmdata.openstreetmap.de). Images of multiple focal layers were stacked using Zerene Stacker 1.04 software. Final maps and the figures were prepared using CorelDRAW®2021 software.

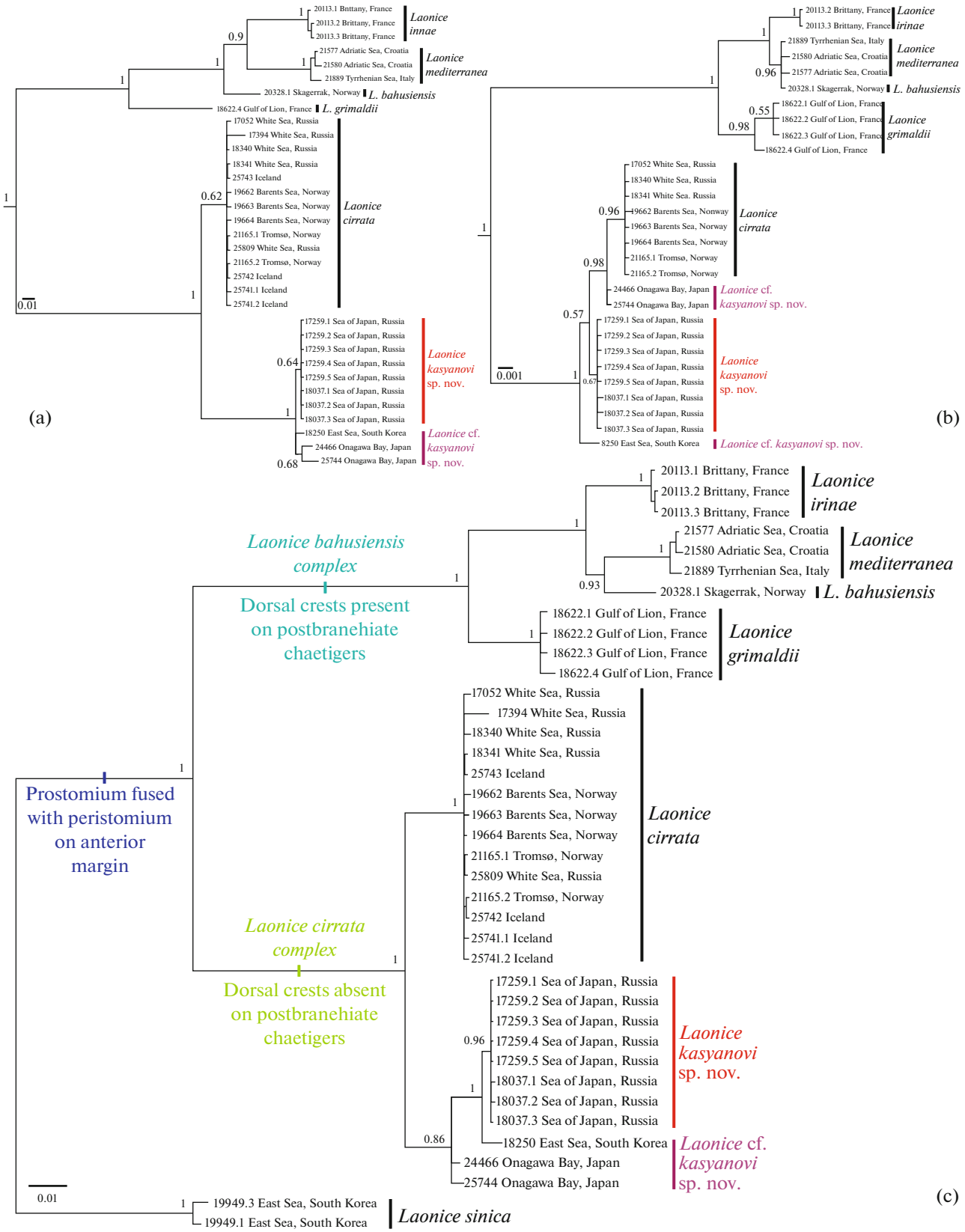
Morphometric Analysis

Relationships between various morphometric variables have been used to distinguish *Laonice* species [16, 30]. Dependant variables include the length of the nuchal organs (NO), the arrangement of branchiae (Br), the first occurrence of lateral pouches (LP), sabre chaetae (SC), and hooded hooks (HH), and arithmetic differences between them, e.g. the last branchiate chaetiger minus the caruncle length (Br-NO). Variables are expressed as the number of the chaetiger to which the NO extend, or the number of the chaetiger where the LP, SC or HH start. The first appearance of LP, SC, and HH, as well as the chaetiger having the last branchiae, is not always simultaneous on both sides of the same chaetiger, so we always used the first (LP, SC, and HH) and last (Br) chaetiger bearing the structure on at least one side. Statements such as "lateral interneuropodial pouches starting from chaetiger 10" mean that the first pouch (or pair of pouches) occurs between the neuropodia of chaetigers 10 and 11. Because *Laonice* worms are often fragmented in samples, the body width has usually been used as an independent variable to estimate the relationships between variables. In our study, only complete individuals were included in the analysis and the total number of chaetigers was used as an independent variable. Correlation coefficients (r) between variables were calculated and relationships were plotted as graphs using Statistica 6.0 software. Normal fit lines on the plots were calculated using the second (quadratic) order of the polynomial fitting function.

DNA Extraction, Amplification, and Sequencing

We used the ReliaPrep gDNA Tissue Miniprep System (Promega Corporation, Madison, WI, USA) for DNA extraction and purification with standard protocol for animal tissue. Polymerase chain reaction (PCR) amplification of nuclear *18S* rDNA, D1 region of *28S* rDNA and *Histone 3*, and mitochondrial *COI* and *16S* rDNA gene fragments was accomplished with the primers and conditions described by Radashevsky et al. [2, 4, 31]. Purified PCR products were sequenced in both directions on an ABI Prism 3500 Genetic Analyzer (Applied Biosystems) using the BrilliantDye Terminator v1.1 Cycle Sequencing Kit (NimaGen) and the same primers as for PCR. We also obtained additional sequences of some genes from specimens that we previously only sequenced for COI [16]. Sequence editing and contig assembly were performed using SeqScape 2.5 (Applied Biosystems).

Fig. 1. Majority rule consensus trees of the Bayesian inference analyses of the combined gene sequences of *Laonice* spp. rooted with sequences of *Laonice sinica*. (a) based on mitochondrial genes *COI* (582 bp) and *16S* rDNA (292 bp). (b) based on nuclear genes *18S* (1690 bp), *28S* (261 bp) and *Histone 3* (320 bp). (c) based on mitochondrial + nuclear genes (3145 bp in total). Posterior probabilities are shown on the branches. The numbers preceding collecting locations are unique numbers from the VIR database linking the individuals on the tree with the sampling data in Supplementary Tables ESM1–ESM3; numbers of individuals are separated from sample numbers by dots. Characters shared by adult worms are marked on the roots of branches.


(a)
20113.1 Bnttany, France
20113.2 Brittany, France
20113.3 Brittany, France
Laonice innae
21577 Adriatic Sea, Croatia
21580 Adriatic Sea, Croatia
21889 Tyrrhenian Sea, Italy
Laonice mediterranea
20328.1 Skagerrak, Norway
L. bahusiensis
18622.4 Gulf of Lion, France
L. grimaldii
17052 White Sea, Russia
17394 White Sea, Russia
18340 White Sea, Russia
18341 White Sea, Russia
25743 Iceland
19662 Barents Sea, Norway
19663 Barents Sea, Norway
19664 Barents Sea, Norway
21165.1 Tromsø, Norway
25809 White Sea, Russia
21165.2 Tromsø, Norway
25742 Iceland
25741.1 Iceland
25741.2 Iceland
Laonice cirrata
0.01
17259.1 Sea of Japan, Russia
17259.2 Sea of Japan, Russia
17259.3 Sea of Japan, Russia
17259.4 Sea of Japan, Russia
17259.5 Sea of Japan, Russia
18037.1 Sea of Japan, Russia
18037.2 Sea of Japan, Russia
18037.3 Sea of Japan, Russia
Laonice kasyanovi sp. nov.
18250 East Sea, South Korea
24466 Onagawa Bay, Japan
25744 Onagawa Bay, Japan
Laonice cf. kasyanovi sp. nov.
(b)
20113.2 Brittany, France
20113.3 Brittany, France
Laonice irinae
21889 Tyrrhenian Sea, Italy
21580 Adriatic Sea, Croatia
21577 Adriatic Sea, Croatia
20328.1 Skagerrak, Norway
L. bahusiensis
18622.1 Gulf of Lion, France
18622.2 Gulf of Lion, France
18622.3 Gulf of Lion, France
Laonice grimaldii
18622.4 Gulf of Lion, France
17052 White Sea, Russia
18340 White Sea, Russia
18341 White Sea. Russia
19662 Barents Sea, Nonway
19663 Barents Sea, Norway
19664 Barents Sea, Norway
21165.1 Tromsø, Norway
21165.2 Tromsø, Norway
Laonice cirrata
24466 Onagawa Bay, Japan
25744 Onagawa Bay, Japan
Laonice cf. kasyanovi sp. nov.
0.001
17259.1 Sea of Japan, Russia
17259.2 Sea of Japan, Russia
17259.3 Sea of Japan, Russia
17259.4 Sea of Japan, Russia
17259.5 Sea of Japan, Russia
18037.1 Sea of Japan, Russia
18037.2 Sea of Japan, Russia
18037.3 Sea of Japan, Russia
Laonice kasyanovi sp. nov.
8250 East Sea, South Korea
Laonice cf. kasyanovi sp. nov.
Laonice bahusiensis complex
Dorsal crests present on postbranehiate chaetigers
Prostomium fused with peristomium on anterior margin
Laonice cirrata complex
Dorsal crests absent on postbranehiate chaetigers
(c)
20113.1 Brittany, France
20113.2 Brittany, France
20113.3 Brittany, France
Laonice irinae
21577 Adriatic Sea, Croatia
21580 Adriatic Sea, Croatia
21889 Tyrrhenian Sea, Italy
Laonice mediterranea
20328.1 Skagerrak, Norway
L. bahusiensis
18622.1 Gulf of Lion, France
18622.2 Gulf of Lion, France
18622.3 Gulf of Lion, France
18622.4 Gulf of Lion, France
Laonice grimaldii
17052 White Sea, Russia
17394 White Sea, Russia
18340 White Sea, Russia
18341 White Sea, Russia
25743 Iceland
19662 Barents Sea, Norway
19663 Barents Sea, Norway
19664 Barents Sea, Norway
21165.1 Tromsø, Norway
25809 White Sea, Russia
21165.2 Tromsø, Norway
25742 Iceland
25741.1 Iceland
25741.2 Iceland
Laonice cirrata
17259.1 Sea of Japan, Russia
17259.2 Sea of Japan, Russia
17259.3 Sea of Japan, Russia
17259.4 Sea of Japan, Russia
17259.5 Sea of Japan, Russia
18037.1 Sea of Japan, Russia
18037.2 Sea of Japan, Russia
18037.3 Sea of Japan, Russia
Laonice kasyanovi sp. nov.
18250 East Sea, South Korea
24466 Onagawa Bay, Japan
25744 Onagawa Bay, Japan
Laonice cf. kasyanovi sp. nov.
0.01
19949.3 East Sea, South Korea
19949.1 East Sea, South Korea
Laonice sinica

GenBank accession numbers of the sequences used in the present analysis are shown in Table 1 and Supplementary Table ESM6.

Data Analysis

We aligned the DNA sequences using the ClustalW method implemented in the MEGA11 software [32]. Complete aligned data sets, without gaps, were used for the comparison of worms identified by morphology as *L. cirrata*. For the analysis of phylogenetic relationships between *Laonice* species, ambiguous positions and gaps were excluded using GBlocks [33]. The nucleotide datasets were combined using SequenceMatrix [34]. Of the 38 individual concatenated sequences used in the present analysis, 6 sequences comprised fragments of one gene, 6 sequences comprised fragments of two genes, 6 sequences comprised fragments of three genes, 5 sequences comprised fragments of four genes, and 15 sequences comprised fragments of five genes. The number of variable and parsimony informative sites in the datasets, and uncorrected values of sequence divergence (pairwise distances, *p*) both within and between groups were calculated in MEGA11 software. We used MrBayes 3.2.6 via the CIPRES web portal [35] for the Bayesian analysis of 10000000 generations, four parallel chains and sample frequencies set to 500, in two separate runs. Based on the convergence of likelihood scores, 25% sampled trees were discarded statistically as burn-in. Analysis of the combined data set was partitioned and the models of substitution were determined using Akaike Information Criterion (AIC) in Modeltest 3.7 [36]: GTR + G was used for *16S*, HKY + G for *COI*, HKY + I for *18S*, TrN for *28S*, and F81 + I for *Histone 3*.

In our analysis, we also included *Laonice* sequences obtained in our previous study [16] and also provided by other authors. Brief information about these sequences and corresponding samples is presented in Table 1 and Supplementary Table ESM6; complete data are presented in Supplementary Table ESM4.

We performed three analyses: 1) based on mitochondrial genes *COI* and *16S* rDNA, 2) based on nuclear genes *18S*, *28S* and *Histone 3* and 3) based on mitochondrial + nuclear genes. The first two analyses were designed to compare the incongruence between mitochondrial and nuclear data sets. The latter analysis was intended to generate a hypothesis about the phylogenetic relationships of the *Laonice* species. Phylogenetic trees were rooted using sequences of *Laonice sinica* Sikorski & Wu, 1998 according to our preliminary phylogenetic analysis of molecular data of Spionidae, where this species was found to be the most basal among *Laonice*.

RESULTS

Molecular Analysis

The combined aligned sequences of *Laonice* spp., with gaps excluded, comprised in total 3145 bp, including 582 bp for *COI* (100% of original aligned sequences), 292 bp (94.8%) for *16S* rDNA, 1690 bp (98.4%) for *18S* rDNA, 261 bp (100%) for *28S* rDNA, and 320 bp (100%) for *Histone 3*. The combined concatenated dataset contained 417 variable sites, 378 of which were parsimony-informative. The frequency of variable sites in the aligned sequences was 33.5% for *COI*, 31.8% for *16S* rDNA, 5.3% for *18S* rDNA, 5.4% for *28S* rDNA, and 8.1% for *Histone 3*. The average *p*-distances for the individual gene fragments between the groups of samples are given in Supplementary Table ESM7.

Comparison of the obtained sequences showed high genetic similarity (p = 0–1.32%, average p = 0.29% for *16S* rDNA; p = 0–1.04%, average p = 0.6% for *COI*) of the worms identified by morphology as *L. cirrata* from the Norwegian, Barents, and White Seas and off Iceland. The *18S* rDNA, *28S* rDNA and *Histone 3* sequences of these worms were identical, except for one *18S* rDNA sequence from the Barents Sea, which differed from the others by one base substitution. The three detected *16S* rDNA haplotypes differed from each other by one to four base substitutions, and one of these haplotypes was present in worms from all localities. The seven detected *COI* haplotypes differed from each other by one to five base substitutions, with one of these haplotypes present in worms from Norway and Iceland. Therefore, the examined worms from all these localities are considered conspecific and referred to *L. cirrata*.

The *16S* rDNA, *18S* rDNA, *28S* rDNA, and *Histone 3* sequences of worms from Russia (the Sea of Japan), identified by morphology as *L. cirrata*, were invariable, while the uncorrected *p*-distance value for *COI* sequences was maximum 0.34% and average 0.11%. The maximum *p*-distance values between sequences of worms from Russia and the only one studied individual from South Korea were 3.09% (18 variable sites) for *COI*, 1.53% (4 variable sites) for *28S* rDNA, and 0.31% (1 variable site) for *Histone 3*. The maximum *p*-distance values between sequences of worms from Russia and two analyzed individuals from Japan were 0.12% (2 variable sites) for *18S* rDNA and 1.37% (5 variable sites) for *16S* rDNA. Four *COI* haplotypes and four *16S* rDNA haplotypes were detected in worms from the Northwest Pacific (Japan, Russia and South Korea), but none of them was common for individuals from different localities. It is noteworthy that, when analyzing only nuclear genes, specimens from Japan (sequenced for *18S* rDNA only) were grouped with *L. cirrata* from Norway (Fig. 1b). Moreover, this analysis placed the single examined specimen from South Korea at the base of a clade

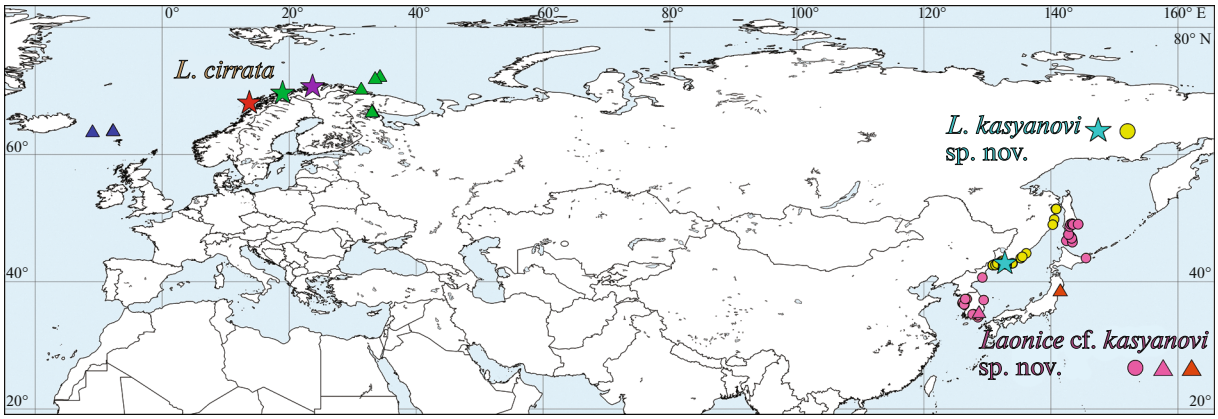


Fig. 2. Map showing localities in the Norwegian Sea (Norway) where M. Sars collected specimens to describe *Laonice cirrata*: (red star) Ure in Lofoten (type locality of *L. cirrata*), (green star) Tromso, (magenta star) Hammerfest. (turquoise star) Type locality of *Laonice kasyanovi* sp. nov. (Vostok Bay, Sea of Japan, Russia), from where specimens were sequenced in the present study. Triangles showing localities where specimens were collected for sequencing: (green and pink) sequenced in the present study; (blue) sequenced by Bogantes et al. [14]; (orange) sequenced by Abe and Sato-Okoshi [66]. Yellow and pink circles showing sampling sites where specimens were identified by morphology only.

including *L. cirrata* and similar worms from the Northwest Pacific (Fig. 1b).

The five-gene analysis revealed two clades among worms identified by morphology as *L. cirrata*: one clade including worms from the Northeast Atlantic (Norwegian, Barents, White Seas and off Iceland) and another clade including worms from the Northwest Pacific (Japan, Korea and Russia) (Fig. 1c). Worms in these clades differed by 92 variable sites in *COI* (582 bp), 19 sites in *16S* rDNA (302 bp), 5 sites in *18S* rDNA (1707 bp), 4 sites in *28S* rDNA (261 bp) and 4 sites in *Histone 3* (320 bp) data sets. The uncorrected *p*-distance values between sequences in these clades ranged from 0.06 to 0.24% for *18S* rDNA, from 0.94 to 1.25% for *Histone 3,* from 2.98 to 5.3% for *16S* rDNA, and from 12.98 to 14.36% for *COI*. The *28S* rDNA sequences were identical in specimens from the Norwegian Sea (Norway), White Sea (Russia) and the Sea of Japan (Russia) and differed from the single sequence from South Korea by four base substitutions ($p = 1.53\%$). The uncorrected pairwise average *p*-distance values between sequences in these clades are shown in Table ESM7.

The phylogenetic analysis of the obtained sequences revealed genetic differences between worms from the Northeast Atlantic and worms from the Sea of Japan (Russia) earlier identified by morphology as *L. cirrata*. Therefore, we consider these worms to be non-conspecific and assign the latter group to the new species *Laonice kasyanovi* sp. nov. The only studied individual from South Korea and two sequenced specimens from Japan are here referred to as *Laonice* cf. *kasyanovi* sp. nov. The final decision on the systematic position of the Japanese and Korean populations should be based on the analysis of more individuals and more genetic data.

Morphology and Systematics

Laonice cirrata (M. Sars, 1851) Fig. 3

Nerine cirrata M. Sars [8]: 207–208.

Laonice cirrata: Söderström [9]: 4, 5, 7, 81, 97, 98, 110, 220–223, Figs. 77, 128. Derjugin [37]: 240. Sikorski [38] (*Part.*): 293–295, text Figs. 1–7; [17] (*Part.*): 408–413, Figs. 1, 2; [18] (*Part.*): 326–332, Figs. 2C, 4A, B, 5C, D, 6G, 7A–G; [39] (*Part.*): 1187–1188, figs. 2b, 4a; [40] (*Part.*): 207, Fig. 1A.

Aonides paucibranchiata: ?Hannerz [41]: 30–32, Fig. 8. ?Cazaux [42]: 205–207, pl. 67: Figs. 1–3. Lebsky [43]: 93–96, Figs. 2–4. Not Southern [44].

Synopsis. Adults up to 126 mm long, 2.6 mm wide for 161 chaetigers. Prostomium anteriorly rounded, fused with peristomium. Caruncle extending to end of chaetiger 40, shorter in small individuals. Nuchal organs U-shaped, on sides of caruncle. Occipital antenna present. One pair of small lateral eyes and one pair of large median eyes present. Chaetiger 1 with capillaries and postchaetal lamellae in both rami. Capillaries in anterior parapodia in two vertical rows. Sabre chaetae in neuropodia from chaetigers 10–30. Hooded hooks in neuropodia from chaetigers 17–55, absent in notopodia; hooks tridentate, with two small upper teeth situated side by side above main fang. Branchiae from chaetiger 2, up to 46 pairs, free from notopodial postchaetal lamellae, with ciliation on inner and outer edges. Dorsal crests absent. Lateral interneuropodial pouches from chaetigers 8–50. Pygidium with one pair of short and thick ventral cirri and up to seven pairs of longer and thinner dorsal cirri. Digestive tract without gizzard-like structure. Dioecious. Spermatids in tetrads. Spermatozoa short-head aquasperm. Oocytes with thick honeycombed envelope ornamented with two circles of vesicles (cortical

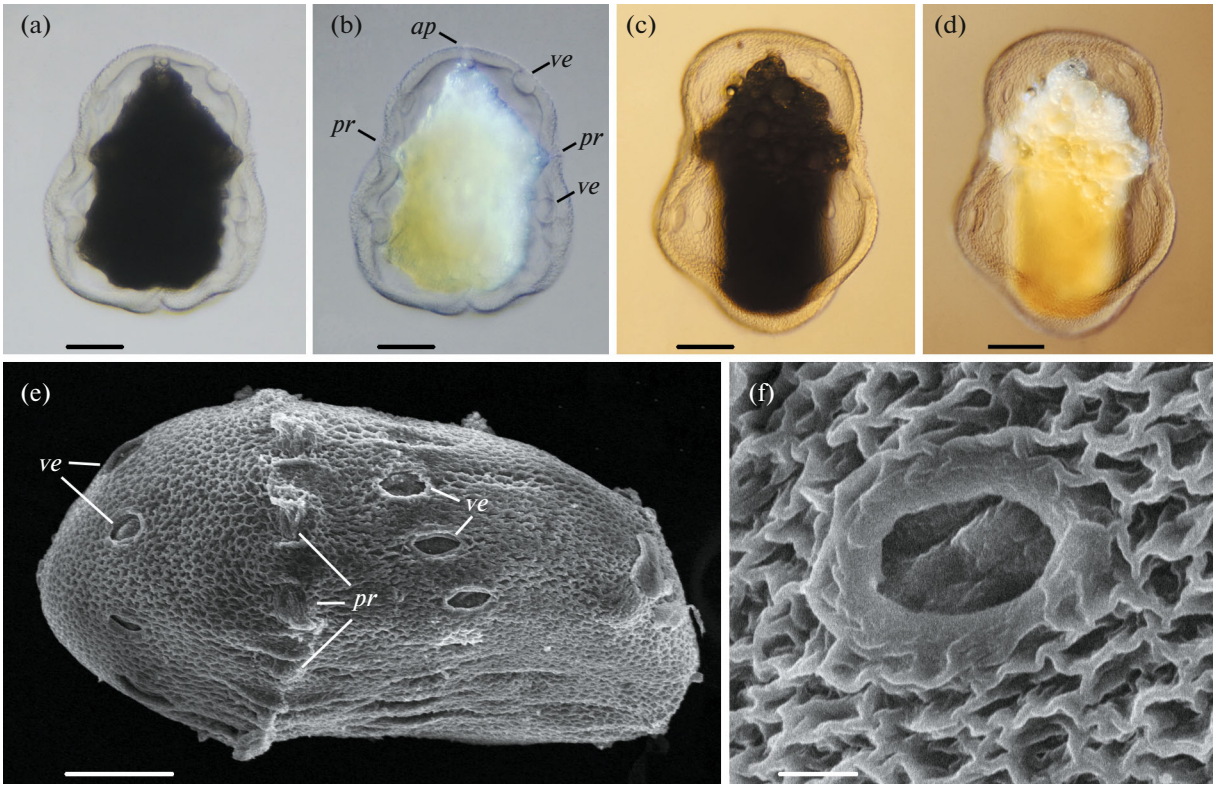


Fig. 3. Larval morphology of *Laonice cirrata* from the White Sea, Russia. (a) Trochophore in transmitted light. (b) The same in reflected light, showing two circles of large subspherical vesicles in thick egg envelope. (c) Advanced trochophore in transmitted light. (d) the same in reflected light. (e) Trochophore. (f) Fragment of trochophore showing honeycombed egg envelope with a vesicle. Abbreviations: *ap*, apical tuft of cilia; *pr*, prototroch; *ve*, vesicles of egg membrane. Scale bars: (a–d) 100, (e) 50, and (f) 5 μm. Larva (a, b) collected in September 2019; larvae (c, d, e) collected on September 8, 2016. Larva (c, d) sequenced for *COI* in the present study (VIR ID 25809). (a–d) Alive, (e, f) SEM.

alveoli). Larval development entirely pelagic, planktotrophic.

Remarks on the type material. The above synopsis is based on specimens from the shallow waters of the Northeast Atlantic and the adjacent Arctic, including the Norwegian and Barents Seas and the waters around Iceland and Greenland.

In the original description of *N. cirrata* Sars [8] (p. 208) noted that the worms were "distributed between boulders in Ure in Lofoten, Tromsö and Hammerfæst in 20–30 fathoms depth, in sand and clay sediments" (see Fig. 2). Söderström [9] was the first to revise the morphology and taxonomy of this species. Söderström ([9]: 221) noted that "With the exception of Hammerfest ... specimens from these localities are preserved in the Kristiania [Oslo] Museum." Later, when the type specimens were thought to be lost, Sikorski [18] incorrectly (see ICZN [45]: Article 73.2.3) suggested Hammerfest to be the type locality of *N. cirrata*. However, when two type specimens from Ure in Lofoten were found, Sikorski [40] designated one of them as the lectotype (UOZM C5232), and designated Ure in Lofoten as the type locality of *N. cirrata* (Fig. 2). Among the paralectotypes, Sikorski [40] noted one specimen from Ure I Lofoten (UOZM C5233), one specimen from Tromsø (UOZM C5234), and two specimens from Vadsø (UOZM C5235). However, specimens from the latter locality cannot be considered paralectotypes of *N. cirrata* because Vadsø was not noted in the original description of this species.

Remarks on the larval development. Hannerz [41] described and illustrated an egg and pelagic larvae with 14 and 15 chaetigers which he collected in the Gullmar Fjord (Sweden) and identified as *L. cirrata*. This was considered the most detailed description of larval morphology of this species which was used to infer phylogenetic relationships between spionids [46]. However, Hannerz [41]: 25 noted that "it has not been possible to get this larva to metamorphose" and "No other larva, which can reasonably be classified under *Laonice*, has been encountered during the course of investigation." He also noted that "*Laonice cirrata* (Sars) has been divided by Söderström (1920) into four species, viz.: *L. bahusiensis*, *L. appelöfi*, *L. sarsi*, and *L. cirrata* s.str. Later investigators have, however, been unable to find any justification for such a division (Fauvel 1927). Since I have found only one larval type

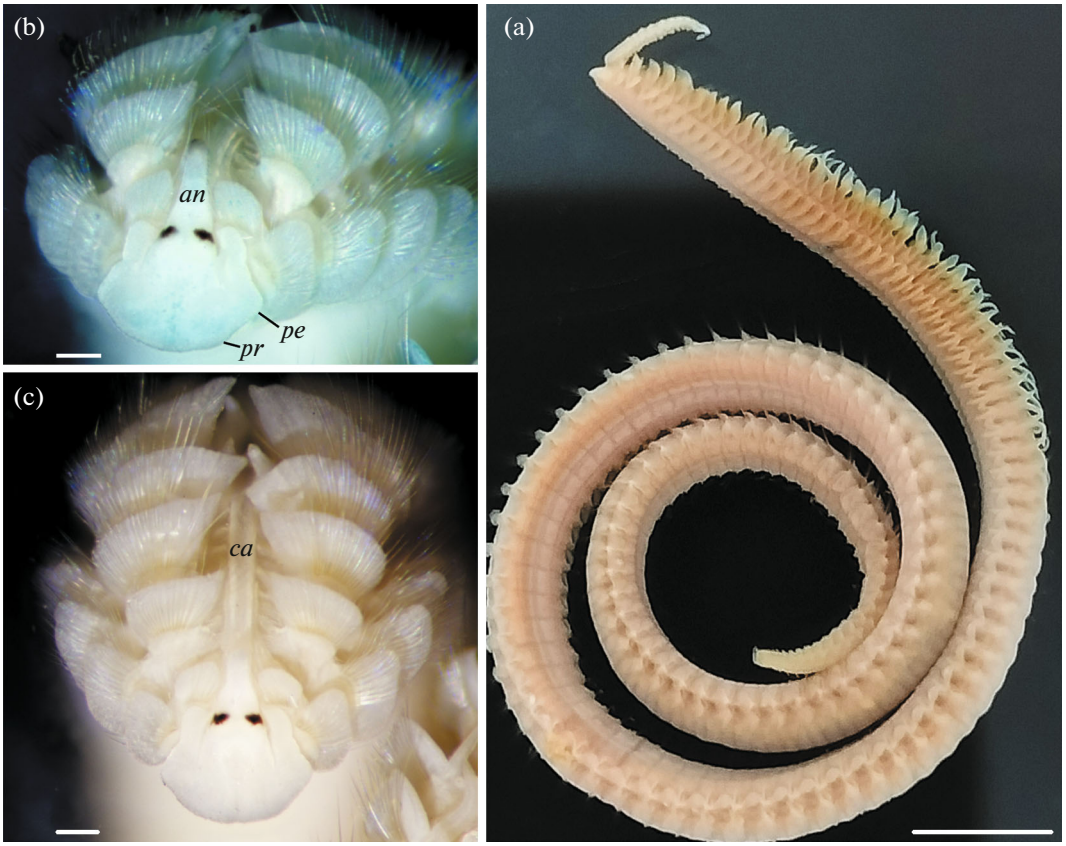


Fig. 4. Adult morphology of *Laonice kasyanovi* sp. nov. from the Sea of Japan, Russia (formalin-fixed type specimens). (a) Holotype, left lateral view. (b) Anterior end, frontal view, palps missing, stained with methylene green. (c) The same, plain. Abbreviations: *an*, occipital antenna; *ca*, caruncle; *pe*, peristomium; *pr*, prostomium. Scale bars: (a) 5, (b, c) 200 μm. (a) Holotype MIMB 42765; (b, c) paratype MIMB 42757.

which can be referred to this species, I feel obliged to describe it under *L. cirrata* (Sars)." It is worth noting that all the species distinguished and named by Söderström [9] are currently considered valid. Thus, both the specific and generic identifications of the *Laonice* larvae by Hannerz [41] were preliminary and hypothetical.

Lebsky [43] described the development of a polychaete species based on eggs and larvae collected from plankton in the White Sea from September 14 to October 26, 1965 and grown in the laboratory. He succeeded in getting these larvae to settle and metamorphose, and he identified them as *Aonides paucibranchiata* Southern, 1914, although he noted that adults of this species had never been recorded in the White Sea. *Aonides* from the White Sea are still unknown [47] and are probably absent there, at least in the northwestern part of the sea, where Lebsky collected his material. The description and illustrations of *A. paucibranchiata* larvae by Lebsky [43] are fully consistent with the larvae collected, sequenced, and identified as *Laonice cirrata* in the present study (Fig. 3). We therefore conclude that Lebsky [43] clearly dealt with this species. Although not mentioned by him, it is likely that Lebsky was influenced by the descriptions of *A. paucibranchiata* larvae from Gullmar Fjord provided by Hannerz [41] and from Arcachon (Bay of Biscay, Atlantic France) provided by Cazaux [42], as well as larvae of *Aonides oxycephala* (Sars, 1862) provided by Hannerz [41] and Sveshnikov [48]. All these descriptions were based on larvae collected from plankton, and some of them underwent metamorphosis. Planktonic eggs and early larval stages have been described as having a thick honeycombed envelope and two circles of cortical alveoli, and these characters were thought to be unique for *Aonides*. However, coelomic oocytes with the same envelope have been described in *Laonice branchiata* Nonato, Bolívar & Lana, 1986 [12] and *Laonice irinae* Sikorski, Radashevsky & Nygren, 2021 [16]. Thus, it remains unknown whether *Aonides* and *Laonice* have eggs and larvae of similar morphology or whether all previous descriptions of *Aonides* are from *Laonice*.

The eggs described by Lebsky [43] for "*A. paucibranchiata*" each had a thick honeycombed envelope 536–604 μm in diameter with two circles of subspherical vesicles. The upper circle (later in larvae located above the prototroch) consisted of eight vesicles 42 ×

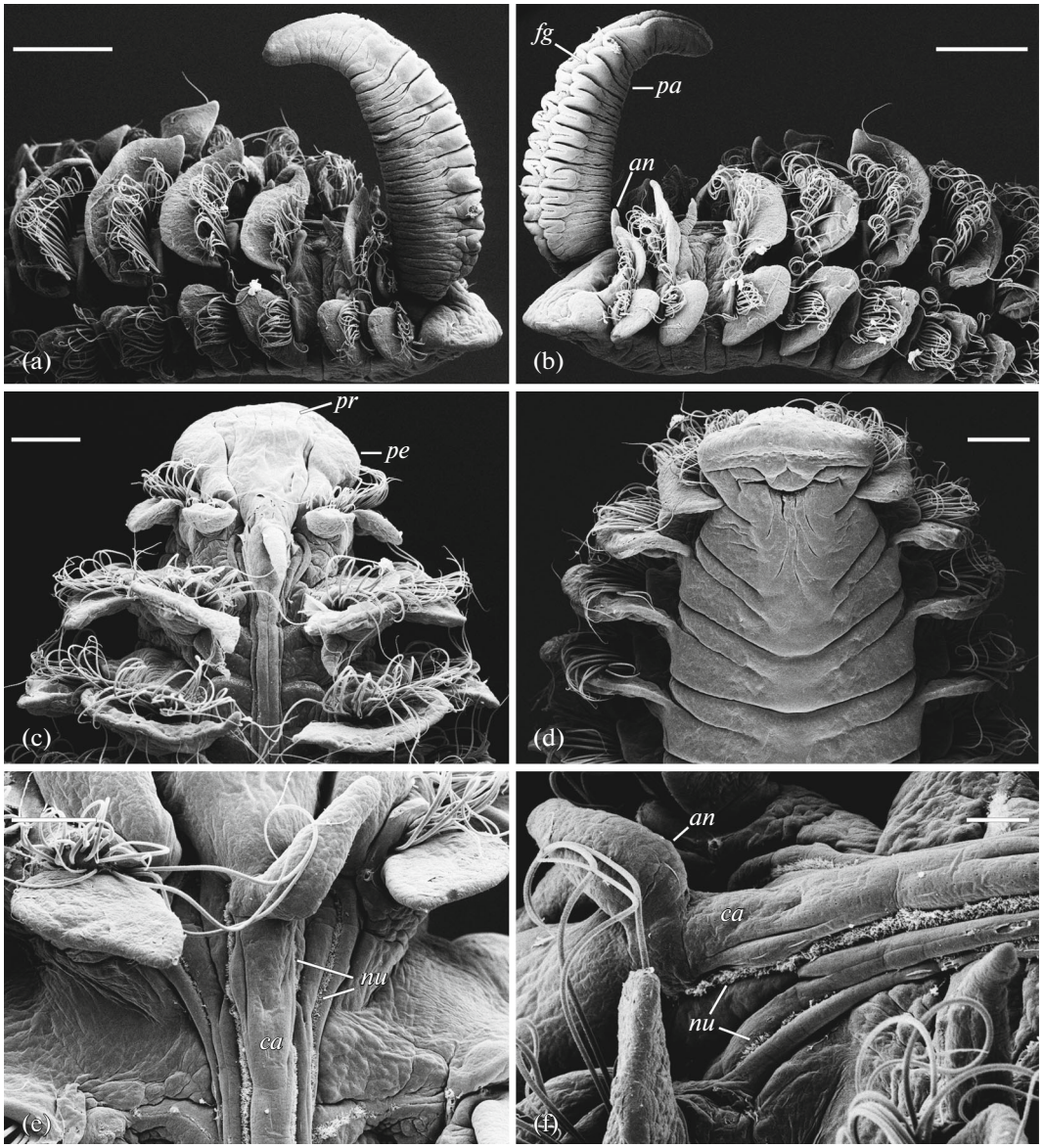


Fig. 5. Adult morphology of *Laonice kasyanovi* sp. nov. from the Sea of Japan, Russia (USNM 1022164, SEM). (a) Anterior end, right lateral view, left palp missing. (b) The same, left lateral view. (c) Anterior end, dorsal view, palps missing. (d) The same, ventral view. (e) Chaetiger 1, dorsal view, showing occipital antenna and nuchal organs ciliation. (f) The same, left lateral view. Abbreviations: *an*, occipital antenna; *ca*, caruncle; *fg*, frontal ciliated groove on palp; *nu*, nuchal organ ciliation; *pa*, palp; *pe*, peristomium; *pr*, prostomium. Scale bars: (a–e) 500, (f) 200 μm.

42 μm in diameter each, and the lower circle (later in larvae located below the prototroch) consisted of 13 vesicles 52 × 42 μm in diameter each ([43]: Fig. 2). Early embryos with a diameter of 300–400 μm were situated in the center, well separated from the egg envelope. Trochophores had a long tuft of apical cilia and a well developed prototroch whose cilia originated from 14 processes of the body and penetrated through the egg envelope. After about a week of development, two pairs of small red eyes and a telotroch appeared. Developed 10–12-chaetiger larvae reached a length of 950 μm. They had nototrochs from chaetiger 1, gastrotrochs from chaetiger 2, tridentate hooded hooks in neuropodia, short palps, and pygidial cirri. They shed out long serrated provisional bristles from notopodia and settled to the bottom to begin their adult life. Trochophores collected in the White Sea in September 2016 and 2019 and sequenced in the present study (Fig. 3) had the same features as those described by Lebsky [43].

Laonice kasyanovi Radashevsky & Sikorski sp. nov.

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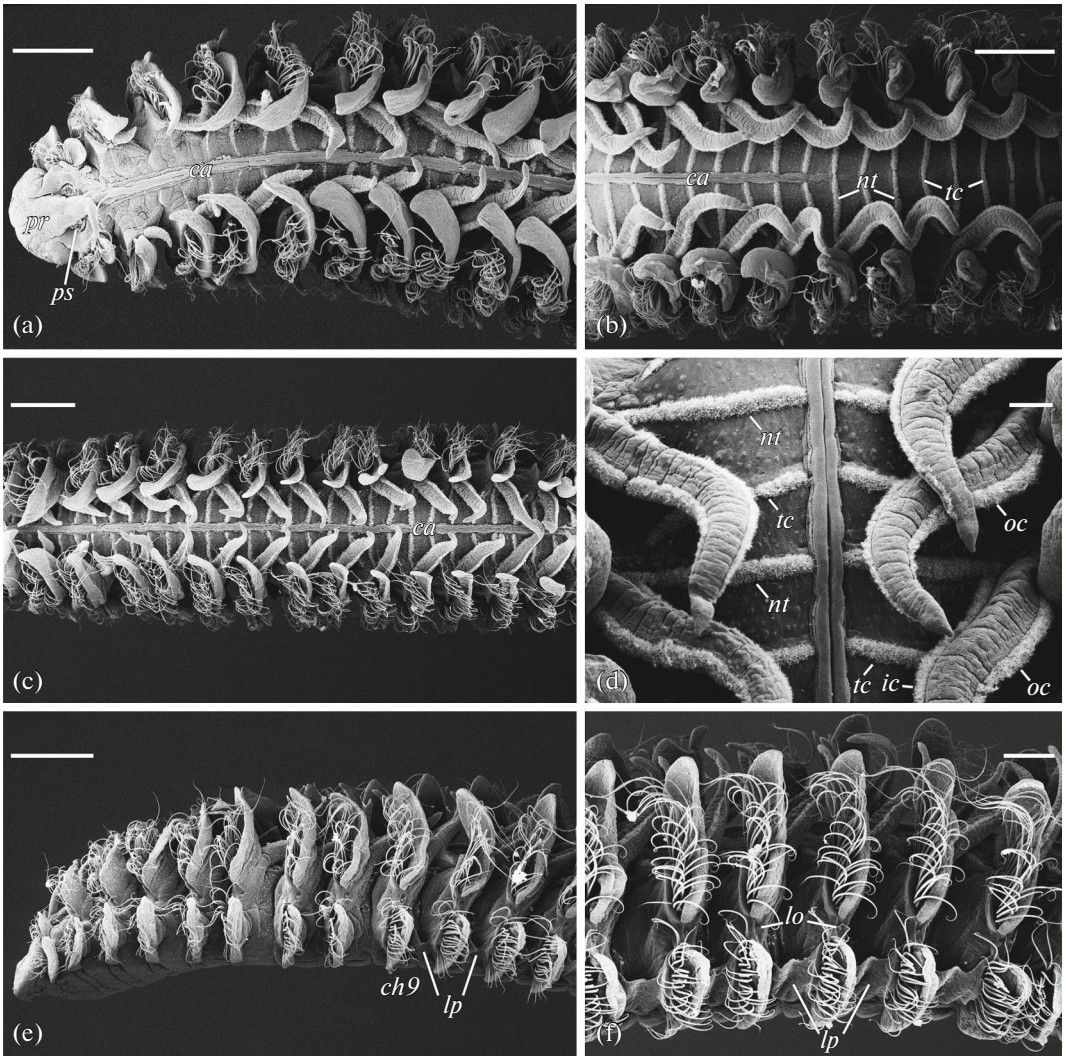

Fig. 6. Adult morphology of *Laonice kasyanovi* sp. nov. from the Sea of Japan, Russia (USNM 1022164, SEM). (a) Anterior end, dorsal view, palps missing. (b) Middle chaetigers, dorsal view, showing posterior part of caruncle and ciliation on chaetigers. (c, d) Anterior chaetigers, dorsal view, showing middle part of caruncle. (e) Anterior end, left lateral view, showing start of lateral pouches from chaetiger 9, palps missing. (f) Middle chaetigers, left lateral view, showing lateral pouches between neuropodia of adjacent chaetigers. All images oriented showing anterior end of body on left, except for (d), showing anterior end of body at top. Abbreviations: *ca*, caruncle; *ch9*, chaetiger 9; *ic*, inner branchial ciliation; *lo*, lateral sensory ciliated organs; *lp*, lateral interneuropodial pouches; *nt*, nototrochs; *oc*, outer branchial ciliation; *pr*, prostomium; *ps*, palp scarf; *tc*, intersegmental transverse ciliation. Scale bars: (a–c, e) 500, (d) 100, and (f) 200 μm.

Figs. 4–7

Laonice cirrata: Zachs [20] (*Part.*): 129. Annenkova [49] (*Part.*): 169; [50] (*Part.*): 172. Uschakov [51] (*Part.*): 265. Stschapova et al. [52]: 79. Buzhinskaja [53] (*Part.*): 102–103; [54] (*Part.*): 126; [55]: 22. Koblikov [56]: 39. Lee [24]: 226; [25]: 60. Ozolinsh [57]: 82. Imajima [58]: 129. Bagaveeva and Zvyagintsev [59]: 48. Ozolinsh and Bagaveeva [60]: 139. Ozolinsh and Kepel [61]: 558, 561, 563, 565, 567, 569. Belan and Belan [62]: 650. Ryu et al. [63]: 725. Khim et al. [64]: S53. Not M. Sars [8].

Laonice sp.: Buzhinskaja and Britayev [65]: 85.

?*Laonice* sp. 1: Abe and Sato-Okoshi [66]: 24–25, Fig. 4D.

?*Aonides oxycephala oligobranchia*: Sveshnikov [48]:145–146, Fig. 4.

Etymology. The species is named in honor of the late academician Vladimir Leonidovich Kasyanov, one of the founders and the second director of the Institute of Marine Biology, Vladivostok, Russia, founder of the Institute's Laboratory of embryology, and a biologist, colleague and a great man.

Type material. **Russia**, Sea of Japan, Vostok Bay of Peter the Great Bay: 42.8925°N, 132.735°E, 9 m, coll. Radashevsky, V.I., 29 May 1991, MIMB 42765 (holo-

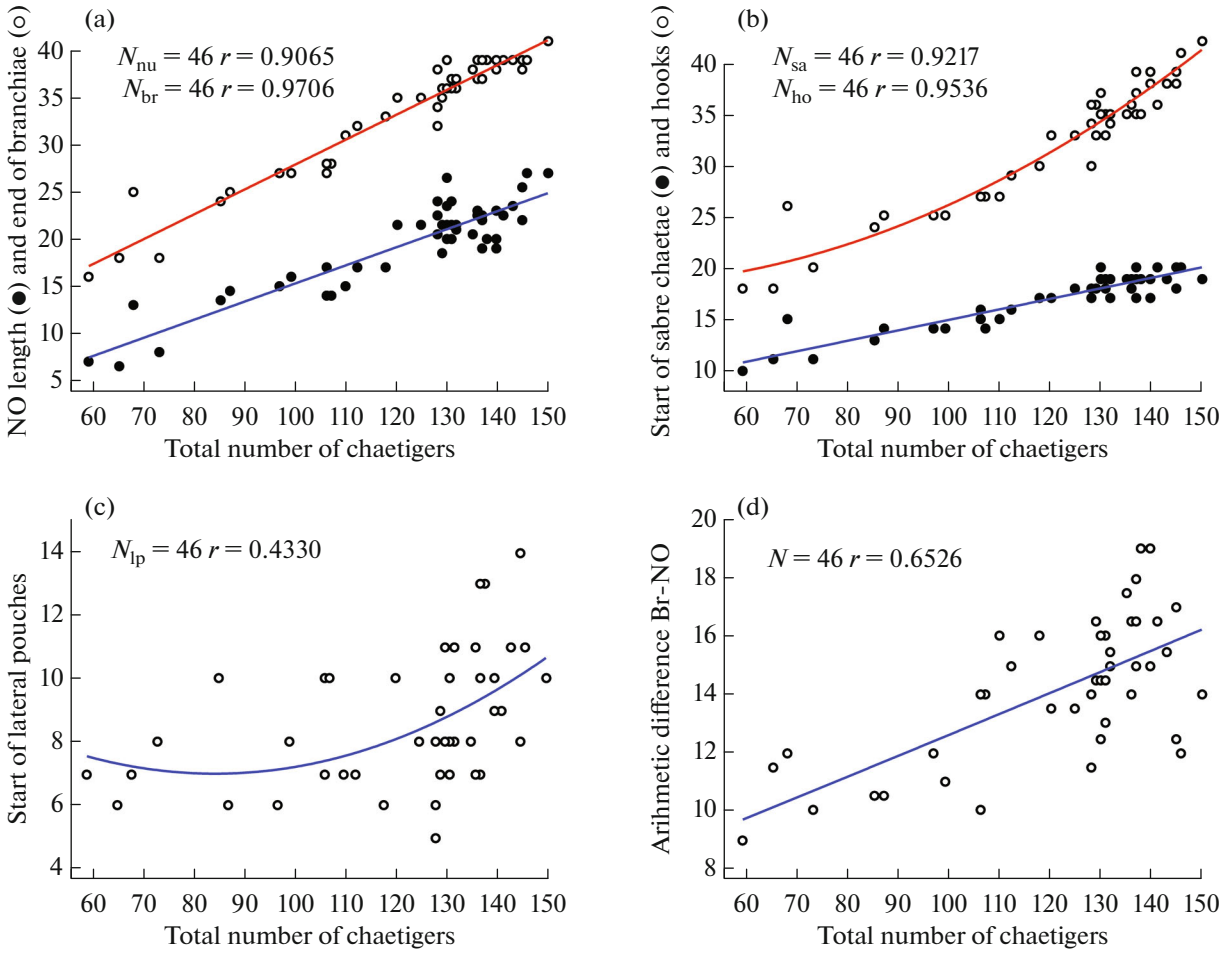

Fig. 7. Adult characteristics of *Laonice kasyanovi* sp. nov. (a) Relationships between length of nuchal organs (NO, in chaetiger numbers) and total number of chaetigers (filled circles), and between distribution of branchiae (referring to number of the last branchiate chaetiger) and total number of chaetigers (empty circles). (b) Relationships between anterior position of sabre chaetae (referring to number of the first sabre-bearing chaetiger) and total number of chaetigers (filled circles), and between anterior position of hooks (referring to the number of the first hook-bearing chaetiger) and total number of chaetigers (empty circles). (c) Relationships between anterior position of lateral interneuropodial pouches (referring to the number of the chaetiger in front of the first pouch) and total number of chaetigers. (d) Relationships between the arithmetic difference between number of last branchiate chaetiger and length of nuchal organs (in chaetiger number) (Br-NO) and total number of chaetigers. Correlation coefficients (r) are presented in the graphs. All correlations are significant ($P < 0.05$).

type); MIMB 12379, 14072–14075, 42756–42764, 42766–42783 (271 paratypes); SMF 13907 (3 paratypes), 13936 (1 paratype); USNM 172571 (8 paratypes), 183517 (9 paratypes), 183518 (1 paratype), 1022164 (10 paratypes); ZISP 49163–49168, 49172 (9 paratypes).

Adult morphology (based on material from Peter the Great Bay, Sea of Japan, Russia). Holotype largest individual, about 130 mm long, 2.5 mm wide for 150 chaetigers (Fig. 4a). Pigmentation on body and palps absent. Prostomium anteriorly broadly rounded, with frontal margin occasionally truncate to slightly concave, completely fused with fronto-lateral parts of peristomium (Figs. 4b, 4c and 5a–5d), posteriorly extending over 27 chaetigers (to end of chaetiger 27 in holotype) as a low narrow caruncle (Figs. 6a–6d), shorter in small individuals (Fig. 7a). Nuchal organs U-shaped ciliary bands on sides of caruncle (Figs. 5e and 5f). Length of nuchal organs was strongly correlated with total number of chaetigers (Fig. 7a, r = 0.9065). Occipital antenna long, cirriform, at level of chaetiger 1, up to twice longer than notopodial lamellae of chaetiger 1 (Figs. 4b, 5b, 5c, 5e and 5f). Two pairs of red eyes arranged trapezoidally to almost in a transverse line, comprising one pair of large median eyes and one pair of small lateral eyes situated below and set slightly wider apart. Median eyes transversally elongated (Figs. 4b and 4c); fine red pigment usually diffused in front of each eye. Lateral eyes usually deeply embedded inside epithelium and hardly discernible, especially in large individuals. Palps as long as 5–15 chaetigers, with deep frontal longitudinal groove lined with numerous short cilia (Figs. 5a and 5b).

Chaetiger 1 with well-developed capillary chaetae and small postchaetal lamellae in both rami; notopodial lamellae triangular; neuropodial lamellae rounded (Figs. 4b and 4c). All notopodia with capillary chaetae only. Low prechaetal lamellae present in noto- and neuropodia on anterior chaetigers after chaetiger 1. Notopodial postchaetal lamellae large, leaf-like on branchiate chaetigers, greatly diminishing in size on posterior abranchiate chaetigers; lamellae on anterior branchiate chaetigers with upper tips pointed (Figs. 4a–4c and 6a–6f). Neuropodial postchaetal lamellae ear-like on branchiate chaetigers, greatly diminishing in size on posterior abranchiate chaetigers.

Branchiae from chaetiger 2, up to 40 pairs (on chaetigers 2–41 in holotype); first pair slightly shorter than notopodial postchaetal lamellae of chaetiger 2; branchiae on chaetiger 3 almost as long as notopodial lamellae; from chaetigers 5–6, branchiae 1.5–2 times as long as notopodial postchaetal lamellae (Figs. 6a–6c), gradually diminishing in size on posterior branchiate chaetigers. Branchiae present on 9–19 chaetigers after end of nuchal organs (Figs. 6b, 7a and 7d) and up to four chaetigers after beginning of hooded hooks in neuropodia; in large individuals, branchiae and hooded hooks beginning from the same chaetiger or hooks beginning 1–2 chaetigers after last branchiate chaetiger. Branchiae free from lamellae, slightly flattened, with surfaces oriented perpendicular to body axis, with ciliation along inner and outer edges (Fig. 6d). Afferent and efferent branchial blood vessels forming a loop and interconnected by numerous circular capillaries giving branchiae annulate appearance. Individual number of branchiae strongly correlated with total number of chaetigers (Fig. 7a, $r = 0.9706$), and with length of nuchal organs ($r = 0.9256$).

Nototrochs and intersegmental ciliation present in immature individuals, females, and males. Nototrochs from chaetiger 2, each composed of one row of small cells with short cilia. On anterior chaetigers nototrochs interrupted by caruncle; on branchiate post-caruncle chaetigers nototrochs extending from tip of one branchia to tip of opposite branchia (Figs. 6a–6d); on posterior abranchiate chaetigers nototrochs extending onto inner edge of notopodial postchaetal lamellae. Short bands of intersegmental longitudinal cilia present on dorsolateral edges of chaetigers between notopodia, beginning from between chaetigers 2 and 3. Single transverse rows of cilia present on anterior edge of branchiate chaetigers beginning from chaetiger 4 (Fig. 6d).

Complete dorsal transverse crests between notopodial postchaetal lamellae absent, although lamellae on middle chaetigers slightly extending to middorsal line.

Lateral pouches between neuropodia from chaetigers 5–14 (from chaetiger 10 in holotype) to almost end of the body (Figs. 6e and 6f). Anterior start of pouches not correlated with total number of chaetigers (Fig. 7c, $r = 0.433$).

Sabre chaetae in neuropodia from chaetigers 10–20 (from chaetiger 19 in holotype), from more anterior chaetigers in small individuals (Fig. 7b), 1–5 in a tuft; chaetae up to three times longer than hooded hooks, with weak granulation on shaft. First appearance of sabre chaetae in neuropodia strongly correlated with total number of chaetigers (Fig. 7b, $r = 0.9217$).

Hooded hooks in neuropodia from chaetigers 15–42 (from chaetiger 42 in holotype), from more anterior chaetigers in small individuals (Fig. 7b), up to 15 in a series in middle chaetigers, up to 21 in a series in posterior chaetigers, fewer in small individuals, accompanied by inferior tuft of sabre chaetae and up to ten thin capillaries alternating with hooks in upper part of hook row. Alternating capillaries slightly longer than hooks. Hooks tridentate, with one pair of upper teeth situated side by side above main fang. First appearance of hooks in neuropodia strongly correlated with total number of chaetigers (Fig. 7b, $r = 0.9536$).

Pygidium with up to eight pairs of cirri arranged around terminal anus, comprising one pair of short ventral cirri and up to seven pairs (six pairs in holotype) of thinner and longer dorsal cirri; fewer cirri in small individuals.

Digestive tract without gizzard-like structure.

Nephridia from chaetiger 4 to chaetigers 16–36, present in all anterior sterile chaetigers except chaetigers 1–3, fewer in small individuals.

Reproduction. *Laonice kasyanovi* is dioecious. Gametes develop in both females and males from chaetigers 27–40 to chaetigers 105–130. Oogenesis is entirely intraovarian; vitellogenesis occurs when oocytes grow while attached to segmental blood vessels. Developed oocytes are about 250 μm in diameter, with thick honeycombed envelope ornamented with two circles of vesicles (cortical alveoli). Spermatogonia proliferate in the testes; spermatogenesis occurs in the coelomic cavity. Spermatids are joined in tetrads. Spermatozoa are ect-aquasperm with a small rounded acrosome, a spherical nucleus 3.5 ± 0.5 μm in diameter, spherical mitochondria, probably four in number and each one less than 1 μm in diameter, and a flagellum 76 ± 2 μm long.

Habitat. Adults of *L. kasyanovi* occur in sandy to silty sediments in coastal shallow waters. The worms crawl freely in sediment and ingest the surrounding sediment without sorting. The intestines of worms are usually tightly filled with sand grains of various sizes. The population density of the species in some places reaches tens of individuals per square meter.

Remarks. Greater variability than described above for shallow-water specimens from Peter the Great Bay was observed in individuals from deeper areas outside the Bay. These non-type specimens usually were broken; they reached 3 mm in width, but their maximum length and total number of chaetigers are unknown.

Their caruncle reached the end of chaetiger 35, branchiae were present until chaetiger 50, lateral pouches first appeared after chaetiger 33, sabre chaetae appeared after chaetiger 29 and hooded kooks appeared after chaetiger 51. It remains unclear whether they are the largest specimens of *L. kasyanovi* collected to date, or if they belong to a different species. To avoid confusion, we based the description of *L. kasyanovi* only on individuals from Peter the Great Bay and used only them as the type material of the species.

Our comparison of adults of *L. kasyanovi* from the Sea of Japan and *L. cirrata* from the Norwegian and Barents Seas did not reveal any reliable morphological character to distinguish these two species. Worms in both regions reach similar maximal size, and have similar individual and ontogenetic variability. Staining with methylene green also did not reveal species specific distinguishing patterns, although the area between the eyes and the occipital papilla was usually stained in Northwest Atlantic specimens but did not absorb the dye in the specimens from the Sea of Japan (Fig. 4b).

Other *Laonice* described to date from the Northwest Pacific include *L. japonica* (Moore, 1907), *L. sinica* Sikorski & Wu, 1998, and *L. rossica* Sikorski, 2003. *Laonice kasyanovi* differs from them by having a prostomium entirely fused with the peristomium on the anterior margin, instead of a prostomium either free from the peristomium or connected to it by a thin fold hidden in prostomium/peristomium groove. Moreover, nuchal organs in *L. sinica* and *L. rossica* are short, not extending beyond chaetiger 13, while in large individuals of *L. kasyanovi* these organs extend to the end of chaetiger 27. In *L. rossica*, hooded hooks are present in the neuropodia and in the posteriormost notopodia, while in *L. kasyanovi* hooks are present only in neuropodia. In *L. sinica*, the notopodial postchaetal lamellae on the postbranchiate chaetigers are interconnected by transverse dorsal crests, while in *L. kasyanovi* such crests are absent. As *L. kasyanovi* and *L. cirrata* are morphologically identical, these characters also serve to distinguish these species from *L. cirrata*.

Imajima and Hartman [67] reported two specimens of *L. cirrata* collected off Shirikishinai (Hokkaido, Japan) at a depth of 30 m. The specimens were up to 120 mm long, 5 mm wide for 160 chaetigers, with branchiae from chaetiger 2 to chaetigers 28–42. Lateral pouches were "first present from the seventh segment, ... or not before the thirties"; hooks in neuropodia were "present from about the fortieth or fiftieth setiger" and were distally bidentate; the pygidium was "surrounded by 8 to 12 short cirri" ([67]: 281–282). No further diagnostic characters of these specimens were provided. Notably, the Smithsonian National Museum of Natural History holds the only specimen of *Laonice* from Japan (USNM 34144), identified by Marian H. Pettibone as *L. cirrata* and assigned to that catalog number on 11 Aug 1966 (Katie Ahlfeld *in litt.*, February 28, 2023). The original label for this specimen reads "Hakodate, Japan" and no additional data are available related to this lot. It is noteworthy that 1) Shirikishinai was founded in 1964 as an administrative unit (https://kotobank.jp), next to Hakodate, on the shore of one bay, and 2) *Boccardia proboscidea* Hartman, 1940 reported by Imajima and Hartman [67] from Shirikishinai, is also in the collection of the Smithsonian Institution (USNM 45198). Thus, it is likely that Imajima and Hartman [67] and USNM 34144 refer to the same locality, and moreover, USNM 34144 was one of the two specimens examined by Imajima and Hartman [67]. Whether these specimens belong to *L. japonica* described by Moore [68] off the coast of Honshu, or to *L. kasyanovi*, remains unknown. We did not yet have a chance to examine the USNM material.

Distribution. North-western part of the Sea of Japan; records from the Korean Peninsula, Sakhalin, South Kurile Island and Japan are to be verified (Fig. 2). Complete information on the type specimens of *L. kasyanovi* is given in Table ESM2; information on the non-type specimens of *L. kasyanovi* and *L.* cf. *kasyanovi* is given in Table ESM3.

DISCUSSION

Despite the long-term need for molecular identity of the true *L. cirrata*, the first genetic data for this species from Norway were obtained by Sikorski et al. [68]. These authors for the first time provided *COI* sequences (MT606420, MT606421) of two specimens collected in Grøtsund Fjord (MIMB 40921), near Tromsø, one of the three sites where M. Sars [8] collected specimens for the description of *N. cirrata* (Fig. 2). In the present study, we obtained the *16S*, *18S*, *28S* and *Histone 3* sequences from these specimens in order to obtain a better molecular identity of the species. Comparison of the sequences of Norwegian worms with the corresponding sequences of worms from the Barents and White Seas, between Iceland and the Faroe Islands (provided by Bogantes et al. [14]) showed their identity (Fig. 1; Table ESM7). Therefore, we consider these worms to be conspecific. Our analysis also showed that *L. cirrata* from the Northeast Atlantic differs genetically from worms from the Sea of Japan (Russia). Therefore, we consider these worms to be the new species *Laonice kasyanovi*. The decision on the systematic position of the Japanese and Korean populations of worms appearing similar to *L. cirrata*, as well as same worms from Sakhalin and South Kurile Islands should be based on the analysis of more gene sequences and more individuals from these regions.

It is noteworthy that in neither the previous [17] nor this study were we able to detect any distinctive morphological features that would distinguish

L. kasyanovi from its sister species *L. cirrata*. Our analyses of the adult morphometric characteristics of these species showed their high and overlapping variability. Therefore, at this point, we consider them as two siblings that can only be confidently distinguished by their genetic data. A similar situation was recently found for *Spiophanes* Grube, 1860 species, including *S. bombyx* (Claparède, 1870), originally described from the Mediterranean (Italy), and three species described from the North Pacific: *S. uschakowi* Zachs, 1933 from the Asian coast, and *S. norrisi* Meißner & Blank, 2009 and S. *hakaiensis* Radashevsky & Pankova, 2020 from the American coast [2]. Although genetic studies have not encompassed *Laonice* from the entire Asian coast, we assume that *L. cirrata* does not occur in the Western Pacific. The presence of this species in the Eastern Pacific should be further investigated.

Our previous analysis of *COI* sequences (483 bp) of *Laonice* spp. from North European and Mediterranean waters ([16]: Fig. 1) showed that species with the prostomium anteriorly fused with the peristomium, and continuous dorsal crests on postbranchiate chaetigers form a clade that was named the *L. bahusiensis* complex. In the present study, we obtained additional sequences of four gene fragments for the same material (see Table ESM6). The analysis of new genetic data also supported the monophyly of the *L. bahusiensis* complex (Fig. 1). The monophyly of the entire *Laonice* clade, marked by the fusion of prostomium and peristomium and referred by Sikorski et al. [69] to the subgenus *Laonice* (*Laonice*), needs further support by analyzing additional species.

ZOOBANK REGISTRATION

This work has been registered with ZooBank under https://www.zoobank.org/C3A3D1B8-A41D-4E69-9EF8-D033D39C5D21.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at https://doi.org/10.1134/S1063074023080060. The following tables are available to authorized users:

Table ESM1. Sampling location data and museum registration numbers of *Laonice cirrata*.

Table ESM2. Sampling location data and museum registration numbers of the type specimens of *Laonice kasyanovi* sp. nov.

Table ESM3. Sampling location data and museum registration numbers of the non-type specimens of *Laonice kasyanovi* sp. nov. and *Laonice* cf. *kasyanovi* sp. nov.

Table ESM4. Sampling location data and museum registration numbers of *Laonice* spp.

Table ESM5. List of the museums and collections (and their acronyms) holding the examined or reported specimens of *Laonice* spp.

Table ESM6. Taxa, sampling location data, museum registration numbers of voucher specimens and GenBank accession numbers of sequences used in the analysis.

Table ESM7. Uncorrected pairwise average genetic distances (*p*, in %) between clades of *COI*, *16S*, *18S*, *28S*, and *Histone 3* gene sequences of *Laonice* spp.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

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

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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