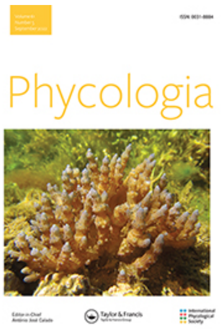

Phycologia

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/uphy20

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To cite this article: Oksana S. Belous, Svetlana Shibneva, Anna V. Skriptsova & Alexander A. Semenchenko (2022): The genus *Schizymenia* (Nemastomatales, Rhodophyta) on the Russian coast of the northwest Pacific and description of *S. tamarae sp. nov*, Phycologia, DOI: 10.1080/00318884.2022.2126244

To link to this article: https://doi.org/10.1080/00318884.2022.2126244

PHYCOLOGIA
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The genus *Schizymenia* (Nemastomatales, Rhodophyta) on the Russian coast of the northwest Pacific and description of *S. tamarae sp. nov.*

Oksana S. Belous[1], Svetlana Shibneva[1], Anna V. Skriptsova[1] and Alexander A. Semenchenko[2]

[1]Laboratory of Autotrophic Organisms, A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences, 17, Palchevskogo str., Vladivostok 690041, Russia
[2]Laboratory of Hydrobiology, Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch of the Russian Academy of Sciences, 100 let Vladivostoku 159, Vladivostok 690022, Russia

ABSTRACT

We analysed *rbc*L and COI sequence data of specimens of *Schizymenia* from the Sea of Okhotsk and Sea of Japan. Our results revealed a new species of *Schizymenia, S. tamarae sp. nov*., from the northwestern Sea of Japan. This species is distinct based on shape and the position of glandular cells. Morphological and genetic analyses confirmed that the previously described *S. jonssonii* is a synonym of *S. dubyi* var. *palmata*, which was originally described from the Kuril Islands. The latter taxon was synonymized with *Neoabbottiella valentinae*. We verified the synonymy of the three names and the affinity of the taxon with the genus *Schizymenia*. Since the name *N. valentinae* has priority at the rank of species we propose *Schizymenia valentinae comb. nov*. The only species of *Schizymenia* currently known to occur along the Russian coast are *S. valentinae* and *S. tamarae*. *Schizymenia valentinae* is distributed along southeastern Kamchatka, on the Commander Islands and Kurile Islands, and *S. tamarae* is known only from the Sea of Japan, where it occurs from Olga Bay to Peter the Great Bay on the Russian coast, and in Japan.

ARTICLE HISTORY
Received 28 April 2022
Accepted 15 September 2022
Published online 28 October 2022

KEYWORDS
COI-5′; Phylogeny; *rbc*L; *Schizymenia jonssonii*; Systematics

INTRODUCTION

The red algal genus *Schizymenia* J. Agardh is one of the five genera of the family Schizymeniaceae of the order Nemastomatales. The history of the systematics of this genus was given in detail by Saunders *et al.* (2015). In total, 25 species of *Schizymenia* have been described, most of which were later synonymized (Funk 1955; Silva *et al.* 1996) or transferred to other genera, some of them belonging to other orders of Rhodophyta (Lindstrom 1985; Hansen 1989; Manghisi *et al.* 2014). At present, 11 species are accepted taxonomically (Guiry & Giury 2022), of which only five have been genetically verified (Gabriel *et al.* 2011; Kim *et al.* 2012; Ramírez *et al.* 2012; Saunders *et al.* 2015; Gunnarsson *et al.* 2020). The placement of several species in *Schizymenia* is questionable. For example, *S. ecuadoreana* (W.R. Taylor) I.A. Abbott has refractive cells in the medulla (Abbott 1967), which is not typical of *Schizymenia*, and its generic position needs to be investigated. *Schizymenia johnstonii* Setchell & N. L. Gardner and *S. violacea* Setchell & N.L. Gardner, from the Gulf of California and Mexico, are synonymous according to Dawson (1944). Moreover, cruciately divided tetrasporangia developed on the blade of *S. violacea* (Setchell & Gardner 1924), hence it was proposed to place it in the genus *Grateloupia* as *G. violacea* (Setchell & N.L. Gardner) E.Y. Dawson (Dawson 1961). *Schizymenia obliqua* (Grunow) F. Schmitz was found in the Indian Ocean, and it is only known from its original collection as *S. erosa* var. *obliqua* Grunow (1868). Kylin (1932) found that the original specimen of *S. erosa* (J. Agardh) J. Agardh was morphologically similar to the genus *Iridaea* Bory.

Schizymenia is widely distributed in the world, including the subantarctic islands (Silva *et al.* 1996) and up to Alaska (Lindstrom 1977). In the North Pacific, three species of *Schizymenia* have been recorded: *S. pacifica* (Kylin) Kylin, *S. dubyi* (Chauvin) J. Agardh and *S. apoda* (J. Agardh) J. Agardh (Perestenko 1994; Lee & Kang 2001; Lee 2008; Liu 2008; Gabriel *et al.* 2011; Kim *et al.* 2012; Yoshida *et al.* 2015). On the Russian Pacific coast two species of *Schizymenia* were reported: *S. dubyi* (Yamada 1928; Okamura 1933; Zinova 1940; Tokida 1954) or its form *S. dubyi* var. *palmata* Yamada (Yamada 1935; Nagai 1941; Zinova & Perestenko 1974) and *S. pacifica* (Perestenko 1994). Abbott believed that only one species, *S. pacifica*, occurred in the northern Pacific, and that *S. dubyi* had been incorrectly identified (Abbott 1967). Despite the fact that *S. dubyi* occurs in Japan (Yoshida *et al.* 2015), Korea (Lee 2008; Kim *et al.* 2012) and China (Liu 2008), this species has not been mentioned in the floristic reports of the Pacific coast of Russia (Perestenko 1994; Klochkova *et al.* 2009, 2021; Selivanova 2011). Lopatina *et al.* (2016) studied the holotype and paratypes of *S. dubyi* var. *palmata* (Hokkaido University, Japan), as well as other herbarium specimens, which were collected near the Kuril Islands and identified by L.P. Perestenko as *S. dubyi* var. *palmata*, and by A.D. Zinova as *S. pacifica*. The absence of glandular cells in the cortex and the similarity of the vegetative anatomy of these samples with *Neoabbottiella*

CONTACT Oksana S. Belous ksu_bio@mail.ru
Supplemental data for this article can be accessed online at https://doi.org/10.1080/00318884.2022.2126244

valentinae N.A. Pisareva & Kloczkova, allowed the authors to conclude that *S. dubyi* var. *plamata* is conspecific with *N. valentinae* (Pisareva & Klochkova 2013; Lopatina *et al.* 2016). Currently, it is believed that only *S. pacifica* grows on the Pacific coast of Russia, where it is distributed from the Sea of Japan to the Commander Islands (Perestenko 1994; Skriptsova 2019; Klochkova *et al.* 2021).

The aim of the present study was to revise the genus *Schizymenia* in Russian waters. Since identification of species in the genus is difficult because of the availability of only few diagnostic characters (Abbott 1967), we used an integrated approach using molecular and morphological data. Such approaches have overcome taxonomic problems in many seaweed groups (e.g. Kraft & Saunders 2017).

MATERIAL AND METHODS

Seaweed collection

We collected and examined 27 specimens of *Schizymenia*. The holotype of *S. tamarae sp. nov.* was deposited in V.L. Komarov Botanical Institute (LE; St. Petersburg, Russia), and the studied specimens were deposited in the Museum of A.V. Zhirmunsky National Scientific Center of Marine Biology (MIMB; Vladivostok, Russia). We also studied the holotypes of *Neoabbottiella valentinae* and *N. decipiens* stored in LE, herbarium specimens of *Schizymenia* species and *N. araneosa* (Perestenko) S.C. Lindstrom stored in MIMB, and two vouchers of *S. pacifica* provided by Gayle Hansen. Collection details are given in Table S1 and Fig. 1.

Morphological observations

Cross-sections were made by hand with a razor blade in basal, middle and apical portions of thalli. A Zeiss AxioVert 200 M inverted microscope was used to examine the sections and take photomicrographs.

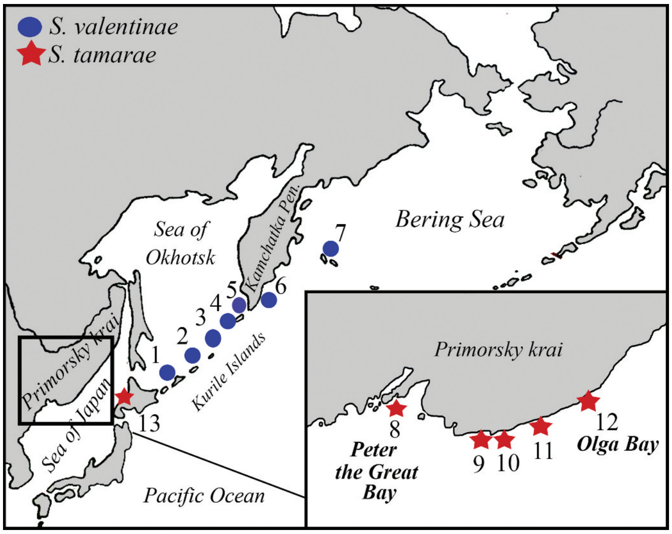


Fig. 1. Sampling localities of *S. valentinae comb. nov.* and *S. tamarae sp. nov.* Kurile Islands: 1, Iturup Island; 2, Simushir Island; 3, Matua Island; 4, Paramushir Island; 5, Shumshu Island. Southeastern Kamchatka: 6, Avacha Bay, Spaceniya Bay. Commander Islands: 7, Mednyi Island. Continental coast of the Sea of Japan: 8, Sukhoputnaya Bay (type locality of *S. tamarae sp. nov.*); 9, Kievka Bay; 10, Petrov Island; 11, Valentin Bay; 12, Olga Bay. Hokkaido Island (Sea of Japan): 13, Oshoro Bay.

Thallus length, width, shape, texture, margins and base were analysed. For the study of anatomy, we measured blade thickness, cell sizes in surface view, sizes of cells of medullary filaments, subcortical and cortical cells, numbers of cells in the cortical rows, shape and size of glandular cells (if available), and sizes of cystocarps and carpospores. Specimens collected in Sukhoputnaya Bay, Kievka Bay (Sea of Japan) and from Kuril Islands (Sea of Okhotsk) were compared with other species of the genus and our own specimens (Table 1).

DNA extraction, polymerase chain reaction, sequence editing, phylogenetic analysis and species delimitation

For molecular analyses fragments of *Schizymenia*, as well as of the holotype of *N. valentinae*, were cut from herbarium samples. Genomic DNA was extracted by the CTAB method (Wang *et al.* 2006). Primers for amplification and sequencing were as follows: for *rbc*L: F57 (forward), rbcLrevNew (reverse) and TLF1 (inner forward); for COI-5′: GazF1 (forward) and GazR1 (reverse; Saunders & Moore 2013). PCR and sequencing were performed as described previously (Shibneva *et al.* 2020). Obtained sequences were manually assembled and edited using FinchTV 1.4 and MEGA7 (Kumar *et al.* 2016), and the datasets were aligned with MUSCLE (Edgar 2004). The inter- and intraspecific COI-5′ and *rbc*L pairwise distances were calculated with MEGA7. PartitionFinder v2.1.1 (Lanfear *et al.* 2012) was used to select the best-fit partitioning scheme and models separately for each codon of *rbc*L and COI-5′. The best model for the first and second codon positions in both *rbc*L and COI-5′ were respectively GTR (Tavaré 1986) + I (gamma distribution) and F81 (Felsenstein 1981) + I (a proportion of invariable sites), whereas for the third position the best model was HKY (Hasegawa *et al.* 1985) + G and HKY + I for *rbc*L and COI-5′, respectively. Bayesian inference was performed with two independent runs of Metropolis-coupled Markov chain Monte Carlo analyses. The chains were run for 5 million generations and sampled every 500 generations, with 25% of the sampled trees discarded as burn-in. Trace files were visually inspected in Tracer v1.7 (Rambaut *et al.* 2018). Maximum likelihood (ML) analysis was implemented using RAxML v8.2.7 (Stamatakis 2006) and bootstrap analysis (1,000 replications). Using the option-raxml in PartitionFinder, we found the best model for the RAxML GTRCATI separately for each codon in *rbc*L and COI-5′. FigTree v1.4.4 was used to visualize phylogenetic trees. *Platoma cyclocolpum* (Montagne) F. Schmitz, *Titanophora weberae* Børgesen and *Titanophora* sp. were used as outgroups. All sequences have been deposited in GenBank (see Table S2 for accession numbers).

The Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al.* 2021), a Poisson Tree Processes (PTP; Zhang *et al.* 2013) and a Multi-rate Poisson tree processes (mPTP; Kapli *et al.* 2016) methods were applied to determine candidate species. The ASAP analysis was run on https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html with three proposed

Table 1. Morphological and anatomical comparison of *Schizymenia* species.

Characteristic	*S. tamarae sp. nov.*	*S. valentinae* from Russian coast	*S. jonssonii* from Iceland	*S. pacifica* from American coast	*S. tenuis*	*S. apoda*	*S. dubyi*	*S. dubyi* var. *palmata*
Blade (cm)	oval, entire or torn in the upper part with uneven notched edges, 3–12 × 2–5	oblong–oval, entire, torn or deeply dissected into lobes, with uneven torn edges and notches 5–24 × 3–22	oblong, sometimes lobed or split, 5–35	entire or irregularly divided into several lobes 15–20(–60)	typically cleft, 5–15	simple lanceolate to broadly rounded with undulate or straight margins. The older blades are cleft and lacerated with or without proliferations, 15–20(–30)	simple to variously and irregularly lobed, often lacerate from above, margin smooth to somewhat ruffled, 10–60 × 5–15	elliptic or elliptic-ovate, often divided into 3–5 lobes
Lamina colour	purple red to brownish red	wine red to brownish red	dark red to brownish red	wine red or dark cherry	similar to *S. pacifica*	from light red to bright orange or dark brownish red	dark red-brown	dark yellowish red
Lamina thickness (µm)	250–375	250–500	250–600(–900)	212–400	100–400	250–600	300–600(–1000)	100–450
Glandular cells (µm)	deeply in cortex, ovoid, pear-shaped or oval-elongated, 9–11 × 10–23	not found	not found	abundant, narrow, elongated, fusiform, close to the surface, 7–10.5 × 32–40(–51)	similar to *S. pacifica*	elongated, 15–25	ellipsoid-ovoid to clavate, 6–10 × 14–30; 4 × 12–20; 6–7 × 26–28	not found
Surface cells (µm)	subspherical or elongated, 2.7–4 × 4–5	roundish to elongated, 4–7	spherical, 7–9	spherical to elongated, 3–4 × 4–5	similar to *S. pacifica*	angular, 3–6	oval, 3–5(7) × 6–10	
Medullary cells (µm)	5.5–8 × 34–48	6.5–10.5 × 17–50	3–7 × <150	4–8.5	similar to *S. pacifica*	4–6 in diameter	3–5(–10) in diameter	abundant, slender
Outer cortex cells (µm)	roundish or elongated, 4 × 6–8 (2–4 rows in the middle and upper part and 5-7 rows at the base)	elongated, square or rectangular, 3–5 × 3–8 [2–3(–4) rows]	elongated, 7.5 × 15 (2–3 rows)	oval elongated, rectangular, 4–8 × 5–8 or almost square, 4–8 (2–3 rows)	similar to *S. pacifica*	4 × 10 (2–3 rows)	elongate, round to subsquare 2–4 (2–3rows)	small, ellipsoid (2–3 rows)
Inner cortex cells (µm)	roundish or oval-elongated, 7–10 × 11–16 (3–5 rows)	roundish or slightly elongated, 6–12.5 × 8–18 (3–4 rows)	spherical, 30 (3–5 rows)	spherical to oval, 4–11 × 5–14 (3–5 rows)	similar to *S. pacifica*	spherical, 6–8 (4–5 rows)	subspherical to ovoid, 6–10(–14) (3–4 rows)	roundish or nearly round
Secondary pit-connections	-	-	-	-	-	+ (occasionally)	-	?
Cystocarps (µm)	compact, 48–132 × 77–116	compact, oval, 123 × 64 or roundish, 125	130–300	oval to round, 120–150 × 100–150	ovoid to round, 100–150 × 80–100	80 × 120	100–240	spherical
Carpospores (µm)	triangular, polygonal or irregular shape with roundish corners 20–28 × 28–42	polygonal, square, rectangular or irregular shape with smoothed or sharp corners 15–18 × 21–38	15–40	–	similar to *S. pacifica*	25–33	ovoid, 15–20	11.5–15 × 15–27
Ostioles (µm)	25–50	30–50	about 50	18–42	25–50	about 50	?	?
Depth (m)	upper to low intertidal	low intertidal to subtidal (20)	low intertidal	low intertidal	low intertidal	intertidal	intertidal	
References	this study	this study	Gunnarsson *et al.* (2020)	this study. Description of the reproductive system according to Saunders *et al.* (2015)	Saunders *et al.* (2015)	D'Archino & Zuccarello (2014); Gabriel *et al.* (2011)	Womersley & Kraft (1994); Ramirez *et al.* (2012); Cormaci *et al.* (2021)	Nagai (1941)

models: Jukes-Cantor (JC), Kimura and *p*-distance. The ASAP delimitation first score was considered as the best partition (Puillandre *et al.* 2021). The PTP and mPTP analysis were implemented on the webserver (http://mptp.h-its.org/#/tree) using the PTP with *p*-value = 0.001 and following default settings. All analyses were performed separately for the COI-5′ and *rbc*L datasets.

As most of the results of ASAP and PTP performed separately for the COI-5′ and *rbc*L data sets were in agreement, we designated the resulting groups as candidate species.

RESULTS

Molecular analyses

Phylogenetic trees constructed based on concatenated COI-5′ and *rbc*L sequences resolved all the specimens from the Russian coast within a monophyletic clade with species of *Schizymenia* (Fig. 2). Specimens from the Sea of Japan were sister to the clade that included *S. dubyi* and *S. apoda* with high support (PP = 1, ML = 97%). On the phylogenetic tree, this group was separated from another clade (PP = 1, ML = 89) containing two other Pacific species, *S. pacifica* and *S. tenuis* G.W. Saunders, T. Birch & K.R. Dixon, and a North Atlantic species, *S. jonssonii* K. Gunnarsson & J. Brodie. *Schizymenia tenuis* was sister to *S. pacifica* (PP = 1, ML = 100). Low genetic distances between these specimens (*rbc*L = 0.4%–0.5%, COI-5′ = 0.8%–1%) suggested their conspecifity. Samples from the Kuril Islands (Simushir Island and Matua Island) formed a clade with *S. jonssonii* from Iceland. The genetic distances between these groups were in a range of 0.16%–0.79% for *rbc*L and 1.14%–1.35% for COI-5′ (Table 2). These values were significantly lower than the divergence between the closely related *S. dubyi* and *S. apoda* (*rbc*L = 1.44%; COI-5′ = 2.28%), and were comparable with maximal *rbc*L intraspecific divergence in these species (Table 2). Unexpectedly, the holotype of *Neoabbottiella valentinae* grouped with samples of *Schizymenia* from the Kurile Islands (PP = 0.99, ML = 98%; Figs 2, S1, S2). In the *rbc*L phylogeny the group of specimens from the Russian coast of the Sea of Japan also formed a clade with a specimen from Japan (Oshoro, Hokkaido; *Schizymenia* sp. 1, AY294390; Fig. S1).

The results of the species delimitation generally agreed. The ASAP performed on the COI-5′ and *rbc*L sequence sets (except *p*-distance model for COI-5′) yielded five candidate species: 1) *S. apoda*; 2) *S. dubyi*; 3) *S. pacifica* complex, including *S. pacifica* and *S. tenuis*, as well as unidentified *Schizymenia* sp. 1 Cal from the north-eastern Pacific; 4) a group combining specimens of *S. jonssonii* from Iceland (North Atlantic) and specimens from the Kurile Islands (Northwestern Pacific), as well as the holotype of *N. valentinae*; and 5) a separate genetic species that contained specimens from the Russian coast of the Sea of Japan and specimen AY294390 from Japan (Fig. S1). PTP and mPTP performed on the basis of the *rbc*L dataset gave the

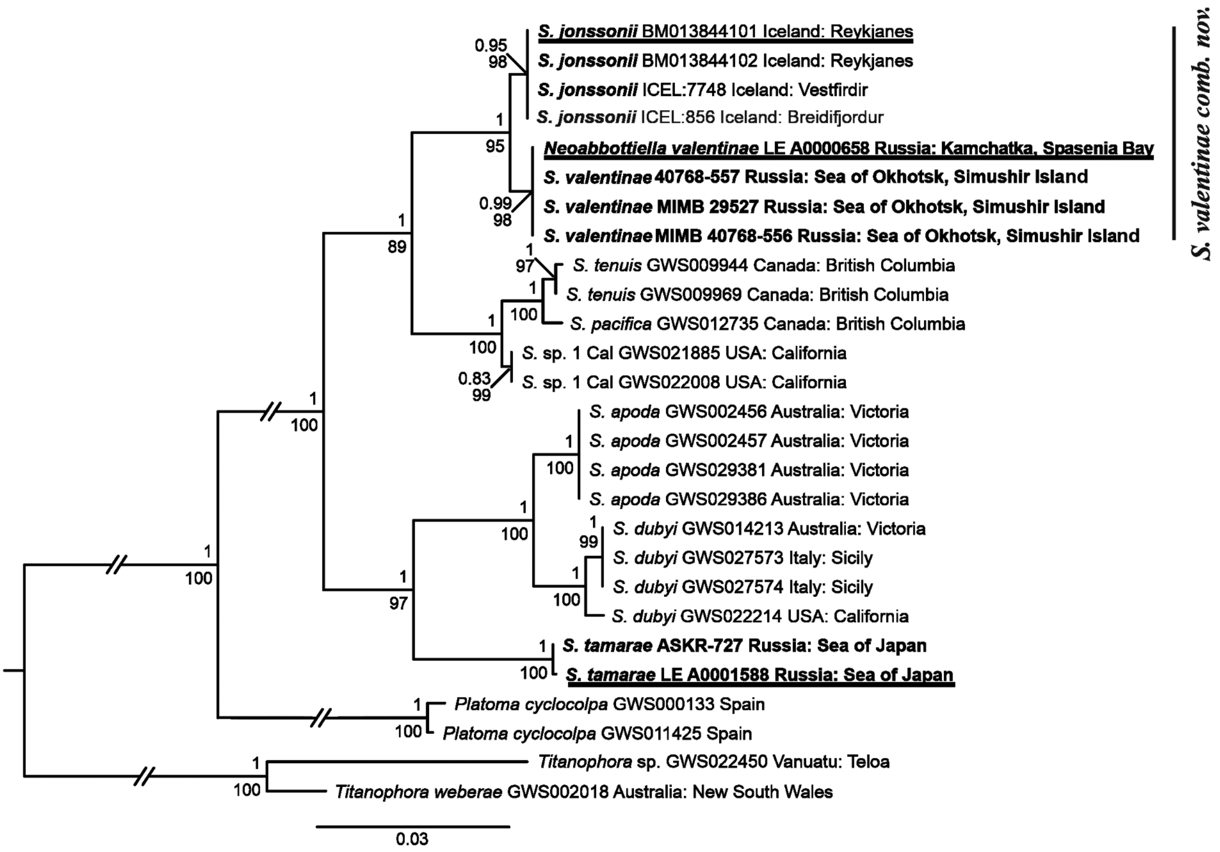


Fig. 2. Bayesian topology of *Schyzimenia* spp based on the concatenated mitochondrial COI-5′ and plastid *rbc*L markers (1,953 bp). Bayesian posterior probabilities and ML bootstrap values are given above and below nodes, respectively. Sequences produced in this study are in bold. Holotypes are underlined.

Table 2. Intraspecific COI-5′ and *rbc*L divergences (%), and distance (%) to nearest neighbour (NN) for the species of the genus *Schizymenia*.

Species	N	Maximal infraspecific divergence (%)	Nearest neighbour (NN)	Average distance to NN (%)
COI-5′				
S. tamarae	3	0	*S. dubyi*	5.55
S. valentinae Russia	3	0	*S. jonssonii*	1.15
Neoabbottiella valentinae	1	–	*S. jonssonii*	1.17
S. pacifica	88	0.16	*S. tenuis*	0.83
S. tenuis	12	0.16	*S. pacifica*	0.83
S. sp. 1 Cal	3	0	*S. tenuis*	1.64
S. dubyi	11	0	*S. apoda*	2.28
S. apoda	5	0	*S. dubyi*	2.28
S. jonssonii	6	0	*S. valentinae*	1.15
***rbc*L**				
S. tamarae	4	0.16	*S. apoda*	2.83
S. valentinae Russia	3	0.57	*S. jonssonii*	0.37
Neoabbottiella valentinae	1	–	*S. valentinae*	0.21
S. pacifica	5	0.54	*S. tenuis*	0.45
S. tenuis	2	0.14	*S. pacifica*	0.45
S. sp. 1 Cal	2	0	*S. pacifica*	0.41
S. dubyi	12	0.86	*S. apoda*	1.44
S. apoda	18	0.67	*S. dubyi*	1.44
S. jonssonii	4	0	*S. valentinae*	0.37

same results, whereas PTP based on the COI-5′ separated *Schizymenia* sp. 1 Cal from the group combining *S. pacifica* and *S. tenuis*, and COI-5′-based mPTP combined *S. apoda* and *S. dubyi* (Fig. S2). ASAP performed on COI-5′ using *p*-distance model separated specimens from the Kuril Islands (including *N. valentinae*) from *S. jonssonii* (Fig. S2).

The combined results of the phylogenetic and species delimitation analyses suggests that *S. pacifica* and *S. tenuis* are conspecific; *N. valentinae, S. jonssonii* and specimens from the Kuril Islands represent a single species, for which we propose the new combination *S. valentinae comb. nov.* (for reasons of priority at the rank of species). The specimens from the Russian coast of the Sea of Japan represent a separate species, which we describe as *S. tamarae sp. nov.*

Morphological observations and taxonomy

Schizymenia valentinae (N.A. Pisareva & Kloczkova) O.S. Belous, Skriptsova & Shibneva *comb. nov.*

Figs 3–9

BASIONYM: *Neoabbottiella valentinae* N.A. Pisareva & Kloczkova 2014, *Russian Journal of Marine Biology* 39, p. 407, figs 1d–1f, 3

HOLOTYPE: LE A0000658, a specimen bearing gonimoblasts and spermatia, collected 2 August 2004 by N.A. Pisareva, deposited in LE herbarium of Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

TYPE LOCALITY: Intertidal zone of Spaseniya Bay, Avacha Gulf, southeastern Kamchatka, Russia.

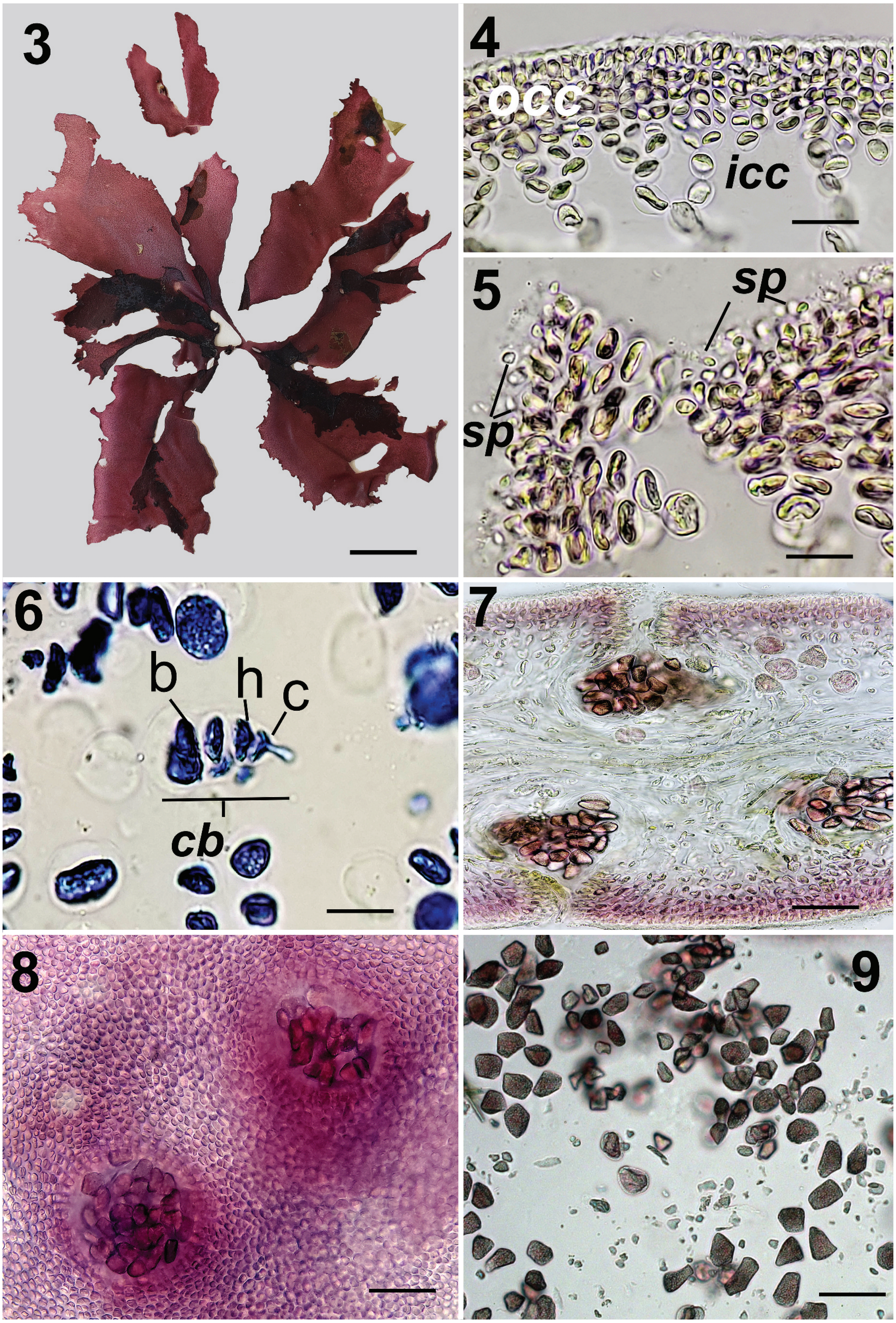
HETEROTYPIC SYNONYMS: *Schizymenia dubyi* var. *palmata* (Yamada 1935), p. 23, pl. 9; *Schizymenia jonssonii* K. Gunnarsson & J. Brodie 2020, p. 326, figs 1, 2, 4.

REPRESENTATIVE DNA BARCODES: *rbc*L: ON341124, ON341123, ON341125, ON341126; COI-5′: ON341116, ON341117, ON341118, ON341119.

HABITAT AND DISTRIBUTION: Grows from the upper intertidal to subtidal zones, at depths of 1–20 m on rocky and stony grounds. It is distributed in the North Atlantic (Iceland), southeastern Kamchatka, Commander Islands and Kurile Islands.

OTHER EXAMINED SPECIMENS: see Table S1.

Examined specimens from Simushir Island (Kuril Islands, Russia) showed the following characteristics. The gametophyte was blade-like, soft, smooth, membranous, oblong-oval, roundish, entire, torn or deeply dissected into lobes, with uneven torn edges and notches, with a narrow wedge-shaped base, turning into a small stipe of 2–3 mm (Fig. 3). The colour was wine red to brownish red. Blades were 5–24 cm long, 3–22 cm wide and 250–500 µm thick. Cortical cells from the surface were rounded to elongated, 4–7 µm in diameter. In cross-section, the blade consisted of inner and outer cortex and a medulla. The medulla was composed of loose, branched anticlinal and periclinal filaments consisting of rod-shaped elongate cells of 6.5–10.5 × 17–50 µm. A refractive cell was absent. Medullary filaments transitioned to short dichotomous branches forming the loose inner cortex and dense outer cortex (Fig. 4). Medullary filaments were connected to cortical cells by pit-connections. The outer cortex consisted of elongated, rectangular or rarely square cells of 3–5 × 3–8 µm, forming 2–3(–4) layers (Fig. 4). Cells of the inner cortex were roundish or slightly elongated, 6–12.5 × 8–18 µm, decreasing in size towards the surface and forming rows of 3–4 cells (Fig. 4). Glandular cells were not found even after staining with aniline blue. The gametophyte was monoecious. Spermatangia were roundish or oval, 2–2.5 µm in diameter, and developed in pairs on mother cells (Fig. 5). The carpogonial branch was four-celled, curved



Figs 3–9. *Schizymenia valentinae comb. nov.* from Simushir Island (Kuril Islands, Russia).

Fig. 3. Habit of fertile plant of *S. valentinae comb. nov*. Scale bar = 2 cm.

Fig. 4. Cells of outer cortex (occ) and inner cortex (icc) in traverse section. Scale bar = 20 μm.

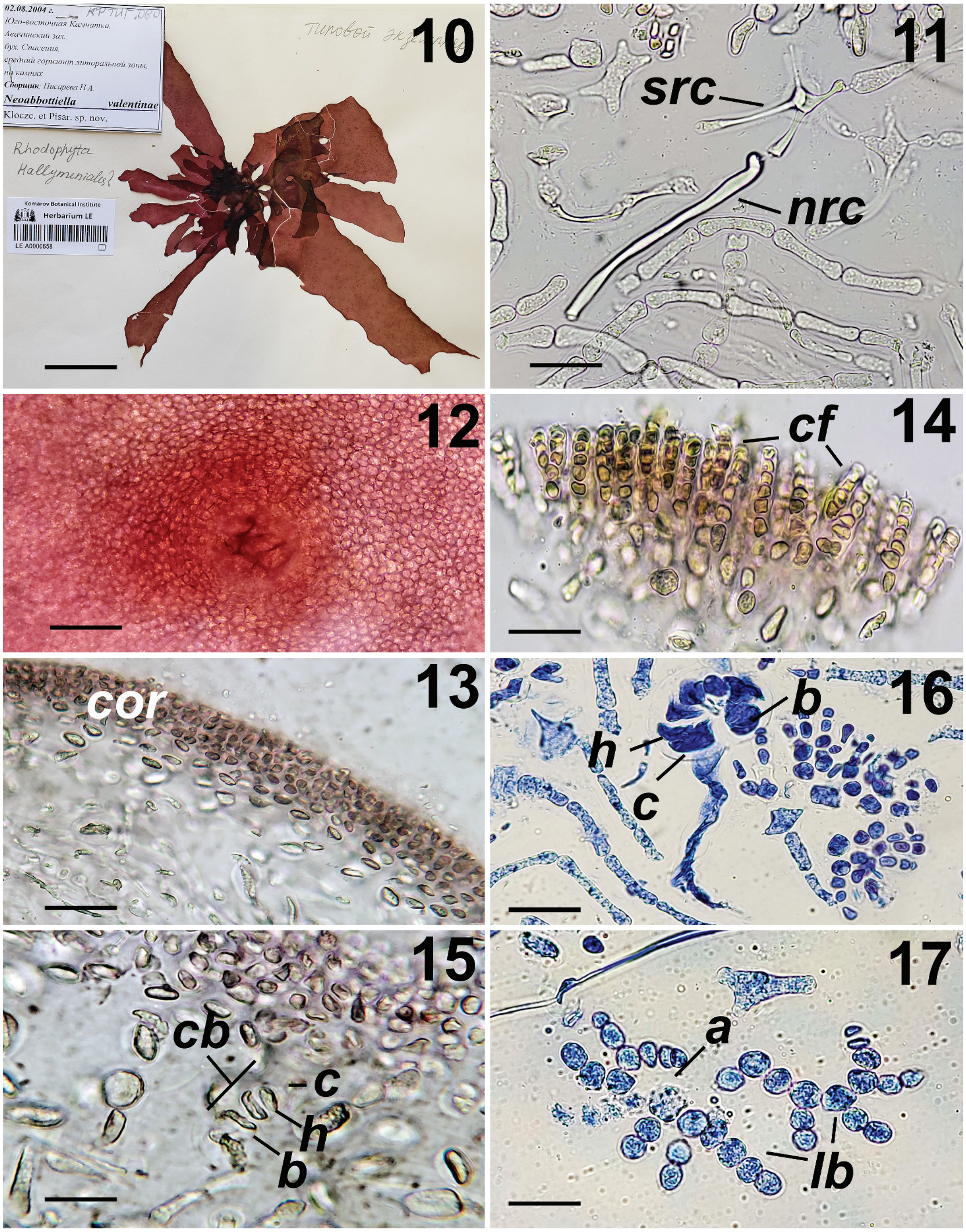
Fig. 5. Outer cortical cells with spermatangia (sp). Scale bar = 10 μm.

Fig. 6. Carpogonial branch (cb): carpogonium (c), hypogenous cell (h) and basal cell (b). Scale bar = 15 μm.

Fig. 7. Mature gonimoblast located on both surfaces of blade between the inner cortex and medulla in transverse section of the blade. Scale bar = 60 μm.

Fig. 8. Surface ostiole of the carposporophyte showing carposporangia. Scale bar = 20 μm.

Fig. 9. Carpospores. Scale bar = 50 μm.



Figs 10–17. Morphology and anatomy of *Neoabbottiella* spp.

Fig. 10. Holotype of *N. valentinae* (LE A0000658) from Spasenia Bay, Avacha Gulf (southeastern Kamchatka, Pacific Ocean). Scale bar = 2.5 cm.

Fig. 11. Cross-section of the blade of *N. araneosa* showing refractive cells: stellate (src) and needle-shaped (nrc) refractive cells. Scale bar = 20 µm.

Fig. 12. Surface ostiole above the carposporophyte of *N. valentinae*. Scale bar = 30 µm.

Fig. 13. Cortex (cor) of the holotype of *N. valentinae*. Scale bar = 60 µm.

Fig. 14. Cortex of the holotype of *N. decipiens* (LE A0000657) showing decaying cell filaments (cf) enclosed in a common mucous membrane. Scale bar = 30 µm.

Fig. 15. Carpogonial branch (cb) in the holotype of *N. valentinae*: carpogonium (c), hypogenous cell (h) and basal cell (b). Scale bar = 15 µm.

Fig. 16. Carpogonial branch (cb) of *N. araneosa*: carpogonium (c), hypogenous cell (h) and basal cell (b). Scale bar = 15 µm.

Fig. 17. Auxiliary cell branch (a) of *N. araneosa*. Lateral branches (lb). Scale bar = 10 µm.

, basal and with oval-elongated hypogenous cells (Fig. 6). Cystocarps were small, compact, oval (123 × 64 µm) or roundish (125 µm in diameter), without pericarp, forming small dark red dots densely covering the entire blade surface excluding the stipe, located on both surfaces of the blade in the inner cortex or in the medulla closer to cortex (Fig. 7). Ostioles were 30–50 µm in diameter and had the appearance of depressions on the blade (Fig. 8). All gonimoblast cells turned into carpospores. Carpospores were 15–18 × 21–38 µm, polygonal, rectangular, square or irregularly shaped with smooth or sharp corners (Fig. 9). Tetrasporic crusts were not found.

This species has recently been described from the Atlantic as *S. jonssonii* (Gunnarsson *et al.* 2020). Apparently, *S. jonssonii* was previously known in the Pacific Ocean as *S. dubyi* var. *palmata*, which was first noted in the Kuril Islands by Yamada (1935) and then Nagai (1941). *Schizymenia dubyi* var. *palmata* was synonymized with *N. valentinae* based on morphological and anatomical similarities between the type specimens (Lopatina *et al.* 2016). Based on genetic and morphological studies of the holotype of *N. valentinae* (LE A0000658; Fig. 10), we confirmed that it is conspecific with our specimens from Simushir Island (Fig. 2). *Neoabbottiella valentinae* clearly differs from the other two species of *Neoabbottiella* by lacking refractive cells in the medulla (Fig. 11), a prominent pericarp over gonimoblast and the characteristic stellate pattern of gonimoblasts, as well as by presence of ostioles (Fig. 12), which are characteristic of the genus *Schizymenia* and absent in *Neoabbottiella* (Perestenko 1994). Also, the cortex of *N. valentinae* (Fig. 13) was typical of *Schizymenia*, whereas in *Neoabbottiella* it is formed by cell filaments of 3–6 cells enclosed in a common mucous membrane (Fig. 14). Most importantly, carpogonial branches found in the holotype of *N. valentinae* consist of four cells (Fig. 15), whereas carpogonial (Fig. 16) and auxiliary branches (Fig. 17) in the genus *Neoabbottiella* are curved and consist of 12–15 cells, and have branches of 2–4 cells (Perestenko 1975).

With the three names *S. dubyi* var. *palmata, N. valentinae* and *S. jonssonii* regarded as synonyms, and the taxon interpreted as a species of *Schizymenia*, the principle of priority determines that the epithet '*valentinae*' is to be used, so a new combination is required. The name *S. dubyi* var. *palmata* (Yamada 1935), although it is the earliest of the three, does not have priority at the rank of species (Turland *et al.* 2018, Art. 11.2).

Schizymenia tamarae O.S. Belous, Skriptsova & Shibneva *sp. nov.*

Figs 18–26

DESCRIPTION: Gametophytes blade-like, membranous, soft, smooth, oval, entire or torn in the upper part with uneven-notched edges, with narrow or wide wedge-shaped base, on short terete stalk 2–6 mm long; thallus attached with small cushion, from which one or several blades can grow (Figs 18, 19). Blades purple red to brownish red in colour, 3–12 cm long, 2–5 cm wide and 250–375 µm thick. In cross-section blade consists of inner and outer cortices, and medulla. Medulla loose, consisting of branched anticlinal and periclinal filaments of cells of 5.5–8 × 34–48 µm, from which short, dichotomously ramified branches develop, forming a loose inner cortex (3–5 cell rows) and a dense outer cortex. Outer cortex of 2–4 cell rows in the middle and upper part of the blade and 5–7 cell rows at the base (Fig. 20). Refractive cells absent. Medullary filaments connected to cortical branches by pit-connections. Cells of outer cortex roundish or elongated, of 4 × 6–8 µm. Inner cortex of roundish or oval-elongated cells of 7–10 × 11–16 µm diameter in cross-section and 2.7–4 × 4–5 µm in surface view. Glandular cells are located deeply in the cortex (Figs 21, 22), formed from the second or third cell of the inner cortex; they are ovoid, pear-shaped or oval-elongated, 9–11 × 10–23 µm (Figs 21–23), abundant at blade base and stalk, clearly visible in fresh specimens, poorly distinguishable in dry material where visible only at surface of thallus. Carpogonial branch and auxiliary cell branch were not observed. Cystocarps in form of small dark red dots scattered over entire surface of blade, including base. Ostioles of 25–50 µm in diameter in surface view, looking like depressions in cortex over carposporophytes (Fig. 24). In cross-section, gonimoblast compact, 48–132 × 77–116 µm, without pericarp, located on both surfaces of the blade in the inner cortex (Fig. 25). All gonimoblast cells turn into carpospores. Carpospores of 20–28 × 28–42 µm, triangular, polygonal or irregular in shape, with roundish corners (Fig. 26). Spermatangia and tetrasporic crusts were not found.

ETYMOLOGY: The specific epithet is dedicated to Dr. Tamara V. Titlyanova from the National Scientific Center of Marine Biology, Vladivostok, Russia, in recognition of her many contributions to the ecology of seaweeds.

HOLOTYPE: LE A0001588, collected 6 June 2020 by A.V. Skriptsova, deposited in Komarov Botanical Institute of the Russian Academy of Sciences (LE, St. Petersburg, Russia). GenBank accession numbers: *rbc*L: ON341120; and COI-5′: ON341113.

ISOTYPE: LE A0001589, deposited in LE.

TYPE LOCALITY: Sea of Japan: Peter the Great Bay, Sukhoputnaya Bay, Russia (42°50′N, 133°41′W), upper to lower intertidal, 0.5–0.8 m.

REPRESENTATIVE SPECIMENS EXAMINED: MIMB 43293, Sea of Japan, Sukhoputnaya Bay, 0.5-1.5 m depth, 18 June 2018; ASKR-M157, Sea of Japan, Sukhoputnaya Bay, 0.5–0.8 m depth, 14 September 2021; ASKR-M156, Sea of Japan, Kievka Bay, low intertidal and subtidal zones, 10 July 2016; Sea of Japan, Olga Bay, 0.5 m depth, 28 September 1967 (LE); Sea of Japan, Valentin Bay, 18 August 1964 (LE); Sea of Japan, Petrov Island, 1933 (LE).

REPRESENTATIVE DNA BARCODES: *rbc*L: ON341120, ON341121, ON341122; COI-5′: ON341113, ON341114, ON341115.

HABITAT AND DISTRIBUTION: The alga grows in the upper to lower intertidal zone on rocky and stony grounds in depressions and crevices under the canopy of other seaweeds, in clusters and does not form thickets; found on open sea coasts with high surf. It is distributed in the Sea of Japan and in Hokkaido (Japan).

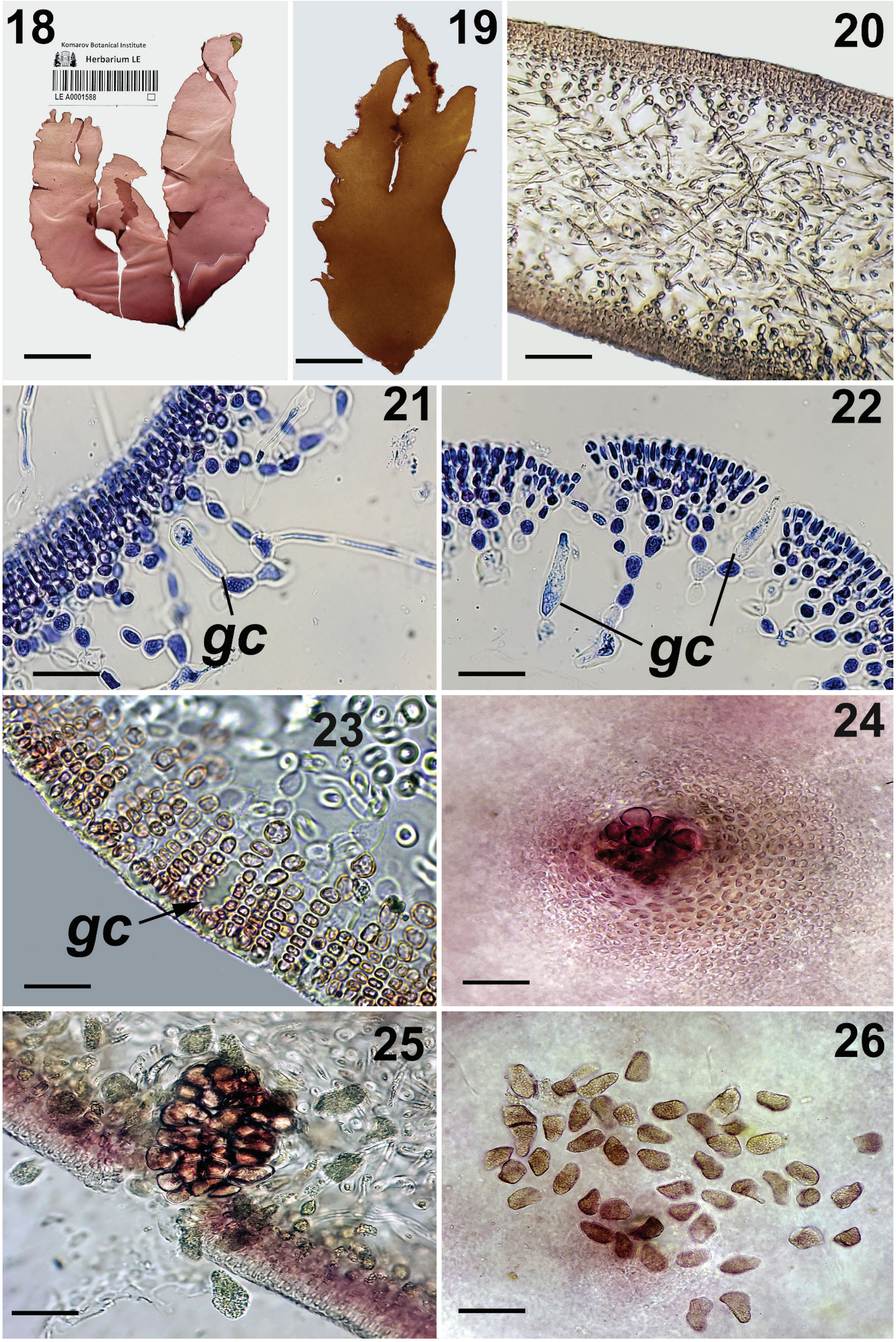
DISCUSSION

The determination of species boundaries and diversity is one of the main tasks of taxonomic studies. This is especially critical in species with simple morphologies, especially in foliose red algae (Filloramo & Saunders 2018.). The use of molecular phylogenetic methods in systematics and taxonomy of macroalgae has a huge advantage over the use of traditional morpho-taxonomic methods in solving these difficult issues.

Based on molecular and morphological analyses of *Schizymenia* from the Pacific coast of Russia, two species were found in this region: *S. valentinae comb. nov.* and *S. tamarae sp. nov.* The distinction of *S. tamarae* is supported by phylogenetic analysis, species delimitation analyses and morphological traits. The main features of this species are its small size and the presence of small, ovoid, elongated or pear-shaped glandular cells located deeply in the cortex (formed from the second or third cell of the inner cortex; Table 1). Small blades are characteristic of *S. tenuis*, but the glandular cells of this species are longer, narrowly fusiform, and extend through the entire cortex to the medulla, as in *S. pacifica* (Saunders *et al.* 2015). Large, elongated, ellipsoid and clavate glandular cells are characteristic of *S. dubyi* and *S. apoda* (Ramírez *et al.* 2012; D'Archino & Zuccarello 2014), and perhaps of *S. binderi* (Kützing) J. Agardh (Agardh 1851), whereas in *S. novae-zelandiae* J. Agardh they are rounded (as illustrated in Adams 1994).

Schizymenia tamarae is only known from the Sea of Japan, where it occurs on the Russian coast, from Olga Bay in the north to Peter the Great Bay in the south, and in northern Japan.

Another result of our study is the conclusion that *S. dubyi* var. *palmata, S. jonssonii* and *Neoabbottiella valentinae* represent the same species of *Schizymenia*, which following the rules of nomenclature must be designated *S. valentinae comb. nov.* The re-evaluation of distributional data for *S. valentinae* reveals a boreal circum-polar distribution of the species. It occurs in the northwestern Pacific from Urup Island in the south to Commander Island in the North, as well as in the North Atlantic in Vestmannacyjar Archipelago off



Figs 18–26. *Schizymenia tamarae sp. nov.*

Fig. 18. Holotype of *S. tamarae sp. nov*. (LEA0001588) from Sukhoputnaya Bay (Sea of Japan) collected 6 June 2020. Scale bar = 1.5 cm.

Fig. 19. Plant with carposporangia collected 14 September 2021. Scale bar = 1 cm.

Fig. 20. Cross-section of sterile blade. Scale bar = 80 µm.

Fig. 21. Cross-section though the cortex showing deeply located glandular cell (gc) formed from the second cell of the inner cortex. Scale bar = 20 µm.

Fig. 22. Elongated glandular cell in the cortex (gc). Scale bar = 20 µm.

Fig. 23. Pear-shaped glandular cell (gc) located in outer cortex. Scale bar = 30 µm.

Fig. 24. Surface ostiole of the carposporophyte showing carposporangia. Scale bar = 30 µm.

Fig. 25. Mature gonimoblast. Scale bar = 50 µm.

Fig. 26. Carpospores. Scale bar = 60 µm.

the South coast of Iceland, where it had recently been described as *S. jonssonii* (Gunnarsson *et al.* 2020).

Eleven species of *Schizymenia* are currently marked as accepted in AlgaeBase (Guiry & Giury 2022). However, the actual number of species in the genus may be lower. As noted above, the placement of three of the species assigned to *Schizymenia* is questionable. The distinctness of *S. tenuis* to *S. pacifica* is doubtful based on our results. Morphologically, these two species are almost identical; the genetic divergence is also low (5–6 bp in COI-5′ and 3–5 bp in *rbc*L); moreover, both species occur in sympatry, although *S. tenuis* is typically more northerly in its distribution (Saunders *et al.* 2015). These values are lower than the divergence between the Pacific and Atlantic populations previously attributed to *S. jonssonii* (this study) and between Australian and Japanese *S. dubyi* (1.34% for *rbc*L, this study). The level of *rbc*L divergence between *S. pacifica* and *S. tenuis* was in the same range as infraspecific divergence in *S. apoda* and *S. dubyi*, and was comparable to divergence within *S. pacifica* (Table 2). Such levels of divergence correspond to geographic variability in other species of red algae: e.g. *Mastocarpus pacificus* (Kjellman) Perestenko (0.7% for *rbc*L and 1.7% for COI-5′ between Japanese and Alaskan populations; Lindstrom *et al.* 2011), *Mazzaella laminarioides* (Bory) Fredericq (0.7%–1.3% for *rbc*L and 3.2%–6.9% for COI along the south-east Pacific; Montecinos *et al.* 2012), *Gracilaria salicornia* (C. Agardh) E.Y. Dawson (up to 1.3% for COI; Yang *et al.* 2013). DNA-based species delimitation methods also suggest that *S. tenuis* and *S. pacifica* belong to a single species (Figs S1, S2). It is likely that further study can show that *S. tenuis* should not be maintained as separate species from *S. pacifica*.

To date three species of *Schizymenia* have been known from the northwestern Pacific: *S. pacifica, S. dubyi* and *S. apoda* (Perestenko 1994; Lee & Kang 2001; Lee 2008; Liu 2008; Gabriel *et al.* 2011; Kim *et al.* 2012; Yoshida *et al.* 2015). The occurrence of *S. dubyi* and *S. apoda* was genetically confirmed in this area (Kim *et al.* 2012). The question of the occurrence of *S. pacifica* in the northwestern Pacific remains open. To clarify this issue further studies are needed. We analysed herbarium specimens stored in the LE Herbarium of V.L. Komarov Botanical Institute (St. Petersburg, Russia), and in the Museum of A.V. Zhirmunsky National Scientific Center of Marine Biology, FEB RAS (MIMB, Vladivostok, Russia) and found that none of the specimens marked as *S. pacifica* can be attributed to this species. Specimens collected at the Kuril Islands, southeastern Kamchatka, and on the Commander Islands were morphologically identical to *S. valentinae*, whereas species collected in Olga Bay and in Peter the Great Bay (Russian coast of the Sea of Japan) were identical to *S. tamarae*.

This study extends our knowledge of species diversity of the genus *Schizymenia*. Four species of the genus occur in the northwestern Pacific: *S. apoda, S. dubyi, S. valentinae* and *S. tamarae*. Along the Russian coast only *S. valentinae* and *S. tamarae* are found.

ACKNOWLEDGEMENTS

We are deeply grateful to the divers A.S. Oskolkov, K.K. Dudka and I.N. Ivanov for collecting seaweeds during the 56th expedition aboard the R/V Academic Oparin to the Sea of Okhotsk and Northwest Pacific. We thank Dr. Gayle Hansen for providing samples of *S. pacifica* from Oregon and Prof. Kazuhiro Kogame (Hokkaido University) for the photos of the original samples of *S. dubyi* var. *palmata*. We also thank Dr. T. Mikhaylova (V.L. Komarov Botanical Institute) for the opportunity to study the herbarium specimens of *Schizymenia* and *Neoabbottiella*.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

FUNDING

The study was funded by the Russian Science Foundation, project number 22-24-00024. “Gigartinales of Russian Far East: diversity, taxonomy, phylogeny”, https://rscf.ru/project/22-24-00024

AUTHOR CONTRIBUTIONS

O.S. Belous: light microscopy, manuscript preparation. S.Yu. Shibneva: analysis of molecular data, manuscript preparation. A.V. Skriptsova: seaweeds collection, original concept, manuscript preparation. A.A. Semenchenko: DNA sequencing, analysis of molecular data.

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