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RESEARCH PAPER

Taxonomic revision of kelp species with rhizome-like holdfast, *Laminaria longipes* Bory and *Laminaria repens* Ruprecht, from Russian Far Eastern seas

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ABSTRACT

In this paper, we describe the historical background of one *Laminaria* J.V. Lamouroux species from the northern Pacific region. In the references, two different *Laminaria* species were recorded under the same name, *Laminaria longipes* Bory, due to errors in the labeling of authentic herbarium specimens, a very brief description, confusion of protologues, and the absence of type specimens. One of them, inhabiting the northern Atlantic Ocean, has rhizoids, whereas the second one from the Pacific Ocean has holdfast with rhizomes. The latter species was described by Ruprecht (1850) as *Laminaria repens* Ruprecht, however, due to various reasons this name was not scientifically accepted and in 19th century, this kelp species has been named differently, until the name *L. longipes* was universally accepted. None of its previous names were typified. We found original specimens collected in the 18th and 19th centuries that were used to describe these species, designated lectotypes and specified synonyms. We propose to return the name *L. repens* for the Pacific *Laminaria* species with rhizomes. Based on molecular-phylogenetic data of our specimens, we confirmed its validity and difference from another species with rhizomes distributed in the Pacific North America, *L. sinclairii* (Harvey ex JD Hooker & Harvey) Farlow, Anderson & Eaton. We also discuss developmental biology and ecology of *L. repens* from the Russian Far East, provide data on the geographical distribution of all known forms of this species and show that their areas, except for the Middle Kurile Islands, where they have been known so far, cover almost the entire distribution of this species.

Keywords: lectotypification, morphology, COI, Laminariales, *Laminaria longipes*, *Laminaria repens*, *Laminaria ruprechtiana*, Avacha Bay, Kamchatka

РЕЗЮМЕ

Климова А.В., Клочкова Т.А., Клочкова Н.Г. Таксономическая ревизия видов ламинарий со стелющимися ризомами, *Laminaria longipes* Bory и *Laminaria repens* Ruprecht, из дальневосточных морей России. Описана запутанная история изучения одного из северотихоокеанских представителей рода *Laminaria* J.V. Lamouroux. Показано, что в научной литературе из-за ошибок в этикетировании аутеничных гербарных образцов, исключительной краткости и путаности протологов и отсутствия типовых образцов название *Laminaria longipes* Bory имели два разных вида этого рода. Один из них, обитатель северной Атлантики, имеет ризоиды, другой, тихоокеанский, прикрепляется стелющимися ризомами. Последний в публикации Рупрехта (1850) был описан как *Laminaria repens* Ruprecht, однако по разным причинам это название в науке не прижилось. В позапрошлом веке его называли по-разному, пока за ним не закрепилось имя *L. longipes*. При этом ни одно из использовавшихся ранее его названий не было типифицировано. Авторы настоящей статьи обнаружили в гербарных коллекциях ламинариевых, собранных в XVIII и XIX веках, образцы, послужившие основанием для описания этих видов, выделили их лектотипы и указали их синонимы. Азиатско-тихоокеанскому виду *Laminaria* с ризомами мы предлагаем вернуть название *L. repens*. Данные молекулярной филогении его представителей из типового места обитания Авачинской губы (восточная Камчатка) подтвердили его валидность и отличие от другого близкого по морфологии тихоокеанского североамериканского вида *L. sinclairii* (Harvey ex J.D. Hooker & Harvey) Farlow, Anderson & Eaton. Также подробно рассмотрены биология развития, экология и участие *L. repens* в формировании водорослевых зарослей на российском Дальнем Востоке. Приведены данные по географическому распространению всех известных форм этого вида и показано, что их ареалы кроме Средних Курил, где они были известны до сих пор, охватывают практически весь ареал этого вида.

Ключевые слова: лектотипификация, морфология, COI, Laminariales, *Laminaria longipes*, *Laminaria repens*, *Laminaria ruprechtiana*, Ачинская губа, Камчатка

In the northern Pacific region, the kelp species were first collected in early 18th century by S.P. Krasheninnikov and G.W. Steller during the Second Kamchatka Expedition by V.J. Bering (1733–1743). Later, these specimens were used by S.G. Gmelin to prepare his phycological-floristic summary entitled "Historia fucorum" (Gmelin 1768). Thereafter, algal species composition of the northern Pacific Ocean was studied during several Russian round-the-world expeditions by the naturalists G.H. Langsdorff, W.G. Tilesius, J.C. Horner (expedition by A.J. Krusenstern and Ju.F. Lisyansky, 1803–1806), A. Chamisso (expedition by O.E. Kotzebue, 1815–1818), and K.H. Mertens, G.J. Kastalsky, and A.G. Postels

(expeditions by F.P. Lütke and M.N. Stanyukevich, 1826–1829). Most herbarium specimens collected during these expeditions were transferred to the Russian Academy of Sciences and subsequently used by A.F. Postels and F.I. Ruprecht to prepare a monograph on seaweeds from the northern Pacific Ocean (Postels & Ruprecht 1840). It included descriptions and high-quality color illustrations of the several members of Laminariales made by A.G. Postels. Also, specimens collected by naturalists mentioned above were transferred to the foreign herbaria and used at different times by V.-S. Dumortier (1822), J.G. Agardh (1848, 1868), J.E.W. Areschoug (1884), and others.

Laminaria longipes was described by Bory de Saint-Vincent (1826) on the basis of herbarium specimens obtained by him from F.K. Mertens, father of K.H. Mertens, who participated in the expedition of F.B. Lütke and M.N. Stanyukevich. In the protologue of the species, Kamchatka was indicated as its distribution area. Later, a reference to F.K. Mertens, an erroneous inclusion of Kamchatka in the range of this species, the extreme brevity of description, and the absence of a type specimen led to the fact that two different kelp species, one from the Atlantic Ocean and the other from the Pacific Ocean, had the same name *L. longipes* until present time.

The reasons behind this confusion based on the history of these species' study are shown below. In accordance with the rules of the Code of Botanical Nomenclature, the replacing name *L. repens* was proposed for the Pacific species *L. longipes*. Its independence is substantiated by sequencing data of specimens collected in the waters off Kamchatka. In addition, we discuss peculiarities of age development and ecology of this species from the Pacific region, as well as the distribution of its known forms.

MATERIAL AND METHODS

Sample collection and specimen observation

The main material for the study of age development, ecology, and morphological variability of *L. repens* was collected by us in 2000–2014 during the algal flora studies in the waters off Kamchatka (Klochkova et al. 2003, 2009) and the study of algal resources (Klochkova & Klochkova 2020).

Herbarium collections from Kamchatka and Ozernaya bays, Northern and Middle Kuril Islands, and Commander Islands, which were collected by M.V. Sukhoveeva, V.S. Ogorodnikov, A.E. Kusidi, and A.V. Klimova, were examined. We also studied herbarium specimens of species with rhizomes that belong to original material from the Komarov Botanical Institute RAS (LE), Muséum National d'Histoire Naturelle (PC), Natural History Museum (BM), and other specimens using online herbarium databases at ALA, F, FHL, MICH, NHA, NY, UC and WTU (open access https://macroalgae.org/portal/). Herbarium codes are given according to Triers (2022). Abbreviations of authors names are given according to IPNI (2022). The protologues, type specimens of all species, information from AlgaeBase (Guiry & Guiry 2022), and Index Nominum Algarum (2022) databases were analyzed during our research.

To refine the range of *L. repens* and morphologically similar species *L. sinclairii*, we used data of The Global Biodiversity Information Facility (GBIF 2020a, 2020b) (Fig. 1). Fresh specimens collected from the Avacha Bay in September 2019 were used to study the features of the internal structure of *L. repens*. To study the anatomy of plants, we made cross sections (6–10 µm thick) in different parts of the thallus using a Starlet 2212 Cryostat microtome (Bright, UK) and examined them using an Olympus BX53 microscope equipped with Olympus DP73 camera (Olympus, Japan).

Samples for molecular genetic analysis were collected on the Paramushir Island (Kuril Islands) on August 16, 2002 by N. Klochkova (Fig. 1).

Molecular identification and phylogenetic analysis

Isolation of DNA and amplification, sequencing, and analysis of nucleotide sequences were performed used the methods described in previous works (Klochkova et al. 2017, Klimova et al. 2018).

The nuclear-encoded ITS was amplified with the primer sets LB1-BC2 (ITS1 region) and YB1-LB2 (ITS2 region) (Saunders & Druehl 1993), and partial mitochondrial COI gene was amplified using the primer set GazF2-GazR2 (Yoon & Boo 1999, Lane et al. 2006, 2007). TaKaRa Ex Taq polymerase (Takara Biomedicals, Otsu, Japan) was used for the polymerase chain reaction (PCR) amplifications. The following PCR program was used: initial denaturation at 95°C for 4 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s, extension at 72°C for 1.5 min and a final extension at 72°C for 10 min. PCR products were checked on 1.2% agarose gel (Agarose LE Analytical, NobleChem, Molecular Grade, NobleBio, Suwon, Korea) for length,

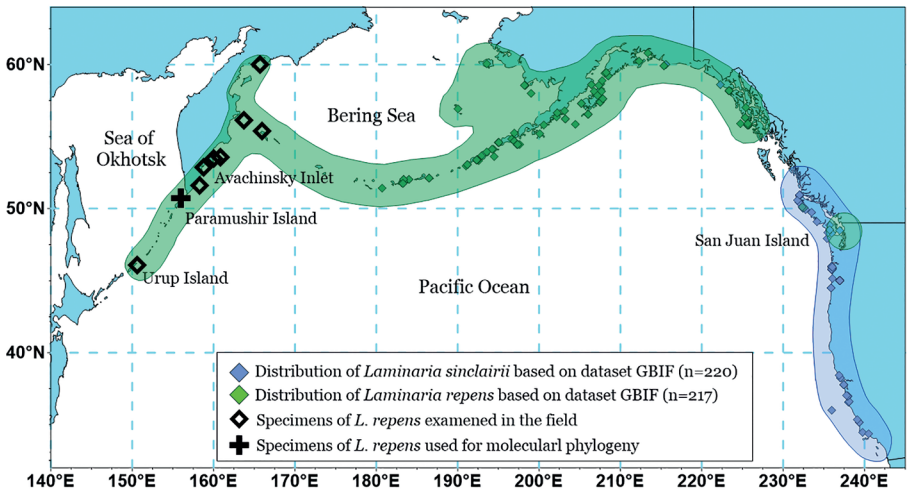

Figure 1 Distribution of *Laminaria repens* and *L. sinclairii* in the North Pacific. Avachinsky Inlet, type locality of *L. repens*. San Juan Island, geographically isolated subtidal population of *L. repens*. +, sampling site for specimens used for DNA extraction; ◊, sampling site for specimens used for morphological and ecological observations

concentration, and purity. Sanger sequencing was performed commercially (Cosmogenetech Co. Ltd., Seoul, Korea).

Our new sequences and sequences from GenBank (NCBI 2022) were aligned using Geneious Prime 2022.0.2 (Biomatters, Auckland, New Zealand) and the alignments were refined by eye. The trees were generated using Bayesian phylogenetic analysis (MrBayes 3.2.2) (Huelsenbeck & Ronquist 2001) using a general time reversible (GTR) substitution model, 2,000,000 generations, sub-sampled every 2,000 generations and a burn-in length of 200,000 generations. Maximum likelihood analysis used RAxML 8.2.11 (Stamatakis 2014) using a GTR + gamma model. Bootstrap support values (%) were calculated based on 1,000 bootstrap replicates. Our new sequences have been deposited in GenBank under the following accession numbers: MH681775 (COI), MH681776 (ITS) and MH681777 (*rbc*L).

RESULTS

Species *L. longipes* was described by Bory de Saint-Vincent. In his protologue, he noted that in comparison with *L. saccharina* (Linnaeus) J.V. Lamouroux (= *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders), *L. longipes* has longer stipe, the blade is narrowed at the base and apex and thinner, reaching the same length but remaining narrow (Bory 1826: 189). In describing its distribution, he literally indicated the following: "Atlantic Ocean (rarely). Kamchatka". At the end of the diagnosis, Bory de Saint-Vincent reported that the studied samples were provided by Mertens and collected off the coast of Kamchatka. The protologue by Bory de Saint-Vincent did not provide more detailed information on *L. longipes* specimens that he used, the collection site and collector's name. Researchers of the past (Agardh 1848, Ruprecht 1850, Le Jolis 1855, Setchell 1899) also noted the lack of information on the authentic material and specimens' collector. They also expressed doubts about its origin from Kamchatka (Fig. 2).

Our analysis of historical information showed that F.K. Mertens has never been to Kamchatka and, therefore, could not be collector of *L. longipes* specimens from Kamchatka. Indeed, his son K.H. Mertens participated in the expedition by F.P. Lütke and M.N. Stanyukevich (1826–1829), but he also could not collect samples until 1826, as he arrived to St. Petersburg in 1826 and was included in the list of participants of the round-the-world expedition onboard "Senyavin" warship. According to historical documents, "Senyavin" arrived in Kamchatka in 1827. Thus, the mention of Kamchatka as the collection site of the specimens described by Bory de Saint-Vincent in the *L. longipes* protologue was an unfortunate mistake that subsequently led to incorrect identification of one of the Pacific species of the genus *Laminaria*.

The kelp specimens observed by Bory de Saint-Vincent is currently stored in the National Museum of Natural History (PC, Paris). To the best of our knowledge, it does not contain kelp specimens under the name *L. longipes*, however, it includes specimen PC0579528, which was collected by Bory de Saint-Vincent and identified by him as *Laminaria saccharina*, and specimen PC0484190, which was collected by Le Jolis. The morphology of both plants is similar to that indicated in the *L. longipes* protologue (Bory 1826), since their blades, indeed, are long, narrowly linear, with narrowed apex and base, extremely long stipes, and branched rhizoids.

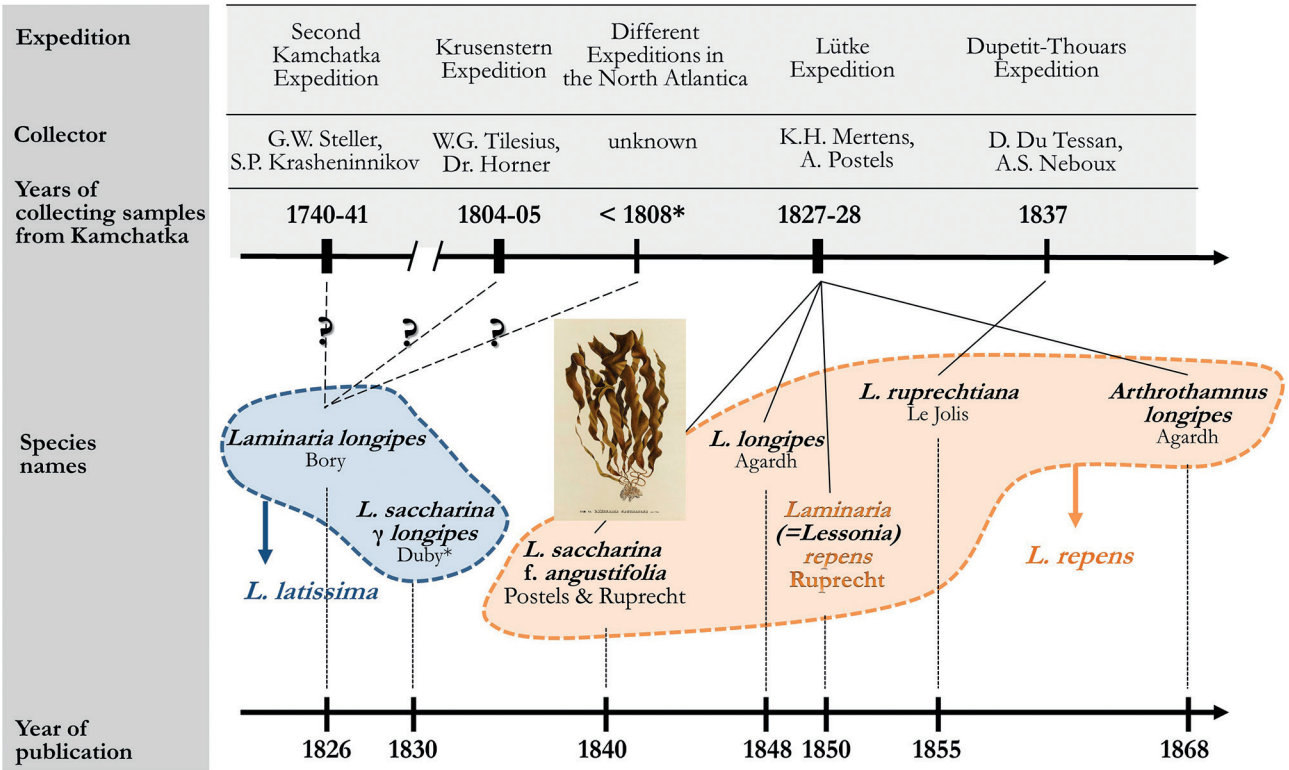

Figure 2 Historical transformation of the names of taxa associated with the species discussed: the herbarium materials that served as a basis for the description of *Laminaria longipes* from the Atlantic Ocean and rhizome *Laminaria* from the Pacific Ocean are shown. *Generalized collections of laminariacean algae made before 1808 off the coast of Europe

In the mid-19th century, French botanist A. Le Jolis, who studied kelp from the Bory de Saint-Vincent's collection, noted that the specimens that were used as a basis for the description of *L. longipes* were obtained from Mertens in 1808 under the name *Laminaria saccharina* var. *longipes* (Bory) Chauvin ex Duby. He also pointed out that, indeed, they belong to *L. saccharina* and are very similar to the specimens of this species from the coast off Normandy [France], which were signed by Bory de Saint-Vincent as *L. saccharina* var. *longipes* (Le Jolis 1855). However, A. Le Jolis also did not specify their collection site and the collector's name.

The herbarium collection by Bory de Saint-Vincent stored in the National Museum of Natural History (PC, Paris) includes specimen PC0579467, which was assigned to *Saccharina latissima* (Fig. 3A,B). It is signed (apparently by Bory de Saint-Vincent) as "*Fucus saccharinus longipes (Mertens. 1808) ex Ocean. Septembr.*" The inscription on its label repeats information provided by A. Le Jolis (1855). The curator of the PC collection of algae informed us that the Bory's collection includes only one specimen with the inscription "*(Mertens. 1808)*". We believe that it was Bory's label data that was included in the *L. longipes* protologue (Bory 1826) and, for this reason, propose to consider the latter a lectotype of this name.

The collection by Bory de Saint-Vincent includes two more specimens (PC0484205 and PC0579513) with very long stipes and narrowly linear blades. They are signed "*Laminaria saccharina var. longipes*" and "*Laminaria cornea (longipes)*" by the same hand as specimen RS0579467. Their collection site is indicated as the Atlantic Ocean. This indirectly indicates that Bory de Saint-Vincent used the material collected in the Atlantic Ocean for the description of *L. longipes*. We believe that, due to the erroneous inclusion of Kamchatka in its range, the name *L. longipes* began to be illegally used for another Northern Pacific species.

The history of the Pacific kelp study developed as follows. Part of the seaweed herbarium collection by F.K. Mertens was lost (Womersley 1967, Dawson et al. 1964), and after his death the remaining specimens were acquired by the Imperial Botanical Garden (now the Komarov Botanical Institute (St. Petersburg, Russia, LE). However, LE herbarium does not contain *L. longipes* specimens marked "Kamchatka".

In the work by Postels & Ruprecht (1840), this species is indicated as a synonym for *L. saccharina* f. *angustifolia* Postels & Ruprecht. In description of this form, it is noted that its stipe is 3–5 inches [7–12 cm] long and more roll-shaped, arranged in clusters; blade is narrow-linear, 1 foot [from 30 cm] long and 1 inch [2.5 cm] wide, rarely widening towards the top, and leathery (Postels & Ruprecht 1840: 10). Rhizomes are not mentioned in the diagnosis. They are also absent in the drawing of *L. saccharina* f. *angustifolia* (Postels & Ruprecht 1840: pl. 11). The plant depicted on it strongly resembles *L. saccharina*, which is currently known as *Saccharina latissima*.

The collection of the Komarov Botanical Institute (LE) includes five herbarium sheets of kelp with rhizomes collected from the Avacha Bay during expedition by F.P. Lütke and M.N. Stanyukevich; three of them retain original labels, indicating "*Laminaria saccharina var. cornea*" (sheet 1), "*Laminaria saccharina f. angustifolia PR (L. longipes Bory)*" (sheet 2), "*L. longipes*" (sheet 3). Sheet 2 also has an additional inscription "*Lessonia repens*" written by Ruprecht (Fig. 3C,D), most likely made by him during the study of algae from the Sea of Okhotsk, when for the first time he described kelp with creeping rhizomes (Ruprecht 1850) under the name *Lessonia repens* Ruprecht.

In addition to LE herbarium, specimens of kelp with rhizomes from the Avacha Bay collected during the expeditions by F.P. Lütke and M.N. Stanyukevich are also stored in herbaria abroad. One of them (MNHN-PC-PC0044629) was discovered by us in the National Museum of Natural History (Muséum National d'Histoire Naturelle, Paris, PC); the second (BM000563288) – in the British Natural History Museum (London, BM).

Agardh (1848: 133) used the name *L. longipes* for the kelp from the Pacific Ocean. He specified Bory de Saint-Vincent as its author and regarded *L. saccharina* f. *angustifolia* described by Postels and Ruprecht (1840) as its synonym. Thus, Agardh returned the species *L. longipes* to the Pacific algal flora and included Kamchatka in its range (Fig. 2).

After the expedition by Lütke and Stanyukevich, kelp in the North Pacific was collected by other collectors, in particular, I.G. Voznesensky, who worked here (including the south of western Kamchatka) in 1839–1849. The specimens collected by him were mentioned by Ruprecht in the discussion of the similarity of the genera *Laminaria* and *Lessonia* in his work on algae from the Sea of Okhotsk (Ruprecht 1850). In this work, he noted that specimens from the Avacha Bay, which was previously identified by him as *L. saccharina* f. *angustifolia*, had rhizomes. On this basis, he assigned them to a separate species, *Laminaria repens* (Ruprecht 1850: 158–159). The species epithet repens is translated from Latin as creeping. It reflects the most significant trait of the species – the presence of rhizomes in it.

When distinguishing *L. repens* as an independent species, Ruprecht used the materials collected in Avacha Bay during the expedition by Lütke and Stanyukevich. Therefore, Avacha Bay, but not western Kamchatka, as it is believed today (Asensi & de Reviers 2009: 213, table 1; Guiry & Guiry 2022), is its typical habitat. In the same work, Ruprecht expressed doubts that *L. saccharina* f. *angustifolia* and *L. longipes* Bory de Saint-Vincen belong to the same biological species, but did not specify the latter as a synonym for *L. repens*.

In estimating the taxonomic characters of *L. repens*, Ruprecht did not definitively determine her generic affiliation. He assigned it first to the genus *Laminaria* and then to the genus *Lessonia* (alternative name). Later, Agardh in his revision of the kelp of the World Ocean indicated the Pacific rhizome kelp as a member of the genus *Arthrothamnus* Ruprecht with the species name *longipes* (Agardh 1868: 26, 27). Fifteen years later, Areschoug (1884) transferred *A. longipes* (Bory) J. Agardh into the genus *Laminaria*, after which the species name "*longipes*," proposed by Agardh, was finally assigned to the rhizome Pacific kelp.

Since Ruprecht considered the same species both as *Laminaria repens* and *Lessonia repens* Ruprecht, Le Jolis proposed a new name for this species – *Laminaria ruprechtiana* Le Jolis (Le Jolis 1855: 308). In the same work, in addition to *L. longipes*

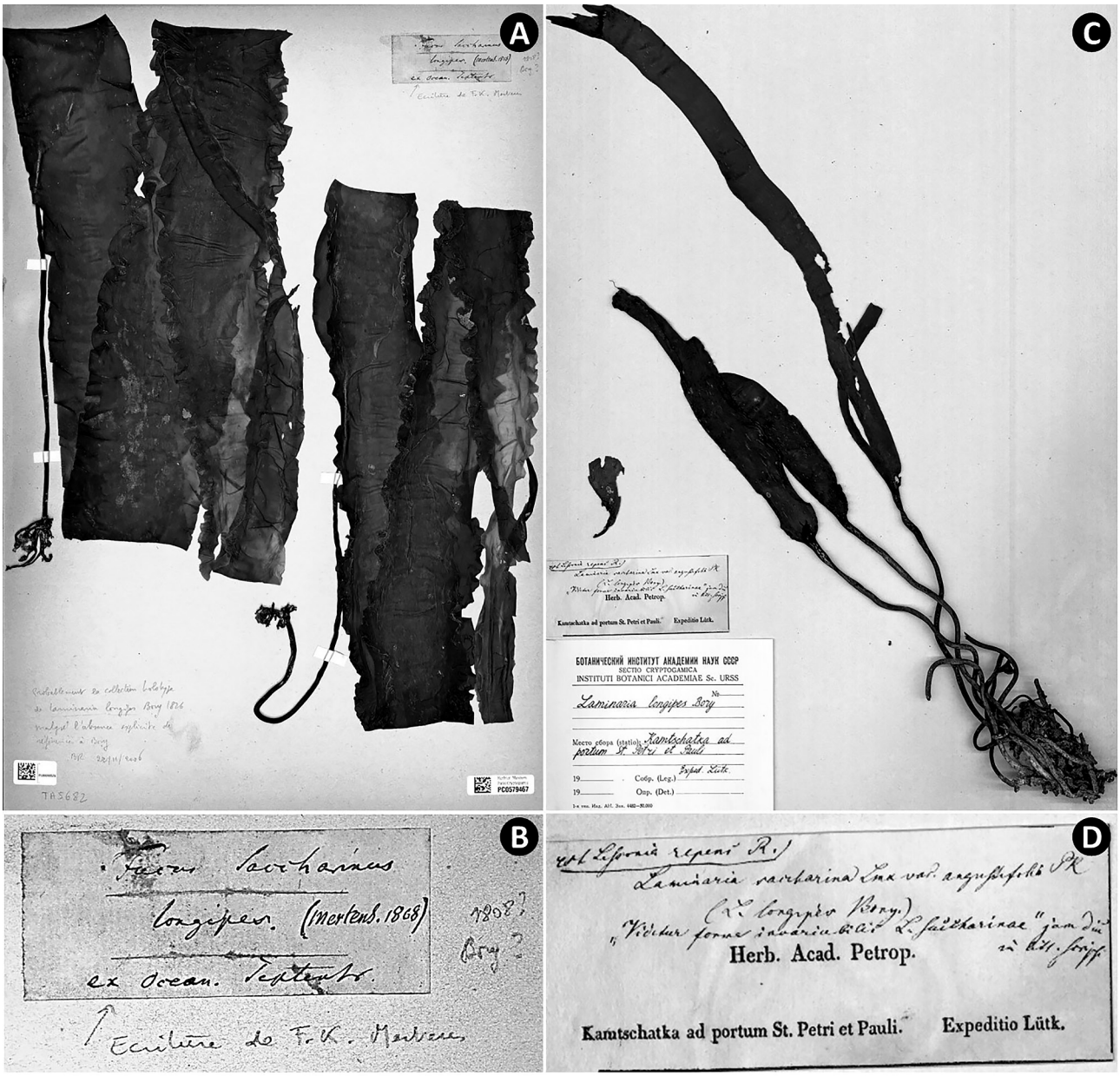

Figure 3 Type specimens of *Laminaria longipes* Bory (A & B) and *L. repens* Ruprecht (C & D). (A & B) Lectotype of *Laminaria longipes* Bory (PC0579467, PC). (C & D) Lectotype of *L. repens* Ruprecht (LE-A0000130, LE)

from the Bory collection, he mentioned the herbarium specimens collected off Kamchatka during the expedition by Petit-Thouars on board the Venera frigate (1836–1839). Among the latter, three herbarium sheets of rhizome kelp have been preserved in PC (PC0513038, PC0515995, and PC0199773), which have inscriptions "… *Laminaria ruprechtii* Le Jolis*, L. saccharina angustifolia* Post & Rupr.*, Laminaria longipes* Ag. – non Bory ... *Kamschatka*..". Another specimen from the same collections, BM000563289, is now stored in the herbarium of VM. It is specified as the type specimen of *Laminaria ruprechtiana*. Its label is the same as that of the PC specimens, with an additional inscription: "*Lessonia longipes Rupr. (non Lam. longipes Bory) ... Kamschatka* ...".

Thus, the history of the study of the Pacific rhizome kelp species shows that, in the century before last, the species names "*longipes*", "*repens*", and "*ruprechtiana*" ("*ruprechtii*" is written on herbarium specimens) were used for its designation, and it was assigned to the genera *Laminaria*, *Lessonia*, and *Arthrothamnus* (Fig. 2). Since the end of the 19th century, its name in the algological literature is *Laminaria longipes*. This can be seen from the revisions of Laminariales (Markham 1972, Petrov 1975, Kain 1979), annotated bibliographies on seaweeds of Alaska (Lindstrom 1977), and the western coast of the Bering Sea and southeastern Kamchatka (Klochkova 1998), as well as from more recent publications (Bartsch et al. 2008, Klochkova et al. 2009, Lindeberg & Lindstrom 2010).

Botanical nomenclature rules prohibit calling different species by the same name. They require that the junior homonym must be renamed. In our case, the species epithet *longipes* was first used for the Atlantic *Laminaria* species described by Bory de Saint-Vincent (1826). Therefore, in the Pacific species with the same name, it must be changed. The publication by Ruprecht (1850) is the first work in which its

species-specific morphological traits are specified: narrowly linear blades, long stipes, and rhizomes. In this work, this species is named *L. repens*, and we believe that this should be the name of the Pacific rhizome species. We propose that the specimen from the LE collection shown in Figure 3C,D with the additional inscription "*Lessonia repens*", made by Ruprecht, should be considered a lectotype of the species *Laminaria repens*, and Avacha Bay, as mentioned above, should be considered its type habitat.

In the scientific literature, three forms of the discussed species from the North Pacific are known: f. *angustifolia* (Post. et Rupr.) Miyabe et Nagai, f. *linearis* Miyabe et Nagai, and f. *latifolia* Yamada (Nagai 1940), although the latter was described by Yamada (1935) in the status of a variety. Tokida (1954) suggested considering *L. longipes* f. *angustifolia* the type form of the species and assigned it to the synonyms *L. longipes* f. *typica* Tokida. However, it cannot be the type form, because, according to ICN, it is a nomen superfluum (Code, Art. 52.1). The form f. *angustifolia*, described by Postels and Ruprecht (1840), also cannot be the type form. In this regard, we propose that plants with the traits typical for the specimens from the type habitat, Avacha Bay, should be assigned to the type form *L. repens* f. *repens*.

The data on the type specimens of the species mentioned in this work, which were collected by us, are summarized below, and new nomenclature combinations are proposed.

***Laminaria longipes* Bory (1826: 189).**

Lectotypus (here designated): − Accurate location not indicated, no date, collector is not identified [ex Ocean. Septembr.] (PC0579467[seen digital image!]), Fig. 3A,B.

= *Laminaria saccharina* var. *longipes* (Bory) Chauvin ex Duby (1830: 940), *Saccharina longipes* (Bory) Kuntze (1891: 915, 940)

Notes: We consider *L. longipes* Bory as heterotypic synonym of *S. latissima* (Linnaeus) CE Lane, C. Mayes, Druehl & GW Saunders.

***Laminaria repens* Ruprecht emend. Klimova et T. Klochkova (Ruprecht, 1850: 158, 159).**

Lectotypus (here designated): − RUSSIA. Kamchatka, Avacha bay, collector is not identified [Kamchatka ad portum St. Petri et Pauli] (LE A0000130!), Fig. 3C,D.

Paralectotypus: LE-A0000131!, LE-A0000132!, LE-A0000133!, LE-A0000134!, MNHN-PC-PC0044629 [seen digital image!], BM000563288 [seen digital image!].

= *Laminaria saccharina* f. *angustifolia* Postels & Ruprecht (1840: 10), *Laminaria longipes* Agardh (1848: 133) non *Laminaria longipes* Bory (1826: 189), *Lessonia repens* Ruprecht (1850: 158, 159); *Arthrothamnus longipes* (Bory) J. Agardh (1868: 26, 27).

≡ *Laminaria ruprechtiana* Le Jolis (1855: 308), *Laminaria longipes* f. *typica* Miyabe et Tokida (1954: 114).

Forms:

Laminaria repens* f. *repens Klimova et T. Klochkova **comb. nov.**

= *Laminaria longipes* f. *angustifolia* (Postels & Ruprecht) Miyabe et Nagai (1940: 68), *Laminaria longipes* f. *typica* Miybe et Tokida (1954: 114).

Laminaria repens* f. *linearis (Miyabe et Nagai) Klimova et T. Klochkova **comb. nov.**

Basionym: *Laminaria longipes* f. *linearis* Myabey et Nagai (1940: 48).

Laminaria repens* f. *latifolia (Yamada) Klimova et T. Klochkova **comb. nov.**

Basionym: *Laminaria longipes* var. *latifolia* Yamada (1935: 18).

Morphology and anatomy

The Pacific species *L. repens* differs well from the overwhelming majority of other members of Laminariales by the specific structure of the holdfast (Fig. 4A). They are creeping rhizomes with numerous stipes extending from them, which bear single blades (Fig. 4B). The creeping rhizome-like holdfast is very rarely found in members of the genus *Laminaria*. In addition to *L. repens*, it is present in only two kelp species – *L. rodriguezii* Bornet, 1888 and *L. sinclairii* (Harvey ex JD Hooker et Harvey) Farlow, Anderson et Eaton, 1878. The former is a deep-sea endemic of the Mediterranean Sea (Boisset et al. 2016), and the latter is found only off the coast of North America and has a rather narrow range there (Abbott & Hollenberg 1976, Markham 1972), which slightly overlaps with the range of *L. repens*. The two Pacific species *L. repens* and *L. sinclairii* are almost identical in terms of their morphology and differ in that the stipe of the latter contains mucous ducts (Markham 1972). The diagnostic value of this trait is not absolute (Petrov 1975, McDevit & Saunders 2010), because their presence or absence strongly depends on the growing conditions (Dankworth et al. 2020). We have repeatedly observed this phenomenon in the Kamchatka kelp species *Laminaria yezoensis* Miyabe and *Hedophyllum bongardianum* (Postels & Ruprecht) Yendo.

The thallus of *L. repens* consists of the blade, stipe, and holdfast. The blades are narrow, belt-like, almost uniform in width and thickness, rigid, with a smooth surface, without bullae even in juvenile age (Fig. 4B). The length of adult plants varies depending on the area and growing conditions from 30 cm to 195 cm, and the width varies from 0.5 to 13 cm. The stipes of this species are thin, long, glossy, fairly flexible, darker than the blade, dark brown or nearly black. Their length in the type form of the species may reach 38 cm, the thickness does not exceed 0.79 cm in diameter. Near the Asian coast, the ratio of the average length of the blade to the average length of the stipe differs in different geographic regions and is, on average, 2.9, 3.7, and 6.4 off Northern Kuriles, Commander Islands, and southeastern Kamchatka, respectively. This rather significant difference can be explained by the confinement of the species to a different range of depths in each of the above-mentioned areas. The holdfast (rhizomes) is creeping, intertwining shoots with loose bundles of branched rhizoidal outgrowths attached to the substrate by small suckers. In multiannual thickets of the species, the rhizomes cover the surface of the substrate with an almost continuous layer (Fig. 4A).

The internal structure of the species is fairly typical of the kelp algae (Fig. 4C–J). The blade thickness in adult plants does not exceed 1.95 mm. The meristoderm consists of 2–3 layers of colored cells (Fig. 4C). The sporiferous tissue develops from the initial meristodermal cells (Fig. 4D). The thickness of mature sporiferous tissue layer varies from 95 to 115 μm, sometimes reaching 130 μm (Fig. 4E). Unicellular paraphyses have well-defined mucous caps up to 25 μm in height (Fig. 4E, dashed arrow). Mature sporangia are 60–80 μm in length, occur singly or in small groups among numerous paraphyses surrounding them (Fig. 4F, solid arrow). The cortical layer consists of 7–10 layers of tightly closed spherical cells. Its medullary tissue

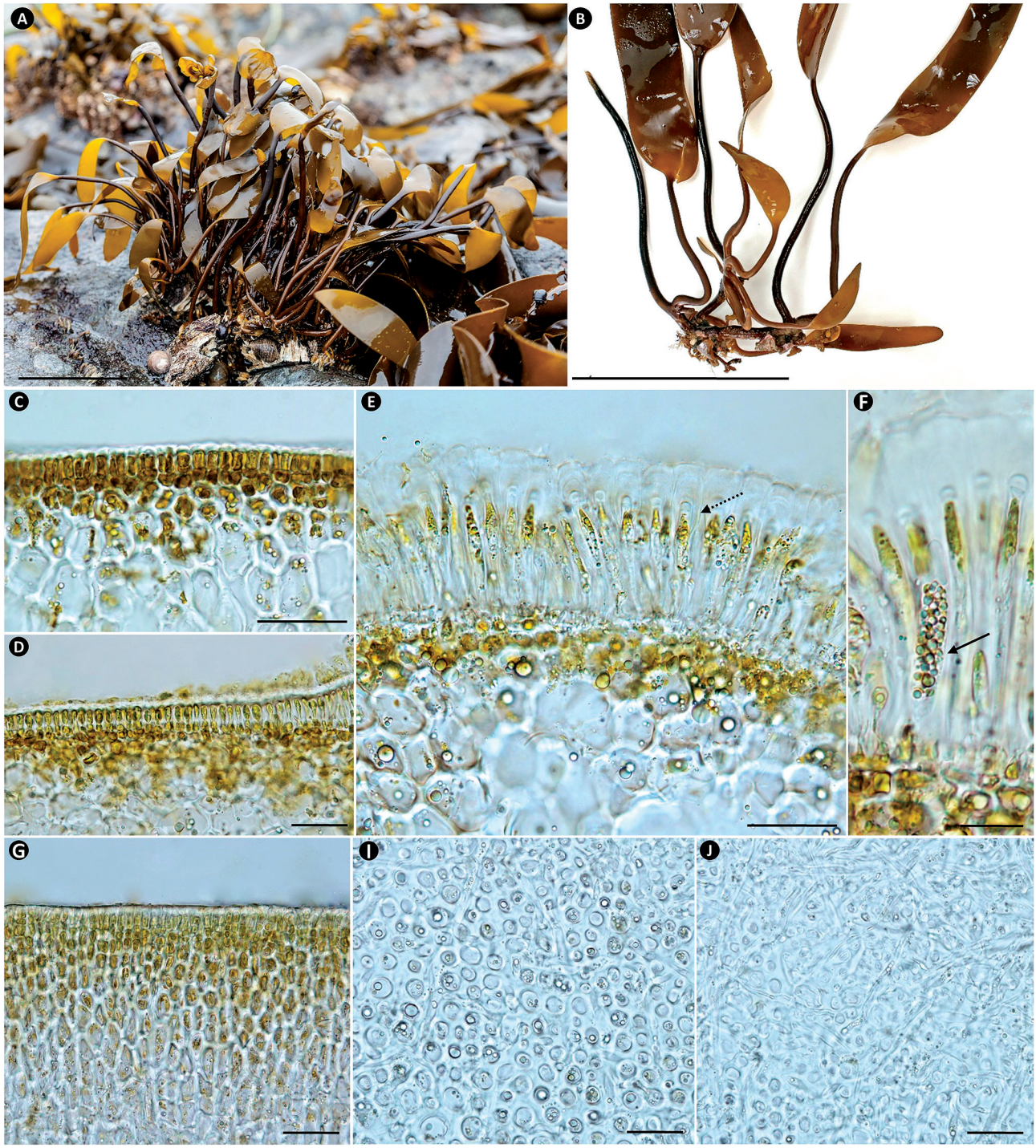

Figure 4 Gross morphology and anatomy of *Laminaria repens* Ruprecht. (A) Plants in Paramushir intertidal, Kuril Islands. (B) Specimen collected from Avachinsky Inlet, eastern Kamchatka. (C–D) Blade in cross-section. (C) Meristoderm is 2-3 cell-layers thick. (D) Region of transition from sterile tissue to sporangial sori. (E) Mature sporangia-bearing tissue with paraphyses (dashed arrow). (F) Unicellular sporangia (solid arrow). (G–J) Stipe in cross-section. (G) Meristoderm is 8–9 cell-layers thick. (I) Inner cortex. (J) Medullar composed of hyphae-like filaments. Scale bars represent: A & B, 10 cm; C–E & G–J – 50 μm; F – 20 μm

is denser, cells (even in young specimens) have rather thick cell walls, the core occupies less than 1/3 of the total cross-sectional thickness. Such internal structure increases the elasticity of thalli and, therefore, the ability to colonize surf habitats with turbulent and high-speed laminar water flows. Sporadic mucous ducts develop in the subcortical layer of the blade. The stipes, judging by the results of our studies, do not have them (Fig. 4G–J).

Molecular-phylogenetic analysis

Today, data of molecular phylogeny of nuclear, plastid, and mitochondrial genes are widely used in the taxonomy of laminariacean algae. The taxonomic affiliation of many members of this group has been confirmed or revised in recent decades (Lane et al. 2006, 2007, Boo et al. 2011, Kawai et al. 2017, Starko et al. 2019). In this regard, the genus *Laminaria* s. l. has undergone significant changes, and currently its members are usually divided into

three groups: *Laminaria* s. s., *Saccharina* Stackhouse and *Hedophyllum* Setchell (Lane et al. 2007, Starko et al. 2019). For many species and genera of Far Eastern kelp algae, the taxonomic position has not yet been clarified. Comparative study of *L. sinclairii* and *L. repens* at the molecular level has not been performed before, because, up to the present studies, data of molecular phylogeny for *L. repens* were absent. The determination of the nucleotide sequences of COI, *r*DNA, and *rbc*L performed by us in representatives of the species of interest, which were collected in the waters off the Kamchatka Peninsula, made it possible to clarify its position among the laminariacean algae. In the presented molecular tree, *L. repens* forms a separate branch in the clade *Laminaria* (Fig. 5). It should also be noted that it is genetically different from the morphologically similar species *L. sinclairii*. To refine the taxonomic position of the species in the system of kelp algae, we used the most representative marker, COI. It should also be noted that, judging by our data, isolation of new taxa from the existing genus *Laminaria* can be expected in the near future, because the Pacific members of this genus significantly differ from its representatives from the Atlantic Ocean. The level of distinctions between them corresponds to that between the genera *Saccharina* and *Hedophyllum*.

Developmental biology of the species in the Asian part of the distributional range and morphogenesis

Laminaria repens is one of the few representatives of kelp algae that are capable of active vegetative reproduction, which is dominant for it. New blades in this species are formed from creeping rhizomes. First, meristematic tubercles appear on the creeping shoots. Then, they give rise to the development of stipes, on the tops of which blades are laid. They grow as the length of stipes increases. After the end of the first growing season, the blades in *L. repens* are not destroyed, unlike the vast majority of other kelp species. After the appearance of a new section of the blade in the second year of life, its last year's section is displaced upwards. During the third growing season, the blade of *L. repens* already consists of three areas of different ages. They are separated from one another by more or less pronounced constrictions and differ in thickness, texture, and color (Fig. 6A,C: solid arrow). The uppermost part of the blade at the end of the growing season is coarser, often with epiphytic and endophytic flora. Sometimes it is completely destroyed even before the end of the third growing season.

In the waters off Kamchatka in the second year of life, the overwintered parts of the blades actively grow and accumulate mass. Due to this fact, this part of the blade is always longer and thicker than the current year's part. In the third growing season, the length of the blades, especially in surf habitats, practically does not increase due to the gradual destruction of the oldest upper part. The stipe reaches its main length during the first year of life. In the second growing season, its growth does not exceed 4 cm, and in the last year of life it stops to grow and only slightly increases in thickness. The main accumulation of thallus mass in *L. repens* is also observed in the second year of life.

The results of comparative analysis of the average length of blades and stipes and their average mass in the Kamchatka plants of the first, second, and third years of vegetation in the period of active spring growth show that they are the highest in the plants of the second year of life. At the end of the third growing season, the average values of all parameters decrease. This can be explained by the fact that the *L. repens* population under the influence of high hydrodynamic load loses, first of all, the oldest plants with the longest stipes. Their removal from the thickets of the species reduces the average size and weight of the representatives of this age group.

The results of our studies show that, in the Asian part of the range, this species shows the following strategy of age development. In the first year of life, it is aimed at increasing the linear sizes and the photosynthetic surface area. In the second year of life, the thallus continues to increase the size parameters due to the active growth of the current year's part of the blade and the less active growth of the last year's part. At the same time, a significant accumulation of thallus mass takes place. Sporangial sori are formed in some specimens. The majority of plants do not have them to the end of the growing season.

The results of the study of seasonal changes in the size and mass parameters in representatives of *L. repens* show that it has only one poorly expressed peak of growth, which is observed in the warmest month of the year, July. Other cold-temperate species of kelp inhabiting waters off Asia have two peaks of linear growth in spring and autumn. The latter to a greater extent leads to the active accumulation of the mass of the blades (Kusidi 2007, Koroleva 2010). Conversely, the water temperature above 15ºC causes an active destruction in them (Klimova 2012).

The presence of rhizomes in *L. repens* and their ability to produce additional blades determines the formation of dense clonal thickets. It colonizes the substrate better than other kelp species and can occupy the same bottom areas for many years. Asexual reproduction for this species is auxiliary.

In *L. repens*, sporiferous tissue develops on both sides of the blade. The sporangial sori on it are located without any particular order, in wide merging spots. Plants at an age of 1.5 years and older begin to reproduce asexually. The fertile tissue is usually formed on the current year's parts of the blade. The area of the sporangial sori in this species is insignificant and does not exceed 5 % of the total photosynthetic surface of the blade. After the release of zoospores, necrotic spots on the sporiferous areas are not formed. This is apparently facilitated by the active tissue regeneration. It should be noted that this ability is absent in other off-Asian kelp algae. Their blades at the sites of development of sporangial sori undergo necrosis and destruction soon after sporulation.

Ecology and involvement in vegetation cover

Near the Asian coast, *L. repens* is most widespread off the Kuril Islands. In the Central Kuriles, it occurs at depths of 0–20 m (Gusarova 1984) and forms a biomass of 0.5–20 kg/m^2 (Sukhoveeva & Sarochan 1986, Gusarova et al. 1993). Its thickets are usually accompanied by *Eualaria fistulosa* (Postels & Ruprecht) M.J. Wynne, *Cymathaere triplicata* (Postels & Ruprecht) J. Agardh, and *C. fibrosa* Nagai. In the Northern

Kuriles, the lower boundary of the species distribution lies at depths of 12–15 m (Ogorodnikov 2007). Near the southern tip of western Kamchatka, near the coast of Cape Lopatka (Cape Kambalny), *L. repens* grows in the lower horizon of the littoral zone and the upper sublittoral zone. On the hydrographic datum level, it forms dense thickets with a projective cover of 80–100 %. Here, its biomass is 3–5 kg/m^2 (Vozzhinskaya 1965).

In the waters off southeastern Kamchatka, this species is rarely found at depths greater than 8 m. The deep-sea specimens are usually larger than those growing in the sublittoral fringe. The last year's parts of the blades are almost entirely preserved until the beginning of autumn. In Avacha and Kronotsky bays, at depths of 0.5–2.5 m, the species forms clonal thickets with a density of 30–40 ind./m^2 and a biomass of over 3.6 kg/m^2 (Klochkova & Berezovskaya 1997). Here, its thickets are often accompanied by *Arthrothamnus bifidus* (S.G. Gmelin) J. Agardh. In the Bering Sea, *L. repens* sinks to a depth of 12–17 m and forms thickets with a biomass of up to 5.6 kg/m^2. To the north of Anapka Bay, it was not found (Klochkova et al. 2003).

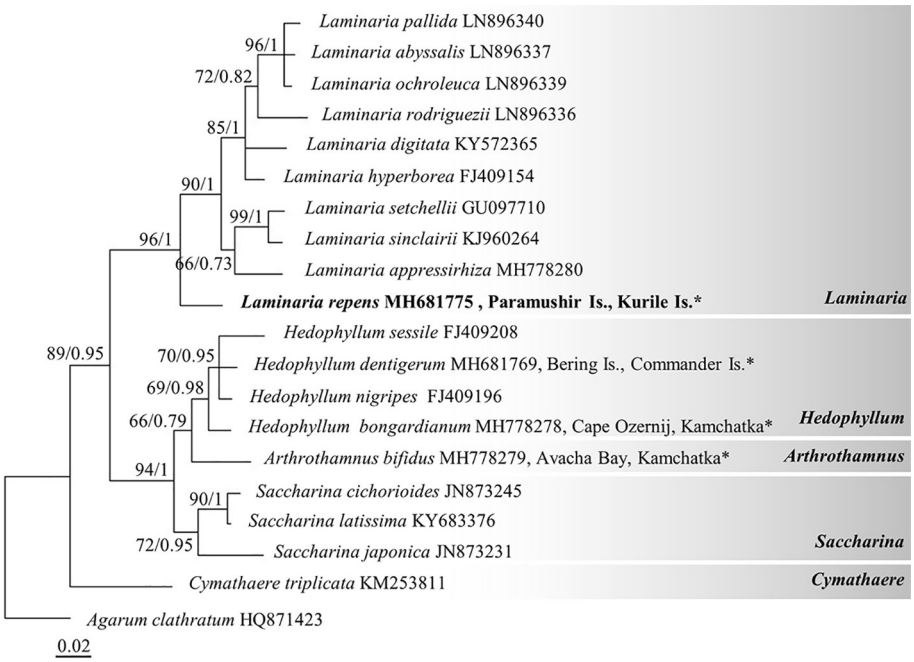

Figure 5 Bayesian inference of phylogenies of the laminariacean algae based on cytochrome c oxidase subunit 1 (COI) sequences. Labels on branches are posterior probabilities and consensus support values. Asterisks "*" indicate our new sequences

On the Commander Islands, the species of interest rises to the lower littoral zone, where it forms small in area, dense thickets with well-developed rhizomes. The maximum value of the *L. repens* biomass near the Mednyi Island is 36 kg/m^2, and the average value is 5.8 kg/m^2 (Kusakin & Ivanova 1995). Near the Bering Island, the species forms very dense thickets numbering up to 200 individuals (including the juveniles) on an area of 200 cm^2. The total mass of plants here was 1.16 kg. After recalculation per 1 m^2, the biomass of the species reaches 65 kg (Kusdi & Klochkova 2008). The thickets of *L. repens* off the Commander Islands are usually accompanied by *Alaria* Greville.

Geographic distribution and forms

Currently, in the waters off the Asian coast, *L. repens* is distributed along the eastern coast of Kamchatka from Ozernaya Bay to Cape Lopatka, in the south of western Kamchatka from Cape Lopatka to Kambalny Bay, as well as off the Commander Islands and Northern and Central Kuril Islands (Fig. 1). It was also found off the Lesser Kuril Chain islands (Sarochan 1969) and off southeastern Sakhalin (Tokida 1954). In more recent algofloristic works, it was not mentioned for the last two regions. Far Eastern zoologists Kusakin & Ivanova (1978) recorded *L. longipes* in Anadyr Bay. In our opinion, this reference is erroneous.

L. repens, similarly to other kelp algae, show wide morphological variability. It is expressed, first of all, in the change in the linear sizes of the blade, its length, width, and thickness, as well as in the length-to-width and length-to-weight ratios. The stipe undergoes less significant morphological changes. In plants of all ages, it is always sufficiently long, uniform in thickness, and, depending on the thallus age, more or less thick. The information on the anatomy, morphology, and ecology of *L. repens* presented in this work is given for its type form. For the forms *linearis* and *latifolia*, it is presented in Table 1.

The form *linearis* includes the plants with long narrowly linear blades (Table 1). According to our observations, they are characteristic of the representatives of this species that are found in the sublittoral fringe under high-surf conditions and in the phase of active linear growth. As noted above, this falls on the summer months, when the wave height and the frequency of waves become minimal, the content of nitrate nitrogen and mineral phosphorus drops to 0.6 and 0.5 µg-atom/l, respectively, and the water temperature reaches its maximum. The length of the light period of the day at this time reaches 16 h. These habitat conditions promote a rapid increase in the length of the blades of *L. repens* without increasing their width. With age, the rapidly grown plants gradually increase in width and gain mass.

The form *latifolia* is characterized by short wide blades with a rounded or even heart-shaped base (Table 1). This morphology is acquired by the representatives of the species growing in gently sloping semi-sheltered littoral zone and in littoral baths. It is, therefore, the result of ecological variability, which is expressed in the inhibition of plant growth. In the cold half of the year, littoral algae are subject to the abrasive effect of ice and the adverse effect of cyclones; therefore, their vegetation period here does not exceed 1.5 years.

Until now, it was believed that the above-mentioned forms of the species are endemic to the Kuril Islands

Table 1. Characteristics of different forms of *Laminaria repens*

Part of thallus	Dimensions / Characteristics (cm)	f. *repens*	f. *linearis*	f. *latifolia*
Blade	Length	30–58 (195)	37–62	n/d
	Width	2–4	0.5–1.2	4–13
	Form of base	cuneate	acute	broadly cuneate / rounded
Stipe	Length	13–37	7–13	3–5
	Diameter	0.3–0.79	0.2–0.3	n/d
Mucilage lacunae	Blade	present	present	n/d
	Stipe	absent	absent	absent
Sori	Side	one side	both sides	one side
	Localization	basal part	elongate patches	whole surface
Distribution	_	North Pacific	Kurile Islands, from Ketoi to Simushir	Kurile Islands, from Paramushir to Urup
Reference	_	Postels & Ruprecht (1840), Nagai (1940), Tokida (1954), present study	Nagai (1940)	Yamada (1935), Nagai (1940)

(Yamada 1935, Nagai 1940). However, the results of the study of the morphological variability of the species in the waters off Kamchatka and the familiarization with the sites of the ALAJ, NHA, MASS, MAINE, FH, and NY herbarium stocks (open accesshttps://macroalgae.org/portal/), containing the photographs of North American herbarium specimens of *L. repens*, showed that the forms described above are, in fact, more widespread and occur within nearly the entire range of this species (Fig. 6). On the photographs of the herbarium specimens from Cook Bay and waters off the San Juan Island, there are short plants with a blade more than 6 cm in width (specimens UC1468798 and FHL-A-00307). They definitely belong to f. *latifolia*. Among the Aleutian specimens, there are plants (specimens H1270989, UC1061583, and NHA-648010) with very narrow blades not more than 1 cm in width. They correspond the description of the form *linearis*.

CONCLUSIONS

In this paper, we present the results of a comprehensive study of one of the Pacific species of the genus *Laminaria* that was previously known in the scientific literature as *L. longipes*. It is shown that its lifespan off the Asian coast is 3 years. Its depth of growth and associated species change with moving from south to north. Due to its pronounced ability for vegetative reproduction in all parts of the range, it forms clonal thickets. The anatomical and morphological organization of this species contributes to its development in areas with strong waves.

The analysis of the papers containing references to this species showed that the true *L. longipes*, which was described by Bory de Saint-Vincent, is one of the many morphological forms of *Saccharina latissima*, formerly known as *L. saccharina*. This is how this species was interpreted by the Russian researchers Postels & Ruprecht (1840). However, the inclusion of Kamchatka along with the Atlantic Ocean in the range of *L. longipes* by Bory de Saint-Vincent, as well as the reference in its protologue to the specimens that were obtained by him from Mertens, gave reason to subsequent researchers to believe that *L. longipes* was described on the basis of the materials collected off Kamchatka by K.H. Mertens during the expedition by Lütke and Stanyukevich. We have shown in our work that this is not true.

The analysis of the publications of algologists of the century before last and the familiarization with the collections of kelp algae that have been stored since the century before last in the LE herbarium, as well as with their digitized images on the websites of foreign herbarium stocks, showed that the Pacific kelp that is now called *L. longipes* was described by Ruprecht (1850) as the independent species *L. repens* on the basis of the presence of creeping rhizomes in it. However, it so happened that, after repeated changes in the genus and species name of *L. repens*, the species name *L. longipes* has stuck to it, which is illegal according to ICN Art. 52.1. In this work, it is shown that the Pacific *L. longipes* is a junior homonym for *L. repens*, and therefore it was restored as a valid species.

As a typus of this species, we selected the specimen collected in Avacha Bay during the expedition by Lütke and Stanyukevich (Fig. 2). Therefore, this area, but not western Kamchatka, as was believed previously (Guiry & Guiry 2022), is the type locality of *L. repens*.

The results of our phylogenetic study confirmed that *L. repens* significantly differs in its molecular genetic organization from the morphologically similar North American species *L. sinclairii*.

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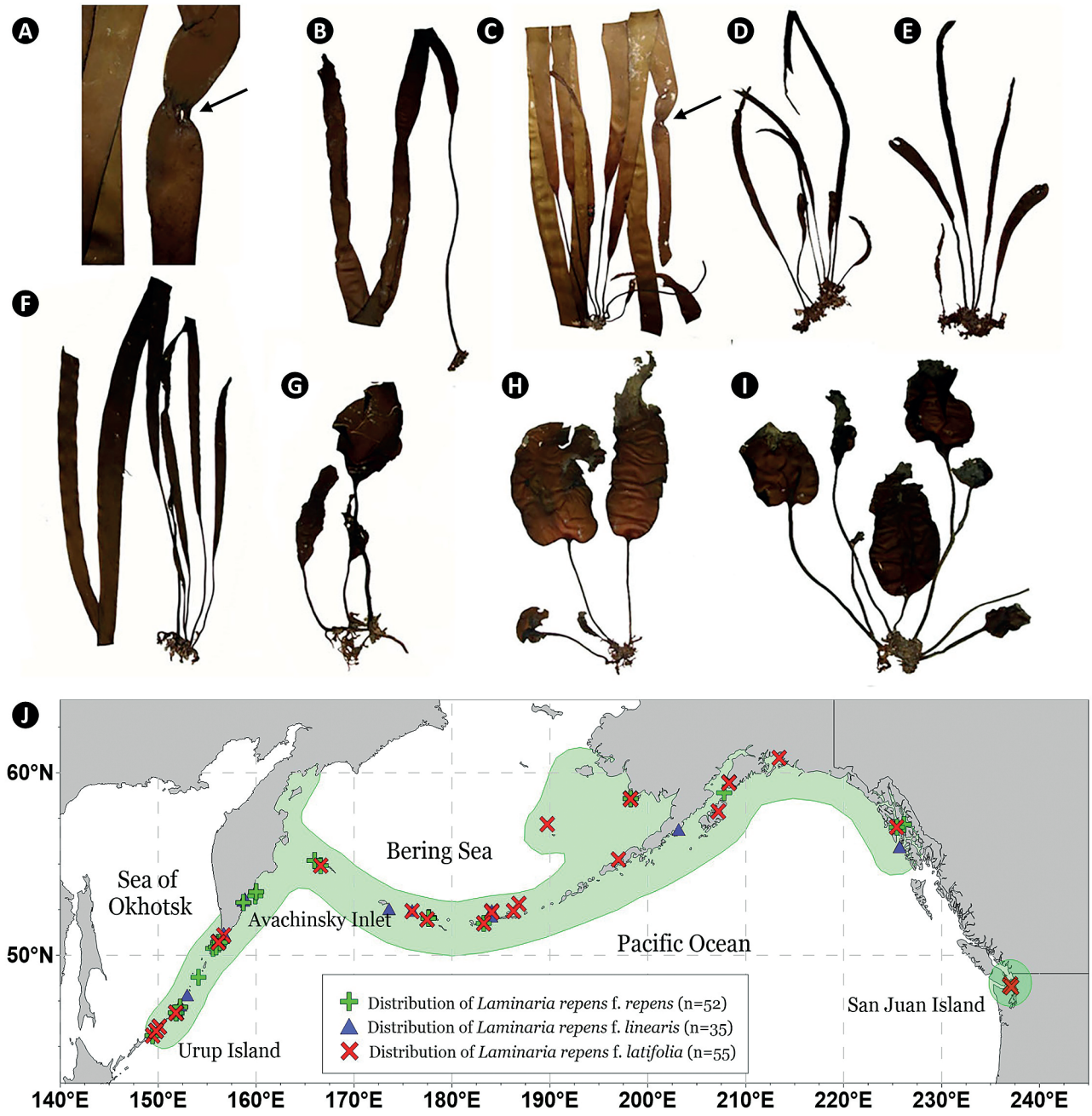

Figure 6 Gross morphology and distribution of three forms of *Laminaria repens* in the North Pacific. (A–C) *Laminaria repens* f. *repens*. Solid arrow indicate blades constrictions. (D-F) *Laminaria repens* f. *linearis*. (G-I) *Laminaria repens* f. *latifolia*. (J) Distribution of forms

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