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Research Article

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Evidence for the reinstatement of *Kallymeniopsis* and the merger of the family Crossocarpaceae within the family Kallymeniaceae (Rhodophyta)

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Abstract: We present a three-gene phylogeny, based on nuclear (short fragment of large subunit ribosomal RNA gene, 1150 base pairs), chloroplast (ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit) and mitochondrial (5′ region of the cytochrome oxidase subunit 1) genes, to determine the position of three species, *Kallymeniopsis verrucosa*, *Beringia castanea* and *Crossocarpus lamuticus* in the Gigartinales. These species were placed by Perestenko in the family Crossocarpaceae, a proposal that was not supported by most phycologists. The goal of this project was to resolve the taxonomic position of these three species and answer the question: Is the Crossocarpaceae a separate family? The concatenated multi-gene phylogeny and the individual gene trees show that these algae nest deeply within the family Kallymeniaceae; *K. verrucosa* and *C. lamuticus* are most closely related to species referred currently to the genus *Erythrophyllum*, whereas *B. castanea* is sister to the recently established *Commanderella ruprechtiana.* Taking into account the data on morphology, vegetative and reproductive anatomy of different species, we propose to revive the genus *Kallymeniopsis* with three species and to retain *Crossocarpus* as a separate genus. *Beringia* is a separate monotypic genus.

Keywords: Gigartinales; phylogeny; Rhodophyta; Russian Pacific; systematics.

1 Introduction

The Kallymeniaceae Kylin is the largest family of the order Gigartinales F. Schmitz (Rhodophyta). It includes 43 genera and 193 species (Guiry and Guiry 2022). Most of the genera are distributed in the Southern Hemisphere. This family consists mainly of taxa with blade-like thalli, which are characterized by very distinctive female reproductive systems with the supporting cell bearing one to several 2–3-celled carpogonial branches and large, often lobed sterile subsidiary cells; the supporting cell functions as an auxiliary cell either for associated carpogonial branches or for another carpogonial branch system (Womersley 1994). According to Perestenko (1975) this family is close to the Crossocarpaceae Perestenko, which she established on the basis of features of post-fertilization development of the first fusion cell, which is formed from supporting and subsidiary cells, but does not incorporate cells of the carpogonial branch (Perestenko 1975), whereas in Kallymeniaceae the fusion cell incorporates the supporting cell and one or two lower cells of the carpogonial branch (Womersley 1994).

When Perestenko described the Crossocarpaceae, she included five genera in the family: *Kallymeniopsis* Perestenko, *Erythrophyllum* J. Agardh, *Crossocarpus* Ruprecht, *Cirrulicarpus* Tokida *et* Masaki, and provisionally *Beringia* Perestenko (1975). Later, two more genera were included in the Crossocarpaceae: *Velatocarpus* Perestenko and *Hommersandia* Hansen *et* Lindstrom (Perestenko 1986). It should be noted that Perestenko's view of the systematics of the Kallymeniaceae and the Crossocarpaceae did not find full support in the phycological community. Hansen and Lindstrom (1984) considered the developmental features of members of the family Crossocarpaceae insufficient to establish an independent family and suggested that the genera *Erythrophyllum*, *Kallymeniopsis*, *Crossocarpus*, *Cirrulicarpus* and *Hommersandia* belong to the family Kallymeniaceae. After that, the family Crossocarpaceae with the seven genera was accepted primarily by Russian phycologists (Perestenko 1994; Selivanova 2008) as well as by Schneider and Wynne (2007), while most scientists limited this family to the genera *Crossocarpus*

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and *Velatocarpus*. Further molecular studies confirmed the correctness of the opinion of Hansen and Lindstrom (1984); therefore, the genera *Kallymeniopsis*, *Cirrulicarpus*, *Beringia*, *Erythrophyllum*, *Hommersandia* and *Velatocarpus* are currently considered within the family Kallymeniaceae (Saunders et al. 2017; Selivanova et al. 2020). The new genus *Commanderella* Selivanova, Zhigadlova *et* G. W. Saunders and combination *C. ruprechtiana* (E. S. Sinova) Selivanova, Zhigadlova *et* G. W. Saunders was proposed for *Cirrulicarpus ruprechtianus* (E. S. Sinova) Perestenko, and *Kallymeniopsis lacera* (Postels *et* Ruprecht) Perestenko was transferred to the genus *Erythrophyllum* as *Erythrophyllum lacerum* (Postels *et* Ruprecht) Selivanova, Zhigadlova et G. W. Saunders (Selivanova et al. 2020). Earlier, based on the data of molecular phylogeny, *Cirrulicarpus gmelinii* (J. V. Lamouroux) Tokida *et* Masaki was restored in the genus *Erythrophyllum* (Saunders et al. 2017). Woelkerling et al. (2019a, 2019b), based on an exhaustive analysis of the complicated nomenclatural history, have presented evidence to treat the name '*E. gmelinii*' (as well as its synonyms '*C. gmelinii*' and '*Kallymenia gmelinii*') as a homotypic synonym of *Cryptonemia palmetta* (S. G. Gmelin) Woelkerling, G. Furnari, Cormaci *et* McNeill, which is currently placed in the family Halymeniaceae of the order Halymeniales (Guiry and Guiry 2022). Because '*K. gmelinii*', '*E. gmelinii*' and '*C. gmelinii*' cannot be used as accepted specific names for algae of the family Kallymeniaceae, we enclose these names in quotation marks in the text.

To date, only one species remains in the Crossocarpaceae, namely, *Crossocarpus lamuticus* (Wynne and Schneider 2022). It should be noted that studies of the Kallymeniaceae/Crossocarpaceae from the Russian Pacific coasts are far from complete. Several taxa inhabiting this area have not yet been included in phylogenetic analyses, e.g. *Beringia castanea*, *C. lamuticus*, *Kallymeniopsis verrucosa*, and *Velatocarpus kurilensis*.

The aim of the present study is to incorporate these Russian species, including *C. lamuticus*, which is currently considered the single species of the family Crossocarpaceae, into molecular phylogenetic analyses to define and update their nomenclature and taxonomy and to resolve the Kallymeniaceae/Crossocarpaceae question.

2 Materials and methods

Algae were collected in the Sea of Okhotsk in June to August 2019 during expedition no. 56 to the Sea of Okhotsk and the northwestern Pacific Ocean, by collectors on board the R/V *Akademik Oparin*.

Specimens of *C. lamuticus* were collected in Ayan Bay (56°25.4′N, 138° 03.9′E) and in Eirineyskaya Bay (Malaya Molta Bay, 59°24.6′N, 145°50′E), from a depth of 1.5–9 m. Specimens of *Commanderella ruprechtiana* were collected on Simushir Island in Roadstead Vodopadny, (47°4.2′N, 152°5.4′E), from the low intertidal zone to depths of 3–6 m, as well as in Milna Bay (46° 52.49′N, 151°52.35′E). *K. verrucosa* was sampled in Roadstead Vodopadny, Milna Bay and in Krasheninnikova Bay on Paramushir Island (50°17.93′N, 155°18.09′E). Specimens were deposited into the Herbarium of the Museum of A. V. Zhirmunsky National Scientific Center of Marine Biology FEB RAS (Vladivostok, Russia) under numbers MIMB41068, MIMB39008, MIMB39780 and MIMB40738 for *C. ruprechtiana*, MIMB40834, MIMB42669–MIMB42671 for *C. lamuticus*; and MIMB41075, MIMB40725, MIMB40716, MIMB40717, MIMB40722, MIMB40729, MIMB40739, MIMB40742, and MIMB40750 for *K. verrucosa*.

Two herbarium specimens of *B. castanea* (5581 and 5373, collected on Matua Island at Cape Clyuv [48°05.068′N, 153°16.113′E] in August 2016 and August 2017 at depths of 13 and 17 m, respectively) and *K. lacera* (KAM0046 and 5584, collected in Grotovaya Bay, Avacha Gulf, South-Eastern Kamchatka on 24 June, 2013) were provided by Galina G. Zhigadlova from the Kamchatka Branch of the Pacific Geographical Institute FEB RAS.

Also, we examined herbarium specimens of *C. lamuticus*, the holotype (LE A0000705) and isotypes (LE A0000706) of *B. castanea* and a specimen identified as '*C. gmelinii*' (LE A0003537) stored in the Algal Herbarium of Komarov Botanical Institute (LE, Saint-Petersburg). The specimen of '*C. gmelinii*' was collected on 12 June, 1964 at Yuri Island, Lesser Kuril Islands at a depth of 8 m; the specimens of *C. lamuticus* were collected in Kawacha Bay (Sea of Okhotsk) on 20 August, 1965 at a depth of 5–6 m and on Belichy Island (Sea of Okhotsk) on 10 August 1964 at a depth 14 m; and the specimens of *B. castanea* were collected from drift material in Korabel'naya Bay on Medny Island (Commander Islands) on 13 July 1972.

Anatomical examinations were carried out on fresh algae and herbarium material. Algae were sectioned manually with a razor blade. The sections were examined under a Zeiss AxioVert 200 M microscope. Species were identified based on their morphology and anatomy using the descriptions in Perestenko (1975, 1986, 1994), Ruprecht (1851) and Zinova and Gussarova (1977)

Genomic DNA was extracted from thallus fragments from herbarium specimens by the CTAB-method (Wang et al. 2006). A partial chloroplast gene fragment, ribulose-1,5-biphosphate carboxylase/oxygenase (*rbc*L), was amplified with specific primers F57 (forward) and rbcLrevNEW (reverse) (Saunders and Moore 2013). The fragment of cytochrome *c* oxidase subunit I (COI-5′) was amplified with the primer pair GazF1 and GazR1 (Saunders 2005). The short fragment of the large subunit of ribosomal DNA (LSU) was amplified with primers T01N and T20 following the published protocol (Saunders and Moore 2013). The preparation of samples for sequencing was carried out as described by Shibneva et al. (2021). The PCR products were bidirectionally sequenced on an ABI 3130× sequencer (Applied Biosystems) and aligned in MEGA-7 (Kumar et al. 2016).

The full set of sequences for each genetic marker used in the analyses, including our sequences and data downloaded from GenBank, is given in Supplementary Table S1. Three single gene alignments were prepared for phylogenetic analysis: LSU (89 sequences, 1150 bp), *rbc*L (71 sequences, 1343 bp) and CO1-5' (95 sequences, 620 bp). In cases where we were unable to obtain sequences of all three genes in GenBank for the same voucher, we combined sequences from two or three vouchers of the same species from nearby localities (where it was possible). This approach was also used by Saunders et al. (2017) and Selivanova et al. (2020, for details see supplementary materials). Single gene alignments were analyzed independently with maximum likelihood (ML, model GTR + Gamma) using raxmlGUI (Edler et al. 2021) and Bayesian approach using MrBayes v3.2.6 (Huelsenbeck and Ronquist 2001). Bootstrap support was assessed with 500 replicates in raxmlGUI. 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. A burn-in of 1,250,000 generations (or 25% of the sampled trees) was used. Since no conflicts were detected between single gene topologies, a final LSU + *rbc*L + COI-5′ concatenated alignment (3113 bp) was constructed and analyzed as outlined for the single gene alignments but with partitioning by gene and then codon for *rbc*L and COI-5′. Partition Finder 2.1.1 (Lanfear et al. 2012) was used to select the best-fit partitioning scheme and models using the greedy algorithm with linked branch lengths for the corrected Bayesian Information Criterion as the optimal criterion for model selection. The best-fit model for LSU, first position in codon for COI-5′, and third position for *rbc*L was GTR + I + G. For second position for COI-5′ and *rbc*L, the best-fit model was SYM + I + G. For COI-5′ in third position of codon and *rbc*L in first position, the best-fit models were GTR + I and HKY + I + G, respectively. The genetic distances (p-distance) were calculated in MEGA 7. FigTree v. 1.4.4 (Rambaut 2016) was used to visualize phylogenetic trees after analysis. *Dilsea lindstromiae* G.W. Saunders, *Dumontia simplex* Cotton and *Constantinea simplex* Setchell (Dumontiaceae) were used as outgroups because this family is genetically closest to the Kallymeniaceae (Fredericq et al. 1996; Tai et al. 2001).

3 Results

3.1 Molecular results

The monophyly of the family Kallymeniaceae was highly supported by BI and ML analysis (Bayesian posterior probability, BPP = 1, bootstrap value ML = 100%). Phylogenetic analysis of our concatenated alignment including sequences of our own collections and those obtained from GenBank resolved at least 33 clear genus-level lineages (Figure 1 and 2). The BI phylogeny revealed two well-supported primary clades, one including *Rhytimenia*, *Psaromenia* and *Meredithia* (BPP = 0.97) and another including the remaining genera of the family Kallymeniaceae (BPP = 0.99). Sequences of *K. verrucosa* and *C. lamuticus* were placed in a clade including members of the genus *Erythrophyllum* (BPP = 1, ML = 100) (Figure 2). Moreover, *K. verrucosa* was placed as sister to *E. lacerum* (without support), and both species were sister to *E. oblongifructum* (BPP = 1, ML = 100). In turn, *C. lamuticus* was sister to ‘*E. gmelinii*’ (ML = 79). The average p-distances between *C. lamuticus* and ‘*E. gmelinii*’ were 2.33 and 0.18% for *rbc*L and LSU genes, respectively. Genetic distances between *K. verrucosa* and the closely related species, *E. lacerum*, *E. oblongifructum* and *E. delesserioides* were 1.54, 5.52 and 9.03% on average for *rbc*L and 0.00, 0.26 and 0.22% for the LSU, respectively.

Beringia castanea was placed as sister to *Commanderella ruprechtiana* with high support (BPP = 1, ML = 100) and the average p-distance was 1.7% for the LSU gene (Figure 1).

The BI phylogeny of just the *rbc*L gene (Supplementary Figure S1) was congruent with the concatenated LSU, COI-5′ and *rbc*L data for all major clades and relevant taxa.

The phylogenetic data clearly show that the Crossocarpaceae should not be supported as a separate family and that all species previously assigned to the Crossocarpaceae (see Perestenko 1994) should be transferred into the Kallymeniaceae.

3.2 Taxonomic proposals

Based on our DNA phylogenies *Kallymeniopsis verrucosa* and *Crossocarpus lamuticus* could be assigned to the genus *Erythrophyllum* following Saunders et al. (2017) and Selivanova et al. (2020), who combined *Kallymeniopsis lacera*, *K. oblongifructum*, ‘*Cirrulicarpus gmelinii*’ and *Beringia wynnei* with the type species of *Erythrophyllum*, *Erythrophyllum delesserioides*, into a single genus based on genetic similarity, without considering morphological features. Nevertheless, the species mentioned show very distinct morphologies; also, they differ by features of their female reproductive system (where it is known), especially *Kallymeniopsis* (Table 1). There is no conflict between the molecular data and recognizing *Kallymeniopsis*, *Crossocarpus* and *Erythrophyllum* as different genera (Figure 1). We here propose to resurrect the genus *Kallymeniopsis* (with three species) and to retain *Crossocarpus* and *Beringia* as separate genera. A new genus is required for *Erythrophyllum wynnei* as well as a new name for the taxon currently known as ‘*E. gmelinii*’ (for reasons, see Discussion). Below we provide figures of the morphology and vegetative anatomy of species from the Russian coast of the Northwestern Pacific to make these species more familiar to a wider audience.

Crossocarpus Ruprecht
Type species: *Crossocarpus lamuticus* Ruprecht, *Algae ochotenses*, p. 72. 1850.
Comments: This genus differs from the genetically close genus *Kallymeniopsis* in the absence of a morphologically distinct auxiliary cell system, in the structure of the medulla and in morphology (Table 1). *Crossocarpus* differs from *Erythrophyllum* in being non-procarpic (Table 1).

Crossocarpus lamuticus Ruprecht (Figures 3 and 4).
Lectotype (designated here): LE A0001131, conserved in the Herbarium of Komarov Botanical Institute, St.-Petersburg, Russia (LE).
Description: Thalli flat, branched in one plane (Figure 3A–E), with a short terete stipe, attached by a small holdfast (Figure 3F). Each branch broadens upwardly (Figure 3D), turning into entire or dissected blades without a midrib. Blades of various shapes, planar, with rounded apices and wedge-shaped base, somewhat flabellate to deeply incised (Figure 3C–E), often with rounded proliferations or small

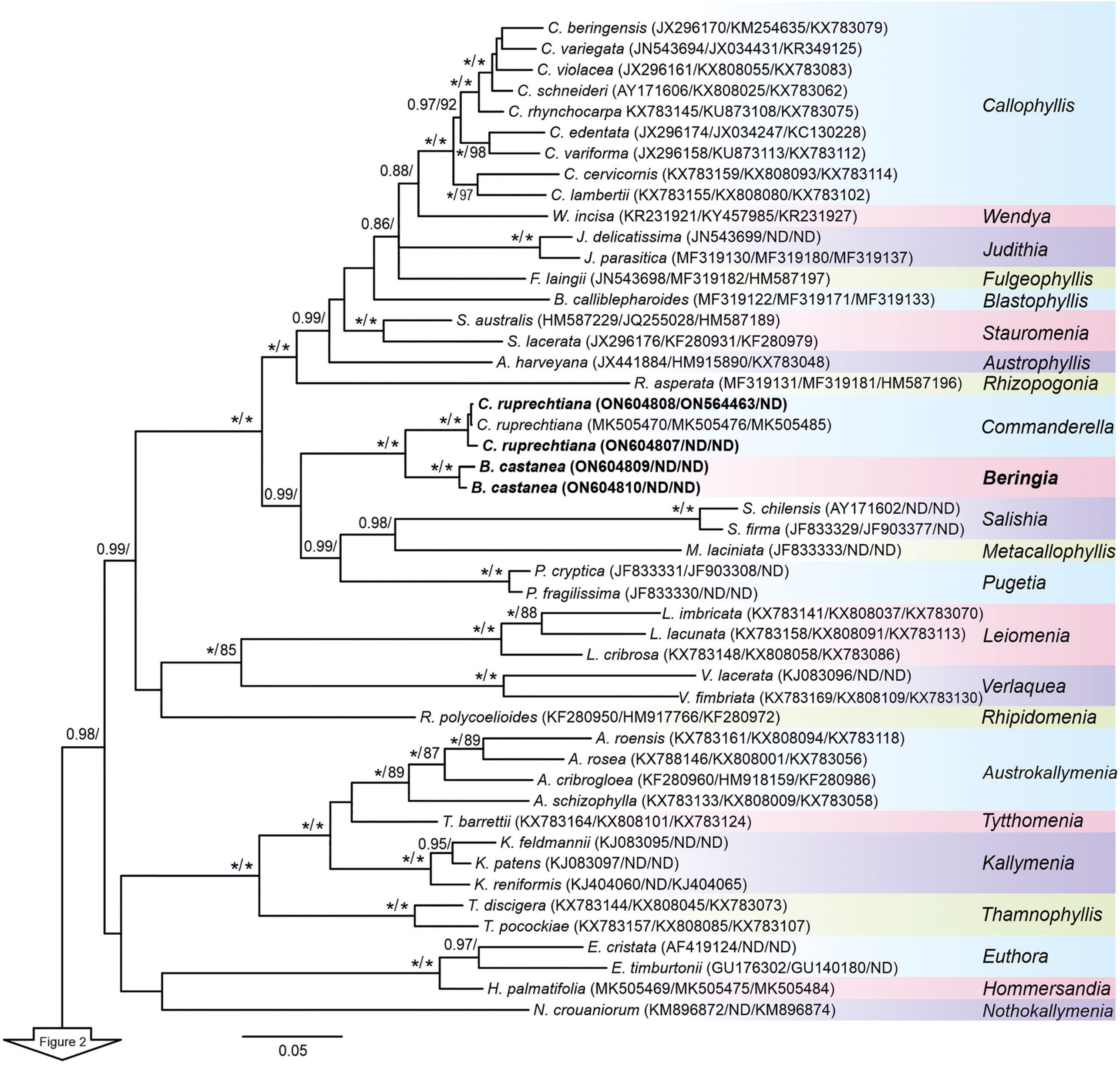

Figure 1: Bayesian tree generated from a three-gene (LSU, COI-5′, *rbc*L) concatenated alignment. Specimens analyzed in this study are highlighted in bold. Numbers in brackets after the species names are GenBank accession numbers (LSU/COI-5′/*rbc*L). Bayesian posterior probability values >0.7 and bootstrap support values >75% are shown and asterisks indicate full node support. Scale bar: substitutions per site.

bladelets along margins (Figure 3G–I). Medulla filamentous, consisting of primary filaments of rounded or ellipsoidal thick-walled cells and secondary filaments of elongated to filiform cells (small round in transverse view) (Figure 4A–D). These types of filaments are intermixed in varying degrees (Figure 4A, C). Medullary cells sometimes are coarsely granular. Refractive cells of various shapes (Figure 4E, F), are rare in the blade and often can be observed only after staining with aniline blue; but they are common in the stipe. Non-procarpic. Carpogonial system of 8–9 cells; supporting cell bears a three-celled carpogonial branch and several clavate, wedge-shaped, or slightly lobed at distal end subsidiary cells, which are twice as large as the first and second cells of the carpogonial branch (Perestenko 1994). Gonimoblasts immersed, developing in rounded marginal proliferations (Ruprecht 1850).

Comments: Despite significant morphological differences, all specimens studied were anatomically and genetically identical. Ruprecht (1850) did not indicate a nomenclatural type. Drawings of three specimens were provided in the

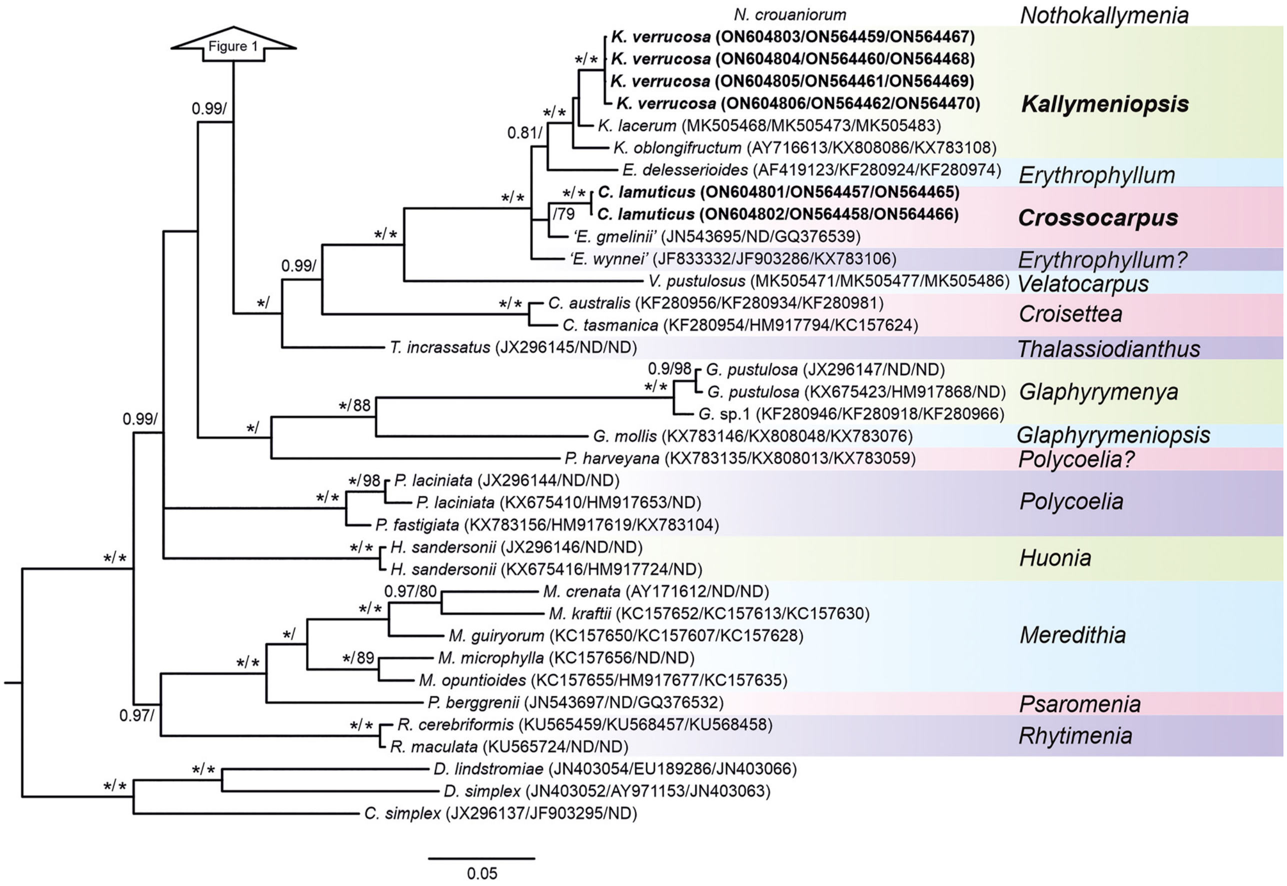

Figure 2: Continuation of Figure 1. For details, see legend for Figure 1.

protologue (Ruprecht 1850). Since no holotype was indicated by Ruprecht (1850), all the illustrated specimens are syntypes. To our knowledge, a lectotype has not been formally designated to date. Here we designated lectotype LE A0001131 collected on 27.08.1844 in Ujakon Bay, Sea of Okhotsk, from drift material in Middendorff's Exp. The designated lectotype is fully consistent with the illustration given in Table 14a (Ruprecht 1850). The second specimen of the same collection (LE A0001132) becomes the isolectotype.

Kallymeniopsis Perestenko in Norris, *Smithsonian Contributions to Botany* 96, p. 344. 2014.

Type species: *Kallymeniopsis lacera* (Postels *et* Ruprecht) Perestenko, *Bot. Zhurnal* 62, p. 398. 1977.

Original description: Perestenko, *Bot. Zhurnal* 60(12), p. 1679. 1975.

Emended description: Plants foliose, obovate or orbiculate in shape, entire or lacerated, with cuneate base. Subsessile or with short stipe. Holdfast discoid. Medulla of long, narrow, branched periclinal filaments, with large, elongate, branched or unbranched needle-shaped or dendroid refractive cells. Monocarpogonial, supporting and subsidiary cells large, elongated, lobed at distal end. Non-procarpic. Auxiliary system of small, rounded cells. Tetrasporophyte and gametophyte isomorphic.

Comments: According Mikhaylova and Sokolova (2020), the genus Kallymeniopsis was invalidly published by Perestenko (1975; 1977); the genus name was subsequently unintentionally validated by Norris (2014, p. 344), who provided the reference to a previously and effectively published description (in accordance with Art. 38.1(a) ICN, Turland et al. 2018) that unequivocally associated the name with Perestenko. According to Art. 46.2 and Note 4 to Art. 46 ICN (Turland et al. 2018), the name is therefore attributed to Perestenko, not Perestenko ex Norris.

Kallymeniopsis lacera (Postels *et* Ruprecht) Perestenko (Figure 5).

Basionym: *Iridaea lacera* Postels *et* Ruprecht, *Illustrationes algarum…*, p. 17. 1840.

Heterotypic synonyms: *Iridaea affinis* Postels *et* Ruprecht, *Illustrationes algarum…* p. 18. 1840.

Kallymeniopsis circinnata Perestenko *nom. inval.*, *Bot. Zhurnal* 60(12), p. 1680. 1975.

Table 1: Morphological comparisons among *Erythrophyllum delesserioides*, '*E. gmelinii*', *E. wynnei*, *Crossocarpus lamuticus* and species of *Kallymeniopsis*.

	Erythrophyllum delesserioides	***Crossocarpus lamuticus***	**'*Erythrophyllum gmelinii*'**	***Erythrophyllum wynnei***	***Kallymeniopsis oblongifructa***	***Kallymeniopsis lacera***	***Kallymeniopsis verrucosa***
Habit	Simple or branched lanceolate blades with midrib running along whole blade and with lateral veins	Various in shape, flat, with dissected lobes to irregularly branched in one plane, proliferous from margin	Flat, stalks branch in one plane. Each branch terminates with a fan-shaped or irregularly lobed blade. Wide mid-rib thickening conspicuous in stems and at blade bases, not along the whole blade	Flat orbicular blades	Simple or somewhat lobed blades, segments broadly wedge-shaped	Simple or somewhat lobed blades, segments wedge-shaped	Simple or somewhat lobed blades, segments wedge-shaped, with few to abundant outgrowths on the blade and margin
Medulla	Long narrow cells	Ellipsoidal and filiform cells	Ellipsoidal and filiform cells	Round cells interspersed with branched filaments of smaller cells	Periclinally directed filaments, 3–4 µm wide	Periclinally directed filaments, 4–5 µm wide and rare thicker filaments, 5–14 µm	Periclinally directed filaments, 2–4 µm wide
Refractive cells	Stellate, periclinally elongated	Various in shape	Irregularly elongated, dendroid to almost stellate	Unknown	Spiniferous, branched periclinally elongated	Needle-shaped with short arms	Large dendroid
Carpogonial system	Monocarpogonial	Monocarpogonial	Monocarpogonial	Unknown	Unknown	Monocarpogonial	Monocarpogonial
Subsidiary cells	2 large elongated clavate or wedge-shaped, slightly lobed at distal end	4–5 large elongated clavate or wedge-shaped, slightly lobed at distal end	2–3 large elongated narrow wedge-shaped, deeply lobed at distal end	Unknown	Unknown	4–8 large elongated clavate or wedge-shaped, slightly lobed at distal end	4–5 large elongated clavate or wedge-shaped, slightly lobed at distal end
Auxiliary system	Procarp	Unknown	Supporting cell in different carpogonial system serves as auxiliary cell	Unknown	Unknown	Separate, auxiliary cell with 6–7 small rounded subsidiary cells	Separate, auxiliary cell with 5–6 small rounded subsidiary cells
Cystocarps	In fruiting papillae scattered over the surface	In marginal proliferations	In upper part of the thalli, arranged in elliptical and occasionally confluent ring	Unknown	On surface of thallus	On surface of thallus	On surface of thallus
Tetrasporangia	Obliquely cruciately divided, in cortex	Unknown	Obliquely cruciately divided, in cortex	Unknown	Cruciately divided	Cruciately divided, in cortex	Obliquely cruciately divided, in cortex
References	Twiss (1911)	Perestenko (1975, 1994), Ruprecht (1851)	Hansen (1977); Norris et al. (1960), Tokida and Masaki (1956); Yendo (1915)	Clarkston and Saunders (2012)	Abbott (1968), Norris (2014)	Zinova and Gussarova (1977), Perestenko (1975, 1994); this paper	(Zinova and Gussarova 1977: this paper)

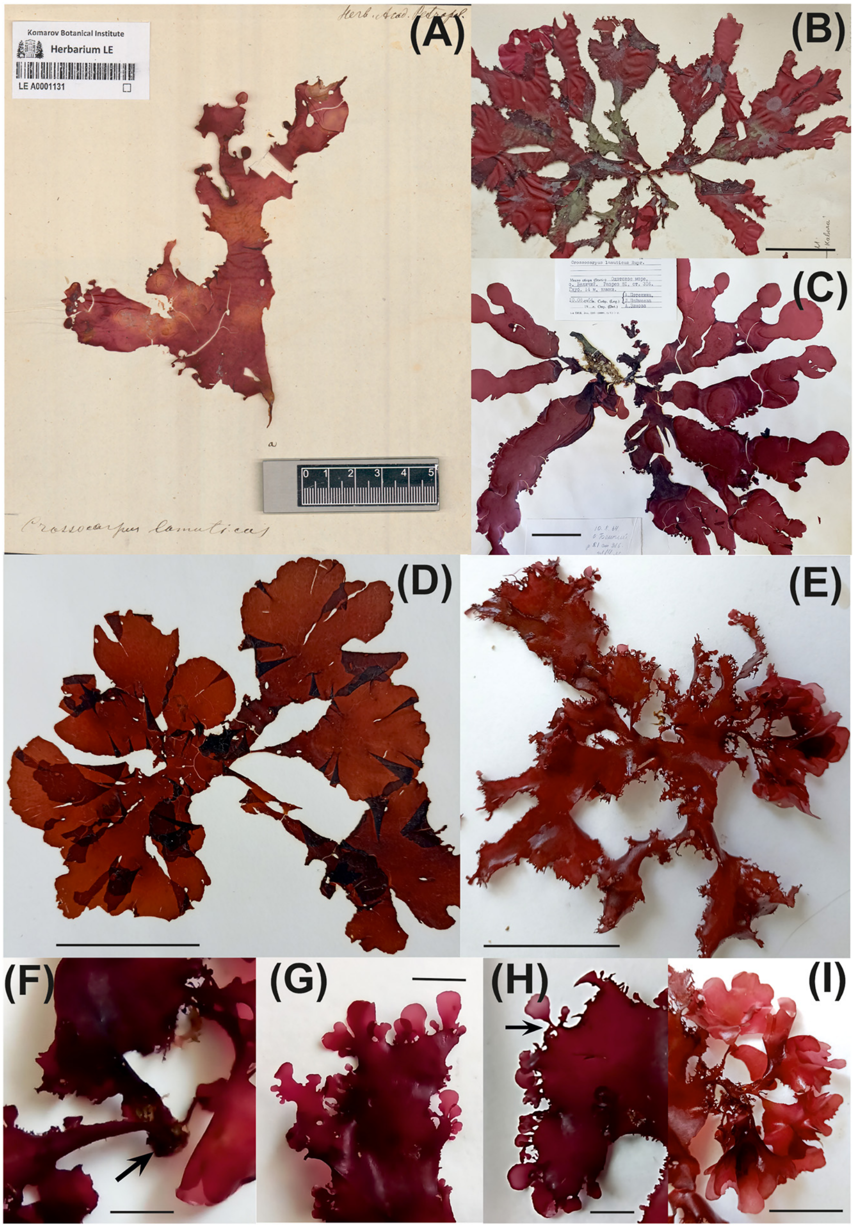

Figure 3: *Crossocarpus lamuticus*.
(A) Designated lectotype (LE A0001131) of *C. lamuticus*. (B) Habit of the plant from Kawacha Bay (Sea of Okhotsk). (C) Habit of the plant from Belichy Island (Sea of Okhotsk). (D and E) Plants from Molta Bay (Eirineyskaya Guba, Sea of Okhotsk). (F) Branched flattened stipe, arrow shows holdfast. (G) Marginal proliferations on the plant shown in Figure 3E. (H) Marginal proliferations with a short stipe (arrow) on the plant shown in Figure 3E. (I) Large marginal proliferations on the plant shown in Figure 3E. Scale bars: (A–E) = 5 cm; (F, G, I) = 1 cm; (H) = 0.5 cm.

Erythrophyllum lacerum (Postels *et* Ruprecht) Selivanova, Zhigadlova *et* G.W. Saunders, *Phycologia* 59(3), p. 203. 2020.

Description and representative illustrations: Perestenko, *Bot. Zhurnal* 60(12), p. 1679, Figure 1. 1975.

Observation: Thalli foliose, entire, dissected to varying degrees (Figure 5A), with a wedge-shaped or cordate base and a short terete stipe, attached by a discoid holdfast. Margins entire, smooth or undulate. Medulla filamentous, of long filiform cells (Figure 5B, D). Refractive cells needle-shaped (Figure 5C). Non-procarpic (Figure 5E). Carpogonial system of 7–12 cells (Figure 5F); supporting cell bears a three-celled carpogonial branch and several subsidiary cells with lobed broad distal ends; subsidiary cells twice or more larger than first and second cells of carpogonial branch. Auxiliary system of 6–11 small, rounded cells (Figure 5G). Fusion cells are large and lobed (Figure 5H). Cystocarps protruded above the blade surface, scattered across the blade. Tetrasporangia in cortex (Perestenko 1994).

Comments: Perestenko (1975) fulfilled all the conditions for valid publication of new combination (Art. 41 and 41.5 ICN (Turland et al. 2018), when she proposed the name *Kallymeniopsis lacera* (Postels *et* Ruprecht) Perestenko. She assigned a binary name to the species, publishing a supporting description, clearly indicated its basionym and gave a full and direct reference to author and place of valid publication of the basionym, with page reference and date

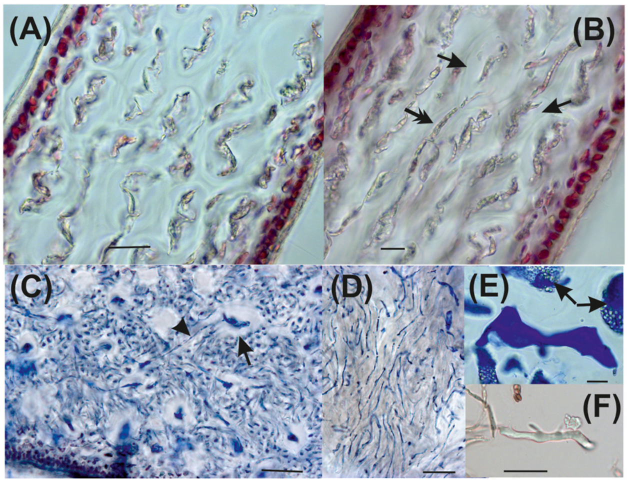

Figure 4: Vegetative anatomy of *Crossocarpus lamuticus*. (A) Traverse section of the young blade showing medulla of thick-walled cells. (B) Longitudinal section of the blade showing primary filaments from thick-walled cells (arrow) and thinner secondary filaments (double arrow) which form from them. (C) Transverse section of stipe showing primary filament (arrow), and secondary filament (arrowhead). (D) Squashed longitudinal section of the stipe showing filiform medullary cells. (E) Refractive cell stained with aniline blue and coarsely granulated medullary cells (arrows). (F) Refractive cell. Scale bars: (A, B, E) = 20 μm; (C, D, F) = 50 μm.

(Perestenko 1975). However, to that date the genus *Kallymeniopsis* was not validly published because Perestenko did not indicate the type of the genus as required by Art. 40.1 ICN (Turland et al. 2018). This specific name was subsequently validated by Norris (2014, p. 344), who unequivocally associated *K. lacera* with the genus *Kallymeniopsis* and unequivocally associated the specific name with Perestenko in the phrase "…the generitype, *Kallymeniopsis lacera* (Postels *et* Ruprecht) Perestenko (1977; basionym: *Iridaea lacera* Postels *et* Ruprecht 1840)" (Norris 2014, p. 344). In accordance with Art. 46.2 ICN, Note 4 and Ex. 23 to Art. 46 ICN (Turland et al. 2018), the name *K. lacera* should be attributed to Perestenko, not Perestenko ex Norris. Unfortunately, the type of the species has not been designated to date. Postels and Ruprecht (1840) did not indicate a type. To our knowledge, at the moment, no type material has been found.

Kallymeniopsis verrucosa A.D. Zinova *et* Gussarova (Figure 6).

Holotype: LE A0000275, collected at Kuril Islands, Simushir Island, Section 1, station 1, depth 14 m, 9 VIII 1968, leg. V.F. Sarochan deposited at Algal Herbarium of the Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg, Russia (LE).

Original description and representative illustrations: Zinova and Gussarova, *Novosti Sistematiki Nizshikh Rastenii* [*Novitates Systematicae Plantarum Non Vascularium*] Vol. 14, p. 26, Figures 1 and 2. 1977.

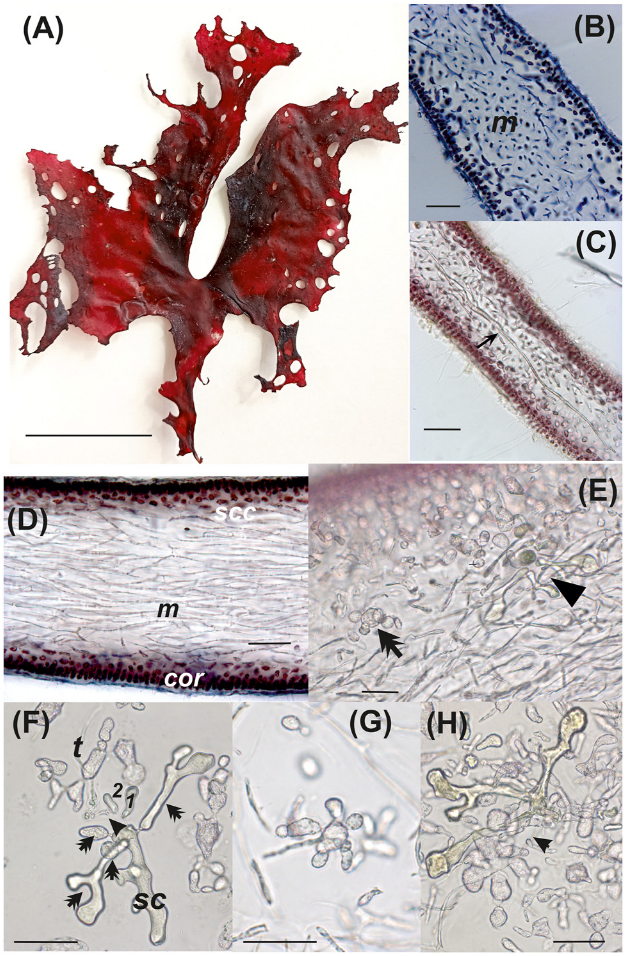

Figure 5: *Kallymeniopsis lacera*. (A) Habit of plant collected in Grotovaya Inlet, Avacha Gulf, Eastern Kamchatka on 24 June, 2006 (voucher KAM0046). (B) Transverse section of the blade: m, medulla. (C) Needle-shaped refractive cell (arrow). (D) Longitudinal section of the blade: scc, subcortical cells; cor, cortex; m, medulla. (E) Carpogonial (arrowhead) and auxiliary (double arrow) systems in transverse section. (F) Carpogonial system: SC, supporting cell; t, trichogyne; 1, 2, basal and hypogynous cells of carpogonial branch, respectively; arrowhead, carpogonium; double arrows, subsidiary cells. (G) Auxiliary system. (H) Fusion cell: arrowhead, connecting filament. Scale bars: (A) = 5 cm; (B–H) = 50 μm.

Observation: Thalli foliose, entire or lacerated to various degrees, with a wedge-shaped base and a short terete stipe attached by a discoid holdfast (Figure 6A). Margins entire, undulate, often with numerous outgrowths (Figure 6B, C). The outgrowths also develop on the blade surface (Figure 6D). Medulla filamentous (Figure 6F, G) rich in large dendroid refractive cells (Figure 6E, G). Auxiliary and carpogonial systems distinct: supporting cell of the carpogonial system bearing 4–5 large elongated, wedge-shaped, or slightly lobed at distal end subsidiary cells; auxiliary system of 6–7 small cells (Zinova and Gussarova 1977). Cystocarps protruding above the blade surface, scattered across the blade. Tetrasporangia in cortex (Figure 6H).

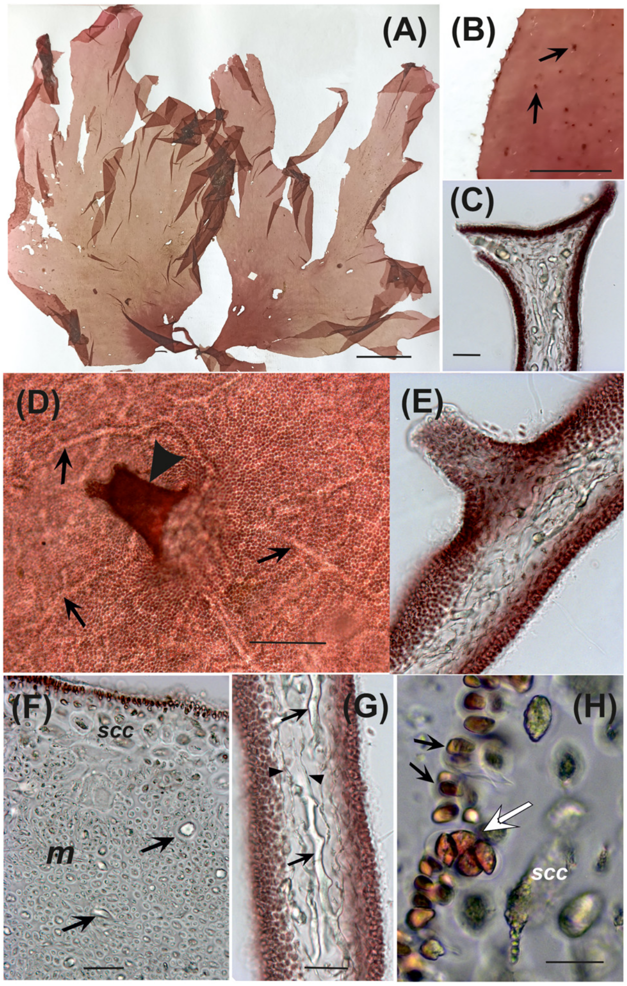

Figure 6: *Kallymeniopsis verrucosa*. (A) Habit of plant collected in Krasheninnikova Bay, Paramushir Island on 11 August, 2012. (B) Margin. (C) Cross-section through the margin. (D) Outgrowth on the blade surface (arrowhead) and refractive cells visible through the surface (arrows). (E) Cross-section through outgrowth. (F) Transverse section through the blade with transversely-cut refractive cells (arrows): m, medulla; scc, subcortical cells. (G) Longitudinal section of the blade with giant refractive cells (arrows) and medullary filaments (arrowheads). (H) Tetrasporangium (white arrow): scc, subcortical cell; black arrows, cortical cells. Scale bars: (A) = 5 cm; (B) = 0.5 cm; (C, D, F–H) = 50 μm; (E) = 30 μm; (H) = 20 μm.

Comments: Our results clearly showed that *K. verrucosa* is genetically close to the generitype *K. lacera* (Figure 2) and should be assigned to the same genus. The binary designation “*K. verrucosa* Zinova *et* Gussarova” was not validly published in 1977 because the name of the genus had not yet been validated at that time (ICN Art. 35.1, Turland et al. 2018). Nevertheless, Zinova and Gussarova (1977) fulfilled the conditions for valid publication of the new species (Arts. 32.1, 38.1, 40.1), when they proposed the binary name *Kallymeniopsis verrucosa*, including designation of the holotype and the supporting description. Therefore, according to Art. 46.2 ICN (Turland et al. 2018), Zinova and Gussarova are the authors of the species name. As noted in Mikhaylova and Sokolova (2020), the information from the type specimen label is quoted incorrectly in the text (Zinova and Gussarova 1977). This error has been corrected in Mikhaylova and Sokolova (2020).

Kallymeniopsis oblongifructa (Setchell) G. I. Hansen in Norris, *Smithsonian Contributions to Botany* 96, p. 344. 2014.
Basionym: *Iridaea oblongifructa* Setchell, *Notes on algae*, I. *Zoe* 5, p. 123. 1901.
Homotypic synonyms: *Kallymenia oblongifructa* (Setchell) Setchell, University of California Publications in Botany 4(14), p. 234. 1912.

Erythrophyllum oblongifructum (Setchell) G.W.Saunders, *Cryptogamie*, *Algologie* 38, p. 92. 2017.
Holotype: UC94395, collected on 9.xii.1897 by N. L. Gardner at Coupeville, Whidbey Island, Washington. Conserved in UC (Herbarium of the University of California, Berkeley, USA).
Original description: Setchell, *Notes on algae*, I. *Zoe* 5, p. 123. 1901.
Emended descriptions: Setchell, *Univ. Calif. Publ. Bot* 4(14), p. 234. 1912; Abbott, J. Phycol 4, p. 197. 1968.
Comments: The binary designation ‘*Kallymeniopsis oblongifructa* (Setchell) G. I. Hansen’ was invalid at the time of publication (Hansen 1997) because the generic name had not been validly published by that time. Norris unequivocally associated this species with the genus *Kallymeniopsis* and unequivocally associated the name with G. I. Hansen (Norris 2014, p. 345). In 2017, the new combination *Erythrophyllum oblongifructum* (Setchell) G. W. Saunders was validly proposed (Saunders et al. 2017). We restore this species within *Kallymeniopsis* based on similarities in morphology and vegetative anatomy (Table 1) and phylogenetic data, although this position is provisional and further study is needed to obtain data on the female reproductive system and its post-fertilization development.

Beringia castanea Perestenko (Figure 7).
Type: LE A0000705, collected on 13.09.1972 by L. P. Perestenko from drift material at Korabelnaya Bay, Mednyj Island, Commander Island, Bering Sea. Conserved in LE (Algal Herbarium of the Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg, Russia).
Description: Blade rounded, dissected or lobed, sessile, with discoid holdfast (Figure 7A, B). Medulla filamentous, consisting of primary filaments of rounded or ellipsoidal thick-walled cells and secondary filaments of elongated to filiform cells (small round in transverse view) (Figure 7C, D). Some thick-walled cells have a stellate protoplast (Figure 7E). Tetrasporangia located in cortex, developing from medullary filaments (Figure 7F). Supporting cell of carpogonial system

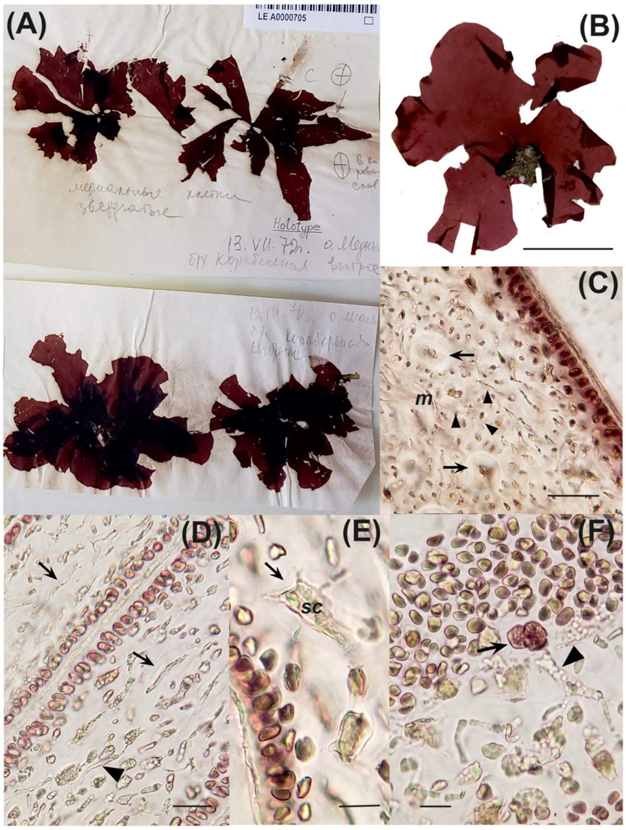

Figure 7: *Beringia castanea*. (A) Holotype (upper right) and isotypes of *B. castanea* collected on Medny Island (Commander Islands) on 13 July, 1972. (B) One of two specimens for which genetic data were obtained. Collected on Matua Island (Kuril Islands) in August 2016. (C) Transverse section of the base of the blade: m, medulla; arrows, thick-walled cells of primary filaments; arrowheads, secondary filaments. (D) Two longitudinal sections of the blade showing primary filaments of thick-walled oval cells (arrows) and thinner secondary filaments (arrowhead). (E) Thick-walled cell (sc) with stellate protoplast and thick cell wall (arrow). (F) Tetrasporangium (arrow) developed from medullary filament (arrowhead). Scale bars: (B) = 2 cm; (C) = 35 μm; (D) = 30 μm; (E–F) = 20 μm.

bearing 3 subsidiary cells, which are 1.5-times larger than the first cell of the carpogonial branch (Perestenko 1975).

4 Discussion

Our molecular-phylogenetic analysis shows that *Crossocarpus lamuticus*, *Beringia castanea*, and *Kallymeniopsis verrucosa*, species included by Perestenko (1975) in the Crossocarpaceae, nest comfortably within the Kallymeniaceae. The evidence that is presented demonstrates that the family Crossocarpaceae should be placed in synonymy with Kallymeniaceae, the name with priority. This relationship was predicted by Saunders et al. (2017) and earlier by Hansen and Lindstrom (1984). According to Saunders et al. (2017) and Selivanova et al. (2020), only four species placed in the Crossocarpaceae by Perestenko (1994) and still recognized in the Kallymeniaceae (*B. castanea*, *K. verrucosa* and *V. kurilensis*) and Crossocarpaceae (*C. lamuticus*), did not have any genetic data to decide their taxonomic position. The present study clarifies the taxonomic positions of three species (*B. castanea*, *C. lamuticus*, and *K. verrucosa*), resurrects one genus (*Kallymeniopsis*), and supports the genus *Crossocarpus*.

Although Saunders et al. (2017) and Selivanova et al. (2020) transferred *Kallymeniopsis lacera*, *K. oblongifructum*, '*Cirrulicarpus gmelinii*' and *Beringia wynnei* to the genus *Erythrophyllum*, this merger was done based on genetic data, without taking into account morphological features. We believe that, until there is a better understanding of how the genetic structure in Kallymeniaceae corresponds to reproductive and vegetative morphology and anatomy, the merger of the four genera in *Erythrophyllum* is premature. The genera within Kallymeniaceae are delimited mainly by reproductive (e.g. by the shape of the cells of the carpogonial branch and, to a lesser extent, the morphology of the auxiliary cell system, procarpy versus non-procarpy, monocarpogonial versus polycarpogonial, and post-fertilization events), and also by vegetative (e.g. thallus branching and internal anatomy) characters (Hansen and Lindstrom 1984; Womersley and Norris 1971). The traditional placement of *E. delesserioides*, *C. lamuticus*, '*E. gmelinii*' (='*C. gmelinii*') and species of *Kallymeniopsis* in different genera was based on the high level of morphological divergence between them. It is evident that vegetative anatomy and the reproductive traits clearly distinguish *Kallymeniopsis* from the other species mentioned (Table 1). Although the structure of the carpogonial system and the development of primary fusion cells are common in these species, *Kallymeniopsis* possesses a separate auxiliary system, which consists of several small rounded cells (Figure 6E; Zinova and Gussarova 1977). In '*C. gmelinii*' an auxiliary cell is the supporting cell of a different unfertilized carpogonial system (Norris et al. 1960), and in *E. delesserioides* the female reproductive system is, presumably, procarpic, and the gonimoblast filaments arise directly from a primary fusion cell resulting from the fusion of cells of the carpogonial system (Twiss 1911). We believe that *Kallymeniopsis* should be kept as a distinct genus with three species: *K. lacera*, *K. verrucosa* and *K. oblongifructa*, although the last species requires more study to obtain data on its reproductive anatomy.

The removal of *Kallymeniopsis* into a separate genus makes the clade, which includes other species currently placed in *Erythrophyllum* and *Crossocarpus lamuticus*, paraphyletic. The only way to resolve this conundrum is to keep *Erythrophyllum* and *Crossocarpus* as separate genera and to propose a new genus for *E. wynnei*.

The proposed taxonomic changes agree with the phylogenetic results. Although genetic distances between genera in the clade including species of *Kallymeniopsis*, *Erythrophyllum* and *Crossocarpus* are small compared to most other Kallymeniaceae, there are significant morphological and anatomical differences between the genera that should be acknowledged in their taxonomy. Smaller genetic distances can be explained by a different rate of evolution in different genetic lineages.

Differences in the habits, vegetative anatomy and position of cystocarps in *E. delesserioides*, *C. lamuticus* and '*E. gmelinii*' (= '*Cirrulicarpus gmelinii*') have traditionally been considered the basis for assigning these species to different genera. Nevertheless, the presence of a yellowish homogeneous substance in some cells of the medulla (Yendo 1915) and reproductive characters, such as monocarpogony, large lobed subsidiary cells and the formation of a fusion cell only from the supporting cell and subsidiary cells (Hansen 1977; Norris et al. 1960; Perestenko 1975) suggest that these species are closely related. '*Erythrophyllum gmelinii*' (= '*C. gmelinii*') and *C. lamuticus* seem to be more closely related to each other than to *E. delesserioides*. In addition to a close sister genetic relationship (Figure 1), '*E. gmelinii*' and *C. lamuticus* share the similar structure of the medulla and post-fertilization development of the female reproductive structure (Table 1). The only significant feature distinguishing '*E. gmelinii*' and *C. lamuticus* is the position and shape of the cystocarps (Table 1).

These facts allow us to suggest that *C. lamuticus* and '*E. gmelinii*' may be assigned to the genus *Crossocarpus* which has priority. However, there is a conflict between the nomenclature and taxonomy of '*E. gmelinii*', which needs to be resolved first. This alga has been listed in large number of publications under the names '*Kallymenia gmelinii*' (Grunow 1870); '*Erythrophyllum gmelinii*' (Okamura 1921; Saunders et al. 2017; Yendo 1915), '*Cirrulicarpus gmelinii*' (Hansen 1977; Kloczkova 1996; Kloczkova et al. 2009; Norris et al. 1960; Perestenko 1994; Tokida and Masaki 1956). The binomial '*Kallymenia gmelinii*' was proposed by Grunow (1870); in the protologue he cited the illustration "Fucus Palmetta insigni magnitudine Gmelin *Hist. Fucor*. t. 23" (Grunow 1870, p. 72, footnote), which was subsequently designated as the lectotype of *Fucus palmetta* S. G. Gmelin (Woelkerling et al. 2019a). This act unequivocally associated '*K. gmelinii*' with *F. palmetta*. Grunow (1870) also stated that he saw specimens from the Kuril Islands in the Berlin herbarium that exactly matched the Gmelin's illustration cited. The same specimen along with specimens from Japan was studied by Yendo (1915) who proposed to transfer '*K. gmelinii*' to the genus *Erythrophyllum* as '*E. gmelinii*'. Later, Tokida and Masaki (1956) proposed the new name '*Cirrulicarpus gmelinii*' for '*E. gmelinii*'. Currently, the specific names '*K. gmelinii*', '*E. gmelinii*' and '*C. gmelinii*' are treated as a homotypic synonyms of *Cryptonemia palmetta* (S. G. Gmelin) Woelkerling, G. Furnari, Cormaci *et* McNeill (Woelkerling et al. 2019b), which is a member of the order Halymeniales (Guiry and Guiry 2022). This synonymy is based on an exhaustive analysis of the complicated nomenclatural history, and the evidence that all these names are based on *Delesseria gmelinii* J. V. Lamouroux, a legitimate replacement name for *Fucus palmetta* S. G. Gmelin (Woelkerling et al. 2019b, pp. 4–5), and are typified by the type of *F. palmetta* (Woelkerling et al. 2019a, 2019b). Despite the fact that the names '*K. gmelinii*', '*E. gmelinii*' and '*C. gmelinii*' are homotypic synonyms of *Cryptonemia palmetta* (Woelkerling et al. 2019b), there is evidence that '*E. gmelinii*' and '*C. gmelinii*' (as understood by Hansen 1977; Norris et al. 1960; Perestenko 1994; Tokida and Masaki 1956; Yendo 1915) do not belong to the order Hallymeniales. Genetically '*C. gmelinii*' is resolved within the Kallymeniaceae clade of the order Gigartinales (D'Archino et al. 2010; Saunders et al. 2017). According to descriptions in Hansen (1977) and Norris et al. (1960), the carpogonial system of '*C. gmelinii*' is typical of kallymeniaceaean algae and consists of a large supporting cell bearing a single three-celled carpogonial branch and two or three subsidiary cells, elongated and lobed at distal end. The auxiliary cell is a supporting cell or one of the subsidiary cells in a distant unfertilized carpogonial system (Norris et al. 1960), whereas carpogonial and auxiliary systems of halymenialean algae are ampulla type (Cormaci et al. 2021; Rodriguez-Prieto et al. 2022). The best solution for resolving the conundrum with '*E. gmelinii*' might be to propose a new species name based on different type than *F. palmetta* for algae referred to, before Woelkerling et al. (2019b), as '*K. gmelinii*', '*E. gmelinii*' and '*C. gmelinii*'. Here we hesitate to do this because we examined only one sterile specimen, which was labeled as '*C. gmelinii*'. Although the morphology and vegetative anatomy of this specimen is certainly consistent with the description of '*E. gmelinii*' and '*C. gmelinii*' (Hansen 1977; Norris et al. 1960; Okamura 1921; Perestenko 1994; Tokida and Masaki 1956; Yendo 1915), it was not possible to obtain amplifiable DNA from the specimen due to its great age.

Another species under study, *Beringia castanea*, is also recognized as a member of the family Kallymeniaceae where it is sister to *Commanderella ruprechtiana*. Another species originally placed in the genus *Beringia*, *B. wynnei*, was transferred into *Erythrophyllum* as *E. wynnei* by Saunders et al. (2017). It is evident that these species are genetically distant. Since *Beringia castanea* is the type species of the genus, a new genus is required for *E. wynnei*. Being anatomically similar to *Crossocarpus*, *Beringia* differs in the structure of the carpogonial system, which is small-celled in comparison with *C. lamuticus* and *K. lacera* (Perestenko 1975, 1994). The supporting and subsidiary cells are only 1.5-times larger than the first cell of the carpogonial branch, whereas, in the species of *Crossocarpus*, they are 2–3-times larger than the basal and hypogenous cells of the carpogonial branch (Perestenko 1975, 1994).

A comparison of the descriptions of various genera of the family Kallymeniaceae shows that they all have a unique combination of characters such as the structure of the medulla, the presence and shape of refractive cells, and, most importantly, the features of the female reproductive system. Therefore, when deciding whether the genera are separate or should be merged, morphological features must be considered along with genetic data. Our study highlights the importance of a combined molecular/morphological approach to resolving the diversity of, and the relationships among, taxa within the Kallymeniaceae.

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Author contribution: A. V. Skriptsova: original concept, seaweeds collection and identification, manuscripts preparation; S. Y. Shibneva: phylogenetic analysis, manuscript preparation; A.A. Semenchenko: sequencing, tree drawing, manuscript preparation.

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