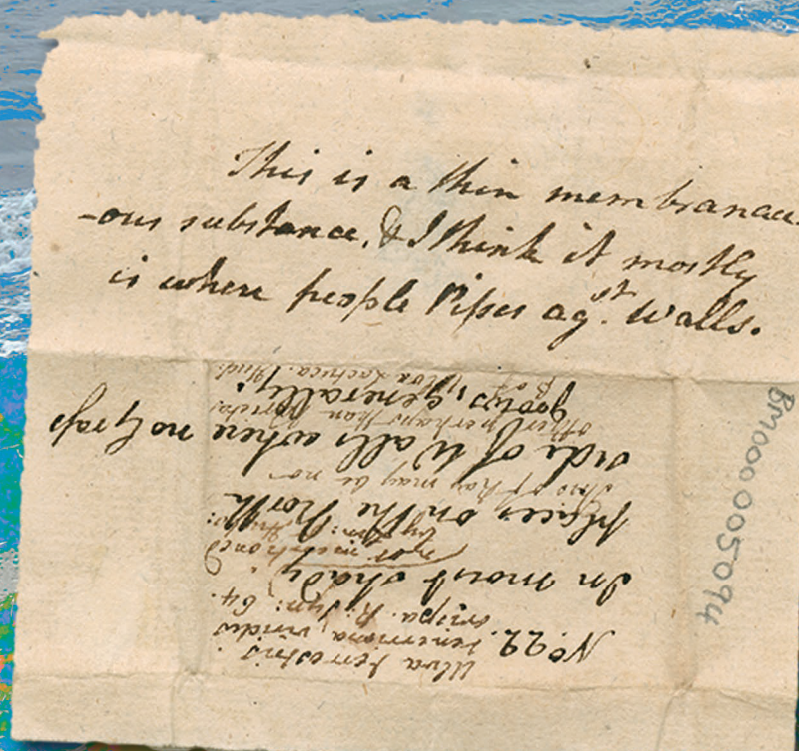


Taxonomic revision of the genus *Prasiola* Meneghini, 1838 (Prasiolaceae, Trebouxiophyceae) results in the establishment of three new genera

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Taxonomic revision of the genus *Prasiola* Meneghini, 1838 (Prasiolaceae, Trebouxiophyceae) results in the establishment of three new genera

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ABSTRACT

With 35 currently recognised species, *Prasiola* Meneghini, 1838 is the largest genus of the family Prasiolaceae (Prasiolales, Trebouxiophyceae). However, recent molecular phylogenetic studies have shown that the genus as currently conceived is polyphyletic, due to a separate genus, *Prasiococcus* Vischer, clearly being nested between the *Prasiola* clades. Since the clade containing the type species *Prasiola crispa* (Lightfoot) Kützinger has priority, we propose three new taxonomic realignments, based on DNA sequence comparisons, for two clades containing four and two species of *Prasiola*, respectively, and for another single species. The genus *Mariprasiola* Heesch, Guiry & Rindi, gen. nov., comprising the four species *M. stipitata* (Suhr ex Jessen) Heesch, Guiry & Rindi, comb. nov., the type, *M. delicata* (Setchell & N.L.Gardner) Heesch, Guiry & Rindi, comb. nov., *M. linearis* (C.-C.Jao) Heesch, Guiry & Rindi, comb. nov. and *M. meridionalis* (Setchell & N.L.Gardner) Heesch, Guiry & Rindi, comb. nov., distributed in marine habitats. Two species of *Vittaprasiola* Heesch, Guiry & Rindi, gen. nov., the strictly terrestrial species *V. calophylla* (Carmichael ex Greville) Heesch, Guiry & Rindi, comb. nov., the type, and the freshwater species *V. fluviatilis* (Sommerfelt) Heesch, Guiry & Rindi, comb. nov., share a belt-like appearance. *Eaprasiola* Heesch, Guiry & Rindi, gen. nov. is currently monospecific, with *E. japonica* (R.Yatabe) Heesch, Guiry & Rindi, comb. nov., found in freshwater habitats in East Asia and with thalli reaching up to 20 cm in length, the largest known representative of the family. Since the remaining 21 species of *Prasiola* lack genetic data, they cannot at present be assigned to any genus and remain in the genus *Prasiola sensu lato*.

KEY WORDS

Prasiolaceae,
molecular phylogeny,
taxonomic revision,
lectotypifications,
epitypification,
new combinations,
new genera.

RÉSUMÉ

Révision taxonomique du genre *Prasiola* Meneghini, 1838 (Prasiolaceae, Trebouxiophyceae) et établissement de trois nouveaux genres.

Avec 35 espèces actuellement reconnues, le genre *Prasiola* Meneghini, 1838 est le plus grand de la famille des Prasiolaceae (Prasiolales, Trebouxiophyceae). Cependant, des études récentes de phylogénétique moléculaire ont montré que le genre tel qu'il est actuellement conçu est polyphylétique, en raison d'un genre distinct, *Prasiococcus* Vischer, clairement imbriqué entre les clades *Prasiola*. Étant donné que le clade contenant l'espèce type *Prasiola crispa* (Lightfoot) Kützinger est prioritaire, nous proposons trois nouveaux réalignements taxonomiques, basés sur des comparaisons de séquences d'ADN, pour deux clades contenant respectivement quatre et deux espèces de *Prasiola*, et pour une autre espèce unique. Le genre *Mariprasiola* Heesch, Guiry & Rindi, gen. nov., comprenant les quatre espèces *M. stipitata* (Suhr ex Jessen) Heesch, Guiry & Rindi, comb. nov., le type, *M. delicata* (Setchell & N.L.Gardner) Heesch, Guiry & Rindi, comb. nov., *M. linearis* (C.-C.Jao) Heesch, Guiry & Rindi, comb. nov. et *M. meridionalis* (Setchell & N.L.Gardner) Heesch, Guiry & Rindi, comb. nov., est réparti dans les habitats marins. Deux espèces de *Vittaprasiola* Heesch, Guiry & Rindi, gen. nov., l'espèce strictement terrestre *V. calophylla* (Carmichael ex Greville) Heesch, Guiry & Rindi, comb. nov., le type, et l'espèce d'eau douce *V. fluviatilis* (Sommerfelt) Heesch, Guiry & Rindi, comb. nov., partagent une apparence en forme de ceinture. *Eaprasiola* Heesch, Guiry & Rindi, gen. nov. est actuellement monospécifique, avec *E. japonica* (R.Yatabe) Heesch, Guiry & Rindi, comb. nov., trouvée dans les habitats d'eau douce d'Asie de l'Est et, avec des thalles atteignant jusqu'à 20 cm de longueur, le plus grand représentant connu de la famille. Étant donné que les 21 espèces restantes de *Prasiola* manquent de données génétiques, elles ne peuvent actuellement être attribuées à aucun genre avec certitude et restent dans le genre *Prasiola sensu lato*.

MOTS CLÉS
Prasiolaceae,
phylogénie moléculaire,
révision taxonomique,
lectotypifications,
épitypification,
combinaisons nouvelles,
genres nouveaux.

INTRODUCTION

Prasiola Meneghini, 1838, *nom. cons.* includes trebouxiophycean green algae formed by monostromatic blades of various shapes arising from short stipes. With 35 species currently recognised, *Prasiola* is by far the largest genus of the family Prasiolaceae (Guiry & Guiry 2024). Most species were described based on morphological characters and habitat preferences. In recent decades, however, DNA sequence data have greatly advanced our understanding of the phylogeny and taxonomic diversity of the genus. Molecular studies have more firmly established the phylogenetic relationships between the various *Prasiola* species and have shown that the genus as presently conceived is polyphyletic (Rindi et al. 2007; Moniz et al. 2012a, b; Heesch et al. 2012, 2016; Sutherland et al. 2016; Nelson & Sutherland 2018).

Prasiola was introduced as a genus by Meneghini (1838: 360) citing “Ulvae Trib. IV (*Prasiola*)”, a tribe name of C.Agardh (1823: 416, “*Tribus Ulvae Crispae. Prasiola*”). Agardh included in his “*Tribus Ulvae Crispae*” two *Ulva* species, *U. crispa* Lightfoot (Lightfoot 1777), and *U. furfuracea* Mertens ex Hornemann (Hornemann 1813: pl. MCCCCLXXXIX). *Prasiola* Meneghini, 1838 is currently conserved against the earlier genus name *Humida* S.F.Gray (type: *Humida muralis* (Dillwyn) S.F.Gray) (Gray 1821) with *Prasiola crispa* (Lightfoot) Kützinger as the type, although *Prasiola* and *Humida* are currently considered heterotypic (Silva 1980).

According to phylogenetic analyses (Moniz et al. 2012b; Heesch et al. 2012, 2016), *Prasiola crispa* belongs to a well-supported clade that includes several other species distributed

mainly in terrestrial habitats such as *P. antarctica* M.Moniz, Rindi, Novis, Broady & Guiry, *P. glacialis* M.Moniz, Rindi, Novis, Broady & Guiry, and *P. furfuracea* (Hornemann) Trevisan, but also in the supralittoral zone of marine shores, such as *P. borealis* M.Reed and *P. novaezealandiae* Heesch & W.A.Nelson, and in freshwater (*P. mexicana* J.Agardh).

A second clade formed by species found in marine habitats (upper intertidal zones and coastal lagoons) consists of *Prasiola stipitata* Suhr ex Jessen, *P. delicata* Setchell & N.L.Gardner, *P. linearis* C.-C.Jao and *P. meridionalis* Setchell & N.L.Gardner. A third clade comprises a freshwater species, *P. fluviatilis* (Sommerfelt) Areschoug ex Lagerstedt, and the strictly terrestrial *P. calophylla* (Carmichael ex Greville) Kützinger. Additionally, phylogenetic analyses consistently place a single freshwater species, *Prasiola japonica* Yatabe, as an individual lineage separated from the other species of *Prasiola* as currently circumscribed (Moniz et al. 2012b; Heesch et al. 2016; Sutherland et al. 2016; Nelson & Sutherland 2018). In all molecular phylogenetic studies to date, the genus *Prasiococcus*, with its only species *Prasiococcus calcarius* (J.B.Petersen) Vischer, forms a lineage nested within *Prasiola sensu auctorum*. *Prasiococcus* does not have the bladed thallus typical of the genus *Prasiola* but consists of sarcinoid cell packets (Vischer 1953). The very different morphology of *Prasiococcus*, together with its placement in phylogenies among the *Prasiola* clades, effectively renders the genus *Prasiola*, as presently circumscribed, polyphyletic (Rindi et al. 2007; Moniz et al. 2012a, b; Heesch et al. 2012, 2016; Sutherland et al. 2016; Nelson & Sutherland 2018).

Here we present a new molecular phylogeny that includes new DNA sequence data, in which the polyphyly of *Prasiola*

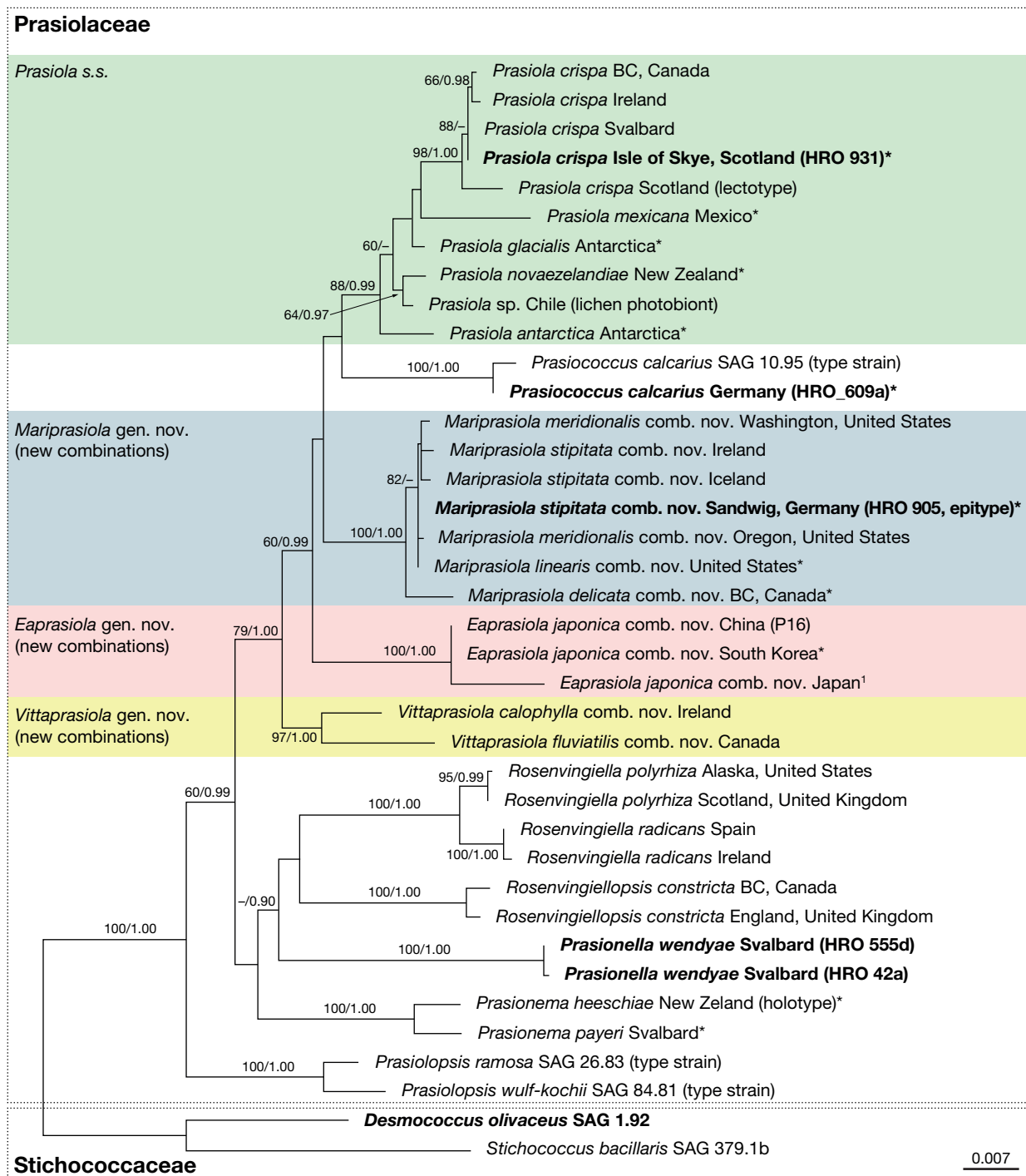


FIG. 1. — Phylogenetic tree of the Prasiolaceae based on ML and Bayesian analyses of a concatenated data set of SSU rDNA and *rbcL* sequences (*: only *rbcL* sequence included; ¹: only SSU sequence included). New sequences are set in bold. Only Maximum Likelihood bootstrap support of 60 and above, and Bayesian probabilities of 0.90 and above are shown.

siola is further confirmed. This calls for a reassessment of the classification within the Prasiolaceae and the splitting of *Prasiola* into several genera, with new generic names for all but the clade containing the generic type of *Prasiola*, *P. crispa*. New genus names are therefore proposed below for the two other clades and the single species. For the remaining 21 taxonomically valid *Prasiola* species (Guiry & Guiry 2024), no genetic data are currently available, and at present these

species cannot be unambiguously assigned to any genus but *Prasiola sensu lato*.

MATERIAL AND METHODS

Sequences (of the plastid-encoded *rbcL* and the nuclear SSU rDNA genes) of representatives of the family Prasiolaceae and

of two outgroup species were downloaded from GenBank (Table 1). New *rbcL* and SSU rDNA sequences were produced from field and cultured material. A sample of *Mariprasiola stipitata* comb. nov. (HRO 905) was collected from the type locality, Sandwig at Flensburg Fjord, Germany, on 21 Oct. 2024, while *Prasiola crispa* (HRO 931) was sampled in Portree on the Isle of Skye, Scotland, on 28 Oct. 2024, i.e. within the general area of the presumed type locality. Smaller species were isolated by serial transfer and cultivated on agarose-solidified media (3N-BBM+V, Aghajanian 1979) at low light and 6–8°C, i.e. *Prasiococcus calcarius* collected from Burg Gleichen, Thuringia, Germany (HRO 609a, 15 Mar. 2023), and two strains of *Prasionella wendyae* Heesch, M. Pazoutová & Rindi collected from Kongsfjord, Spitsbergen, Svalbard (HRO 42a, Aug. 2019, HRO 555d, 27 Aug. 2022). Material of the outgroup species *Desmococcus olivaceus* (Persoon ex Acharius) J.R. Laundon was obtained from the Culture Collection of Algae at the University of Göttingen, Germany (strain SAG 1.92).

Genomic DNA was extracted from dried or frozen material using the NucleoSpin Plant II kit (Macherey & Nagel, Germany) following the manufacturer's instructions. The DNA extract of a sample of *Prasiola japonica* from a previous study (Moniz *et al.* 2012a, as *Prasiola yunnanica* C.C. Jao) was included in PCRs amplifying the *rbcL* and SSU rDNA genes, following the PCR protocol of Heesch *et al.* (2012, 2016), using published primers for *rbcL* (SHF5 and SHR8; Heesch *et al.* 2012) and SSU (EAF3 and ITS055R; Marin *et al.* 2003).

PCR products were visualised on agarose gels, purified using the NucleoSpin Gel and PCR Clean-up kit (Macherey & Nagel, Germany) and sequenced by a commercial supplier (Eurofins, Germany) using the same primers as for PCRs. Sequence data were aligned in PhyDE (Müller *et al.* 2010), and were transformed for subsequent phylogenetic analyses with the online tool ALTER (ALignmentTransformationEnvironment; Glez-Peña *et al.* 2010). The SSU alignment comprised 999 basepairs and the *rbcL* alignment 1148 basepairs, but not all positions were available for all sequences. To avoid creating possible chimeric sequences, both markers were included only if they were sequenced from the same sample. The concatenated data set therefore contained 25 (SSU) and 37 (*rbcL*) sequences, respectively, for a total of 38 specimens, including the two outgroup taxa (*Desmococcus olivaceus* and *Stichococcus bacillaris* Nägeli) from the sister family Stichococcaceae. Before the analyses, the data set was partitioned by marker and codon position. Phylogenetic reconstructions were performed using the Maximum Likelihood criterion in RAxML v.7.3.1 (Stamatakis 2014), and Bayesian inference was performed using MrBayes v.3.2 (Huelsenbeck & Ronquist 2001; Ronquist *et al.* 2012). Support for ML analyses, based on the TIM3+I+G4 model suggested by Modeltest implemented in RAxML, was estimated by 1000 pseudoreplicate runs in RAxML. Bayesian probabilities were estimated in MrBayes by running Markov Chain Monte Carlo analyses for 3 million generations, sampling trees every 100 generations, with the first 5000 discarded as burnin, and 50% majority rule consensus trees calculated from the remaining trees. Trees were visualised using FigTree v.1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>).

ABBREVIATIONS

ML	Maximum Likelihood;
PCR	polymerase chain reaction;
<i>rbcL</i>	large subunit of the plastid operon coding for the ribulose biphosphate carboxylase oxygenase enzyme;
SSU	small subunit of the nuclear encoded ribosomal DNA.

RESULTS

In the phylogenetic analyses, deep branches generally received weak or no support, especially for the early diverging lineages, while most currently recognized genera were highly supported, i.e. *Prasiolopsis*, *Prasionella*, *Prasionema*, *Rosenvingiella* and *Rosenvingiellopsis* (Fig. 1). Sequences of the genus *Prasiola*, on the other hand, were assigned to four distinct, unambiguously supported clades, rendering the genus polyphyletic. Three of the clades contained species from marine habitats (i.e. *P. stipitata*, *P. delicata*, *P. linearis* and *P. meridionalis*), freshwater and terrestrial habitats (*P. calophylla* and *P. fluviatilis*), or freshwater habitats (*P. japonica*). These three clades were separated from the fourth clade, with moderate support, by another, fully supported clade of two sequences from a distinct genus, *Prasiococcus* (Fig. 1). Since this fourth clade comprised, amongst other species, the generitype of the genus *Prasiola*, *P. crispa*, entities included in this clade were identified as belonging to *Prasiola sensu stricto*. To amend the polyphyly of the genus, new combinations are required for the other three clades. These are assigned to the new genera *Mariprasiola* gen. nov., *Vittaprasiola* gen. nov. and *Eaprasiola* gen. nov., as follows.

TAXONOMIC REVISIONS

Family PRASIOACEAE F.F. Blackman & Tansley

Genus *Mariprasiola* Heesch, Guiry & Rindi, gen. nov.

TYPE. — *Mariprasiola stipitata* (Suhr ex Jessen) Heesch, Guiry & Rindi, comb. nov. (basonym: *Prasiola stipitata* Suhr ex Jessen) below.

ETYMOLOGY. — Derived from “mari-”, a prefix denoting the marine habitat typical of the genus.

DESCRIPTION

Thalli adhering to the substratum by a callus- or crust-like holdfast, from which a pluriseriate stipe arises, gradually expanding into a linear, lanceolate, wedge-shaped, spoon-shaped or fan-shaped blade, ranging in width and length from a few mm to approximately 1.5 cm. Reproduction sexually by oogamy or asexually by aplanospores. The genus includes both species with sexual reproduction and species with entirely asexual life histories. Algae living in upper intertidal and supratidal habitats of marine rocky shores often subject to inputs of organic nitrogen, or of coastal lagoons.

TABLE 1. — Origin and GenBank accession numbers of taxa included in the sequence alignments, with collection details of additional samples for which new sequences were generated in this study (GenBank accession numbers in **bold**). n/d, no data available.

species	origin	references or collection details for new samples	nrDNA	rbcL
<i>Prasiococcus calcarius</i>	Switzerland (SAG 10.95)	Rindi <i>et al.</i> 2007	EF200527	EF203011
	Germany	Obtained in this study. Cultured material (HRO 609a): Burg Gleichen, Thuringia, Germany. coll.: S. Heesch & M. Janssen, 15 Mar. 2023	n/d	PQ605268
<i>Prasiola antarctica</i>	Antarctica	Moniz <i>et al.</i> 2012a	n/d	JQ669721
<i>Prasiola crispa</i>	Ireland	Rindi <i>et al.</i> 2004, 2007	EF200530	AY694196
	BC, Canada	Rindi <i>et al.</i> 2007	EF200531	EF203018
	Svalbard	Richter <i>et al.</i> 2017	KP791868	KP791900
	Scotland, UK	Moniz <i>et al.</i> 2012a (lectotype)	n/d	JQ669725
	Scotland, UK	Obtained in this study. HRO 931, Portree, Isle of Skye, Argyll; coll. S.Heesch, 28 Oct. 2024	n/d	PQ605265
<i>Prasiola glacialis</i>	Antarctica	Moniz <i>et al.</i> 2012b (holotype)	n/d	JQ669710
<i>Prasiola mexicana</i>	Mexico	Moniz <i>et al.</i> 2012b (sample P46/F5)	n/d	JQ669719
<i>Prasiola novaezelandiae</i>	New Zealand	Heesch <i>et al.</i> 2012	n/d	HQ174306
<i>Prasiola</i> sp.	Chile	Thüs <i>et al.</i> 2011 (lichen photobiont)	JN573862	JN573838
<i>Eaprasiola japonica</i> comb. nov.	China	This study; Moniz <i>et al.</i> 2012a (as <i>P. yunnanica</i>)	PQ586995	JQ669708
	Japan	Moat War & Hara 2002	AB079032	n/d
	South Korea	Sutherland <i>et al.</i> 2016	n/d	KT354067
<i>Mariprasiola delicata</i> comb. nov.	British Columbia, Canada	Saunders & Kucera 2010 (as <i>Prasiola</i> sp.)	n/d	HQ603498
<i>Mariprasiola linearis</i> comb. nov.	USA	Sherwood <i>et al.</i> 2000	n/d	AF189065
<i>Mariprasiola meridionalis</i> comb. nov.	Washington, USA	Sherwood <i>et al.</i> 2000	AF189074	AF189066
	Oregon, USA	Rindi <i>et al.</i> 2004, 2007	EF200528	AY694191
<i>Mariprasiola stipitata</i> comb. nov.	Ireland	Rindi <i>et al.</i> 2004, 2007	EF200526	AY694192
	Iceland	Rindi <i>et al.</i> 2007	EF200524	EF203014
	Germany	Obtained in this study; HRO 905, Sandwig, Flensburg Fjord; coll. S. Heesch, 21 Oct. 2024 (epitype)	n/d	PQ605264
<i>Vittaprasiola calophylla</i> comb. nov.	Ireland	Rindi <i>et al.</i> 2004, 2007	EF200521	AY694194
<i>Vittaprasiola fluviatilis</i> comb. nov.	Canada	Sherwood <i>et al.</i> 2000	AF189072	AF189063
<i>Prasiolopsis ramosa</i> Vischer	Switzerland (SAG 26.83)	Karsten <i>et al.</i> 2005; Rindi <i>et al.</i> 2007	AY762600	EF203015
<i>Prasiolopsis wulf-kochii</i> Darienko & Pröschold	Amazonia, Brazil (SAG 84.81)	Karsten <i>et al.</i> 2005; Rindi <i>et al.</i> 2007 (as <i>Trichophilus welckeri</i>)	AY762601	KM464713
<i>Prasionella wendyae</i>	Svalbard	Obtained in this study. Cultured material (HRO 42a): Kongsfjord, Spitzbergen. coll.: U. Karsten, Aug. 2019	PQ586996	PQ605266
	Svalbard	Obtained in this study. Cultured material (HRO 555d): Kongsfjord, Spitzbergen. coll.: S. Heesch, V. Lacombe & H. de Lauzon, 18 Aug. 2022	PQ586997	PQ605267
<i>Prasionema heeschiai</i> W.A.Nelson & J.E.Sutherland	New Zealand	Nelson & Sutherland 2018	n/d	MF347442
<i>Prasionema payeri</i> Heesch, M.Pazoutová & Rindi	Svalbard	Heesch <i>et al.</i> 2016	n/d	LN877815
<i>Rosenvingiella polyrhiza</i> (Rosenvinge) P.C.Silva	Alaska, USA	Rindi <i>et al.</i> 2007	EF200520	EF203013
	UK	Rindi <i>et al.</i> 2004, 2007	EF200515	AY694206
<i>Rosenvingiella radicans</i> (Kützinger) Rindi, L.M.McIlvor & Guiry	Ireland	Rindi <i>et al.</i> 2004, 2007	EF200516	AY694204
	Spain	Rindi <i>et al.</i> 2004, 2007	EF200517	AY694199
<i>Rosenvingiellopsis constricta</i> (Setchell & N.L.Gardner) Heesch, M.Pazoutová & Rindi	UK	Rindi <i>et al.</i> 2004, 2007	EF200523	AY694197
	British Columbia, Canada	Rindi <i>et al.</i> 2007, Moniz <i>et al.</i> 2014	EF200529	EF203019
outgroup				
<i>Desmococcus olivaceus</i>	SAG 1.92	Pröschold unpublished	KM020049	PQ605269
<i>Stichococcus bacillaris</i>	SAG 379.1b	Negrisolo <i>et al.</i> unpublished; Nyati <i>et al.</i> 2007	AJ311637	AM260442

***Mariprasiola stipitata* (Suhr ex Jessen)
Heesch, Guiry & Rindi, comb. nov.**

Prasiola stipitata Suhr ex Jessen, *Prasiolae generis algarum monographia*: 16, pl. II: figs 11–16 (Jessen 1848).

LECTOTYPE. — Original illustration (Jessen 1848: pl. II, fig. 11; “*frondes Slesvicenses*” designated by Burrows 1991: 24).

EPITYPE (here designated for the above lectotype). — B 40 0046812 (ZE Botanischer Garten und Botanisches Museum, Freie Universität Berlin); Sandwig, Flensburg Fjord, Germany; dried herbarium specimen; 21.X.2024; *HRO 905*; S. Heesch coll./det.; GenBank accession no.: PQ605264 (*rbcl* sequence).

TYPE LOCALITY. — “*Sandwieck in ducatu Slesvicensi*” [Duchy of Schleswig, now in the state of Schleswig-Holstein, Germany] (Jessen 1848: 16) (Sandwig, Flensburg Fjord, Germany).

REMARKS

Karl Friedrich Wilhelm Jessen (1821–1889) was a German botanist born in Schleswig (then a fiefdom of Denmark) whose doctorate at the University of Kiel was a monograph of the genus *Prasiola*, effectively published at Kiel by the university.

At the time this species was described, the duchy of Slesvic (current German spelling: Schleswig) comprised the southern part of the Jutland peninsula, with Sandwieck (presently spelled Sandwig) situated on the southern coast of Flensburg Fjord in the middle of the duchy. In 1920, the northern part of the duchy was assigned to Denmark, while the southern part, including the southern part of Flensburg Fjord (and Sandwig), was integrated into the German Reich.

***Mariprasiola delicata* (Setchell & N.L.Gardner)
Heesch, Guiry & Rindi, comb. nov.**

Prasiola delicata Setchell & N.L.Gardner, *University of California Publications in Botany* 7: 291, pl. 22: fig. 3a–f; pl. 25: fig. 1; pl. 24: fig. 8 (Setchell & Gardner 1920).

TYPE MATERIAL. — *N.L. Gardner 3981* (Setchell & Gardner 1920: 292, but the specimen is “currently missing”, *fide* Dr Kathy-Ann Miller, UC).

LECTOTYPE (here designated). — Original illustration in Setchell & Gardner (1920: pl. 22: fig. 3e).

TYPE LOCALITY. — “Sitka, Alaska” (United States) (Setchell & Gardner 1920: 292), growing at or near the upper tide mark on rocky islets.

REMARKS

William Albert Setchell (1864–1943), Professor of Botany at the University of California, Berkeley, and Nathaniel Lionel Gardner (1864–1937), also of the University of California at Berkeley, described many algae from Alaska to the Gulf of California and elsewhere. Their types are generally to be found in the Jepson Herbarium at UC.

***Mariprasiola linearis* (C.-C.Jao)
Heesch, Guiry & Rindi, comb. nov.**

Prasiola linearis C.-C.Jao, *Papers of the Michigan Academy of Sciences, Arts and Letters* 22: 105, pl. XIII, figs 5–7 (Jao 1937).

TYPE MATERIAL. — *C.-C. Jao No. 1261*; 17.XII.1935 [the place of deposition of the type cannot be ascertained].

LECTOTYPE (here designated). — Original illustration in Jao (1937: pl. XIII, fig. 5).

TYPE LOCALITY. — “Growing on gravel and grasses in the upper littoral belt, Argyle Lagoon, San Juan Island” (Washington State, United States).

REMARKS

Chin-Chih Jao (1900–1997) carried out his doctoral research at the University of Michigan in the 1930s, but a search of MICH by Dr M. J. Wynne revealed no type or any other material, even though a footnote on p. 99 of his publication specified that types were deposited there. Original material may have been brought to China by Dr Jao (MBMCAS) but its current location is unknown.

***Mariprasiola meridionalis* (Setchell & N.L.Gardner)
Heesch, Guiry & Rindi, comb. nov.**

Prasiola meridionalis Setchell & N.L.Gardner, *University of California Publications in Botany* 7: 291, pl. 25: fig. 2 (Setchell & Gardner 1920).

TYPE MATERIAL. — *N.L. Gardner 3824* (Setchell & Gardner 1920: 291, but the specimen is “currently missing”, *fide* Dr Kathy-Ann Miller, UC).

TYPE LOCALITY. — “Neah Bay, Washington” (United States) (Setchell & Gardner 1920: 291).

LECTOTYPE (here designated). — Original illustration in Setchell & Gardner (1920: pl. 25: fig. 2).

Genus *Vittaprasiola* Heesch, Guiry & Rindi, gen. nov.

ETYMOLOGY. — The Latin noun *vitta* (*pl. vittae*), a belt or ribbon, is here employed as a prefix.

TYPE. — *Vittaprasiola calophylla* (Carmichael ex Greville) Heesch, Guiry & Rindi, comb. nov. (basonym: *Prasiola calophylla* Carmichael ex Greville), below.

DESCRIPTION

Thalli adhering to the substratum by a basal cell or a callus-like holdfast, from which a uniseriate or pluriseriate stipe arises, gradually expanding into a linear, ribbon-shaped blade up to a 2 cm wide and up to 10 cm long. Asexual reproduction by aplanospores; sexual reproduction not known, presumed but not observed. When known, life history consists of an alternation of two asexual heteromorphic generations. Algae living in freshwater habitats and in terrestrial habitats often subject to inputs of organic nitrogen.

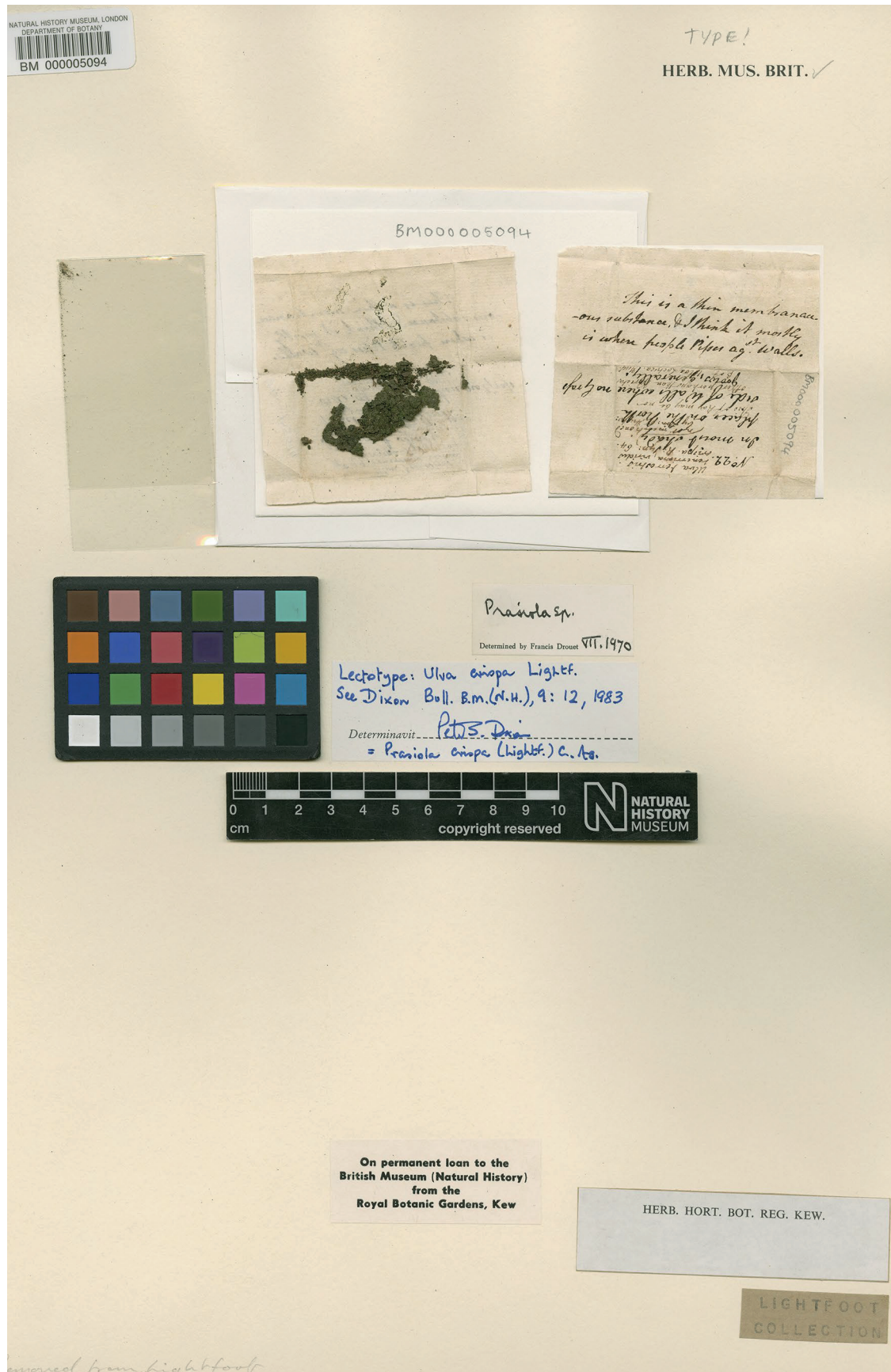


FIG. 2. — Lectotype specimen of *Ulva crista* Lightfoot in the Lightfoot herbarium (BM000005094). The specimen was labelled "*Prasiola* sp." in 1970 by Francis Drouet, when he examined the specimen of *Ulva montana* Lightfoot [synonym of *Sorospora montana* (Lightfoot) Hassall] in which folder the *Ulva crista* material was then included. The specimen was also annotated as lectotype by Peter S. Dixon in 1983. Reproduced by kind permission of the Natural History Museum, London.

Vittaprasiola calophylla (Carmichael ex Greville)

Heesch, Guiry & Rindi, comb. nov.

Bangia calophylla Carmichael ex Greville, *Scottish Cryptogamic Flora* 1826: pl. 220 (Greville 1826). — *Prasiola calophylla* (Carmichael ex Greville) Kützing, *Phycologia germanica, d. i. Deutschlands Algen in bündigen Beschreibungen. Nebst einer Anleitung zum Untersuchen und Bestimmen dieser Gewächse für Anfänger*: 243 (Kützing 1845).

POTENTIAL TYPE. — E00500045, which is the only specimen listed in the Greville collection as having been collected by Carmichael.

TYPE LOCALITY. — “On a block of stone near the Clergyman’s house in the Island of Lismore. October. Captain Carmichael.” [Argyll & Bute, Scotland] (Greville 1826: expl. pl. 220).

REMARKS

Greville (1826: expl. pl. 220) attributed the name to “Carmichael MSS”. Captain Dugald [Dughall] Carmichael (1772-1827) was a Scottish surgeon-soldier-adventurer and friend of Robert Brown (1773-1858); Carmichael retired to Ardtur, Appin, about 1817, spending much of his time studying the local algae and communicating many of his discoveries to his contemporaries.

Vittaprasiola fluviatilis (Sommerfelt)

Heesch, Guiry & Rindi, comb. nov.

Ulva fluviatilis Sommerfelt, *Magazin for Naturvidenskaberne* 9 (1): 27, pl. III: figs 1 a-d (Sommerfelt 1828). — *Prasiola fluviatilis* (Sommerfelt) Areschoug ex Lagerstedt, *Om algsläktet Prasiola. Försök till en Monographi*: 28 (Lagerstedt 1869).

TYPE MATERIAL. — University of Oslo Natural History Museum (O)? (not seen).

TYPE LOCALITY. — Leerdalsören, Bergen, Norway (Sommerfelt 1828: 28)

REMARKS

Søren Christian Sommerfelt (1794-1838) was a Norwegian clergyman and botanist whose collections are currently held by the University of Oslo Natural History Museum (O).

Genus *Eapراسيولا* Heesch, Guiry & Rindi, gen. nov.

ETYMOLOGY. — Derived from “Ea”, a prefix based on the abbreviation of “East Asian” as a connotation of the three east Asian countries where this species has so far been recorded from, i.e. Japan, South Korea and China (Guiry & Guiry 2024).

TYPE. — *Eapراسيولا japonica* (Yatabe) Heesch, Guiry & Rindi, comb. nov. (basonym: *Prasiola japonica* Yatabe), below.

DESCRIPTION

Thalli consisting of oval or linear blades, up to 4 cm wide and 20 cm long, attached to the substratum by a small, callus-like holdfast. Reproduction takes places sexually by oogamy and asexually by aplanospores. Life history consists of a repetition of the same generation that reproduces both asexually and sexually. Living in freshwater.

Eapراسيولا japonica (Yatabe)

Heesch, Guiry & Rindi, comb. nov.

Prasiola japonica Yatabe, *Botanical Magazine, Tokyo* 5 (52): 186, pl. XXV: figs 1-5 (Yatabe 1891).

TYPE MATERIAL. — University of Tokyo (TI).

SYNTYPE LOCALITIES. — Nikko (province of Shimotsuke), Kiri (Kozuke), Shibakawa (Suruga), and Oimura (Mino) [Japan] (Yatabe 1891: 188). The figures in Yatabe’s pl. XXV are of material sent to him by “Mr. I. Ogasawara” collected in March 1891 from Kiriugawa, “[...] a rapid stream near the town of Kiri”, Kozuke Province [now Gunma Prefecture, central Honshu]. This material would be the most suitable for lectotypification.

REMARKS

Ryōkichi (Ruōkichi) Yatabe (1851-1899) was the first professor of botany at the University of Tokyo’s School of Science during the Meiji-period. His algal specimens are at the University of Tokyo (Dr Taiju Kitayama pers. comm.) and not at the University of Sapporo (Prof. Kazuhiro Kogame pers. comm.).

DISCUSSION

The molecular phylogeny presented here confirms the polyphyly of *Prasiola* reported by previous studies and justifies the proposed splitting of *Prasiola* into several genera. An alternative to this split would be to accommodate *Prasiococcus calcarius* in the genus *Prasiola*. However, this is prevented by the different morphologies of these two genera, with *Prasiola* species consisting of many cells organised in single-layer blades, while *Prasiococcus* has few-celled sarcinoid thalli. The habit of *Prasiococcus* appears to be very consistent and not affected by environmental conditions; the strains of *Prasiococcus* that we isolated and observed in culture never showed any transition to bladed stages similar to those of *Prasiola*. The phylogenetic position of the new genera provides further support for multiple separate colonisations of aquatic habitats in the family Prasiolaceae, previously highlighted by Moniz *et al.* (2012a).

At present, there are no characters that permit us unambiguously to separate the *Prasiola*-like genera, as there is wide morphological and ecological overlap among the species belonging to the new genera and the type of *Prasiola*, the Lightfoot material of *Ulva crista*. This also prevents the assignment based on morphology of the 21 species of *Prasiola* currently without genetic data, to any genus other than *Prasiola*. On the other hand, within the *Maripراسيولا* gen. nov. clade, neither of the two markers support a separation of *M. meridionalis* comb. nov. and *M. linearis* comb. nov. from the generitype *M. stipitata* comb. nov., as relationships are not resolved between the three species, leading to a supposed polyphyly of the two sequences of *M. meridionalis* comb. nov. included in the analyses. However, morphological differences that persisted in cultures led Moniz *et al.* (2014) to refrain from synonymising these entities. For the present, therefore, we continue to follow this viewpoint until such time when a higher number of sequenced markers may be available that support their conspecificity.

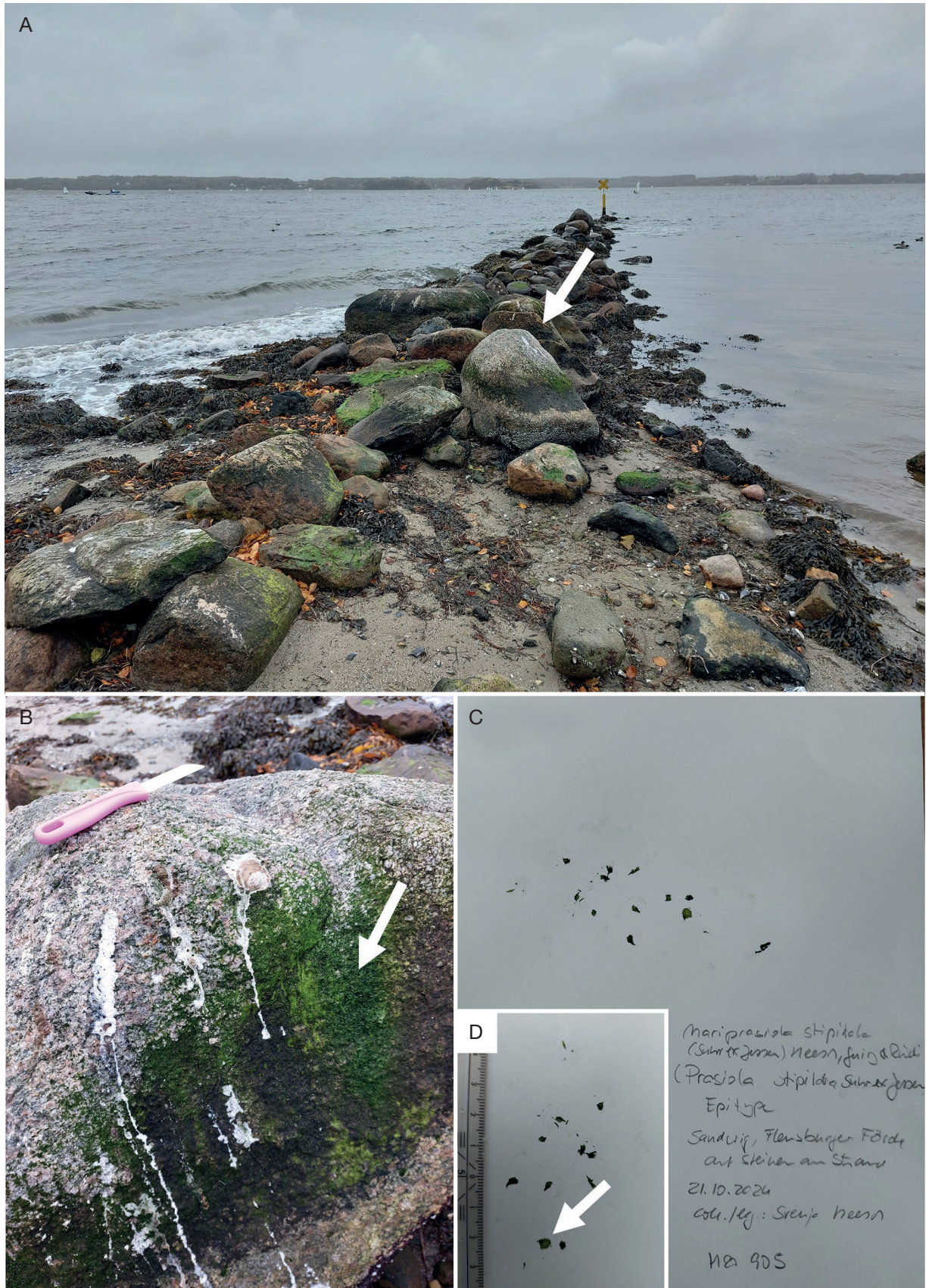


FIG. 3. — Epitype of *Mariprasiola stipitata* comb. nov.: **A**, **B**, type locality, Sandwig, Flensburg Fjord, Germany, 21.X.2024: Wave breaker at Sandwig beach, consisting of large rocks; **B**, rock with seagull feces and dark green patches of *Mariprasiola stipitata* comb. nov. (arrow, length of pink kitchen knife: 16 cm); **C**, herbarium voucher (B40 0046812) with epitype material; **D**, detail of epitype specimen (arrow).

Also, we note here some issues concerning the types of some of the species that we transfer to the new genera. Although these species are validly published, for some the type was an illustration, a type specimen was not formally designated, or the original type specimens appear to have been lost. No actual holotype specimen exists for *Mariprasiola stipitata* comb. nov., except for an illustration (Jessen 1848), which was designated as lectotype by Burrows (1991). We herein epitypify this lectotype with material collected at the type locality in October 2024.

Mariprasiola delicata comb. nov. and *Mariprasiola meridionalis* comb. nov. were described (as *Prasiola delicata* and *Prasiola meridionalis*, respectively) by Setchell & Gardner (1920). Most of the original collections of William Albert Setchell and Nathaniel Lyon Gardner are conserved in the Jepson Herbarium at the University of California, Berkeley (UC), which should therefore have the type specimens of these two species. However, no original specimens of these two species collected or examined by Setchell and Gardner are currently present in UC (Dr Kathy Ann Miller, personal communication), and we here lectotypify both names with the original material in accordance with best nomenclatural practice. The same problem pertains to *Prasiola linearis*, described by Jao (1937) based on collections from the Argyll Lagoon (Washington State, United States). Chin-Chih Jao (1900–1997) carried out his doctoral research at the University of Michigan, Ann Arbor in the 1930s (Wynne 1997), but a search of MICH by Dr M.J. Wynne revealed no type or any other material, even though a footnote on p. 99 of his publication (Jao 1937) indicated that type material was deposited there.

With respect to the type of *Ulva crispa*, Lightfoot (1777: 972) does not mention any specific locality, although it is probable from the title, *Flora scotica*, that his specimen was collected in Scotland. Dixon (1983: 12) found in the Lightfoot herbarium in the London Natural History Museum what “...appears to be the original Lightfoot material of *U[lva] crispa* ... in the folder annotated *U[lva] montana*.” and annotated “*Prasiola* sp.” by Francis Drouet (1907–1982), presumably while Drouet, a cyanophyte specialist, was examining the *Ulva montana* Lightfoot material [currently the coccoid cyanophyte *Sorospora montana* (Lightfoot) Hassall]. This latter folder was annotated “Mountain Dulse Skye”, and this probably gave rise to later claims (e.g. Burrows 1991: 21) that the type locality of *Ulva crispa* Lightfoot was the Isle of Skye, Argyll, Scotland. In fact, no locality is indicated on the sole specimen in Lightfoot’s herbarium (Fig. 2) annotated in Lightfoot’s hand “No. 22. In moist shady places on the North side of Walls where no Grass grows, generally. This is a thin membranaceous substance, & I think it mostly is where people Pisses ag[ain]st Walls.” Bryant *et al.* (2012: 32) comment “This observation agrees with the known ecology of this taxon which is often associated with sites rich in organic nitrogen (such as urine or guano).” Dixon (1983: 12) and Bryant *et al.* (2012: 32) referred to this specimen as the lectotype of *Ulva crispa* Lightfoot. The phrase “*hic*

designatus” or an equivalent (ICN Art 7.11) was not used by Dixon (1983: 12), but was not required prior to 1st January 2001, and Dixon’s lectotypification is thus valid. The lectotype now bears the number BM000005094 and is annotated as such by Peter S. Dixon as the lectotype (Fig. 2). The lectotype was sampled by Moniz *et al.* (2012a) and a partial *rbcL* sequence produced (GenBank accession JQ669725). We furthermore included in our data set a partial *rbcL* sequence from material collected on the Isle of Skye, Argyll, Scotland, in October 2024, the overall morphology of which agreed with that of the description of *P. crispa*, and which clustered unambiguously with other strains of this species.

These typification issues, however, do not invalidate our proposed transfers to new genera and the new combinations proposed here for these species. If original type specimens are not located, sequenced neotypes and/or epitype material should be designated based on new material collected from the type localities and morphologically agreeing with the original descriptions.

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