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Article

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First records of the genus *Seiria* (Peyssonneliales, Rhodophyta) in the western Pacific with descriptions of three new species

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Abstract

The red algal genus *Seiria* (order Peyssonneliales) is newly reported from the western Pacific based on collections from Guam, Japan, and Kosrae. Three new species are described based on morphological observations and molecular analyses: *Seiria guamensis sp. nov.*, *S. japonica sp. nov.*, and *S. kosraeana sp. nov.* All species are attached by unicellular rhizoids, the only vegetative feature shared among all known species of the genus. *Seiria japonica sp. nov.* and *S. kosraeana sp. nov.* produce serially arranged tetrasporangia characteristic of the genus, whereas the examined specimen of *S. guamensis sp. nov.* was not reproductive. The three new species are distinguished from one another and from their congeners by unique combinations of morphological traits and by significant sequence divergence in COI-5P and *rbc*L molecular markers. *Seiria* and other peyssonnelioid algae are severely under-reported globally, underscoring the need for expanded collections to reveal their true diversity.

Key words: *Seiria*, DNA barcoding, marine biodiversity, Peyssonneliales, taxonomy, coral reefs, Guam, Mariana Islands

Introduction

The red algal order Peyssonneliales (Krayesky *et al*. 2009) has undergone substantial systematic revision since the turn of the century including the description, recognition, or reassessment of several genera and species (e.g., Zhang & Zhou 1981; Kato *et al*. 2006; Dixon & Saunders 2013; Sherwood *et al*. 2020; Mills & Schils 2021; Pestana *et al*. 2021). Among the 15 currently recognized genera in the Peyssonneliales (Guiry & Guiry 2025), the genus *Seiria* K.R. Dixon (2018) was described on the basis of phylogenetic divergence and a distinctive morphology including unicellular rhizoids, extensive directional cell fusions in the lower and mid perithallus, and the serial production and release of tetrasporangia (Dixon 2018). *Seiria* is closely related to the genera *Incendia* K.R. Dixon (2013) and *Ramicrusta* D.R. Zhang & J.H. Zhou (1981).

Seiria was initially described as a monospecific genus whose generitype, *Seiria magnifusa* K.R. Dixon (2018: 241), was collected from subtidal reefs in western Australia (Dixon 2018). The second species, *Seiria mesophotica* A.R. Sherwood (2021: 20), was described from mesophotic reefs in Hawaii (Sherwood *et al.* 2021a). *Seiria mesophotica* does not possess the extensive directional cell fusions reported for the generitype, but displays unicellular rhizoids and the serial production and release of tetrasporangia that characterize the genus (Sherwood *et al.* 2021a). Additional phylogenetic analyses done when describing *S. mesophotica* also helped solidify the phylogenetic placement of *Seiria* as a distinct clade (Sherwood *et al.* 2021a), while a recent taxonomic revision of the Peyssonneliales further established *Seiria* as sister to *Incendia* (Pestana *et al.* 2021). In addition to *S. magnifusa* and *S. mesophotica*, one additional undescribed *Seiria* species has recently been reported from New Zealand based on DNA sequence data (Nelson *et al.* 2022).

An ongoing investigation of crustose calcifying red algal (CCRA) diversity in Guam and the rest of Micronesia has shown that Guam harbors one of the most diverse CCRA floras reported worldwide (Mills *et al.* 2022). To that end, two specimens corresponding to *Seiria* were collected from shallow tropical reefs in Guam and Kosrae as part of the persistent effort to document Micronesian CCRA diversity. One additional specimen in the University of Guam

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Herbarium (GUAM) had recently been collected from Okinawa, Japan. Below, we report the first records of the genus *Seiria* from Japan, the Mariana Islands, Micronesia, and the broader Western Pacific. Furthermore, we describe three new species using a combination of morphological characterization and comparative molecular analyses.

Materials and methods

Collection and Morphological Analysis

Specimens were sampled by diving on shallow reefs in Guam, Japan, and Kosrae (Figure 1). Samples were preserved in formalin, silica gel, and air dried before being deposited at the University of Guam Herbarium (GUAM). Anatomical observations were made using light microscopy (LM). For anatomical observations, material was decalcified in 0.08 M HCl, optionally stained with aniline blue, hand-sectioned, and mounted on glass slides. LM observations were conducted and photographed using a Nikon Eclipse 80i light microscope (Nikon Corporation, Shinagawa, Tokyo, Japan).

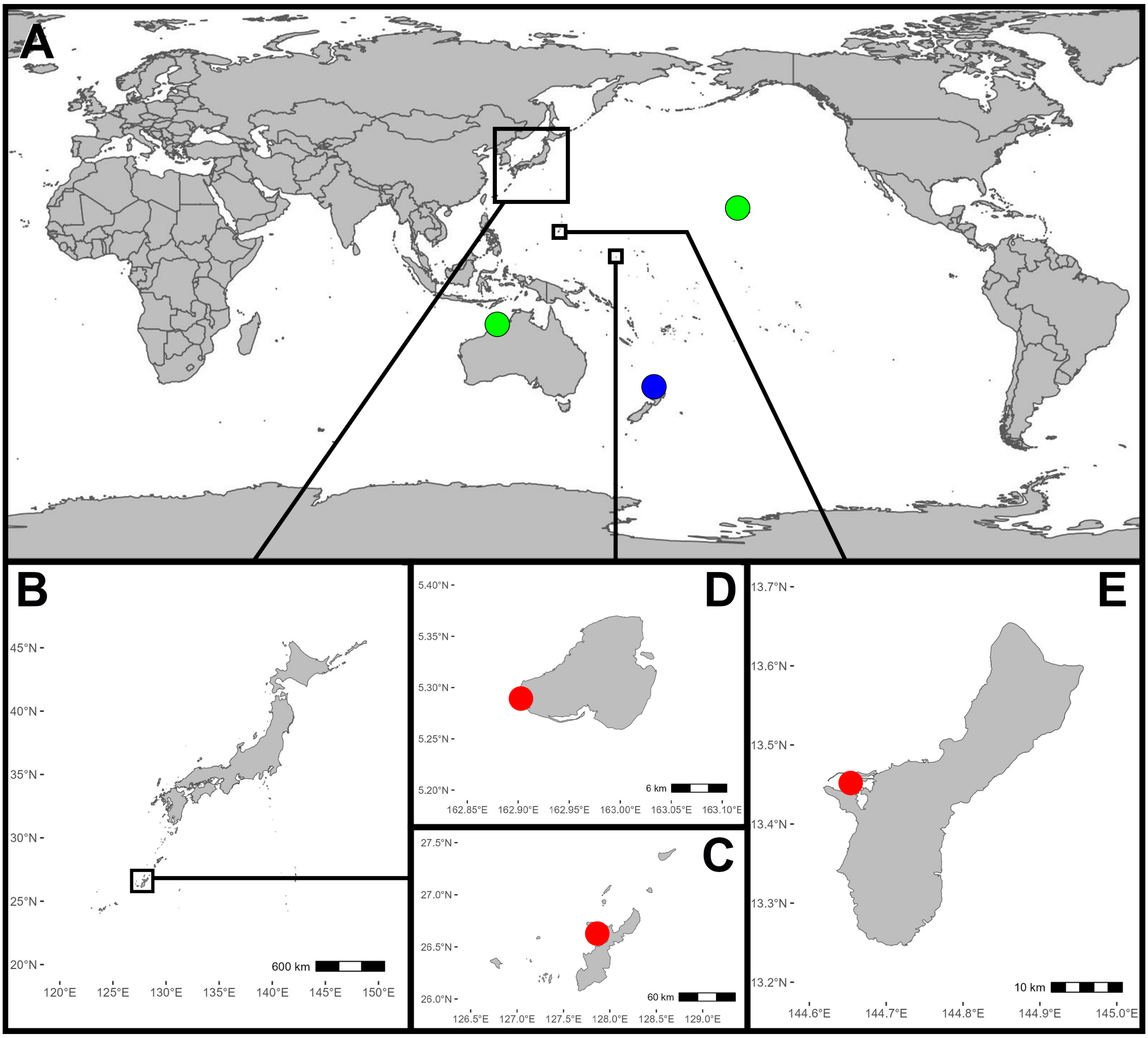

FIGURE 1. Maps of the type localities of *Seiria* species. (A) Pacific-centered map showing the locations of Guam, Japan, and Kosrae (black boxes). The type localities of the two previously described *Seiria* species and the collection location of an undescribed species from northern New Zealand are indicated by green and blue dots, respectively. (B) Map of Japan showing the location of the Okinawa prefecture (black box). Scale bar = 600 km. The red dots in panels C–E show the collection sites of the new *Seiria* species from Okinawa (C; scale bar = 60 km), Kosrae (D; scale bar = 6 km), and Guam (E; scale bar = 10 km).

Molecular Analysis

Total genomic DNA was extracted following the protocol described by Saunders & McDevit (2012) or using the GenCatch Blood & Tissue Genomic Mini Prep Kit (Epoch Life Science, Inc., Missouri City, TX) following the manufacturers' bench protocol. The 5' end of the mitochondrial cytochrome c oxidase subunit 1 (COI-5P) was amplified via polymerase chain reaction (PCR) using the forward primer TS_COI_F01_10 (Mills & Schils 2021), the reverse primer GWSRx (Saunders & McDevit 2012), and following the profile described by Mills & Schils (2021). The 3' end (~ 750 bp) of the plastid ribulose-1,5-biphosphate carboxylase large subunit (*rbc*L) was amplified using the primers F492 and RrbcS Start (Freshwater & Rueness 1994) following the profile reported by Kucera & Saunders (2012). Amplification of the chloroplast *psb*A gene was performed with primers psbA-F and psbAR2 (Yoon *et al.* 2002) under the thermal cycling conditions detailed by Mills & Schils (2021). All PCR products were sent to Macrogen Inc. (Seoul, Republic of Korea) for DNA sequencing.

Individual COI-5P and *rbc*L alignments were generated using the MAFFT v7.450 plugin (Katoh *et al.* 2002; Katoh & Standley 2013) in Geneious Prime 2023.2.1. (Kearse *et al*. 2012). The general time reversal + invariable sites + gamma distribution (GTR+I+G) evolutionary model was selected as the optimal model for both gene alignments using jModeltest 2.1.3 (Darriba *et al*. 2012). Sequences generated during this study were aligned with those belonging to members of the closely related genera *Seiria* and *Incendia*, as well as representatives of other genera in the Peyssonneliales (Table 1). While *psb*A sequences were successfully obtained for two species, they were not used in phylogenetic analyses due to a lack of *psb*A sequences available for most described peyssonnelioid species. Alignments of 97 COI-5P and 92 *rbc*L sequences were used confirm the monophyly of *Seiria* and to determine the phylogenetic relationship between the three newly described *Seiria* species and the other two currently described species in the genus. For all alignments and trees, selected outgroup taxa belonged to the Rhodymeniales, a relatively divergent order from the Peyssonneliales that belongs to the same subclass (Yang *et al.* 2016). All newly generated COI-5P, *rbc*L, and *psb*A sequences were deposited in GenBank (Table 1).

Phylogenetic analyses were performed for both alignments using maximum likelihood (ML) methods in IQ-TREE (Nguyen *et al*. 2015), and Bayesian inference was completed using the MrBayes (Ronquist & Huelsenbeck 2003) plugin in Geneious Prime. ML node support was estimated using nonparametric bootstrapping (1,000 replicates). Bayesian trees were run for 1,500,000 generations with trees sampled every 100 generations and the first 3,000 trees discarded as burn-in. The average standard deviation of split frequencies reached less than 0.01 for all Bayesian trees. Phylogenetic analyses were used in conjunction with anatomical observations to describe new species and provide new generic records of *Seiria* for Japan and Micronesia.

TABLE 1. List of species, accession numbers, and voucher numbers of COI-5P and *rbc*L sequences used in phylogenetic analyses. Accession numbers of two obtained *psb*A sequences were also included where applicable. Species and sequences that are new to this study are in bold type.

	GenBank Accession Number			
Organism	**COI-5P**	***rbc*L**	***psb*A**	**Voucher number**
Agissea amadoi		MW822572		ALCB 132953
Agissea densissima		MW822573		ALCB 132955
Agissea distenta		AB325856		SAP 098401
Agissea distenta		EU349140		K235
Agissea harveyana		AB325859		SAP 097591
Agissea harveyana		MF668134		TC13191
Agissea inamoena		EU349122		K194
Agissea inamoena		EU349127		K160
Agissea novae-hollandiae	JX969736	JX969794		PLD001
Agissea orientalis		AB325865		SAP 102071
Agissea orientalis		MZ047755		ARS09966

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TABLE 1 (Continued)

	GenBank Accession Number			
Organism	**COI-5P**	***rbc*L**	***psb*A**	**Voucher number**
Agissea simulans		EU349130		K121
Agissea sp.Australia	JX969699			LAG02
Agissea sp.Australia	JX969709			PLD007
Agissea sp.Malaysia		AB325862		SAP 091284
Agissea stoechas		EU349128		K106
Agissea stoechas		EU349129		K176
Agissea taberniforma		MW822575		ALCB 132952
"*Agissea valentinii*"		EU349132		K104
"*Agissea valentinii*"		EU349133		K228
Agissea villatlantica		MW822574		ALCB 132951
Agissea yemonjasagbae		MW822571		ALCB 132954
Brasilophycus roseomarginatus	MW822580	MW822578		ALCB 132722
Brasilophycus similis	MW822579	MW822577		ALCB 132723
Brasilophycus similis		MW822576		ALCB 132727
Incendia basilii	JX969745			VT030
Incendia crenata	JX969689			VT015
Incendia crenata	JX969714			VT095
Incendia crenata	JX969723			VT114
Incendia cryptica	HM918344			GWS016759
Incendia cryptica	HM918347			GWS016762
Incendia cryptica	HM918354			GWS016771
Incendia cryptotricha	JX969738			VT070
Incendia glabra	JX969688	JX969774		VT141
Incendia homosorora	HM918345			GWS016760
Incendia homosorora	HM918361			GWS016780
Incendia homosorora	HM918362			GWS016781
Incendia homosorora	HM918377			GWS016801
Incendia lisianskiensis	MZ043101	MZ047757		ARS09969
Incendia regularis	JX969750	JX969803		VT039
Incendia sp. PCC 2021	MN920390			TP3S010
Incendia undulata	JX969706			VT005
Incendia yoneshigueana		MN990096		ALC132951/P19
Metapeyssonnelia corallepida		EU349214		K85
Metapeyssonnelia sp. DLB-8375		JQ429756		DLB-8375
Olokunia atropurpurea		AB325853		SAP 098399
Olokunia atropurpurea	JX969703	JX969782		CM04

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TABLE 1 (Continued)

	GenBank Accession Number			
Organism	**COI-5P**	***rbc*L**	***psb*A**	**Voucher number**
Olokunia boudouresquei		AB325813		SAP 102065
Olokunia boudouresquei		KC998947		RHO2031
Olokunia immersa		AB325861		SAP 098402
Olokunia japonica		AB325817		SAP 102040
Olokunia japonica		AB325819		SAP 097597
Olokunia japonica		AB325821		SAP 102053
Olokunia japonica		AB325823		SAP 102064
Olokunia meridionalis		AB325864		SAP 098403
Peyssonnelia coriacea		KR732900		LAF6390
Peyssonnelia coriacea		KR732906		LAF5464
Peyssonnelia coriacea		KR732909		LAF5360
Peyssonnelia heteromorpha		KR732912		LAF5361
Peyssonnelia replicata		EU349182		K241
Peyssonnelia rubra		KR732915		LAF5461
Peyssonnelia squamaria	JX969741	JX969797		GWS018179
Polystrata dura		AB325869		SAP 098388
Polystrata dura	JX969712	JX969784		VT097
Polystrata erupta	OM902807			GH0015121
Polystrata erupta	OM902088			GH0015123
Polystrata erupta	PP131398			GWS037166
Polystrata erupta	PP131415			GWS034720
Polystrata erupta	PP131436			GWS034749
Polystrata erupta	PP131448			GWS037119
Polystrata erupta		PP131463		GWS016779
Polystrata fosliei		AB325872		SAP 098397
Polystrata kimberleyensis	PP131409			GWS034782
Polystrata kimberleyensis	PP131432			GWS034627
Polystrata kimberleyensis	PP131445			GWS034758
Polystrata kimberleyensis	PP131451			GWS034757
Polystrata sp. Costa Rica		AB325871		SAP 102074
Ramicrusta adjoulanensis	MW960726	MW960752		GH0015334
Ramicrusta adjoulanensis	MW960727			GH0015394
Ramicrusta adjoulanensis	MW960728			GH0015525
Ramicrusta adjoulanensis	MW960729			GH0015652
Ramicrusta appressa	HM918340			GWS016794
Ramicrusta appressa	JX969707			GWS025723

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TABLE 1 (Continued)

	GenBank Accession Number			
Organism	**COI-5P**	***rbc*L**	***psb*A**	**Voucher number**
Ramicrusta appressa	JX969695			VT108
Ramicrusta aranea	JX969701	JX969780		VT106
Ramicrusta asanitensis	MW960730	MW960754		GH0015054
Ramicrusta asanitensis	MW960731	MW960755		GH0015060
Ramicrusta asanitensis	MW960732			GH0015151
Ramicrusta asanitensis	MW960733	MW960756		GH0015152
Ramicrusta asanitensis	MW960734			GH0015259
Ramicrusta asanitensis	MW960735			GH0015291
Ramicrusta australica	JX969724	JX969787		PLD004
Ramicrusta bonairensis	KX417374			DLB-7890
Ramicrusta fujiiana	MN990086	MN990099		ALCB 1298839/P12
Ramicrusta fujiiana	MN990087	MN990100		ALCB 1298839/P13
Ramicrusta fujiiana	MN990088	MN990102		ALCB 129844/P22
Ramicrusta fujiiana	MW960736	MW960757		GH0015078
Ramicrusta hawaiiensis	MN623629	MN623630		ARS09600
Ramicrusta labtasiensis	MW960737	MW960751		GH0015097
Ramicrusta labtasiensis	MW960738			GH0015399
Ramicrusta labtasiensis	MW960739			GH0015524
Ramicrusta labtasiensis	MW960740			GH0015617
Ramicrusta labtasiensis	MW960741			GH0015717
Ramicrusta labtasiensis	MW960742			GH0015719
Ramicrusta labtasiensis	MW960743			GH0015723
Ramicrusta lateralis	MW960744	MW960750		GH0015072
Ramicrusta lateralis	MW960745			GH0015230
Ramicrusta lateralis	MW960746			GH0015631
Ramicrusta lateralis	JX969721			VT109
Ramicrusta lehuensis	MN623631	MN623632		ARS09609
Ramicrusta monensis	KX417375			DLB-8208
Ramicrusta nanhaiensis	JX969713			GWS002520
Ramicrusta paradoxa	MN990091	MN990103		ALCB 129745/P1
Ramicrusta paradoxa	MN990092	MN990104		ALCB 129746/P7
Ramicrusta sp. Belize	OM460697			US:D&ML 63797
Ramicrusta sp. Tunisia	MG030799			RM0115
Ramicrusta taogamensis	MW960747	MW960753		GH0015094
Ramicrusta taogamensis	MW960748			GH0015103
Ramicrusta taogamensis	MW960749			GH0015641

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TABLE 1 (Continued)

	GenBank Accession Number			
Organism	**COI-5P**	***rbc*****L**	***psb*****A**	**Voucher number**
Ramicrusta textilis	JX969749	KC130226		GWS001755
Ramicrusta textilis	JX969690	JX969775		VT079
Ramicrusta textilis	MK616538	MK616530		SD17079
Ramicrusta textilis	KX417373			DLB-7794
Ramicrusta trichaurea	JX969719			VT105
Rhodowynnea indica	JX969742	JX969798		VT081
Rhodowynnea mariti		AB325863		SAP 102070
Rhodowynnea nordstedtii		EU349148		K208
Rhodowynnea nordstedtii		EU349149		K109
Rhodowynnea sp. Vanuatu		JX969799		VT173
Riquetophycus polypus		EU349170		K183
Riquetophycus sp. Taiwan		EU349171		K236
Riquetophycus sp. USA		EU349160		K102
Seiria guamensis	**PV668558**	**PV668549**		**GH0013146**
Seiria japonica	**PV668557**	**PV668548**	**PV668551**	**GH0012093**
Seiria kosraeana	**PV668559**	**PV668550**	**PV668552**	**GH0013672**
Seiria magnifusa	HM918333	MW996699		GWS016727
Seiria magnifusa	HM918341			GWS016756
Seiria magnifusa	HM918342			GWS016757
Seiria magnifusa	HM918343			GWS016758
Seiria magnifusa	MW996536			GWS034602
Seiria mesophotica	MZ043099	MZ047754		ARS09966
Seiria mesophotica	MZ043100	MZ047756		ARS09967
Seiria sp. New Zealand		KC998950		RHO225
Sonderophycus capensis		EU349186		K214
Sonderophycus cauliferus		AB325854		SAP 098400
Sonderophycus cauliferus		MF668136		TC13194
Sonderophycus copusii	MT012464	MT012465		ARS09651
Sonderophycus coriaceus	JX969698			GWS015628
Sonderophycus fervens	KC130203	KC130225		G0418
Sonderophycus sp. Australia	JX969739			GWS024474
Sonderophycus sp. Taiwan		EU349189		K237

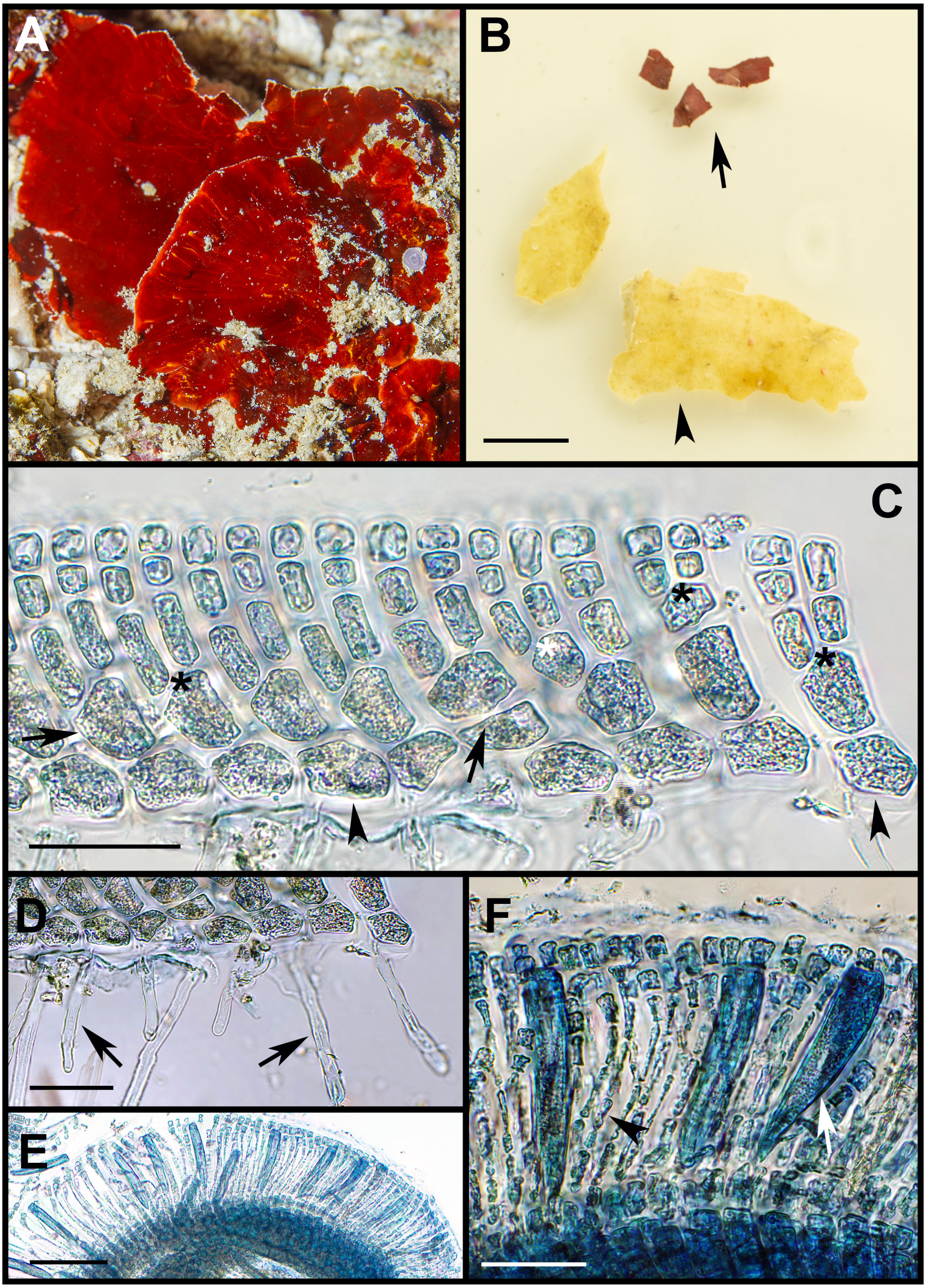

FIGURE 2. *Seiria japonica sp. nov.* (A) *In-situ* image of the holotype specimen. (B) Habit of the holotype specimen. Dried specimen is indicated with the arrow and formalin-preserved specimen is indicated by the arrowhead. Scale bar = 1 cm. (C) Radial section showing the thallus configuration including basal hypothallus (arrowheads) and perithallial filaments that contain large cells (arrows) that bifurcate into parallel files of smaller cells (asterisks). Scale bar = 50 µm. (D) Close-up showing variable length unicellular rhizoids (arrows) embedded in the hypobasal cuticle. Scale bar = 50 µm. (E) Radial-vertical section of a tetrasporangial nemathecium showing frequently produced tetrasporangia. Scale bar = 100 µm. (F) Close-up of tetrasporangial nemathecium showing mature tetrasporangia (arrow) and paraphyses of up to 6 cells (arrowhead). Scale bar = 50 µm.

Results

Morphological Results

Seiria japonica M.Mills & Schils *sp. nov.* (Figure 2A–F)

Type:—Japan. Okinawa Prefecture, Sesoko Island, 26.6410°N, 127.8565°E, 15 m depth, 28 June 2011, *T. Schils & A. Simeon* (holotype GH0012093)

Distribution and Habitat:—Known only from the type locality.

Etymology:—Named for the type locality due to this species also representing the first generic record for Japan.

Description:—Plants deep red to crimson, heavily calcified, and tightly adherent to the substratum but with free blade-like margins (Figure 2A–B). Crusts relatively thin, typically ranging from 90–125 µm, but more than double in thickness when nemathecia are present. Hypothallus monostromatic and composed of parallel files of semi-rectilinear cells 24–34 µm wide and 14–26 µm tall (Figure 2C). Perithallial filaments arise at 60–90° angles from the hypothallus and are typically 3–5 cells in length (Figure 2C). Perithallial filaments composed of one or occasionally two large quasi-rectangular cells (15–27 µm wide and 15–38 µm tall) that bifurcate once or rarely twice into smaller filaments of laterally compressed-to-isodiametric cells (Figure 2C). Hair cells absent. Plants attached by frequently occurring unicellular rhizoids of variable length, ranging from 50–150 µm long and up to 12 µm wide (Figure 2D). Gametangia not observed. Tetrasporangial nemathecia raised, scattered on the thallus surface, and composed of simple paraphyses up to six cells in length and up to 165 µm long (Figure 2E–F). Lower cells of the paraphyses laterally compressed and rectilinear, but decrease in height distally until terminal cells are approximately isodiametric (Figure 2F). Within nemathecia, tetrasporangia are frequently occurring and moderately variable in shape and size (Figure 2E–F).

Remarks:—Like the generitype, *Seiria japonica* possesses abundantly produced tetrasporangia of variable shape and size, but the tetrasporangial nemathecia are composed of paraphyses that are longer and composed of fewer cells than *S. magnifusa* and *S. mesophotica*. Apart from the attachment by unicellular rhizoids, the vegetative anatomy of *S. japonica* distinctly differs from other members of the genus. In particular, the perithallial filaments composed of large basal cells that bifurcate into smaller parallel filaments differentiates *S. japonica* from all other *Seiria* species. ML and Bayesian phylogenetic analyses of both COI-5P and *rbc*L (presented below) alignments further support the recognition of *S. japonica* as a new, distinct species.

Seiria guamensis M.Mills & Schils *sp. nov.* (Figure 3A–E)

Type:—Mariana Islands. Guam, Apra Harbor, Western Shoals, 13.4510°N, 144.6548°E, 12 m depth, 29 May 2012, *T. Schils & A. Simeon* (holotype GH0013146)

Distribution and Habitat:—Known only from the type locality.

Etymology:—Named for the type locality as part of an ongoing effort to characterize the diverse algal flora of the Mariana Islands.

Description:—Crusts firmly attached to the substrate proximally (Figure 3A, arrow) but form relatively small free blades at the margins (Figure 3A, arrowhead). Thallus prostrate, dark red to maroon, and heavily calcified but relatively brittle (Figure 3A). Crusts thin, typically 70–100 µm, but occasionally reach around 175 µm near the margins. Monostromatic hypothallus consists of unbranched, parallel files of quasi-isodiametric to laterally compressed (20–33 µm tall and 12–20 µm wide) cells that give rise to assurgent perithallial filaments dorsally (Figure 3B–C). Perithallus composed of short filaments that arise at approximately 90° angles from the hypothallus and are typically 3–4 cells long but can reach up to 7 cells long in the occasional thicker portions near the margins (Figure 3D). Cell fusions and secondary pit connections are absent in the perithallus. Basal perithallial cells often laterally compressed and much taller than wide (up to 30 µm long and 18 µm wide), while mid and upper perithallial cells are dorsally compressed and typically quasi-isodiametric (Figure 3C). Hair cells absent. Plants attached to substrate via long (up to 150 µm long and 13 µm wide), frequently occurring unicellular rhizoids (Figure 3E). Reproduction not observed.

Remarks:—This sample broke apart upon collection, effectively separating the firmly attached crust and free bladed margins. As such, the free blade was selected for formalin preservation due to it being larger and more conducive to morphological observation, while the smaller appressed portions were preserved in silica gel. Attachment by unicellular rhizoids is the only vegetative feature shared among all *Seiria* species, and *S. guamensis* is no exception. However, the combination of all other vegetative features, including the short perithallial filaments, monostromatic hypothallus, lack of cell fusions, and laterally compressed basal perithallial cells differentiate *S. guamensis* from all other members of the genus. Since the sole collected specimen of *S. guamensis* is not reproductive, the presence of serially produced tetrasporangia for which the genus was named was not observed. Despite this, phylogenetic analyses establish its generic placement, and the substantial sequence divergence separating *S. guamensis* from all other congeners (presented below) supports its recognition as a new species.

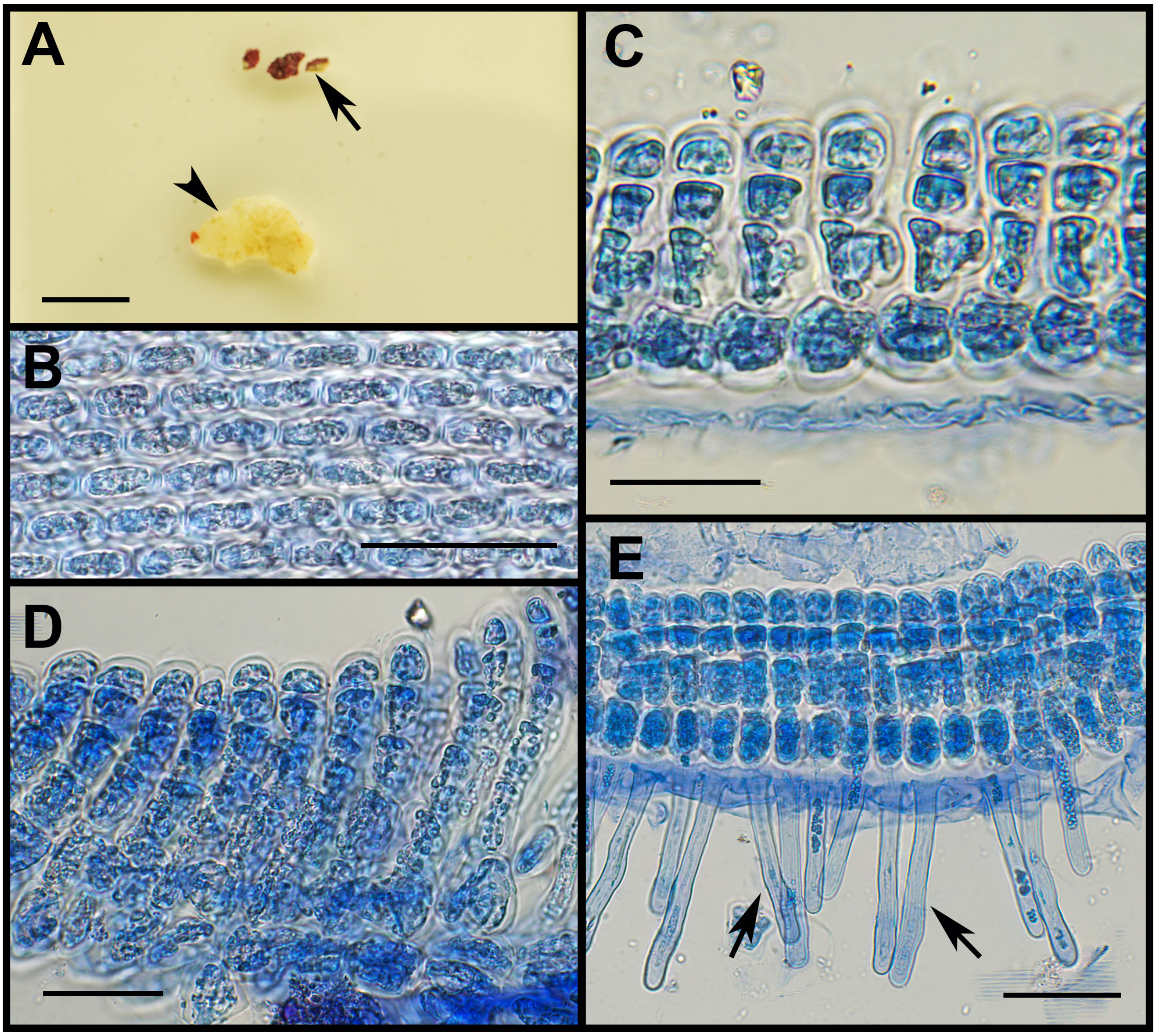

FIGURE 3. *Seiria guamensis sp. nov.* (A) Habit of the holotype specimen. Firmly attached dried specimen is indicated with the arrow, and formalin-preserved free blade is indicated by the arrowhead. Scale bar = 1 cm. (B) Ventral view of the plant showing unbranching, parallel hypothallus. Scale bar = 25 µm. (C) Radial section of the thallus showing the typical thallus configuration, including perithallial filaments that are typically 3–4 cells in length. Scale bar = 50 µm. (D) Radial section showing a portion of thicker crust near the margin, with perithallial filaments comprised of up to 7 cells. Scale bar = 50 µm. (E) Transverse section showing frequent unicellular rhizoids (arrows). Scale bar = 50 µm.

Seiria kosraeana M.Mills & Schils *sp. nov.* (Figure 4A–F)

Type:—Federated States of Micronesia. Kosrae, Buoy 28B, 5.2918°N, 162.9010°E, 12 m depth, 8 September 2012, *T. Schils & A. Simeon* (holotype GH0013672)

Distribution and Habitat:—Known only from the type locality.

Etymology:—Named in recognition of the type locality.

Description:—Living plants burnt-orange to deep maroon, but lose much of their orange coloration when dried (Figure 4A–B). Thallus heavily calcified, encrusting, and almost completely adherent to the substratum apart from small blades that occasionally form at the margins (Figure 4A–B). Crust relatively thick, ranging from 170–310 µm,

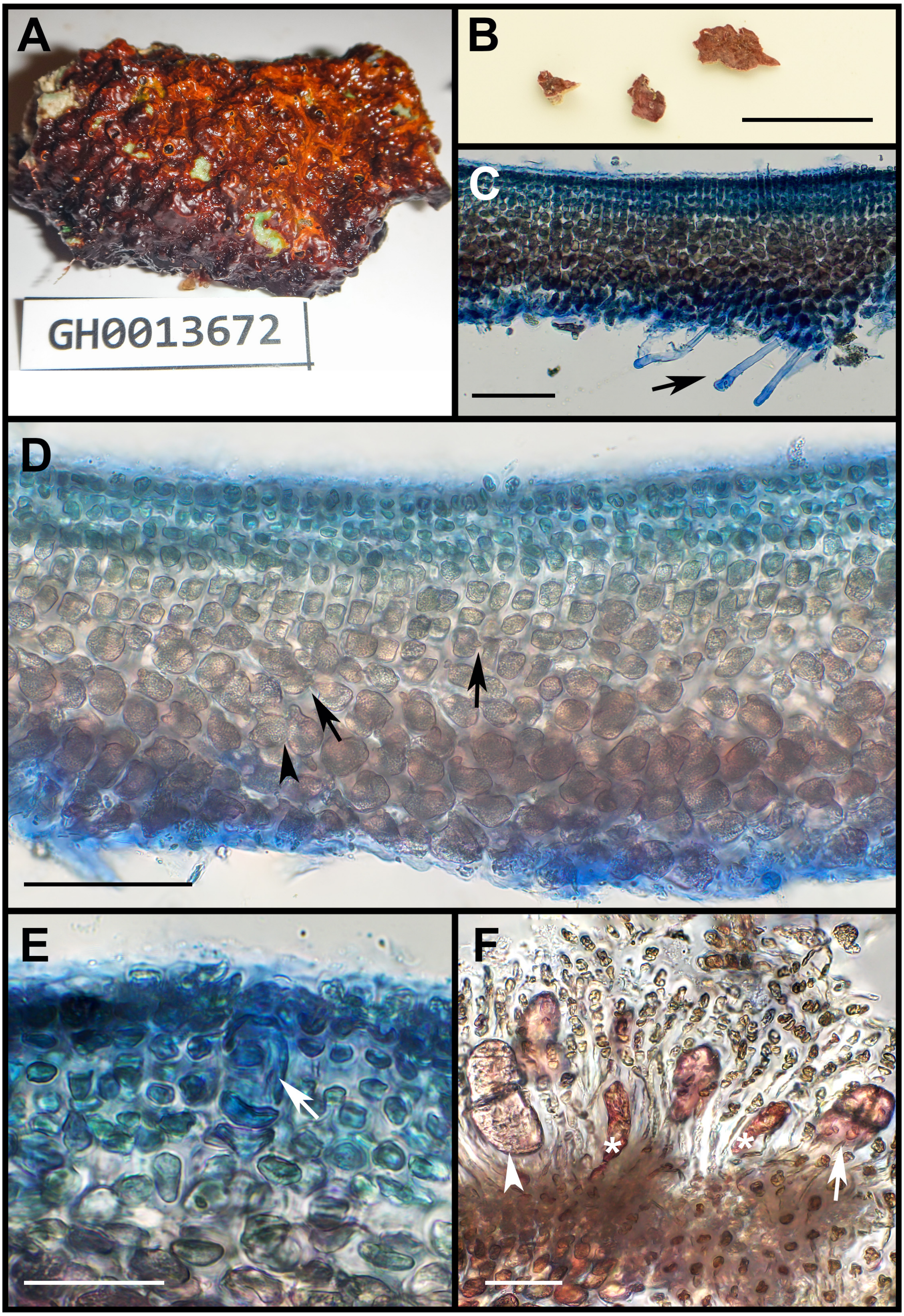

FIGURE 4. *Seiria kosraeana sp. nov.* (A) *Ex-situ* image of the holotype specimen taken shortly after collection. (B) Habit of the holotype specimen. Scale bar = 1 cm. (C) Section showing thin crust, hypothallus composed of irregularly shaped cells, perithallus, and unicellular rhizoids (arrow). Scale bar = 100 µm. (D) Radial section showing densely packed and irregularly projected filaments in the lower perithallus with cellular fusions (arrowheads) and secondary pit connections (arrows). Thin, well-organized upper perithallus delineated by the blue-green stain. Scale bar = 100 µm. (E) Radial section showing large bullet-shaped hair cell (arrow) in the upper perithallus. Scale bar = 50 µm. (F) Radial through tetrasporangial nemathecium with immature (asterisks), intermediate (arrowhead) and mature (arrow) tetrasporangia surrounded by paraphyses. Scale bar = 50 µm.

but typically between 210–230 µm thick (Figure 4C–D). Monostromatic hypothallus composed of parallel, mostly unbranched filaments of irregularly shaped cells that give rise to assurgent perithallial filaments above and long, relatively thick (up to 150 µm long and 18 µm wide) unicellular rhizoids below (Figure 4C). The perithallus is composed of distinct upper and lower zones (Figure 4D). Cells in the lower perithallus are irregularly round-to-globose and form filaments that are densely packed and occasionally irregularly projected (Figure 4D). Secondary pit connections frequently connect cells in the lower perithallus, and some cells are fused to those of adjacent filaments (Figure 4D). Perithallial cells become laterally and dorsoventrally compressed as they approach the thallus surface. The upper perithallus contains predominantly well-organized, parallel files of 3–6 quasi-isodiametric cells that typically lack cell fusions and secondary pit connections (Figure 4D). Large, bullet-shaped hair cells (28–38 µm tall and 15–22 µm wide) infrequently embedded in the upper perithallus (Figure 4E). Tetrasporangial nemathecia raised, up to 170 µm high, scattered on the thallus surface, and composed of simple paraphyses up to eight cells in length (Figure 4F). Within nemathecia, tetrasporangia occur abundantly and at various stages of development including immature, an intermediate stage that resembled bisporangia, and mature (Figure 4F). Mature tetraspores are cruciate decussate and highly variable in shape and size, ranging from 60–100 µm tall and 28–65 µm wide. Gametangia not observed.

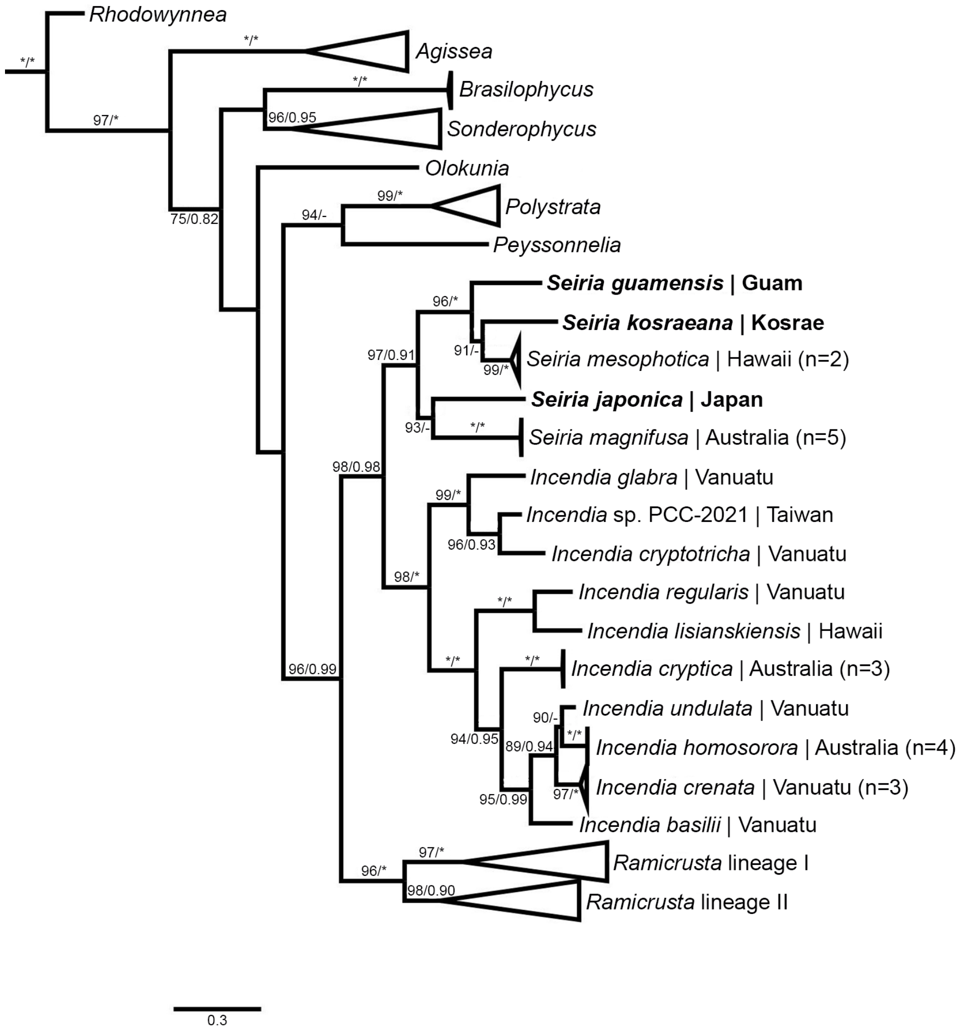

FIGURE 5. Maximum likelihood phylogenetic tree of COI-5P sequences for *Seiria*, *Incendia*, and other genera in the Peyssonneliales with the outgroup *Botryocladia hawkesii* (GenBank Accession: KU687546) and *Botryocladia skottsbergii* (GenBank Accession: HQ423124) pruned. Bootstrap support and Bayesian posterior probability values are printed for each node. Bootstrap support values < 75 and posterior probability values < 0.8 are indicated with a hyphen (-), nodes lacking sufficient support are blank, and an asterisk (*) indicates full support. Newly described species are in bold type.

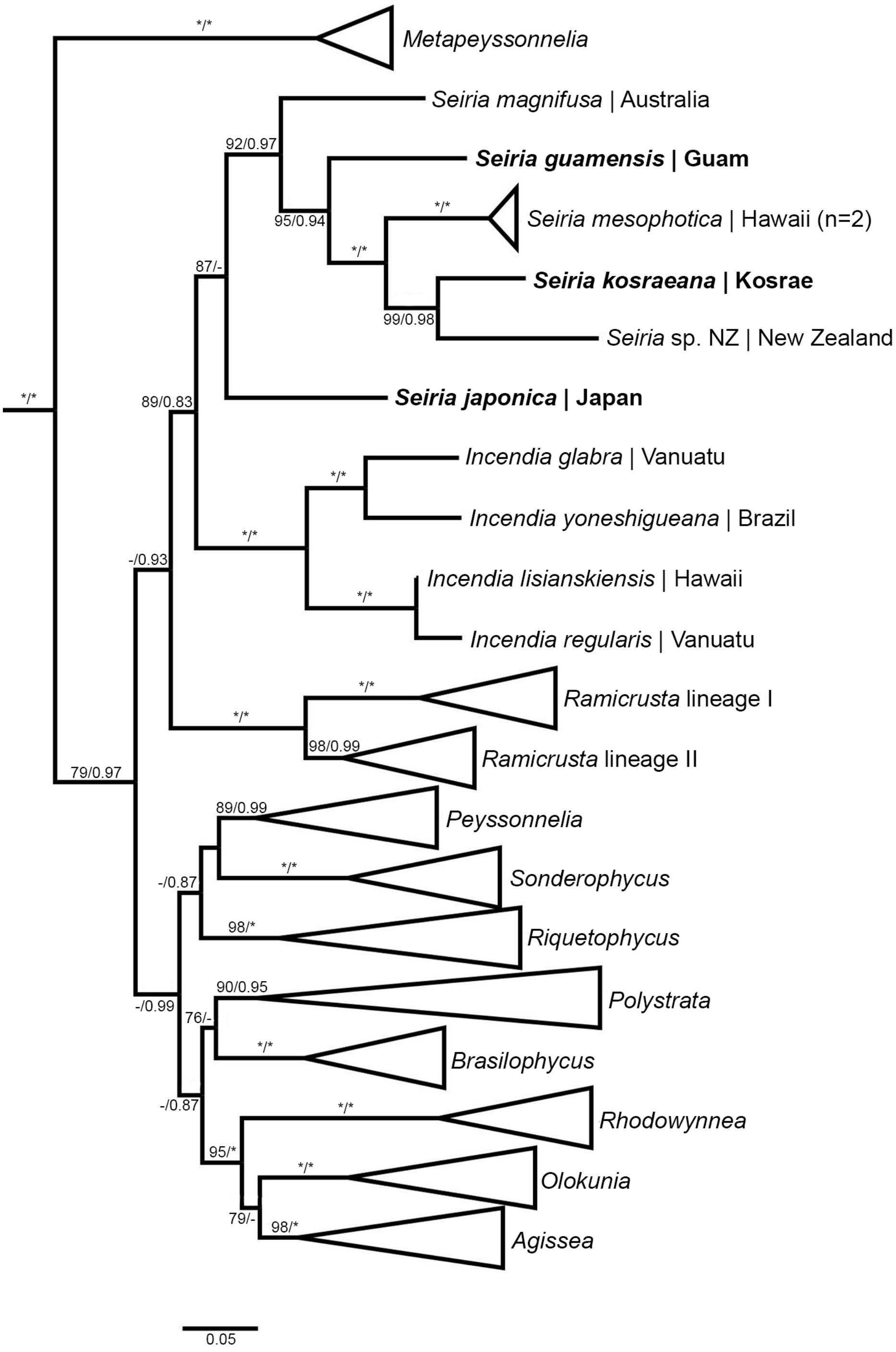

FIGURE 6. Maximum likelihood phylogenetic tree of *rbc*L sequences for *Seiria*, *Incendia*, and other genera in the Peyssonneliales with the outgroup (*Botryocladia hawkesii*, GenBank Accession: KU687828) removed. Bootstrap support values < 75 and posterior probability values < 0.8 are indicated with a hyphen (-), nodes lacking sufficient support are blank, and an asterisk (*) indicates full support. Newly described species are in bold type.

Remarks:—While possessing unicellular rhizoids common among all members of the genus, the vegetative anatomy of *Seiria kosraeana* distinguished it from all other *Seiria* species and is more reminiscent of some species in the closely related genus *Ramicrusta*. The distinct zonation and frequent secondary pit connections present in the perithallus, as well as the presence of hair cells renders *S. kosraeana* recognizably distinct from its congeners. The serially produced tetrasporangia observed in *S. magnifusa*, *S. mesophotica*, and *S. japonica* also occur in *S. kosraeana*. However, tetrasporangial sorus paraphyses in *S. kosraeana* were longer than the other three species and were composed of fewer cells than *S. mesophotica* and more cells than both *S. magnifusa* and *S. japonica*. In addition to marked anatomical differences, analysis of COI-5P and *rbc*L sequence data presented below strongly supports the recognition of *S. kosraeana* as a new species.

Molecular Results

A total of 3 COI-5P, 3 *rbc*L, and 2 *psb*A sequences were obtained for *Seiria* species from Japan and Micronesia. Phylogenetic analyses of COI-5P, the primary barcode marker for red algae (Saunders & McDevit 2012), and *rbc*L both supported the recognition of *Seiria japonica*, *S. guamensis*, and *S. kosraeana* as new species (Figures 5–6). However, COI-5P and *rbc*L trees presented different topologies, where COI-5P trees resolved *S. japonica* as sister to *S. magnifusa* (Figure 5), while *rbc*L trees resolved *S. japonica* as basal to the rest of the genus (Figure 6). A concatenated analysis of both genes resolved the same topology as the *rbc*L analyses (Supplementary Figure S1). Despite this, both analyses supported a monophyletic group that contained all three species, *Seiria magnifusa*, *S. mesophotica*, and an undescribed *Seiria* species from northern New Zealand, further supporting the placement of the three species described herein within this recently described genus. *Seiria japonica*, *S. guamensis*, and *S. kosraeana* all demonstrated more than 9% interspecific COI-5P divergence and differed from their nearest congeners by 10.5%, 9.0%, and 9.6% respectively (Table 2). Results of *rbc*L analyses were similar, with *S. japonica*, *S. guamensis*, and *S. kosraeana* differing from their nearest congeners by 10.8%, 9.0%, and 9.0% respectively (Table 2). The lack of *psb*A sequences available for previously described species did not allow for a comprehensive evaluation of phylogenetic relationships in the genus. However, the two species described herein for which *psb*A sequences were obtained, *S. japonica* and *S. kosraeana*, exhibited 9.5% interspecific *psb*A sequence divergence.

TABLE 2. Table showing the range of inter- and intraspecific divergences (p-distances) of COI-5P and *rbc*L sequences for all *Seiria* species used in molecular analyses. Newly described species are in bold type.

Species	COI-5P Interspecific divergence (%)	Intraspecific divergence (%)	*rbc*L Interspecific divergence (%)	Intraspecific divergence (%)
Seiria guamensis	9.0–11.7	-	9.0–13.9	-
Seiria japonica	10.5–12.5	-	10.8–15.4	-
Seiria kosraeana	9.6–13.1	-	9.0–13.5	-
Seiria magnifusa	10.5–13.1	0–0.15	11.0–14.6	-
Seiria mesophotica	9.0–12.3	3.3	9.0–13.9	3.6
Seiria sp. New Zealand	-	-	10.5–15.4	-

Discussion

Molecular techniques have been instrumental in investigations of diversity and systematics of the Peyssonneliales (e.g., Dixon & Saunders 2013; Mills & Schils 2021; Pestana *et al.* 2021). Recent collections of peyssonnelioid crustose calcifying red algae in Micronesia have led to the discovery of several new species (Mills & Schils 2021) and documented substantial peyssonnelioid algal diversity including the occurrence of several previously unreported genera such as *Polystrata* Heydrich (1905), *Ramicrusta,* and *Incendia* (Mills & Schils 2021; Mills *et al.* 2022). Additionally, recent taxonomic revisions and collections of shallow and mesophotic specimens have revealed several undescribed species (e.g., Akita *et al.* 2019) and reported the occurrence of multiple new genera from Japan including *Olokunia* Pestana, Lyra, Cassano & J.M.C. Nunes (2021)*, Rhodowynnea* Pestana, Lyra, Cassano & J.M.C. Nunes (2021), and *Incendia* (Pestana *et al.* 2021; Suzuki & Terada 2025). This study builds upon the previous studies by providing the first record of *Seiria* for Japan and Micronesia, and the three species described herein doubles the number of recognized species in the genus.

Phylogenetic analyses of COI-5P and *rbc*L, which included representatives of nearly all recognized peyssonnelioid genera, further established the position of *Seiria* as sister to *Incendia* within the order. As such, the resulting phylogenetic trees demonstrate the relationship between all *Seiria* and *Incendia* species, while all other species were grouped according to genus and collapsed (Figures 5–6). The sole exception to this was *Ramicrusta*, which was split into two distinct lineages that were separated by a minimum of 10% COI-5P sequence divergence. The first lineage contained the generitype and was comprised of most of the described *Ramicrusta* species, while the second lineage contained *R. australica* K.R. Dixon (2013: 103), *R. paradoxa* Pestana, G.N. Santos, V. Cassano & J.M.C. Nunes

(2020: 45), and two undescribed species from Belize and Taiwan. The generic distinction of *Seiria* was resolved with strong support in the COI-5P analyses (Figure 5). While the support was lower in the *rbc*L analyses (Figure 6), the concatenated analysis strongly supported the lineage containing the three new species, *S. magnifusa*, *S. mesophotica*, and an undescribed species from northern New Zealand (Supplementary Figure S1; Nelson *et al.* 2022). Studies of the closely related genera *Incendia*, *Ramicrusta*, and *Seiria* have reported 0–2.0% intraspecific COI-5P sequence divergence and a minimum interspecific COI-5P divergence of 2.0–4.0% (Dixon & Saunders 2013; Dixon 2018; Pestana *et al.* 2020; Mills & Schils 2021; Sherwood *et al.* 2021a; Sherwood *et al.* 2021b). Similar intra- and interspecific divergence thresholds have been reported for *rbc*L in the Peyssonneliales (e.g., Pestana *et al.* 2021). This is contrary to expectations considering *rbc*L is more conserved than COI-5P, particularly since *rbc*L divergences between several other closely related species of red algae have been reported to be much lower (e.g., Boo and Kim 2020; Taylor and Saunders 2025). Accordingly, the observed minimum of 9% sequence divergence in both COI-5P and *rbc*L between *S. japonica*, *S. guamensis*, and *S. kosraeana* and their closest congeners provides strong molecular support for their recognition as distinct species within the genus. The discordant topologies resolved by COI-5P and *rbc*L analyses, as well as the similar divergence values for both genes, could be a product of differences in mitochondrial and plastid organellar genes, the genomes of which can resolve different topologies at even the ordinal level (e.g. Pestana *et al.* 2025). This emphasizes the need for multi-gene analyses to better understand the relationships among peyssonnelioid taxa. These differences could also be a result of the small number of currently known species, all of which are highly divergent from one another. Increased collection and sequencing of peyssonnelioid taxa would likely substantially improve our understanding of the distribution of species, elucidate phylogenetic relationships, and estimate divergence between and within species.

The genus *Seiria* was defined morphologically by serially produced tetraspores and the extensive directional fusion of lower and mid-perithallial cells observed in the generitype (*S. magnifusa*; Dixon 2018). However, few anatomical features are shared across *Seiria* species. Attachment by unicellular rhizoids is consistent among members of the genus, yet *S. guamensis*, *S. japonica*, and *S. kosraeana* each possess vegetative anatomies that differ markedly from one another and from the two previously described species. Serially produced tetraspores, the feature for which the genus is named, have been observed in *S. magnifusa*, *S. mesophotica*, *S. japonica*, and *S. kosraeana* (Dixon 2018; Sherwood *et al.* 2021a). However, since the single collected specimen of *S. guamensis* was non-reproductive, the presence of this feature was not observed. Despite this, molecular and phylogenetic analyses strongly supported the position of *S. guamensis* (Figures 5–6). Among the species examined, *S. guamensis* and *S. mesophotica* exhibited the most similar vegetative anatomies, though the former can be distinguished by its entirely unbranched hypothallus and generally shorter perithallial filaments (3–4 vs. 4–8 cells; Sherwood *et al.* 2021a). In contrast, *S. kosraeana* is readily recognized by its distinct perithallial zonation, the presence of cell fusions and secondary pit connections in the lower perithallus, and hair cells embedded in the upper perithallus. The perithallial filaments of *S. japonica*, composed of large basal cells that bifurcate into smaller parallel filaments, are also unique among congeners. The distinct diagnostic features observed among *Seiria* species are noteworthy within the Peyssonneliales, where simple morpho-anatomy, convergent vegetative morphologies, and the scarcity of sexual reproductive structures typically hinder reliable morphological discrimination between species and genera (Dixon & Saunders 2013; Pestana *et al.* 2020; Mills & Schils 2021; Pestana *et al.* 2021).

All three newly described species are represented by single collections. Although not ideal, describing species from single specimens is common in the Peyssonneliales (e.g., Dixon & Saunders 2013; Dixon 2018; Pestana *et al.* 2020; Sherwood *et al.* 2021a). The combination of high interspecific sequence divergence and diagnostic morphological features allowed for a reliable description of *S. japonica*, *S. guamensis*, and *S. kosraeana*. DNA barcoding studies increasingly reveal that global peyssonnelioid diversity is greatly underestimated (Kato *et al.* 2006; Kato *et al.* 2009; Manghisi *et al.* 2019; Sherwood *et al.* 2020; Pestana *et al.* 2021; Chen *et al.* 2022; Mills *et al.* 2022; Nelson *et al.* 2022). Despite the broad geographic ranges observed in most peyssonnelioid genera, *Seiria* appears to have a more limited distribution, occurring only in the Pacific and eastern Indian Oceans (Guiry & Guiry 2025). The broad latitudinal but limited longitudinal range of *Seiria* (Figure 1) reinforces the likelihood that *Seiria* and other peyssonnelioid algae remain substantially underreported worldwide. The increasing prevalence of spatially aggressive peyssonnelioid algal crusts (PACs), which can overgrow corals, prevent settlement, and persist under ocean acidification (Dutra *et al.* 2016; Edmunds *et al.* 2019; Stockton & Edmunds 2021; Edmunds *et al.* 2023), underscores the need for expanded research on peyssonnelioid diversity and ecology. Broader sampling across climatic regions will be key to revealing their true global diversity.

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References

Akita, S., Takano, Y., Nagai, S., Kuwahara, H., Kajihara, R., Tanabe, A.S. & Fujita, D. (2019) Rapid detection of macroalgal seed bank on cobbles: Application of DNA metabarcoding using next-generation sequencing. *Journal of Applied Phycology* 31: 2743–2753.
https://doi.org/10.1007/s10811-018-1730-9

Boo, G.H. & Kim, K.M. (2020) A new species of marine algae from Korea based on morphology and molecular data: *Gelidium palmatum* sp. nov. (Gelidiales, Rhodophyta). *Algae* 35: 33–43.
https://doi.org/10.4490/algae.2020.35.3.6

Chen, P.-C., Perez, C.J.J. & Liu, S.-L. (2022) DNA-assisted inventory and community structure of benthic marine algae in Taiping Island (or Itu Aba Island), South China Sea. *Regional Studies in Marine Science* 55: 102496.
https://doi.org/10.1016/j.rsma.2022.102496

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772.
https://doi.org/10.1038/nmeth.2109

Dixon, K.R. & Saunders, G.W. (2013) DNA barcoding and phylogenetics of *Ramicrusta* and *Incendia* gen. nov., two early diverging lineages of the Peyssonneliaceae (Rhodophyta). *Phycologia* 52: 82–108.
https://doi.org/10.2216/12-62.1

Dixon, K.R. (2018) Peyssonneliales. *In*: Huisman,J.M. (Ed.) *Algae of Australia. Marine benthic algae of north-western Australia. 2. Red algae*. ABRS & CSIRO Publishing, Canberra & Melbourne, pp. 208–244.

Dutra, E., Koch, M., Peach, K. & Manfrino, C. (2016) Tropical crustose coralline algal individual and community responses to elevated *p*CO2 under high and low irradiance. *ICES Journal of Marine Science* 73: 803–813.
https://doi.org/10.1093/icesjms/fsv213

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.
https://doi.org/10.1093/nar/gkh340

Edmunds, P.J., Zimmermann, S.A. & Bramanti, L. A spatially aggressive peyssonnelid algal crust (PAC) threatens shallow coral reefs in St. John, US Virgin Islands. *Coral Reefs* 38: 1329–1341.
https://doi.org/10.1007/s00338-019-01846-0

Edmunds, P.J., Schils, T. & Wilson, B. (2023) The rising threat of peyssonnelioid algal crusts on coral reefs. *Current Biology* 33: R1140–R1141.
https://doi.org/10.1016/j.cub.2023.08.097

Freshwater, D.W. & Rueness, J. (1994) Phylogenetic relationships of some European *Gelidium* (Gelidiales, Rhodophyta) species, based on *rbc*L nucleotide sequence analysis. *Phycologia* 33: 187–194.
https://doi.org/10.2216/i0031-8884-33-3-187.1

Guiry, M.D. & Guiry, G.M. (2025) *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. Available from: http://www.algaebase.org (accessed 5 May 2025)

Heydrich, F. (1905) *Polystrata*, eine Squamariacee aus den Tropen. *Berichte der deutsche botanischen Gesellschaft* 23: 30–36.
https://doi.org/10.1111/j.1438-8677.1905.tb06368.x

Kato, A., Baba, M., Kawai, H. & Masuda, M. (2006) Reassessment of the little-known crustose red algal genus *Polystrata* (Gigartinales), based on morphology and SSU rDNA sequences. *Journal of Phycology* 42: 922–933.
https://doi.org/10.1111/j.1529-8817.2006.00238.x

Kato, A., Guimarães, S.M.P.B., Kawai, H. & Masuda, M. (2009) Characterization of the crustose red alga *Peyssonnelia japonica* (Rhodophyta, Gigartinales) and its taxonomic relationship with *Peyssonnelia boudouresquei* based on morphological and molecular data. *Phycological Research* 57: 74–86.
https://doi.org/10.1111/j.1440-1835.2008.00523.x

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–3066.
https://doi.org/10.1093/nar/gkf436

Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780.
https://doi.org/10.1093/molbev/mst010

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. & Drummond, A. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649.
https://doi.org/10.1093/bioinformatics/bts199

Krayesky, D.M., Norris, J.N., Gabrielson, P.W., Gabriel, D. & Fredericq, S. (2009) A new order of red algae based on the Peyssonneliaceae, with an evaluation of the original classification of the Florideophyceae (Rhodophyta). *Proceedings of the Biological Society of Washington* 122: 364–391.
https://doi.org/10.2988/08-43.1

Kucera, H. & Saunders, G.W. (2012) A survey of Bangiales (Rhodophyta) based on multiple molecular markers reveals cryptic diversity. *Journal of Phycology* 48: 869–882.
https://doi.org/10.1111/j.1529-8817.2012.01193.x

Manghisi, A., Miladi, R., Minicante, S.A., Genovese, G., Le Gall, L., Abdelkafi, S., Saunders, G.W. & Morabito, M. (2019) DNA barcoding sheds light on novel records in the Tunisian red algal flora. *Cryptogamie, Algologie* 40: 5–27.
https://doi.org/10.5252/cryptogamie-algologie2019v40a3

Mills, M.S. & Schils, T. (2021) The habitat-modifying red alga *Ramicrusta* on Pacific reefs: A new generic record for the Tropical Northwestern Pacific and the description of four new species from Guam. *PLoS ONE* 16: e0259336.
https://doi.org/10.1371/journal.pone.0259336

Mills, M.S., Deinhart, M.E., Heagy, M.N. & Schils, T. (2022) Small tropical islands as hotspots of crustose calcifying red algal diversity and endemism. *Frontiers in Marine Science* 9: 898308.
https://doi.org/10.3389/fmars.2022.898308

Nelson, W., Ngauma, B., Norman, J.H., Ringham, S. & Sutherland, J. (2022) *Agissea teruruhau sp. nov.* (Peyssonneliales, Rhodophyta) and epiphyte *Piriora waewaeiti gen. & sp. nov.* (Gigartinales, Rhodophyta) from Manawatāwhi, New Zealand. *Phycologia* 62: 1–18.
https://doi.org/10.1080/00318884.2022.2132054

Nguyen, L.-T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32: 268–274.
https://doi.org/10.1093/molbev/msu300

Pestana, E.M.S., Lyra, G.M., Santos, G.N., Dos Santos, C.C., Casano, V. & Nunes, J.M.C. (2020) Integrative approach reveals underestimated Peyssonneliales diversity in Brazil: registering the first occurrence of *Ramicrusta* and *Incendia*, with the description of three new species. *Phytotaxa* 439: 39–55.
https://doi.org/10.11646/phytotaxa.439.1.2

Pestana, E.M.S., Nunes, J.M.C., Cassano, V. & Lyra, G.M. (2021) Taxonomic revision of the Peyssonneliales (Rhodophyta): circumscribing the authentic *Peyssonnelia* clade and proposing four new genera and seven new species. *Journal of Phycology* 57: 1749–1767.
https://doi.org/10.1111/jpy.13207

Pestana, E.M.S., Lyra, G.M., Zhang, H., Davis, C.C. & Nunes, J.M.C. (2025) Conflicting placements shed doubts on the ordinal status of the Peyssonneliales: Is it a clade in the mega diverse Gigartinales? *Taxon*: 70001.
https://doi.org/10.1002/tax.70001

Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
https://doi.org/10.1093/bioinformatics/btg180

Saunders, G.W. & McDevit, D.C. (2012) Methods for DNA barcoding photosynthetic protists emphasizing the macroalgae and diatoms. *Methods in Molecular Biology* 858: 207–222.
https://doi.org/10.1007/978-1-61779-591-6_10

Sherwood, A.R., Paiano, M.O., Spalding, H.L. & Kosaki, R.K. (2020) Biodiversity of Hawaiian Peyssonneliales (Rhodophyta). 2.

Sonderophycus copusii, a new species from the Northwestern Hawaiian Islands. *ALGAE* 35: 145–155. https://doi.org/10.4490/algae.2020.35.5.20

Sherwood, A.R., Cabrera, F.P., Spalding, H.L., Alvarado, E.A., Smith, C.M., Hauk, B.B., Matadobra, S.J., Kosaki, R.K. & Paiano, M.O. (2021) Biodiversity of Hawaiian Peyssonneliales (Peyssonneliaceae, Rhodophyta): new species in the genera *Incendia* and *Seiria*. *Phytotaxa* 524: 14–26. https://doi.org/10.11646/phytotaxa.524.1.2

Sherwood, A.R., Paiano, M.O., Wade, R.M., Cabrera, F.C., Spalding, H.L. & Kosaki, R.K. (2020) Biodiversity of Hawaiian Peyssonneliales (Rhodophyta). 1. Two new species in the genus *Ramicrusta* from Lehua Island. *Pacific Science* 75: 185–195. https://doi.org/10.2984/75.2.2

Stockton, L. & Edmunds, P.J. (2021) Spatially aggressive peyssonnelid algal crusts (PAC) constrain coral recruitment to *Diadema* grazing halos on a shallow Caribbean reef. *Journal of Experimental Marine Biology and Ecology* 541: 151569. https://doi.org/10.1016/j.jembe.2021.151569

Suzuki, M. & Terada, R. (2025) DNA-based floristic survey of red algae (Rhodophyta) growing in the mesophotic coral ecosystems (MCEs) offshore of Tanegashima Island, northern Ryukyu Archipelago, Japan. *PLoS ONE* 20: e0316067. https://doi.org/10.1371/journal.pone.0316067

Taylor, K.E. & Saunders, G.W. (2025) Assessment of rhodolith-forming species diversity in British Columbia uncovers novel cryptic diversity in the genera *Boreolithothamnion* and *Rhodolithia* gen. nov. (Florideophyceae, Rhodophyta) and the occurrence of hybrid rhodoliths. *Journal of Phycology* 61: 1371–1393. https://doi.org/10.1111/jpy.70066

Yang, E.C., Boo, S.M., Bhattacharya, D., Saunders, G.W., Knoll, A.H., Fredericq, S., Graf, L. & Yoon, H.S. (2016) Divergence time estimates and the evolution of major lineages in the florideophyte red algae. *Scientific Reports* 6: 21361. https://doi.org/10.1038/srep21361

Yoon, H.S., Hackett, J.D. & Bhattacharya, D. (2002) A single origin of the peridinin- and fucoxanthin-containing plastids in dinoflagellates through tertiary endosymbiosis. *Proceedings of the National Academy of Sciences* 99: 11724–11729. https://doi.org/10.1073/pnas.172234799

Zhang, D.R. & Zhou, J.H. (1981) *Ramicrusta*, a new genus of Peyssonneliaceae. *Oceanologia Limnologia Sinica* 12: 538–544.

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

SUPPLEMENTARY FIGURE S1. Maximum likelihood phylogenetic tree of concatenated COI-5P and *rbc*L sequences for *Seiria*, *Incendia*, other genera in the Peyssonneliales, and an outgroup (*Botryocladia hawkesii* and *Botryocladia skottsbergii)*. Bootstrap support values are printed for each node, and Bayesian posterior probability values are included for nodes resolving the genus *Seiria*. Newly described species are in bold type.