

Biodiversity of Hawaiian Peyssonneliales (Rhodophyta): *Sonderophycus copusii* sp. nov., a new species from the Northwestern Hawaiian Islands

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Specimens of red algae corresponding to the peyssonnelioid genus *Sonderophycus* were collected at Kure Atoll, Hawai‘i, at a depth range of 88–94 m depth during mesophotic surveys of the Papahānaumokuākea Marine National Monument, Hawaiian Islands, and were analyzed using morphological and molecular approaches. Analyses of mitochondrial cytochrome oxidase subunit 1 and chloroplast *rbcL* DNA sequences demonstrated that the Hawaiian specimens were identical to one another yet distinct from the three other species currently recognized within the genus (*S. capensis* [Montagne] M. J. Wynne, *S. coriaceus* [Womersley & Sinkora] M. J. Wynne, and *S. fervens* Dixon), as well as the likely congener, *Peyssonnelia caulifera* Okamura, and are proposed here as a new species: *Sonderophycus copusii* A. R. Sherwood. *Sonderophycus copusii* is morphologically distinct from other members of the genus by the following combination of characters: the presence of occasional secondary perithallial growth, emergence of rhizoids from the hypobasal cuticle at a strongly acute angle, a lack of horizontally directed filaments in the lower perithallus, and the lack of a stipe. This is the first record of the genus *Sonderophycus* in the Hawaiian Islands. *Sonderophycus copusii* was documented as a dominant member of the algal community at Kure Atoll, and thus may play a significant ecological role in the deep-water benthic community of Kure Atoll, along the lines of reports of deep water peyssonnelioid beds in the Mediterranean, Red Sea, and Caribbean. This study further highlights the unexplored diversity of the Peyssonneliales in Hawai‘i, and emphasizes more generally the degree of as yet undiscovered biodiversity of algae at mesophotic depths.

Key Words: COI; Hawai‘i; mesophotic; Peyssonneliales; *Sonderophycus*; *rbcL*; Rhodophyta

Abbreviations: BOLD, Barcode of Life Database; COI, cytochrome oxidase subunit I; MCE, Mesophotic Coral Ecosystems; NOAA, US National Oceanographic and Atmospheric Administration; NWHI, Northwestern Hawaiian Islands; PMNM, Papahānaumokuākea Marine National Monument; *rbcL*, ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit gene

INTRODUCTION

The peyssonnelioid genus *Sonderophycus* has a confusing taxonomic history. Denizot (1968) described the genus based on morphological differences between *Peyssonnelia australis* Sonder and other species in the genus

Peyssonnelia. *Sonderophycus* was established with the combination *Sonderophycus australis* (Sonder) Denizot. Subsequently, Womersley and Sinkora (1981) established the genus *Sonderopelta* (based on *S. coriacea* Womersley



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& Sinkora) after examining the type specimen of *P. australis* Sonder in MEL and determining that it represented a species of *Peyssonnelia*. Thus, *Sonderopelta coriacea* Womersley & Sinkora was used to re-describe the taxon known as *Sonderophycus australis* (Sonder) Denizot. Further adding to the confusion, Silva et al. (1996) cited *Peyssonnelia australis* Sonder as a synonym of *P. capensis* Montagne. A phylogenetic analysis of the Peyssonneliales by Kravesky et al. (2009) demonstrated that the types of *Sonderophycus* (*S. australis*) and *Sonderopelta* (*S. australis* = *P. capensis*) formed a genus-level clade separate from *Peyssonnelia* based on *rbcL* and ribosomal large subunit sequence data, but in synonymizing the two genera they recognized the junior synonym, *Sonderopelta*. Wynne (2011, 2016) established that *Sonderophycus* had priority over *Sonderopelta* and established the type of the former as *S. capensis* (Montagne) M. J. Wynne.

The genus *Sonderophycus* is small, comprising only three currently recognized species: the type species, *S. capensis* (Montagne) M. J. Wynne, *S. coriaceus* (Womersley & Sinkora) M. J. Wynne, and *S. fervens* K. R. Dixon. *Peyssonnelia caulifera* Okamura is also a likely member and is not currently recognized as part of the genus only by virtue of a nomenclatural error in citation of the basionym when proposing the combination (Jeong et al. 2017, Guiry and Guiry 2020). The genus is distinctive from others in the Peyssonneliales in forming a well-defined clade in molecular phylogenetic analyses (Kravesky et al. 2009, Dixon and Saunders 2013, Dixon 2018), but also morphologically in the tomentum of fibrous rhizoids that anchor the thalli to the substratum, the lack of hair cells, and the tendency of lower perithallial filaments to be sharply angled (Denizot 1968, Jeong et al. 2017, Dixon 2018).

Studies of the peyssonnelioid algae of the Hawaiian Islands are relatively few. Four species of *Peyssonnelia* have been reported from Hawai'i, namely, *P. conchicola*

Piccone & Grunow, *P. inamoena* Pilger, *P. rubra* (Greville) J. Agardh by Abbott (1999), and *P. japonica* (Segawa) Yoneshigue by Kato et al. (2009). A number of sequences of Peyssonneliales were presented in Sherwood et al. (2010), but the species-level taxonomy of peyssonnelioid specimens in Hawai'i was not investigated in further detail at that time. The genus *Ramicrusta* was recently reported for the first time from the Hawaiian Islands, with the proposal of two (presumably) endemic species; *R. hawaiiensis* A. R. Sherwood and *R. lehuensis* A. R. Sherwood (Sherwood et al. in press). Thus, a total of six peyssonnelioid species have been reported from Hawai'i, representing *Peyssonnelia* and *Ramicrusta*; no species of *Sonderophycus* or its synonyms have been previously recorded.

This study is part of the ongoing effort to characterize the mesophotic algae of the Hawaiian Islands. During mesophotic expeditions to Papahānaumokuākea Marine National Monument (PMNM) led by the US National Oceanic and Atmospheric Administration (NOAA) in 2015 and 2016, three specimens attributable to the genus *Sonderophycus* were collected. These algae were observed as a dominant member of the benthic community at Kure Atoll, suggesting an ecologically important role for this species. Molecular and morphological characterization of these specimens is here used to support the proposal of these specimens as a new species of *Sonderophycus*.

MATERIALS AND METHODS

Three specimens of *Sonderophycus* were collected in 2015–2016 by technical rebreather diving as part of marine survey expeditions to Kure Atoll, PMNM in the Northwestern Hawaiian Islands (NWHI), between 88 and 92 m depth (Table 1). Field work was conducted under PMNM permit PMNM-2015-029 to R. Kosaki. Specimens

Table 1. Specimens of *Sonderophycus* from the Hawaiian Islands characterized as part of the current study

Species	Sherwood Lab collection	Herbarium accessions	Collection information (latitude / longitude in decimal degrees)	GenBank accession (COI)	GenBank accession (<i>rbcL</i>)
<i>Sonderophycus copusii</i> sp. nov.	ARS 09651	BISH 776117	Kure Atoll, Hawai'i (28.48716, -178.37304), 94 m depth, Jun 4, 2016, leg. J. Leonard (NWHI-535)	MT012464	MT012465
<i>Sonderophycus copusii</i> sp. nov.	ARS 09653	BISH 776116, HAW-43388	Kure Atoll, Hawai'i (28.49845, -178.34171), 90 m depth, Jun 5, 2016, leg. J. Hansen & B. Hauk (NWHI-543)	MT012466	MT012467
<i>Sonderophycus copusii</i> sp. nov.	ARS 09686	BISH 776118	Kure Atoll, Hawai'i (28.49007, -178.29113), 88 m depth, Sep 21, 2015, leg. R. Kosaki & B. Hauk (NWHI-451)	MT012468	MT012469

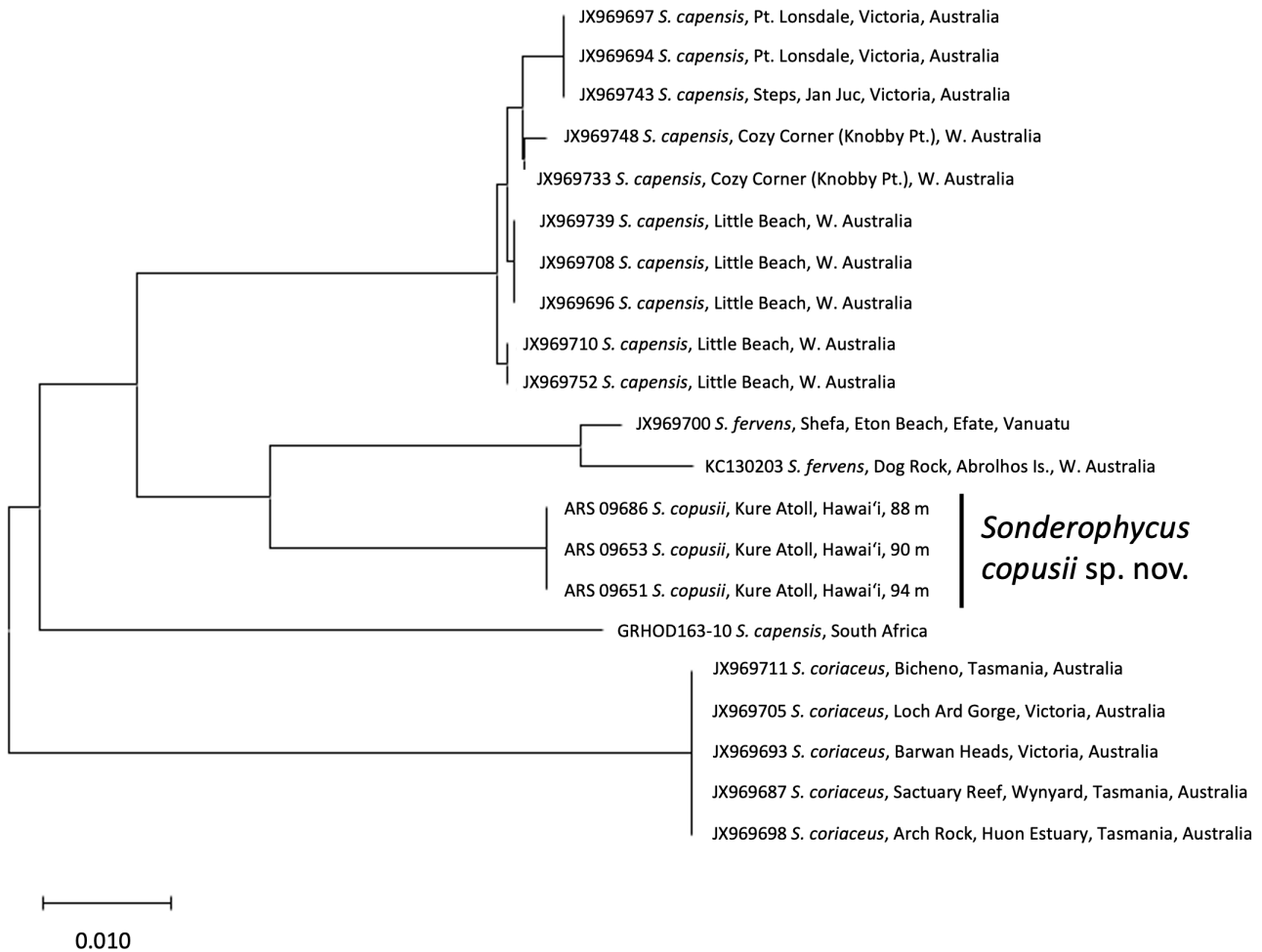


Fig. 1. Neighbor-joining phylogram (Kimura-2-parameter distances) of cytochrome oxidase subunit I sequences of *Sonderophycus*, demonstrating the sequence divergence of *S. copusii* samples from other represented members of the genus. Scale bar represents: substitutions per site.

were pressed as herbarium vouchers for morphological analysis and preserved in silica gel desiccant for molecular characterization. Specimens were examined and cleaned under a Zeiss SteREO Discovery v12 dissecting microscope (Pleasanton, CA, USA). Morphological and anatomical investigations of the samples were conducted by rehydrating small pieces of the specimens in a detergent (Modified Pohl's Solution, Clark unpublished data: https://www.eeob.iastate.edu/research/bamboo/pdf/anatomy_protocols.pdf) for 30 min, decalcifying small pieces of attached coral rubble in 5% HCl for 15 min, hand sectioning with a double-edged razor blade, staining with 1% aniline blue, and mounting in 30-50% Karo. Photomicrographs were taken on a Zeiss AxioImager A1 compound light microscope (Pleasanton, CA, USA) with an Infinity2-1RC digital camera (Lumenera Corporation, Ottawa, ON, Canada).

Specimens were extracted for genomic DNA using an OMEGA E.Z.N.A. Plant DNA DS Kit (OMEGA Biotek, Norcross, GA, USA). The cytochrome oxidase subunit I (COI) DNA barcode marker (658 bp) was amplified using the GazF1 and GazR1 primers (Saunders 2005). The *rbcl* (ribulose-1,5-bisphosphate carboxylase / oxygenase large subunit, 1,335 bp) marker was amplified as three overlapping fragments using the following primer pairs: F7 and R753 (Gavio and Fredericq 2002), F492 (or alternatively F577) and R1150 (Freshwater and Rueness 1994), and F993 and R-rbcS start (Freshwater and Rueness 1994). Successful PCR products were submitted for sequencing to the University of Hawai'i at Mānoa Advanced Studies for Genomics, Proteomics, and Bioinformatics core facility or through GENEWIZ (South Plainfield, NJ, USA). Raw sequence reads for each gene were assembled, edited, and aligned using the MUSCLE v. 3.8.425 plug-in (Edgar

2004) in Geneious Prime 2019.1.3 (<http://www.geneious.com>) with other available sequences for *Sonderophycus* and related genera from GenBank and the Barcode of Life Database (BOLD) (Supplementary Table S1). DNA barcode analysis of the COI sequences was performed by constructing a neighbor-joining framework based on Kimura-2-parameter distances using MEGA X (Kumar et al. 2018). For the *rbcL* phylogenetic analyses, newly generated sequences were aligned with reference sequences and analyzed with PartitionFinder v. 1.1.1 (Lanfear et al. 2012). Maximum likelihood analyses were performed on all alignments using RAXML-HPC2 on XSEDE v. 8.2.10 (Stamatakis 2014) via the CIPRES gateway (Miller et al. 2010) with 1,000 bootstrap replicates, and using the GTRCAT model. Bayesian inference was performed using the MrBayes plug-in v. 3.2.6 (Huelsenbeck and Ronquist 2001) through Geneious Prime 2019.1.3 (<http://www.geneious.com>) using four chains of Metropolis-coupled Markov Chain Monte Carlo for 1,000,000 generations and sampling every 100 generations; 100,000 chains were removed as burn-in prior to determining posterior probabilities.

RESULTS

DNA barcoding analysis of COI sequences of the three new Hawaiian *Sonderophycus* specimens and 18 additional specimens of *Sonderophycus* representing *S. capensis*, *S. coriaceus*, and *S. fervens* clearly indicated that the Hawaiian specimens were identical to one another yet distinct from other species of the genus (Fig. 1). Of the currently recognized and likely members of the genus, only *P. caulifera* was not represented in the COI barcoding analysis. All taxa represented in the analysis include specimens from, or close to, their type locality. The Hawaiian specimens shared 95.0–95.1% identity with their most similar congeners (*S. fervens*; JX969700, KC130203). In addition, COI sequence data for *S. capensis* clearly distinguished specimens from South Africa (type locality = Durban, South Africa) and Australia, demonstrating that the Australian material is likely a distinct species from *S. capensis*. Phylogenetic analysis of *rbcL* sequences representing all known members of *Sonderophycus* plus *P. caulifera*, as well as other representatives of the Peyssonneliales, yielded a well-resolved phylogeny that indicated full support for the monophyly of the genus *Sonderophycus* (Fig. 2). Clades corresponding to *S. capensis*, *S. coriaceus*, *S. fervens*, *P. caulifera*, and the Hawaiian specimens plus one additional GenBank sequence (see below) were

all resolved with full support. The Hawaiian specimens characterized in this study were allied with a sequence from Magang Harbor, Taiwan, at 4 m depth (EU349189), differing from this sequence by only two nucleotides (Fig. 2). The closest relative of the Hawaiian *Sonderophycus* is the Australian taxon, *S. fervens*.

The Hawaiian specimens are here recognized as a new species of *Sonderophycus* based on the molecular distinctiveness of the specimens within the context of other species of the genus, as well as on morphological characters, as outlined below.

Sonderophycus copusii A. R. Sherwood sp. nov. (Fig. 3A–J)

Description. Thallus encrusting with the margins free, typically on rock or coral rubble, attached by rhizoids. Deep brick red to dark dusky rose in color, radial striations, and faint concentric rings visible on dorsal surface. Thallus composed of a single, broadly lobed blade, orbicular in shape, and cartilaginous, reaching 8.5 cm in diameter. Cystoliths and hypobasal calcification present. Blades 65–210 µm thick, composed of 6–10 cell layers. Hypothallus composed of radiating and parallel filaments, cells 8–9 µm diameter × 11–18 µm length. Occasional secondary perithallial growth. Perithallial filaments arising at approximately 45° to the hypothallus, but straightening to upright (90°) near the dorsal surface of the thallus. Perithallial cells elongate in shape toward basal region of perithallus, 10–12 × 30–45 µm (diameter × length), and closer to isodiametric in upper region of perithallus, 8–13 × 6–16 µm (diameter × length). Rhizoids multicellular, 8–15 µm diameter, long and fibrous, tangled, felt-like, and cut off at an acute angle from the distal end of the hypothallus towards the growing margin; on emergence from the hypobasal cuticle the angle sometimes lessens; cuticle 10–13 µm thick. Hair cells absent. Tetrasporangia 15–20 µm diameter and 50–80 µm long, cruciately divided, borne on paraphyses produced in elevated, subcircular gelatinous nemathecia (500–1,200 µm diameter) on thallus surface. Gametangial reproduction not observed.

Holotype. BISH 776116 (ARS 09653, Kure Atoll, Hawai'i, 28.49845, -178.341712, depth 90 m, Jun 5, 2016, leg. J. Hansen & B. Hauk [NWHI-543], sheet 1). Tetrasporangial plants.

Isotype. HAW-43388 (ARS 09653, as above for holotype).

Etymology. Named for Joshua Copus, our colleague and friend, and a doctoral student at the University of Hawai'i at Mānoa who passed away on Nov 12, 2019,

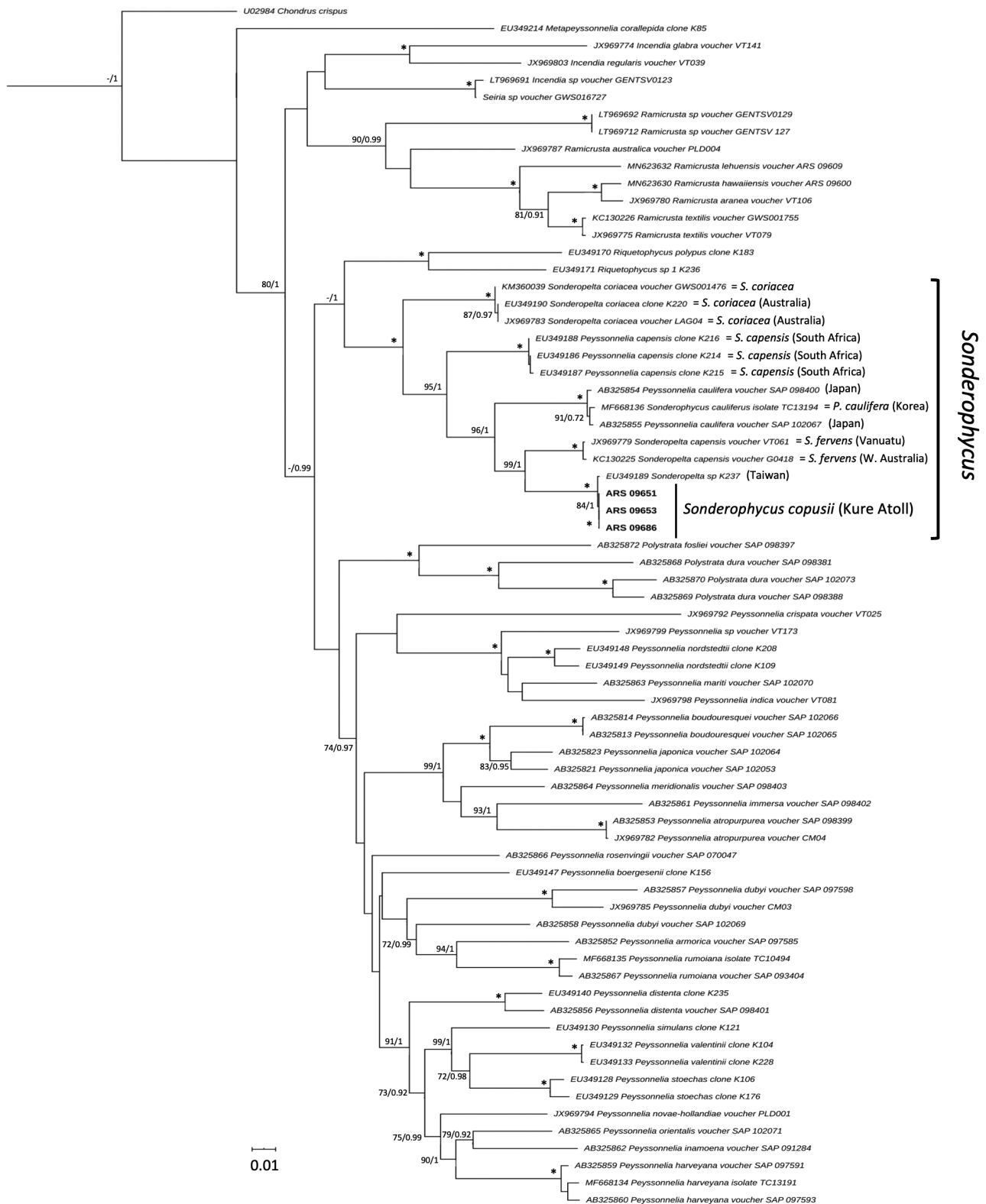


Fig. 2. Maximum likelihood phylogenetic tree of *rbL* sequences for *Sonderophycus* and closely related genera in the red algal order Peyssonneliales. Where known, geographical origins of *Sonderophycus* (or presumed members of the genus) specimens are indicated. Numbers along branches indicate nodal support (first value, bootstrap support; second value, Bayesian posterior probabilities). Nodes with full support are indicated with an asterisk. Scale bar represents: substitutions per site.

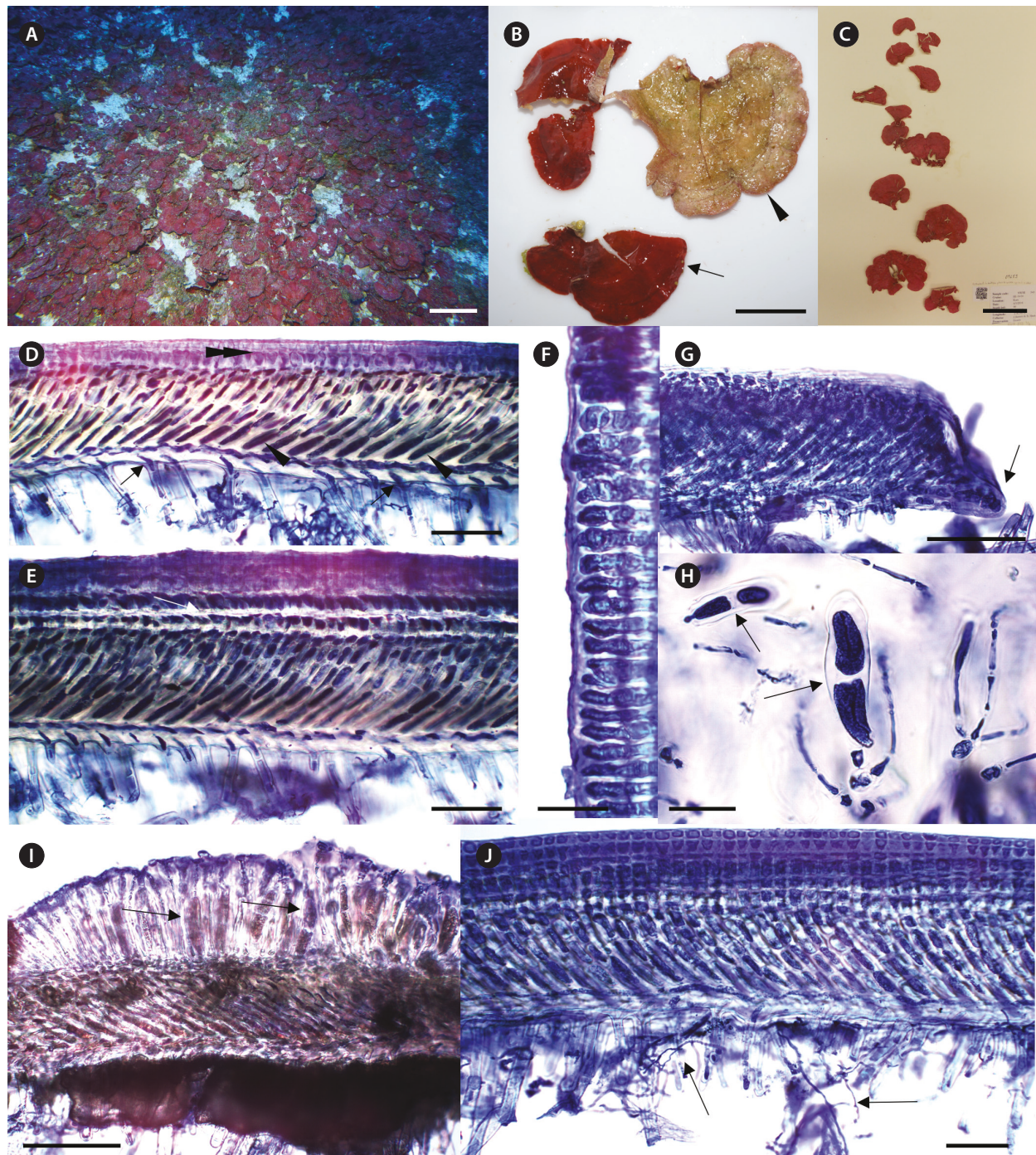


Fig. 3. Morphology of *Sonderophycus copusii* sp. nov. (A) Bed of *Sonderophycus copusii* at Kure Atoll at 90 m, illustrating the dominance of the species in the algal assemblage. (B) Live specimens (ARS 09686, BISH 776118) prior to being processed, showing both dorsal (arrow) and ventral (arrowhead) views. (C) Image of the holotype (ARS 09653, BISH 776116). (D) Radial vertical section through the thallus, demonstrating multicellular rhizoids emerging from the hypobasal cuticle at a bent angle (arrows), perithallial filaments arising from the hypothallus at a 45° angle (arrowheads), and the near isodiametric upper perithallial cells (double arrowhead) (ARS 09651, BISH 776117). (E) Radial vertical section illustrating zone of secondary perithallial growth (arrow) (ARS 09651, BISH 776117). (F) View of growing edge of hypothallus (ARS 09651, BISH 776117). (G) Radial vertical section through growing edge of thallus, illustrating the prominent apical cell (arrow) (ARS 09651, BISH 776117). (H) Crucially divided tetrasporangia (arrows) among nemathecial paraphyses (ARS 09653, BISH 776116). (I) Section through a tetrasporangial nemathecium on the dorsal surface of the thallus, with developing tetrasporangia (arrows) (ARS 09653, BISH 776116). (J) Radial vertical section illustrating an association with filamentous fungi (arrows) among rhizoids (ARS 09686, BISH 776118). Scale bars represent: A, 10 cm; B, 3 cm; C, 5 cm; D, E & J, 50 µm; F, 30 µm; G & I, 100 µm; H, 25 µm.

while diving during a research expedition to study the mesophotic coral reefs of the Solomon Islands.

Distribution. Kure Atoll, Papahānaumokuākea Marine National Monument, Hawai'i, USA, from 88–94 m depth.

Specimens examined. ARS 09651 (BISH 776117), ARS 09653 (BISH 776116), ARS 09686 (BISH 776118).

DNA sequence data. GenBank accessions MT012464, MT012466, MT012468 (COI) and MT012465, MT012467, MT012469 (*rbcL*).

Habit and morphology. Dense beds of *Sonderophycus copusii* were photographed at Kure Atoll, with the species covering more than 50% of the substratum. In cross-section, this taxon strongly resembles other members of the genus, with perithallial filaments arising at an angle of approximately 45° from the hypothallus. Specimens also have an obvious, protruding marginal apical cell at the thallus margin, which corresponds to reports of other species of *Sonderophycus*. The rhizoids of *S. copusii* form a remarkably thick tomentum, which are frequently entangled with fungal hyphae. Cystoliths are evident in material that has not been decalcified. Although male and female gametophytes were not observed, tetrasporangial plants were among those characterized.

Key to the species of *Sonderophycus* (including *P. caulifera*)

- 1a. Thallus possessing a distinct stipe *S. coriaceus*
- 1b. Thallus lacking a stipe 2
- 2a. With horizontally directed filaments in the lower perithallus *S. fervens*
- 2b. Lacking sideways-growing filaments in the lower perithallus 3
- 3a. Rhizoids markedly bent upon emergence from the basal cuticle 4
- 3b. Rhizoids not markedly bent upon emergence from the basal cuticle *P. caulifera*
- 4a. Thallus entire, not composed of multiple lobes *S. copusii*
- 4b. Thallus composed of 2–5 fan-shaped lobes *S. capensis*

DISCUSSION

Dixon (2018) remarked that *Peyssonnelia* and *Sonderophycus* cannot be unequivocally distinguished based on morphology despite some characters appearing consistent within *Sonderophycus*, and that molecular phylogenetic analyses provide the strongest evidence for the

monophyly of *Sonderophycus* within a polyphyletic *Peyssonnelia*. Recognition of peyssonnelioid genera in recent years through combined molecular and morphological analyses has led to the description of several new genera (e.g., *Incendia* and *Seiria*) (Dixon and Saunders 2013, Dixon 2018), the clarification of others that have been recognized for some time (e.g., *Polystrata*, *Ramicrusta*, *Sonderophycus*) (Zhang and Zhou 1981, Kato et al. 2006, Kravesky et al. 2009, Pueschel and Saunders 2009, Ballantine et al. 2016), and the reinstatement of others (e.g., *Ethelia*, which was recently reinstated as distinct from *Polystrata* and placed into its own family) (Dixon et al. 2015). This theme of phylogenetic clarification followed by intensive taxonomic overhaul has been common across the red algae in recent decades (e.g., recognition of many new and resurrected genera within the Batrachospermales, Gracilariales, Kallymeniaceae) (e.g., Entwistle et al. 2009, Saunders et al. 2017, Gurgel et al. 2018), and is an indication of the taxonomic revival that is currently underway in the field of phycology (De Clerck et al. 2013).

Recognition of the Hawaiian specimens as a new species, *Sonderophycus copusii*, is supported by both morphological and molecular phylogenetic comparisons, and sequence data for the *rbcL* and COI markers clearly distinguish the species from all other described taxa in the Peyssonneliales. However, no single morphological character is diagnostic for *S. copusii*, and the distinction of this species from others in the genus relies on a combination of features: the presence of occasional secondary perithallial growth, emergence of rhizoids from the hypobasal cuticle at a strongly bent angle, a lack of horizontally directed filaments in the lower perithallus, and the lack of a stipe. Secondary perithallial growth was reported for *S. fervens* (Dixon 2018) and was occasionally observed in *S. copusii* specimens but is not known in other species of *Sonderophycus*. The emergence of the rhizoids from the hypobasal cuticle at a strongly bent angle appears to be a character shared by several species of *Sonderophycus* (*S. capensis*, *S. copusii*, and *S. fervens*), while the presence of a stipe is known only in *S. coriaceus* (which is prominently three-dimensional, with thallus lobes raised from the substratum) (Womersley and Sinkora 1981, Dixon 2018). *Sonderophycus copusii* is similar to both *S. fervens* and *Peyssonnelia caulifera*; *S. fervens* and *S. copusii* are distinguished by the former having prominent radial streaks on the thallus surface, which are present but not prominent in the latter, and the lack of horizontally directed filaments in the lower perithallus (as per Dixon 2018) in *S. copusii*. Similarly, *S. copusii* differs from *P. caulifera* in having acutely bent rhizoids at the point of emergence

from the hypobasal cuticle (Dixon 2018).

The *Sonderophycus copusii* specimens reported in the current study are almost identical in *rbcL* sequence (differing by only 2 bp) to a specimen published by Kravesky et al. (2009) (as “*Sonderopelta* sp. K237”), which was collected at 4 m depth in Magang Harbor, Taiwan. Interestingly, the Hawaiian *S. copusii* specimens were collected from mesophotic depths (the taxon is known only from 88–94 m depth), and thus far are limited in distribution to the Hawaiian Islands. Given the lack of comparative morphological data for the Taiwanese specimen, it is unknown whether the Hawaiian and Taiwanese specimens represent the same species, although they are certainly very closely related, and their close relationship may shed light on the biogeographic affinities of the Hawaiian mesophotic *Sonderophycus*. Molecular phylogenetic analyses that have been conducted to date on the biogeographic patterns of Hawaiian mesophotic algae have started to yield insight into the biogeographic affinities of the flora. For example, one of four new sea lettuces was closely allied with an undescribed taxon from the Kermadec Islands and western Australia, two were closely associated with specimens from Mage Island, Japan, and the fourth species was not closely associated with any other known sea lettuce species (Spalding et al. 2016). A recent analysis of the red algal genus *Martensia* from Hawai‘i revealed the presence of five species, all with mesophotic representation, four of which were newly described in the study and presumed endemic to the Hawaiian Islands, and one that was demonstrated to be a new record for the islands (*M. albida* Y. Lee) and previously known only from Korea (Sherwood et al. 2019). Two new species described in the peyssonnelioid genus *Ramiscrusta* from Lehua Island, Hawai‘i (one from mesophotic depths) were distinct from all other described species thus far but were allied with taxa known from the western Pacific / Australasia and the Caribbean (Sherwood et al. in press). Thus, the close association of *S. copusii* with a Taiwanese specimen is consistent with the majority of known biogeographic associations of Hawaiian mesophotic algae to taxa from the Asia-Pacific region. As the species-level taxonomy of the Hawaiian mesophotic flora is clarified in the coming years, our understanding of the biogeographic associations of the flora will also be resolved in greater detail.

The beds of *Sonderophycus copusii* from Kure Atoll are consistent with the Corallinales / Peyssonneliales assemblages noted in Mesophotic Coral Ecosystems (MCEs) of the Caribbean, Mediterranean, and the Red Sea, and may be part of a broader pattern of dominant assemblages at

depth in these ecosystems. The Kure Atoll *Sonderophycus* beds bear similarity to the “*Peyssonnelia* beds” reported from deep waters (30–163 m depth) of various areas of the Mediterranean, which are reported to be patchy in distribution (Augier and Bourdoursque 1978, Ballesteros 1994). Similarly, Aponte and Ballantine (2001) reported mesophotic peyssonnelioids abundant from 60–120 m in the Bahamas, and as part of dominant assemblages in that island group. Likewise, Dullo et al. (1990) noted dominant Corallinales / Peyssonneliales assemblages to 110 m in deep forereef environments in the Red Sea. The ecological role and significance of these mesophotic peyssonnelioid beds is unknown, but it has been hypothesized that they may contribute substantially to sediment production (Ballesteros 1994).

The genus *Sonderophycus* has a relatively broad, pantropical-warm temperate distribution, but with the majority of species known from the Pacific (Guiry and Guiry 2020). *Sonderophycus capensis* has by far the broadest reported distribution of all the species in the genus, with its distribution including Africa, the Indian Ocean, Asia, Australia, and New Zealand, the Pacific Islands, South America, and the Red Sea (e.g., Guimarães and Fujii 1999, Kang et al. 2006, Guiry and Guiry 2020). *Peyssonnelia caulifera* is moderately broad in distribution, with reports from Asia and southeast Asia, and the Pacific Islands (Guiry and Guiry 2020). The remaining species have much more restricted distributions, with *S. fervens* known from northwest Australia, Indonesia, the Philippines, and Vanuatu, *S. coriaceus* known from south Australia and Tasmania, and *S. copusii* known only from the Northwestern Hawaiian Islands. The center of diversity for the genus is clearly in the Pacific, with all species known from this ocean basin, and only one species (*S. capensis*) known outside it (Guiry and Guiry 2020).

Studies of the biodiversity of MCEs have indicated some preliminary trends that will be interesting to explore as more of the algal diversity in these deep-water environments is characterized. For example, fishes have been shown to generally have narrower geographic distributions than their shallow counterparts, high levels of endemism are suggested for all groups of organisms in Hawaiian MCEs, and the degree of shallow-to-deep connectivity has been shown to vary by taxon (Pyle and Copus 2019). Combined with the impressive diversity of peyssonnelioid species that have been described in recent years (e.g., Pueschel and Saunders 2009, Ballantine and Ruíz 2010, 2011, 2012, Dixon and Saunders 2013), it is clear that future contributions to mesophotic algal systematics and taxonomy will be important for under-

standing not only the floristic composition of individual regions, but to clarify the interpretation of these broader patterns of diversity in the mesophotic.

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SUPPLEMENTARY MATERIALS

Supplementary Table S1. Sequences used in phylogenetic analyses (<https://www.e-algae.org>).

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