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Diversity of Kallymeniaceae (Gigartinales, Rhodophyta) associated with Hawaiian mesophotic reefs

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ABSTRACT

Small red algal morphologically variable blades have been extensively collected from Hawaiian reefs, but for many specimens their taxonomy remains poorly understood. In surveys of the Papahānaumokuākea Marine National Monument (PMNM) and Main Hawaiian Islands (MHI), we discovered two taxa of undescribed small (< 5 cm) red blades that matched the genera *Psaromenia* and *Meredithia*, based on morphology and molecular analyses. Neither genus has been previously recorded in the Hawaiian Islands, and neither group of specimens matched currently described species in these two genera. Accordingly, these specimens are described here as new species within the family Kallymeniaceae. *Psaromenia laulamaula* sp. nov., exclusively found at mesophotic depths (83–94 m) in PMNM, is easily distinguished from other members of the genus by its comparatively large, procarpic carpogonial branch system and solitary obovate pink-to-magenta blades. Conversely, *Meredithia hawaiiensis* sp. nov., occurring in both shallow (0–17 m) and mesophotic depths (55 m), has high morphological plasticity, with characters that overlap with other *Meredithia* species, and can only be distinguished based on DNA sequences. This study provides additional evidence of the extent of diversity in the Kallymeniaceae that is poorly characterized from mesophotic depths and provides further evidence that members of the macroalgal flora contain overlooked biodiversity.

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KEY WORDS biodiversity; biogeography; distribution; endemism; Hawai`i; mesophotic; overlooked diversity; red algae; red blade; subtidal

Introduction

The Kallymeniaceae Kylin (Gigartinales, Rhodophyta) is a marine red algal family of ~46 genera united by a morphology of expanded red blades and unique reproductive traits (Saunders *et al.*, 2017; Guiry & Guiry, 2020). Currently, there are two members of the family known in the Hawaiian flora: *Kallymenia sessilis* Okamura and *K. thompsonii* I.A.Abbott & McDermid. The extent to which morphological characters of these species overlap with each other and possibly with related genera has been considered in several publications (e.g. Abbott, 1999; Abbott & McDermid, 2002), highlighting the difficulty in assigning species to an appropriate genus based on morphology alone. With the reinforcement of molecular information, the status and phylogenetic relationships of many species in the family have been clarified (Saunders *et al.*, 2017), and the genus *Kallymenia* J.Agardh was revealed to be non-monophyletic (Huisman *et al.*, 2016; Saunders *et al.*, 2017). An emerging consensus has been to divide *Kallymenia* into several genera, as a necessary step to address problems associated with the uncertain taxonomy within the genus and family (Huisman *et al.*, 2016; Saunders *et al.*, 2017).

Floristic surveys conducted over the last two decades in the Hawaiian Islands have yielded over a hundred expanded red-bladed specimens, including many large (> 20 cm) macroalgal species that cannot be placed in currently recognized taxa, and highlighted a breadth of diversity overlooked in published accounts (Sherwood *et al.*, 2019). One group that thus far has received little taxonomic attention is the smaller blades. During targeted algal surveys of the Papahānaumokuākea Marine National Monument (PMNM) and Main Hawaiian Islands (MHI), small-sized (≤ 15 cm) stipitate red blades were collected that matched the kallymeniacean genera *Psaromenia* and *Meredithia* based on molecular and morphological analyses.

Psaromenia D'Archino, W.A.Nelson & Zuccarello presently includes two species from New Zealand and Bermuda (Schneider *et al.*, 2019), while *Meredithia* J. Agardh includes 12 species that are mostly endemic to Australia and its offshore islands, with the exception of one species from the Caribbean (Puerto Rico) and one from the North Atlantic (British Isles, Norway) (Schneider *et al.*, 2014; Bringloe *et al.*, 2019). The *Psaromenia-Meredithia* clade has recently gained attention due to its broad geographic range

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and occurrence in Mesophotic Coral Ecosystems (MCEs) (Saunders *et al.*, 2017; Schneider *et al.*, 2019). MCEs are deep fore-reef communities comprised of light-dependent organisms including macroalgae, corals and sponges stretching from 30 m to over 150 m depths in the tropics and subtropics (Hinderstein *et al.*, 2010). Some MCEs have a high abundance and diversity of macroalgae, which remains one of the most taxonomically understudied groups of organisms in these environments (Spalding *et al.*, 2019). Atlantic *Psaromenia* and *Meredithia* species are the few thus far recorded from mesophotic depths, at least in the family Kallymeniaceae. *P. septentrionalis* C.W.Schneider, Popolizio & G.W. Saunders was discovered at 90 m in Bermuda (Schneider *et al.*, 2019), and *M. pulchella* D.L. Ballantine, H.Ruíz & J.N.Norris was collected at depths to 70 m in Puerto Rico (Ballantine *et al.*, 2015). In this study, we assessed morphological and molecular (COI-5P and *rbc*L) characters for species delimitation of two Hawaiian kallymeniacean species associated with the MCEs and described two new species belonging to the *Psaromenia-Meredithia* clade, which are also new genus records for the Hawaiian marine algal flora.

Materials and methods

Specimens were sampled during shallow water surveys on Maui in 2007, and from mesophotic depths from 2014–2019 in the PMNM by NOAA divers using mixed gas closed circuit rebreathers. The approximate locations of the sampling sites are shown in Supplementary figure S1 and the specimen collection details and GenBank accession numbers for newly determined sequences are presented in Supplementary table S1. Specimens were preserved as herbarium presses and as formalin vouchers for morphological characterization and in silica gel for DNA extraction.

Morphological characterization

Anatomical and reproductive features were observed in material that was hand-sectioned with a double-edged razor blade. Sections were rehydrated in modified Pohl's solution (Clark, unpubl.: https://www.eeob.iastate.edu/research/bamboo/pdf/anatomy_protocols.pdf) for ~5 min, stained with 0.5% aniline blue for ~5 min, and then mounted in 30% Karo™ Syrup (ACH Foods, Memphis, Tennessee, USA). Sections of stipe and basal regions, which are generally thicker than apical cross sections, were rehydrated and stained for longer periods. Rehydration and staining longer than 20 min caused the blades to disintegrate into a viscous mass of cells. Photomicrographs were taken on a Zeiss AxioImager A1 compound light microscope (Pleasanton, California, USA) with an Infinity2-1RC digital camera (Lumenera Corporation, Ottawa, Ontario, Canada). To illustrate the full view of the sections, several successive images from individual sections were combined using Autostitch free software (Ma *et al.*, 2007). Images of herbarium sheets were taken in the Joseph F. Rock Herbarium (HAW) using a Canon EOS 5D Mark II Digital Camera and a MK Direct Photo-eBox PLUS 1419.

DNA sequencing and phylogenetic reconstruction

Total genomic DNA was extracted from silica gel-preserved or herbarium specimens using the OMEGA E.Z.N.A Plant DNA Kit (OMEGA Biotek, Norcross, Georgia, USA) following the manufacturer's protocol. The mitochondrial COI-5P region was amplified using the primer pairs GazF1 and GazR1 and the recommended PCR amplification profile from Saunders (2005) while the plastid *rbc*L gene was amplified using the following primer pairs: F7 and R753, F577 and R1381, and F993 and RrbcS start (Freshwater & Rueness, 1994), and the PCR amplification profile of Gavio & Fredericq (2002). Bidirectional DNA sequencing was performed at the Advanced Studies in Genomics, Proteomics and Bioinformatics (ASGPB) sequencing facility of the University of Hawai`i at Mānoa. Sequence data generated for all available herbarium or silica vouchers were submitted to GenBank (Supplementary table S1) and were edited and aligned with additional sequences representative for all *Psaromenia* and *Meredithia* species available in GenBank (Supplementary table S2).

Sequence alignment was performed using the MUSCLE plug-in (Edgar, 2004) with default settings in Geneious Prime (http://www.geneious.com) to construct sequence alignments for each gene: COI-5P with 25 sequences of 664 base pairs (bp), and *rbc*L with 26 sequences of 1358 bp, which were subsequently checked by eye. This alignment included a representative of the Dumontiaceae (*Dudresnaya hawaiiensis* R.K.S.Lee) as the outgroup (Saunders *et al.*, 2017). We analysed the *rbc*L and COI datasets both separately and concatenated, and used PartitionFinder v.1.1.1 (Lanfear *et al.*, 2012) to determine the best partitioning strategy for the alignments. Analyses suggested the General Time Reversible model with a gamma distributed rate variation among sites and a proportion of invariant sites (GTR+I+G) involving four partitions for the concatenated data set: (1) COI-5P and (3) codon positions of *rbc*L. The concatenated dataset, partitioned by gene and codon position, was used in phylogenetic reconstruction performed with Maximum likelihood (ML) (GTR +I+G) using RAxML (https://www.geneious.com/plugins/raxml-plugin/; Stamatakis, 2014) with 1000 bootstrap replicates, and Bayesian inference (BI) using MrBayes v. 3.2.6 (https://www.geneious.com/plugins/mrbayes-plugin/; Ronquist *et al.*, 2012) based on the

nucleotide substitution models as determined by the Akaike Information Criteria (AIC) in MrModeltest 2.3 (Nylander *et al.*, 2008) through tree builder plugins in Geneious Prime. The Bayesian analysis was run with 2000000 generations of Markov Chain Monte Carlo iterations until the standard deviation of split frequencies was below 0.01. The first 10% of trees of each run were discarded as burn-in. Visualization of the trees was performed via the interactive Tree of Life (https://itol.embl.de/) (Letunic & Bork, 2019).

Results

Phylogenetic analysis

The COI+*rbc*L concatenated alignment was 2022 bp in length and included both newly determined sequences and reference sequences of *Meredithia* and *Psaromenia* from GenBank. The ML and BI analyses produced identical topologies; thus, only the ML tree, with support values from both analyses superimposed, is shown (Fig. 1). Phylogenetic analyses confirmed the placement of the Hawaiian specimens with full support; one distinct lineage belonging to the genus *Meredithia*, and another one belonging to the genus *Psaromenia*. The concatenated COI+*rbc*L analyses demonstrated the distinctiveness of Hawaiian *Psaromenia* from the other two recognized species in the genus: *P. berggrenii* (J. Agardh) D'Archino, W.A.Nelson & Zuccarello, the type species, and *P. septentrionalis* C.W.Schneider, Popolizio & G.W.Saunders, which were 8.83% and 7.96% divergent from the Hawaiian lineage of *Psaromenia*, respectively. The closest relative of the Hawaiian *Psaromenia* was an undescribed species collected from Jeju Island, Korea, with 4.15% divergence. Hawaiian *Meredithia* was 9.73% divergent from *M. microphylla* (J.Agardh) J.Agardh, the generitype, and was resolved as a close ally to *M. norfolkensis* G.W. Saunders & C.W.Schneider from Australia with 1.88% sequence divergence. Of the described species of *Meredithia*, only *Meredithia pulchella* D.L.Ballantine, Ruíz & J.N.Norris, for which only LSU sequence data are available, was not included in our analyses; however, it has been previously determined to be a sister species to *M. crenata* C.W.Schneider, G.W.Saunders & C.E.Lane (Ballantine *et al.*, 2015). Thus, the two Hawaiian species have been determined to be phylogenetically distinct taxonomic units within the *Meredithia-Psaromenia* lineage and are proposed below as new species.

Psaromenia laulamaula* F.P.Cabrera, Huisman & A. R.Sherwood, *sp. nov. (Figs 2–16)

Description

Thallus red, blade-like, solitary, stipitate, simple, lobed or rounded with smooth to undulate margins, becoming spatulate at maturity, from 1–11 cm in height, 0.3–8 cm in width. Blades rose-pink,

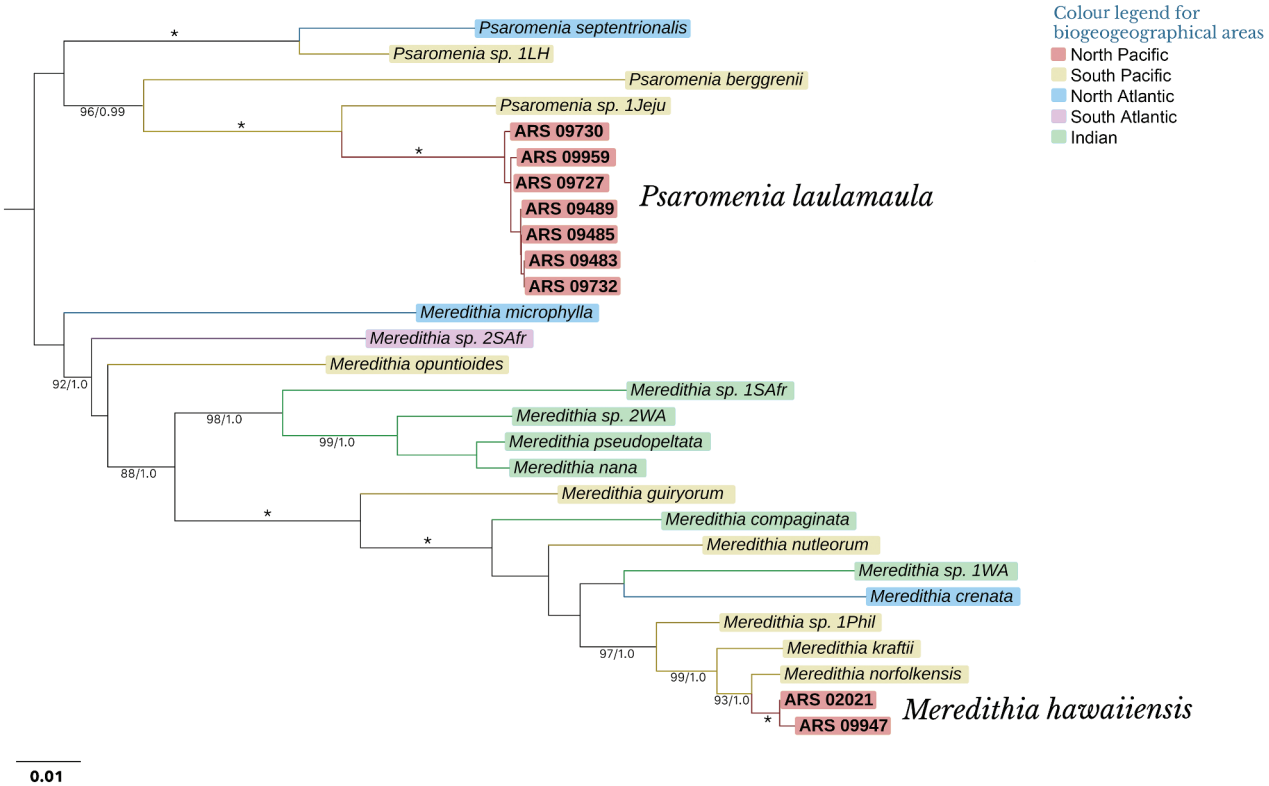


Figure 1. Combined COI and *rbc*L Maximum likelihood tree of *Meredithia* and *Psaromenia* specimens in the context of published GenBank sequences. Outgroup (*Dudresnaya hawaiiensis*) pruned to facilitate presentation. Scale bar = substitutions per site. Numbers at nodes greater than 70% (bootstrap, first value) and 0.9 (Bayesian posterior probabilities, second value) are shown. Full support is indicated by an asterisk (*).

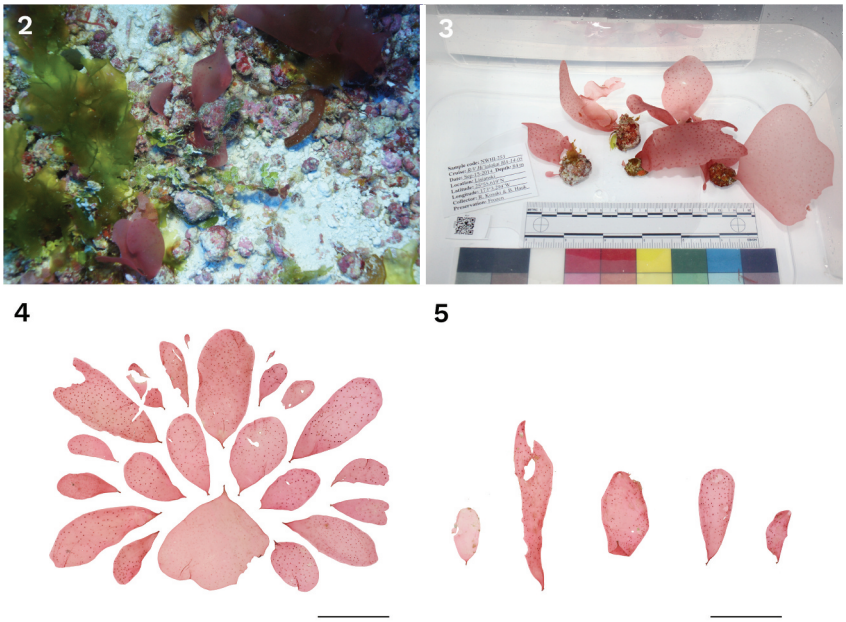
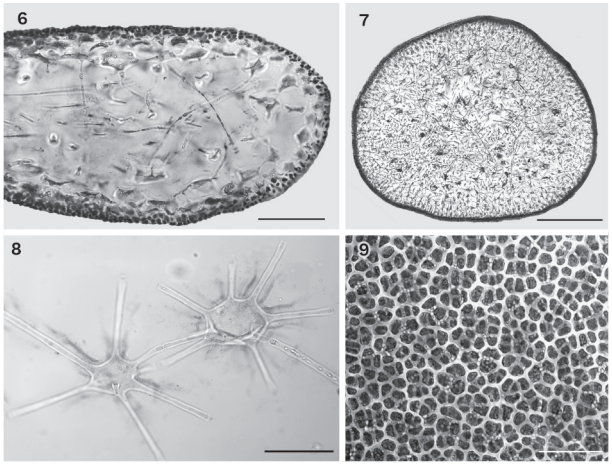
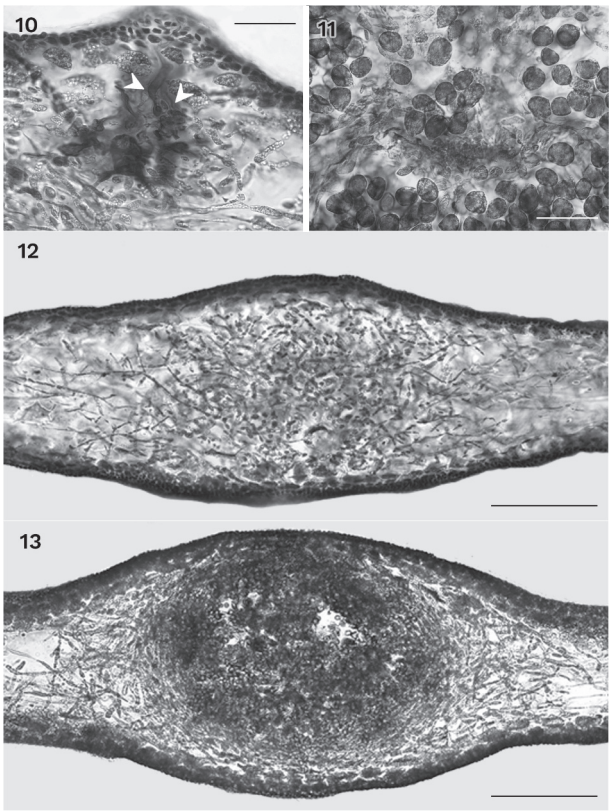


Figure 2–5. *Psaromenia laulamaula* sp. nov. *in situ* and habit images. **Fig. 2**. Holotype specimen (BISH 776061) *in situ*, collected at Lisianski at 84 m. **Fig. 3**. Live holotype specimen (BISH 776061) cleaned of epiphytes. **Fig. 4**. Herbarium voucher of the holotype specimen (BISH 776061), female blades. **Fig. 5**. Isotype (BISH 776062), male and female blades. Scale bars: Figs 2–5, 5 cm.

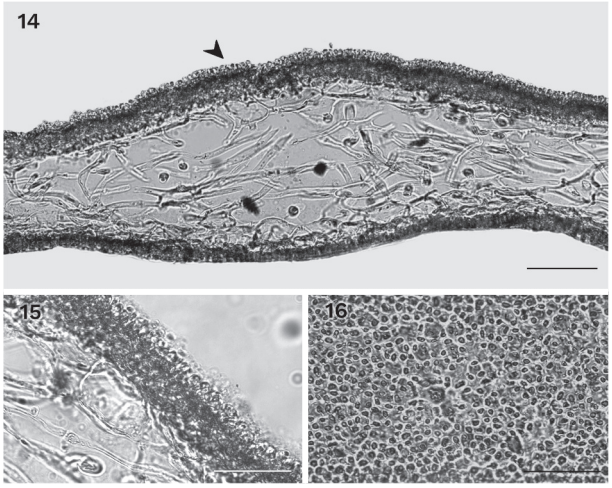


Figs 6–9. Vegetative anatomy of mature blades of *Psaromenia laulamaula* sp. nov (BISH 776061). **Fig. 6**. Cross section through thickened margin in the median part of the blade. **Fig. 7**. Cross section through basal part of stipe. Fig. 8. Fully developed stellate ganglionic cells. **Fig. 9**. Surface view of cortical cells. Scale bars: Fig. 6, 100 µm, Fig. 7, 300 µm, Figs 8–9, 50 µm.

progressing to a rich magenta at margins and basal regions of blade. Stipe 1–5 mm in length with a small discoidal holdfast. Blades multiaxial in structure, composed of a mostly filamentous medulla with abundant, lightly staining stellate ganglionic cells with a diameter of 450–880 µm throughout the blade. Blades 250–300 µm thick near the margins, 200–225 µm thick in apical part of the blade, and 270–300 µm thick in basal regions. Cortex composed of 1–3 cell layers decreasing in size towards the surface with the largest inner cortical cells



Figs 10–13. Female reproductive anatomy of *Psaromenia laulamaula* sp. nov (BISH 776062). **Fig. 10**. Cross section showing a developing carpogonial branch attached near inner cortical cells showing trichogynes (arrowheads). **Fig. 11**. Cross section showing close up of a mature carposporophyte showing carposporangia in compact clusters. **Fig. 12**. Cross section through an immature carposporophyte. **Fig. 13**. Cross section through a mature carposporophyte. Scale bars: Figs 10–11, 50 µm, Figs 12–13, 200 µm.

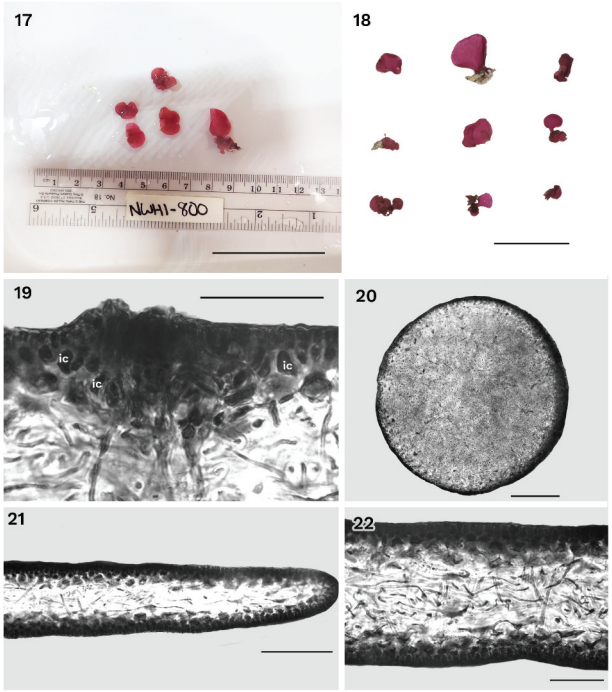


Figs 14–16. Male reproductive structures of *Psaromenia laulamaula* sp. nov (BISH 776063). **Fig. 14**. Cross section through a spermatangial sorus, with spermatia (arrowhead) produced on outer cortical cells. **Fig. 15**. Detail of a cross section of a spermatangial sorus showing the formation of spermatangia. **Fig. 16**. Surface view of spermatangial sorus. Scale bars: Fig 14, 100 µm, Figs 15–16, 50 µm.

measuring to 3–7 × 8–14 µm. Polycarpogonial branch systems borne on supporting cells produce mature cystocarps (up to 2 mm in diameter). Cystocarps scattered singly throughout the blades, extending at least 500 µm above and below the thallus surface. Spermatangial mother cells (3–7 µm length × 5–10 µm breadth) present in sori on one side of the blade. Tetrasporangia not observed.
HOLOTYPE: BISH 776061 (ARS 09483; 84 m, 14. IX.2014, collected by R. Kosaki & B. Hauk).
HOLOTYPE DNA ACCESSION NUMBERS: MW250212 (COI) and MW250215 (*rbc*L).
ISOTYPE: BISH 776062 (ARS 09485;84 m, 14. IX.2014, collected by R. Kosaki & B. Hauk).
ISOTYPE DNA ACCESSION NUMBERS: MW250211 (COI).
TYPE LOCALITY: Lisianski Island (Papa'āpoho), Hawai`i (25.92698, −173.05490).
ETYMOLOGY: The epithet '*laulamaula*' is derived from the Hawaiian language and was developed by Kalani Quiocho of the PMNM Native Hawaiian Cultural Working Group (refer to Appendix in the Supplementary Information).
DISTRIBUTION: Throughout the Papahānaumokuākea Marine National Monument from Kure Atoll (Hōlanikū), Midway Atoll (Kuaihelani), Pearl and Hermes Atoll (Manawai), Lisianski (Papa'āpoho) and French Frigate Shoals (Lalo), and exclusively collected from a mesophotic depth range of 83–94 m.
SPECIMENS EXAMINED: Supplementary table S1.
DNA SEQUENCE DATA: Supplementary table S1.
Habit and vegetative structure: Thalli are simple, almost leaf-like blades that are rounded to spatulate in shape with smooth margins that are ~ undulate. Rather than upright, blades are curled, almost sprawling or lying prostrate on the substrate *in situ* (Figs 2–3, Supplementary fig. S1). The rose pink to red magenta blade colour is retained even when dried. The solitary blades are 4–23 cm in height and 8–29 cm in width, attached by a 5–8 mm long stipe (Figs 4–5). Blades are 250–300 µm thick along the margins (Fig. 6), 200–225 µm thick at the apex of the blade and increase in the basal region to 270–300 µm thick. The stipe is densely packed with medullary filaments (Fig. 7). The medulla is composed of densely aggregated stellate ganglionic cells that are 450–880 µm in diameter (Fig. 8). Surface cortical cells are polygonal to subspherical in shape, 14–25 µm in diameter, loosely packed so that subcortical cells are visible in surface view (Fig. 9).
Reproductive morphology: Cystocarps are up to 2 mm in diameter, and are scattered over the entire blade, protruding on both sides. Carpogonial branches are initiated laterally from subcortical cells with multiple trichogynes (Fig. 10). Mature carposporangia are 12–20 µm wide by 25–40 µm long, and obovoid in shape (Fig. 11). Carposporophytes are 320–450 µm in height and 600–800 µm in diameter when developing (Fig. 12), and 500–550 µm in height and 850–1000 µm in diameter when mature (Fig. 13). Spermatangial sori (Figs 14–16) are scattered over one surface of blades. Tetrasporophytes were not observed.

Meredithia hawaiiensis F.P.Cabrera, Huisman & A.R. Sherwood, *sp. nov.* (Figs 17–22)

DESCRIPTION: Reniform to semi-peltate red blades associated in small clumps, 0.5–1.5 cm in diameter, typically wider than tall. Thalli stipitate or non-stipitate. Stipes 415–440 µm in diameter, 1–2 mm long, densely packed with medullary filaments, bearing a single blade with smooth margins. Non-stipitate blades foliose with loosely undulate margins. Blades multiaxial in structure, composed of a filamentous medulla with occasional lightly staining stellate medullary cells throughout the blade, with 1–2 layers of subcortical cells, 8–17 µm in diameter. Blades 55–108 µm thick in apical margins, 230–275 µm thick in medial region, and 340–370 µm thick in basal portion. Cystocarps 100–200 µm diameter, fully embedded when developing and protuberant when mature, scattered throughout the blades. Male gametophytes and tetrasporophytes not observed.
HOLOTYPE: BISH 776207 (ARS 09947; 17 m, 31. VII.2019, collected by B. Hauk).
HOLOTYPE DNA ACCESSION NUMBERS: MW250209 (COI) and MW250214 (*rbc*L).
TYPE LOCALITY: Pearl and Hermes Atoll (Manawai), Hawai`i (27.91062, −175.90483).
ETYMOLOGY: The specific epithet refers to its occurrence in the Hawaiian Islands.



Figs 17–22. *Meredithia hawaiiensis* sp. nov. **Fig. 17**. Live holotype specimen (BISH 776207), collected at Lisianski at 55 m. Scale bar = 2.5 cm. **Fig. 18**. Herbarium voucher of the holotype specimen (BISH 776061). **Fig. 19**. Cross-section through basal part of the blade showing a carpogonial branch (arrow), and inner cortical cells (ic). **Fig. 20**. Cross section through stipe. **Fig. 21**. Cross section through margins of the blade. **Fig. 22**. Cross section through the apical part of the blade. Scale bars: Figs 17–18, 2.5 cm, Figs 19–22, 100 μm.

DISTRIBUTION: Geographic range extends from shallow and mesophotic depths in the Papahānaumokuākea Marine National Monument at Lisianski (Papa'āpoho) (at 55 m) to the MHI (Maui) in the shallow intertidal (less than 1 m).

SPECIMENS EXAMINED: Supplementary table S1.

DNA SEQUENCE DATA: Supplementary table S1.

Habit and vegetative structure: Thalli consist of simple, semi-peltate to lobed blades, 0.5–1.5 cm in diameter, typically wider than tall. Blades are erect and solitary. *In situ*, blades are rose pink to red magenta in colour, turning to dark fuchsia when dried (Figs 17–18). Blades have smoother margins and are single-lobed when a stipe is present, undulate margins and irregularly lobed when stipes are absent. Inner cortical cells are polygonal to subrounded in surface view and are 5–15 μm in diameter (Fig. 19). Stipes are 415–440 μm in diameter and 1–2 mm long (Fig. 20). Blades are 230–275 μm thick at the apical portion of the blade, progressively thickening at the basal part of the blade (340–370 μm) and becoming thinner at the margins (55–108 μm) (Figs 21–22).

Reproductive morphology: Specimens included occasional blades with protruding cystocarps (0.2–0.4 mm in diameter), such as those observed in the holotype (BISH 776207). However, observations of reproductive development were limited by a paucity of material. Carpogonial branches are initiated laterally from subcortical cells (Fig. 19), but further development was not observed. Male gametophytes and tetrasporophytes were not observed.

Discussion

The discovery of the two novel kallymeniacean species in Hawai`i, *Psaromenia laulamaula* and *Meredithia hawaiiensis*, demonstrates that the archipelago, despite a long history of phycological studies, still harbours an undescribed marine flora. These species have possibly been overlooked due to their relatively small size and unique habitats. *Psaromenia laulamaula* represents the third species formally described in the genus, and the first to be described from the North Pacific, extending the known distribution of *Psaromenia* beyond Bermuda, New Zealand, Korea and Australia. Its closest relative in our analyses, '*Psaromenia* sp.1_Jeju', is an undescribed Korean species (Schneider *et al.*, 2014). Biogeographic links between Hawaiian and Korean material have been observed recently for other mesophotic red algal species in Hawai`i (i.e. *Martensia albida* Y.Lee, *Herposiphonia* spp. Nägeli, *Gracilaria parvispora* I.A.Abbott; Kim *et al.*, 2008; Koh *et al.*, 2018; Sherwood *et al.*, 2019), and this biogeographic pattern for *Psaromenia* represents an additional potential link between the two floras.

In terms of gross morphology, *P. laulamaula* is easily distinguished by its simple blades that usually lie prostrate on the substratum, which contrasts with the foliose to much divided and erect blades of *P. berggrenii* (D'Archino *et al.*, 2010) and *P. septentrionalis* (Schneider *et al.*, 2019). In contrast to *P. berggrenii* and *P. septentrionalis* which both have divided to branched blades, blades of *P. laulamaula* are solitary and undivided. Moreover, the cystocarps of *P. laulamaula* are comparatively larger (Table 1) and possess more densely packed carposporangia than all other currently described species. As with *P. berggrenii* the generitype, *P. laulamaula* is a variable species, especially with respect to its blade morphology. The holotype material has spatulate blades, whereas other collections include blades that are only slightly broadened at the apex. It has been noted that the morphology of *P. berggrenii* is variable in relation to age and depth (D'Archino *et al.*, 2010). Like all other members of *Psaromenia*, no tetrasporangial plants of *P. laulamaula* were observed (D'Archino *et al.*, 2010; Schneider *et al.*, 2019). Given the isolation of the PMNM and the uniqueness of its macrofloral community, we suspect that the new species is endemic to the reefs of Hawai`i.

Meredithia hawaiiensis represents the twelfth species formally described in the genus, with other

Table 1. Comparison of morphological characters of members of the genus *Psaromenia*.

	P. laulamaula F.P.Cabrera, Huisman & A.R.Sherwood	*P. berggrenii* D'Archino, W.A.Nelson & Zuccarello – generitype	*P. septentrionalis* C.W.Schneider, Popolizio & G.W.Saunders
Gross morphology			
Blade shape	narrowly to broadly spatulate	lobed, laciniate to foliose	ligulate
Branching	non-branching	non-branching	subdichotomously branched
Margins	smooth to undulate	smooth to eroded margins	marginal proliferations
Blade dimensions	0.3–8 × 1–13 cm	up to 38 × 26 cm	up to 13 cm tall
Blade colour	rose pink to magenta red	dark red to dark brown	rosy red
Blade thickness	220–300 µm	220–650 µm	300–500 µm thick
Stipe	always present, 0.2–1 × 1–5 mm	if present, 0.5 cm	absent
Vegetative structures			
Outer cortical cells	narrowly to broadly spatulate	polyhedral; 5–9 µm	polyhedral; 3.5–7.5 µm
Inner cortical cell layers	1–3 cell layers	2–4 cell layers	1–2 cell layers
Inner cortical cells	smooth to undulate	isodiametric; 28–32 µm	subglobose; 33.5–67.5 µm
Medulla	filamentous	filamentous	filamentous
Stellate cells	150–300 µm	200–300 µm	–o.n.d
Reproductive structures			
Carpogonial branch system	polycarpogonial	variable, mono-polycarpogonial branches	monocarpogonial
Cystocarp	~2.0 mm	1–1.5 mm	~1.3 mm
Carpospores	12–20 × 25–40 µm	18–21.5 µm	obpyriform to spherical; 9.5–17.0 µm
Spermatangia	3–7 × 5–10 µm	ovoid spermatangia; 2.6–4.3 × 4.4–7 µm	–o.n.d
Tetrasporangia occurrence	not observed	not observed	not observed
Geographic distribution	NWHI	New Zealand	Bermuda
Depth distribution	84–94 m	3–25 m	90 m

–o.n.d, observed but not described.

species reported from the Atlantic, Indian and Pacific Oceans. The available material for *M. hawaiiensis* consists of young blades, which are difficult to distinguish from other members of the genus. For this reason, recognition of *M. hawaiiensis* is based primarily on the molecular analysis. Gross and vegetative morphological observations demonstrated high polymorphism with substantial overlap among *Meredithia* species, and unfortunately reproductive morphology also provides little power in delineating species, as reproductive structures in more than half of the species were either not observed or observed but not described in sufficient detail (Tables 2 and 3). Diagnostic morphological features of *Meredithia* species are often difficult to establish because morphological differences between the species are small and subtle, and thus weakly differentiated. Considerable morphological variability in *Meredithia* remains poorly reflected in dichotomous identification keys and is not easily related to the phylogenetic patterns, which is why species within the genus are still largely distinguished from each other on a molecular basis (Schneider *et al*., 2014; Saunders *et al*., 2017). All members of *Meredithia* except *M. nana* have average blade lengths of 3–5 cm. This underlines an important level of morphological constraint related to size and illustrates how molecular tools will continue to be paramount in distinguishing species. Nevertheless, we found a small set of vegetative characters (blade shape, blade thickness and presence of stipe; Tables 2 and 3) that can be useful in distinguishing *Meredithia* species. Given its limited recorded distribution in Hawai`i, we also suspect that *M. hawaiiensis* is endemic to Hawaiian reefs.

Our work on Hawaiian stipitate red blades is inconclusive with respect to the Deep Reef Refuge Hypothesis, which postulates that mesophotic reefs may function as refugia when there is considerable extent of species overlap with shallow-water counterparts (Bongaerts *et al*., 2017).

Psaromenia laulamaula is documented exclusively at deeper mesophotic depths (with water temperatures as low as 16°C at > 80 m), similar to its Atlantic congener, *P. septentrionalis* (with slightly warmer water temperatures at ~19–20°C year-round at 100 m). A number of other members of the endemic Hawaiian flora, including *Codium campanulatum* P.C. Silva & M.E.Chacana (95 m), *Martensia abbottiae* A.R. Sherwood & S.-M.Lin (65–93 m) and *M. lauhiekoeloa* A.R.Sherwood & S.-M.Lin (61–67 m), have only been found at lower mesophotic depths, while *C. hawaiiense* P.C.Silva & M.E.Chacana (35 m) and *C. intermedium* P.C.Silva & M.E.Chacana (45–55 m) have only been found at upper mesophotic depths. In contrast, *Meredithia hawaiiensis* was first collected in 2007 in the intertidal on Maui, MHI and at mesophotic depths at Lisianski (55 m) in PMNM, exhibiting distributional overlap between shallow and mesophotic communities. Some members of the endemic Hawaiian flora such as *C. desultorium* P.C.Silva & M.E.Chacana (27–37 m) exhibit a narrow range of distributional overlap, while *Martensia hawaiiensis* A.R.Sherwood & S.-M.Lin (1–65 m), *M. tsudae* A.R.Sherwood & S.-M. Lin (~126 m) and *Halimeda kanaloana* Vroom

Table 2. Comparison of morphological characters of members of the genus *Meredithia*.

	Meredithia hawaiiensis F.P. Cabrera, Huisman & A.R.Sherwood	*Meredithia microphylla* (J. Agardh) J.Agardh – generitype	*Meredithia kraftii* G.W. Saunders & C. W.Schneider	*Meredithia opuntioides* G.W. Saunders & C.W. Schneider	*Meredithia pseudopeltata* G. W.Saunders & C. W.Schneider	*Meredithia pulchella* D.L. Ballantine, H. Ruíz & J.N. Norris
Gross morphology						
Blade shape	reniform, semi-peltate to foliose	semi-peltate, auriculate	prostrate	opuntioid	spiralling oval to elongate	peltate, irregularly circular
Branching pattern	non branching	alternate to marginal branching	anastomosing	marginal branching with secondary stipes	marginal branching	marginal branching with secondary stipes
Margins	smooth	smooth to crenulated	undulate to crispate	smooth to irregular	broadly undulate	irregular to crenulated
Blade dimensions	0.5–1.5 cm	–o.n.d	1-3 cm	2.0–3.5 cm	2.5–4.0 cm × 2.5 cm.	
Blade colour	red magenta to dark fuchsia	rose-red, brick red to purplish	–o.n.d	–o.n.d	–o.n.d	3 cm tall
Blade thickness	55–370 µm	–o.n.d	200–275 µm	200–350 µm	250– 400 µm	110 µm
Stipe	0.02–0.4 mm × 1–2 mm	10–30 mm	1.5–2.0 mm × 1.5–2.0 mm	~1 mm × 1–2 mm	1.5 mm wide	–o.n.d
Vegetative structures						
Outer cortical cells	2.5–5.0 µm × 5.0–7.5 µm	3.5–6 µm	dimorphic; 3–6 µm × 5–8 µm	–o.n.d	obclavate; 2.5–3.5 µm × 5.0–10 µm	–o.n.d
Inner cortical cell layers	1–2 cell layers	2–4 cell layers	2–3 cell layers	2–3 cell layers	2–3 cell layers	2–3 cell layers
Inner cortical cells	polygonal to sub-rounded; 5–15 µm	3.5-6 µm	isodiametric	dimorphic; 3–5 µm × 5–9 µm	–n.d	–n.d
Medulla	filamentous; 3–6 µm	filamentous	filamentous	moderately filamentous; 8 µm wide	densely filamentous	filamentous; 2 µm
Stellate cells	150–200 µm	200–300 µm	–o.n.d	–o.n.d	–o.n.d	–o.n.d
Reproductive structures						
Carpogonial branch system	not observed	monocarpogonial	not observed	monocarpogonial ?	not observed	not observed
Cystocarp	1 mm	2–3 mm	not observed	not observed	not observed	not described
Carpospores	not observed	7.5–15 µm	not observed	not observed	not observed	not observed
Spermatangia	not observed	oval to spherical; 1.5-3.5 µm	not observed	not observed	not observed	not observed
Tetrasporangia occurrence	not observed	–n.d.	not observed	not observed	not observed	not observed
Geographic distribution (*Type locality)	NWHI* and MHI	Bergen, Norway British Isles*, Canary Isles, Bardsley Island and Western Mediterranean	Lord Howe Island*, Australia	South-eastern Tasmania*, Australia	Rottnest Island*, Pt. Peron in Western Australia	Bermuda, Florida, Caribbean, Puerto Rico*
Depth distribution	0–17 m, 55 m	1.5–30 m	15 m	6 m	2.5 m	17–70 m

–o.n.d, observed but not described, –n.d, not described.

(1–85 m) have wider ranges of distributional overlap between shallow and mesophotic depths. The variability observed in terms of distributional overlap within shallow and mesophotic communities in this study corroborates trends from other Hawaiian mesophotic studies (Sherwood *et al.* 2019; Spalding, 2012; Silva & Chacana, 2014), in that the evidence for connectivity among MCE and shallow macroalgal populations can differ by species.

Currently observed patterns of geographic distribution of the *Psaromenia-Meredithia* clade show different aspects of the natural history of both genera (D'Archino *et al.*, 2010; Schneider *et al.*, 2014, 2019). Patterns are complex as species are not clustered by biogeographic region, suggesting that alternative biogeographic processes or dispersal routes are playing a role in the observed patterns (McDermid & Abbott, 2006). Hawaiian *Psaromenia* and *Meredithia* species display *rbc*L divergence typically in the 7–9% range from their Atlantic congeners, which denotes separation ~11.66–15 Ma based on the strict (median) molecular clocks of Bringloe (2018) where the *rbc*L clock normal priors 0.30%/Ma. This timeframe of separation between Atlantic and Pacific species pre-dates the gradational closure of the Panama seaway (~4 Ma), when gene flow between marine organisms on either Pacific and Atlantic ocean basins was likely to have been achieved (Jacobs *et al.* 2004). Detailed molecular clock analyses including increased taxonomic sampling and additional molecular markers are needed before stronger conclusions can be drawn about the biogeographic and diversification patterns of the Hawaiian marine flora.

In summary, this study represents a step towards increasing our understanding of mesophotic diversity and taxonomy, tripling the number of known genera in the family Kallymeniaceae in Hawai`i (Abbott, 1999), and joining a growing body of work characterizing the algal diversity of Hawaiian MCEs Spalding, 2012; Silva

Table 3. Continuation of comparison of morphological characters of members of the genus *Meredithia*.

	Meredithia nana J. Agardh	*Meredithia norfolkensis* G.W. Saunders & C.W. Schneider	*Meredithia nutleorum* G.W. Saunders & C.W. Schneider	*Meredithia compaginata* G. W.Saunders	*Meredithia crenata* C. W.Schneider, G.W. Saunders & C.E.Lane	*Meredithia guiryorum* G.W. Saunders & C.W. Schneider
Gross morphology						
Blade shape	flattened	opuntioid	foliose	peltate	reniform to flattened	non-peltate
Branching	regularly alternately to				subdichotomously branched	marginal branching
rarely, marginal branching	marginal branching	marginal branching with secondary stipes	non-branching			
Margins	smooth to slightly irregular	–o.n.d	loosely undulate to prostrate	smooth to irregularly crenulate	crenulated with finger-like projections	irregular
Blade length	5–15 cm	1– 2 cm	1.0–2.5 cm	0.25–1.20 cm	1.5–6 cm	1.0–2.5 cm
Blade colour	dark red	–o.n.d	–o.n.d	–o.n.d	–o.n.d	–o.n.d
Blade thickness	200–450 µm	200–300 µm	200–300 µm	140-210 µm	300 µm	200–270 lm
Stipe	–o.n.d	<1 mm × 2–4 mm	~1 mm × 1–2 mm	0.5–0.8 mm × 0.5–0.8 mm	–o.n.d	~0.5–1.0 mm × 1–2 mm
Vegetative structures						
Outer cortical cells	ovoid, 1.5–2 µm	2.5–5.0 µm × 5.0–7.5 µm	3–6 µm × 3–8 µm	4–8 µm	–n.d.	2.5–5.0 µm × 5.0–7.5 µm
Inner cortical cell layers	1–2 cell layers	2–3 cell layers	1–2 cell layers	2–3 cell layers	4–5 cell layers	2–3 cell layers
Inner cortical cells	–o.n.d	–o.n.d	–o.n.d	7-10 µm × 5–7 µm	–o.n.d	–o.n.d
Medulla	moderately dense filamentous; 2–6 µm	moderately filamentous	moderately filamentous	rectilinear filaments; 3–6 µm	finely filamentous; 1.5 µm	–o.n.d
Stellate cells	150–200 µm	–o.n.d	–o.n.d	–o.n.d	–o.n.d	–o.n.d
Reproductive structures						
Carpogonial branch system	not identified	not observed	not observed	polycarpogonial	not observed .	not observed
Cystocarp	1–2 mm	not observed	not observed	not observed	400 µm	not observed
Carpospores	10–15 µm	not observed	not observed	not observed	3 µm	not observed
Spermatangia	–o.n.d	not observed	not observed	2.5 µm	2 µm	not observed
Tetrasporangia occurrence	25–38 µm	not observed	not observed	not observed	not observed	not observed
(*Type locality)	Port Phillips Head*, Australia	Norfolk Island*, Australia	Fish Bowl, Nepean Island, Norfolk* Island, Australia	Cocos (Keeling) Islands*, Australia	Bermuda*, Western Atlantic	Lord Howe Island, Australia
Depth distribution		12 m	10 m	5 m	2-6 m	

–o.n.d, observed but not described, –n.d, not described.

& Chacana, 2014; Spalding *et al.*, 2016; Wade *et al.*, 2018; Sauvage *et al.*, 2019; Sherwood *et al.*, 2019). Additionally, the present study underscores how much undescribed biodiversity remains in the archipelago, and that even dwarf stipitate red blades deserve systematic attention for detection of biodiversity. Further phycological studies, particularly of specimens that remain unidentified and material associated with mesophotic environments, is likely to further increase known algal biodiversity in the Hawaiian Archipelago.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Supplementary information:

The following supplementary material is accessible via the Supplementary Content tab on the article's online page at https://doi.org/10.1080/09670262.2021.1891462.

Supplementary table S1. List of *Meredithia hawaiiensis* and *Psaromenia laulamaula* samples used in morphological characterization, combined COI and *rbc*L phylogenetic analysis and accession numbers in GenBank.

Supplementary table S2. List of additional *Meredithia* and *Psaromenia* species used in combined COI and *rbc*L phylogenetic analysis and accession numbers in GenBank.

Supplementary figure S1. Map of collection sites around the Main Hawaiian Islands (MHI) and North-western Hawaiian Islands (NWHI).

Appendix. Memorandum on developing the specific nomenclature of *Psaromenia laulamaula*.

Author contributions

F. Cabrera: original concept, drafting and editing manuscript; J. Huisman: editing manuscript and morphological work; H. Spalding: collection of samples and sample processing; R. Kosaki: collection of samples; A. Sherwood: original concept, editing manuscript.

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