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New species in the cryptic genus *Gloiocladia* J.Agardh (Faucheaceae, Rhodophyta) from Hawaiian Mesophotic Coral Ecosystems

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ABSTRACT
Crypsis – high morphological similarities of adult thalli of distinct species of algae – is a common challenge in algal taxonomy, where multiple taxa are characterized as the same species due to identical morphologies. Algal genera with cryptic species and similar morphologies may contain underestimates of both diversity and endemism. Extensive studies of Mesophotic Coral Ecosystems (MCEs; from *c.* 30 to >150 m depths) have revealed high levels of endemism in the Hawaiian Archipelago using DNA sequence-based analyses augmented by morphological analyses. Here, we characterize specimens collected from both the Papahānaumokuākea Marine National Monument and the Main Hawaiian Islands corresponding to the genus *Gloiocladia* J.Agardh; previous reports from Hawai'i included only a single subtidal species (*G. iyoensis* (Okamura) R.E.Norris). Phylogenetic analyses using both plastidial (ribulose-1.5-biphosphate carboxylase/oxygenase) and mitochondrial (cytochrome oxidase subunit 1) markers revealed three clades of Hawaiian specimens with strong sequence divergence. However, the gross morphology of these specimens was nearly identical, except for small differences in the number of layers and sizes of cortical and medullary cells, which can easily be overlooked. This study extended the depth record of *G. iyoensis* to 63 m (aside from a previous report of a dredge sample from 66 m) and revealed one new species exclusive to MCEs (described here as *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov.), as well as one new intertidal species (formal description awaiting analysis of further collections) present in the Hawaiian Archipelago, including the Papahānaumokuākea Marine National Monument (PMNM) and the Main Hawaiian Islands.

KEY WORDS
COI,
*rbc*L,
cryptic diversity,
mesophotic coral ecosystem,
morphology,
phylogeny,
new species.

RÉSUMÉ
Nouvelle espèce du genre cryptique Gloiocladia *J.Agardh (Faucheaceae, Rhodophyta) des écosystèmes coralliens mésophotiques hawaïens.*
La Crypsis – similitudes morphologiques élevées des thalles adultes d'espèces d'algues distinctes – est un défi courant dans la taxonomie des algues, où plusieurs taxons sont caractérisés comme la même espèce en raison de morphologies identiques. Les genres d'algues comportant des espèces cryptiques et des morphologies similaires peuvent contenir des sous-estimations de la diversité et de l'endémisme. Des études approfondies des écosystèmes coralliens mésophotiques (MCE ; d'environ 30 à >150 m de profondeur) ont révélé des niveaux élevés d'endémisme dans l'archipel hawaïen à l'aide d'analyses basées sur des séquences d'ADN complétées par des analyses morphologiques. Nous caractérisons ici les spécimens collectés à la fois dans le monument national marin de Papahānaumokuākea et dans les principales îles hawaïennes correspondant au genre *Gloiocladia* J.Agardh, qui était auparavant représenté à Hawai'i par une seule espèce subtidale (*G. iyoensis* (Okamura) R.E.Norris). Les analyses phylogénétiques utilisant à la fois des marqueurs chloroplastiques (ribulose-1,5-biphosphate carboxylase/oxygénase) et mitochondriaux (sous-unité 1 de la cytochrome oxydase) ont révélé trois clades de spécimens hawaïens présentant de fortes divergences entre les séquences d'ADN. Cependant, la morphologie globale de ces spécimens est presque identique, à l'exception du nombre de couches et de la taille des cellules corticales et médullaires. Cette étude étend la gamme de profondeur de *G. iyoensis* aux MCE supérieurs (63 m, confirmant une occurence précédente sur un échantillon de drague à 66 m) et a révélé une espèce exclusive aux MCE, *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov., ainsi qu'une espèce intertidale (description formelle en attente d'analyse de collections ultérieures), présente dans l'archipel hawaïen, notamment le monument national marin de Papahānaumokuākea (PMNM) et les principales îles hawaïennes.

MOTS CLÉS
COI,
*rbc*L,
diversité cryptique,
écosystèmes coralliens mésophotiques,
morphologie,
phylogénie,
espèce nouvelle.

INTRODUCTION

Species in the red algal order Rhodymeniales exhibit a high level of morphological similarity and cryptic diversity associated with their plastic body plan, which can lead to misidentifications and taxonomic reassessments at various levels within the order (Saunders *et al.* 2006). In particular, the families Faucheaceae and Rhodymeniaceae contain many species that are barely distinguishable based on gross morphology (Le Gall *et al.* 2008). Within the family Faucheaceae, considerable debate has surrounded the separation of two genera, *Gloiocladia* J.Agardh and *Gloioderma* J.Agardh (e.g. Le Gall *et al.* 2008; Nelson & Dalen 2016; Norris 1991; Sánchez & Rodríguez-Prieto 2005). Although morphological features were originally used to distinguish the two genera based on the presence of *tela arachnoidea* in the cystocarp (Kylin 1956; Norris 1991), recent genetic and morphological analyses have yielded considerable confusion regarding their separation (Sánchez & Rodríguez-Prieto 2005; Rodríguez-Prieto *et al.* 2007). Currently, the family Faucheaceae comprises eight genera and 59 species (Guiry & Guiry 2023), with 34 (58%) currently classified in *Gloiocladia* and five (8%) in *Gloioderma*, following phylogenetic re-evaluation of the family and the subsequent transfer of many species from *Gloioderma* and *Fauchea to Gloiocladia* (Rodríguez-Prieto *et al.* 2007).

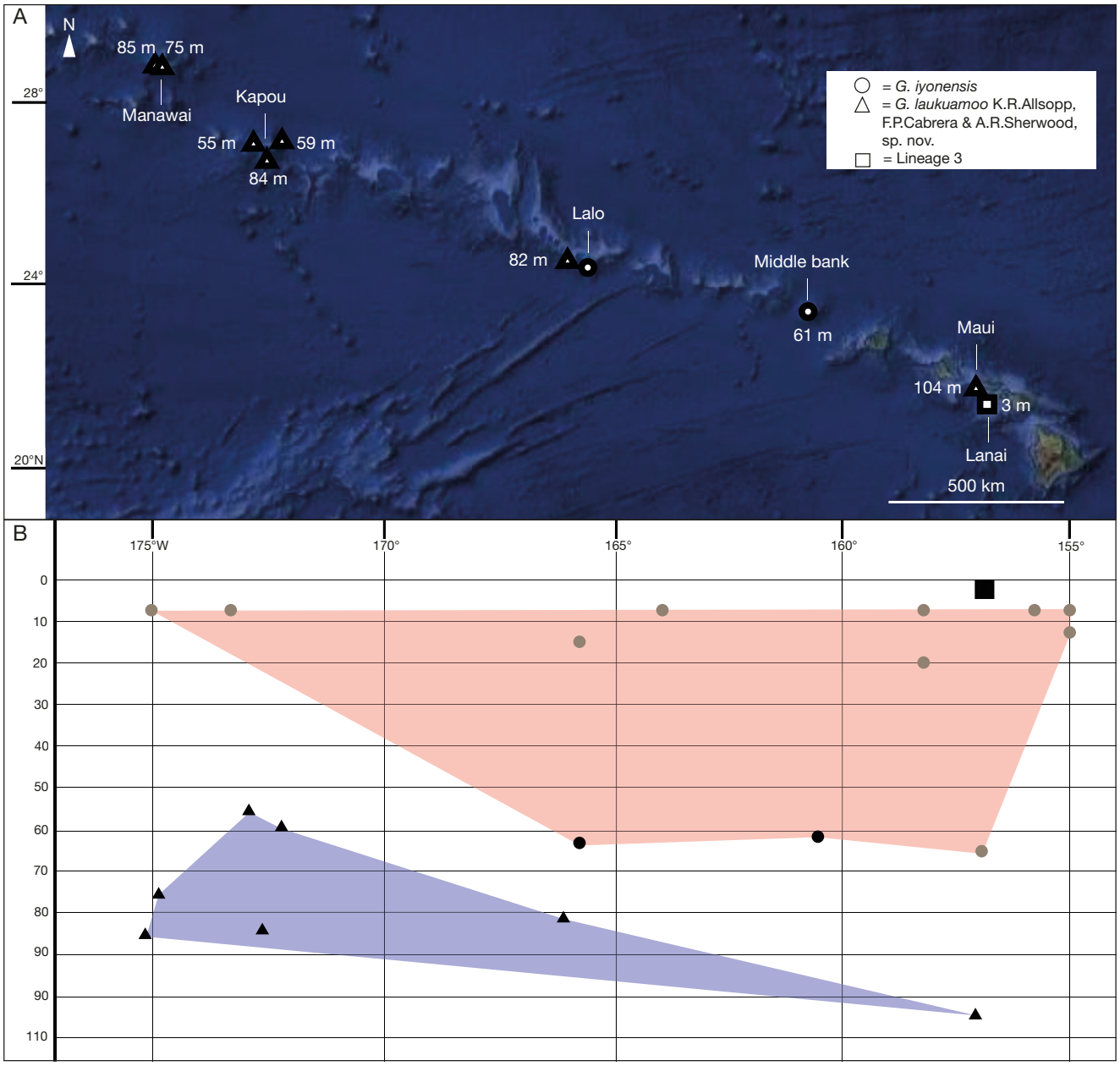

FIG. 1. — Map showing the collection localities and depths for the specimens analyzed for this study (**A**), and depth distribution diagram of all *Gloiocladia* J.Agardh records in the Hawaiian Islands (**B**). **Red shade** represents the biogeographical distribution of *G. iyoensis* (Okamura) R.E.Norris, while **blue shade** represents that of *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. Previously collected specimens (from Abbott 1999) are indicated with **grey dots**, and specimens examined in this study as **black dots**.

Gloiocladia, including the species that were originally described as *Gloioderma*, is characterized by a lubricous thallus with a discoid holdfast and erect, solid, cylindrical, compressed or flattened fronds that are dichotomously, pinnately or radially branched (Norris 1991; Abbott 1999; Rodríguez-Prieto *et al.* 2007). Often, but not always, specimens have marginal protrusions or branchlets that do not extend to full length branches along the edges of blades. Reproductive plants often produce sori along the blade edges as well. Thalli are multiaxial and are composed of small cortical cells, a layer of subcortical cells laterally connected via secondary pit connections, and a medulla of large, axially elongated cells (Agardh 1842; Norris 1991).

The first Hawaiian record of *Gloiocladia* was reported by Abbott (1999), as *G. iyoensis* (Okamura) R.E.Norris. Its Hawaiian distribution includes Manawai (Pearl & Hermes), Kapou (Lisianski), Mokumanamana (Necker), O'ahu, Maui, and Hawai'i from the low intertidal to 66 m depth (Abbott 1999). This depth record suggests that the species occurs throughout the Hawaiian Archipelago from the intertidal to depths within the range of Mesophotic Coral Ecosystems (MCEs). The type locality of *G. iyoensis* is Ehime Prefecture,

TABLE 1. — Collection details for *Gloiocladia* J.Agardh specimens examined in this study.

Lineage and Taxon	Sherwood lab accession	Herbarium accession	Collection details	COI accession	*rbc*L accession
Lineage 1 *G. iyoensis* (Okamura) R.E.Norris	ARS10720	BISH789098	Middle Bank, Hawai'i, 22°39'43"N, 161°2'31"W, 61 m, coll. H. Spalding (NWHI-1081)	OR881946	OR881954
Lineage 1 *G. iyoensis* (Okamura) R.E.Norris	ARS11146	BISH789099	Lalo, Hawai'i, 20 May 2013, 23°37'44"N, 166°11'38"W, 63 m, coll. D. Wagner (NWHI-174-3)	–	OR881956
Lineage 2 *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. (Holotype)	ARS10279	BISH789091	Kapou, Hawai'i, 14 September 2014, 26°2'13"N, 173°47'31"W, 59 m, coll. J. Leonard (NWHI-246)	OR881945	OR881952
Lineage 2 *G. laukuamoo* sp. nov. (Paratype)	ARS10164	BISH789092	Kapou, Hawai'i, 30 July 2019, 26°1'30"N, 174°9'24"W, 55 m, coll. B. Hauk (NWHI-847)	–	OR881951
Lineage 2 *G. laukuamoo* sp. nov.	ARS10286	BISH789093	Lalo, Hawai'i, 8 September 2015, 23°43'36"N, 166°21'17"W, 82 m, coll. D. Wagner (NWHI-347)	–	OR881953
Lineage 2 *G. laukuamoo* sp. nov.	ARS11120	BISH789094	Manawai, Hawai'i, 6 August 2019, 27°44'28"N, 175°57'30"W, 75 m, coll. B. Hauk (NWHI-1025)	OR881947	OR881955
Lineage 2 *G. laukuamoo* sp. nov.	ARS11147	BISH789095	Kapou, Hawai'i, 16 September 2014, 25°52'56"N, 173°57'43"W, 84 m, coll. R. Pyle & D. Wagner (NWHI-265-b)	OR881948	OR881957
Lineage 2 *G. laukuamoo* sp. nov.	ARS11148	BISH789096	Manawai, Hawai'i, 18 September 2014, 27°44'23"N, 175°57'41"W, 85 m, coll. R. Kosaki (NWHI-294-b)	OR881949	OR881958
Lineage 2 *G. laukuamoo* sp. nov.	ARS11390	BISH789097	Maui, Hawai'i, 5 April 2009, 104 m, coll. H. Spalding (P5-736-68)	–	OR881959
Lineage 3 *Gloiocladia* J.Agardh sp.	ARS03705	N/A	Kaumalapau Harbor, Lāna'i intertidal, 26 March 2008, coll. A. Kurihara	HQ422982.1	OR881950

Japan, and the species can be found worldwide in the Atlantic, Pacific, and Indian Oceans (Guiry & Guiry 2023). Although depth data are limited, records suggest the presence of collections from shallow reefs at 1-5 m worldwide. Recent collections from Hawaiian mesophotic reefs present an opportunity to more fully characterize the diversity of this genus across an expanded range of depths in Hawai'i, and explore the possibility of novel and cryptic diversity.

Exploration of MCEs has intensified in recent years, resulting in the discovery and description of numerous new species and genera in Hawai'i (e.g., Paiano *et al.* 2020; Sherwood *et al.* 2020a, b; Cabrera *et al.* 2022; Alvarado *et al.* 2022). These novel taxa have been shown to contribute to unique and diverse algal assemblages in MCEs and exhibit a high degree of endemism. Recent research has also expanded the known native range of some species (Sherwood & Guiry 2023). In this study, molecular and morphological characterization of *Gloiocladia* specimens from Hawaiian MCEs was conducted to investigate the cryptic diversity and distribution of the genus in Hawai'i.

MATERIAL AND METHODS

Extensive surveys of Hawaiian MCEs have been conducted since 2006, and the algal specimens characterized in this study were collected from the Papahānaumokuākea Marine National Monument (PMNM) and the Main Hawaiian Islands by technical diving or submersibles (Table 1; Fig. 1). Specimens were preserved in silica gel and/or pressed as herbarium vouchers. Specimens resembling *Gloiocladia* were selected for further characterization. Small pieces of tissue of *G. iyoensis* specimens collected from 1936-1956 were also sent from the personal collection of Dr. Segawa Japan (type locality) to attempt to establish a molecular type concept for this species.

DNA was extracted using the Nucleospin® Plant II Kit (Macherey-Nagel GmbH & Co., Düren, Germany) or a cetyltrimethylammonium bromide (CTAB) protocol (Doyle & Doyle 1987) with overnight lysis steps and Qiagen (Valencia, California, United States) purification spin columns for washing and elution. The mitochondrial cytochrome oxidase subunit I (COI) barcode marker was amplified following the protocols outlined in Saunders & Moore (2013) and Saunders (2005). The plastidial ribulose-1.5-bisphosphate carboxylase/oxygenase large subunit (*rbc*L) marker was amplified following Saunders & Moore (2013), Gavio & Fredericq (2005) or Freshwater & Rueness (1994). PCR products were submitted for sequencing by Azenta (South Plainfield, NJ, United States). Raw sequence data were edited in Geneious Prime 2019.1.3 (http:// www.geneious.com) and aligned using the MUSCLE v. 3.8.425 plug-in (Edgar 2004), along with available sequences for *Gloiocladia* and related genera from NCBI GenBank (Table 3), following Filloramo & Saunders (2018). Sequences of *Fryeella gardneri* (Setchell) Kylin were used as an outgroup for both alignments. The COI and *rbc*L alignments were concatenated with partitioning of COI from bp 1-663,

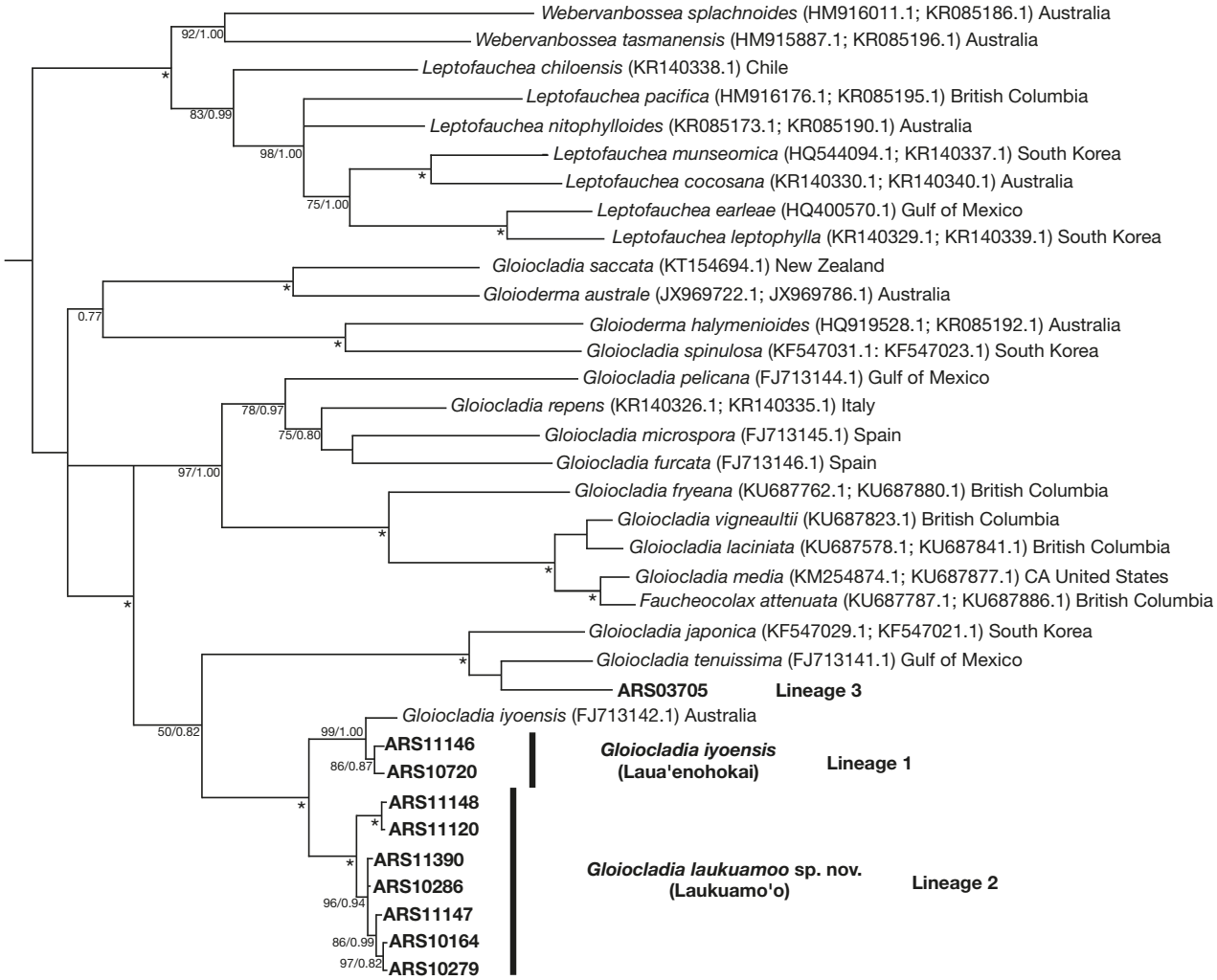

FIG. 2. — Phylogenetic tree inferred in RAxML and MrBayes from the analysis of concatenated COI-*rbc*L sequences from Hawaiian *Gloiocladia* J.Agardh specimens and other representatives of the family Faucheaceae. The topology of the shown tree is represented by the Bayesian Inference. A member of the Gigartinaceae (*Fryeella gardneri* (Setchell) Kylin was used as the outgroup, which was pruned to facilitate presentation. Sequences from this study are indicated in **bold**. The numbers next to tree nodes indicate maximum likelihood bootstrap values and Bayesian posterior probability support values. Full support (100/1.00) is indicated with an asterisk (*). Support values smaller than 50 or 0.5 are not shown.

and *rbc*L from bp 664-2026. ML analysis and Bayesian Inference (BI) were performed on Geneious Prime 2020.2.3 (http://www.geneious.com). For ML, GTR GAMMA I was used as the evolutionary model with 1 000 bootstrap replicates using RAxML plug-in v.8.2.11 (Stamatakis 2014). For BI, the MrBayes plug-in v.3.2.7 (Huelsenbeck & Ronquist 2001) was used with four chains of Metropolis-coupled Markov Chain Monte Carlo (MCMC) for 1 000 000 generations, sampling every 500 generations, burn-in of 100 000 generations, and GTR as the substitution model.

Specimens were photographed in the Joseph F. Rock Herbarium (HAW) with a Canon EOS 5D Mark II Digital Camera (Tokyo, Japan) in an MK Direct Photo-eBox PLUS 1419. Microscope slides for light microscopy were prepared by hydrating specimens in water for 30-60 min and cross-sectioning with a razor blade under a dissecting scope. Samples were stained with 0.5% aniline blue for 5 min, washed, and mounted in 30-50% Karo™. Photomicrographs were taken on a Zeiss AxioImager A1 compound light microscope (Pleasanton, CA) with an Infinity2-1RC digital camera (Lumenera Corporation, Ottawa, Ontario, Canada) to observe the thallus structure and other morphological and anatomical features.

ABBREVIATIONS

Institutional Abbreviations

BISH Bishop Museum's *Herbarium Pacificum*, Honolulu;
NCBI National Center for Biotechnology Information, Bethesda;
PMNM Papahānaumokuākea Marine National Monument; northwestern Hawaiian archipelago.

Other Abbreviations

bp base pair;
COI Cytochrome C Oxidase Subunit I;

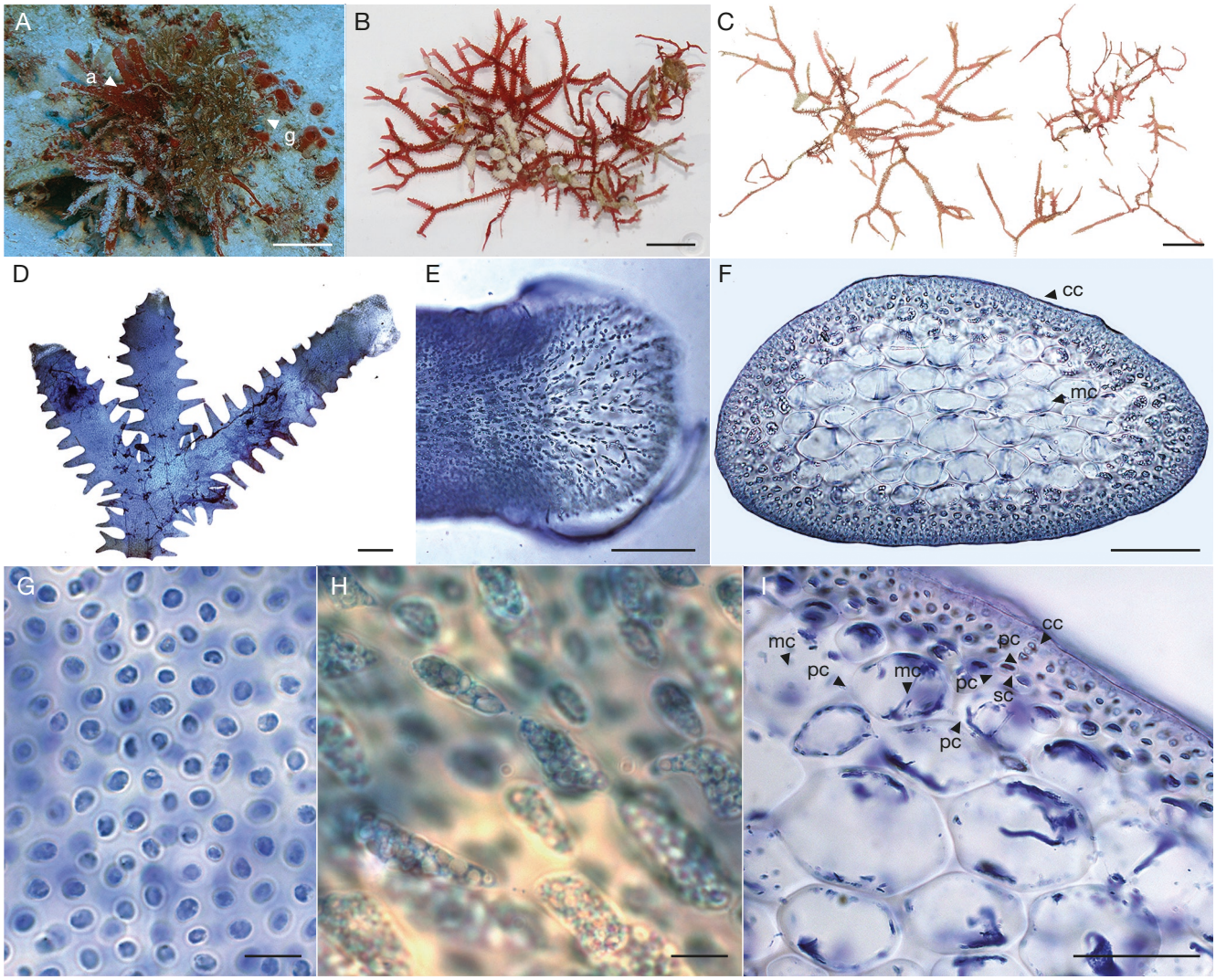

FIG. 3. — Vegetative morphology of *Gloiocladia laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov: **A**, *in situ* photograph of the holotype collection (BISH 789091, ARS 10279). Dark red plant is a species of Amansia (**A**), and *Gloiocladia laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. (**G**) is the yellowish-brown epiphyte; **B**, hydrated holotype collection (BISH 789091, ARS 10279); **C**, pressed specimens of holotype (BISH 789091, ARS 10279); **D**, branched blade with pinnate sawtooth branchlets along the blade margins. Some sawtooth branchlets developing dichotomous apices. (BISH 789095, ARS 11147); **E**, apical region of the plant, showing cortical filaments and gelatinous layer around the apex (BISH 789095, ARS 11147); **F**, cross section of thallus showing medullary (**mc**) and cortical cells (**cc**) (BISH 789091, ARS 10279); **G**, surface view of cortical cells (BISH 789091, ARS 10279); **H**, top-down microscopy of subcortical cells forming lateral secondary pit connections (BISH 789091, ARS 10279); **I**, cross section of *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. showing (**mc**), subcortical (**sc**), and (**cc**) cells connected via pit connections (**pc**) (BISH 789091, ARS 10279). Scale bars: A, 20 mm; B, C, 10 mm; D, 500 µm; E, I, 50 µm; F, 100 µm; G, H, 10 µm. Photo credits: all microscopy images and pressed specimens, K. R. Allsopp; The *in situ* and live specimen images, L. Spalding, Taylor M. Williams, Randall K. Kosaki, Jason Leonard & Brian Hauk.

CTAB	Cetyltrimethylammonium bromide;
DRRH	Deep Reef Refugia Hypothesis;
MCE	Mesophotic Coral Ecosystem;
MCMC	Markov Chain Monte Carlo;
MHI	Main Hawaiian Islands;
ML	Maximum Likelihood;
NHCWG/CWG	Native Hawaiian Cultural Working Group;
*rbc*L	ribulose-1.5-bisphosphate carboxylase.

RESULTS

Of three Japanese *Gloiocladia iyoensis* specimens, only one was successfully sequenced. We were able to generate an *rbc*L sequence; however, the sequence BLASTed at 94% similarity to the gigartinalean species *Cubiculosporum koronicarpis* Kraft (KC174802), and 99% to *Cubiculosporum* sp. (KC174803), which were both collected from Taiwan. Thus, we were not able to confidently generate a topotype sequence for *G. iyoensis*, and current sequences labeled as this species in GenBank must be considered provisionally identified.

Phylogenetic analysis of Hawaiian *Gloiocladia* specimens resolved three Hawaiian lineages, which included one previously reported species (*G. iyoensis*) and two undescribed species (Fig. 2). The COI-*rbc*L concatenated analysis yielded relatively small divergences among lineages; the divergence between some *Gloiocladia* species was as low as 1.1% (e.g.,

G. vigneaultii Filloramo & G.W.Saunders and *G. laciniata* (J.Agardh) N.Sánchez & Rodríguez-Prieto). Lineage 1 was composed of two sequences from Hawaiian MCE specimens (ARS11146 and ARS10720) and an Australian *G. iyoensis* sequence from GenBank. Based on morphological similarity to the published description of *G. iyoensis* (i.e., Norris 1991; Abbott 1999), this lineage may correspond to that species, but this identification will remain unconfirmed until comparison with type material can be accomplished. The remaining Hawaiian MCE specimens were resolved as Lineage 2, which was sister to *G. iyoensis* (with full support), and was 2.2-3.3% divergent from *G. iyoensis*. Lastly, a COI sequence in NCBI GenBank listed as *G. iyoensis* (HQ422982, Sherwood *et al.* 2010) was shown to represent a distinct species in the phylogenetic tree (Lineage 3). This lineage currently consists of a single specimen positioned in a broader clade with *G. japonica* (Okamura) Yoshida and *G. tenuissima* Gavio & Fredericq (Fig. 2).

Based on the phylogenetic analyses (Fig. 2) and morphological comparisons of gross vegetative features presented below (Table 2), we confirm the presence of one previously reported species (Lineage 1, *G. iyoensis*), formally propose the description of one new species (Lineage 2), and note one additional species (Lineage 3) to be described at a later date once additional material is collected and characterized.

Family Faucheaceae Strachan, G.W.Saunders & Kraft
Genus *Gloiocladia* J.Agardh

Gloiocladia laukuamoo K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov.
(Fig. 3A-I)

Type material. — **Hawai'i** • Kapou (Lisianski), Papahānaumokuākea Marine National Monument; 26°2'13"N, 173°47'31"W; 59 m a.s.l.; 14.IX.2014; collected by J. Leonard (NWHI-246); BISH 789091 (ARS 10279); GenBank accessions OR881954 (*rbc*L) and OR881946 (COI).

Etymology. — Laukuamo'o (noun in apposition, and hence non-declinable) is derived from multiple Hawaiian nouns. The name was developed using traditional Hawaiian naming practices in collaboration with the Nomenclature Subcommittee of the Papahānaumokuākea Native Hawaiian Cultural Working Group (CWG) (Appendix 1). "Lau" refers to a leaf or blade of a plant and can also refer to multiplicity. "Kua" refers to the back or the shape of a human spine, while "mo'o" refers to the mourning gecko species found in Hawai'i (*Lepidodactylus lugubris* Duméril & Bibron), which exhibits a similar sawtooth-like pattern on its back. By connecting all three terms, the name accentuates the intertwined sawtooth-like body plan and the biogeography of the species found in the "geological backbone" of the Hawaiian Archipelago, the Northwestern Hawaiian Islands or Papahānaumokuākea Marine National Monument.

Material examined. — BISH 789092 (ARS 10164), BISH 789093 (ARS 10286), BISH 789094 (ARS 11120), BISH 789095 (ARS 11147), BISH 789096 (ARS 11148), BISH 789097 (ARS 11390).

Substrate/host. — Small pebbles (epilithic), or other larger macroalgae such as *Amansia* sp. (epiphytic).

Habit and vegetative morphology. — Thalli are thin and elongated, oval in cross section, rounded at tips and exhibiting a distinctive construction of the blades with sawtooth-like branchlets, although a few specimens lack branchlets. Plants prostrate, and can be epiphytic on other macroalgae such as *Amansia*, by entangling their sawtooth-like branchlets with host thalli. Plants appear brown-yellow in situ when compared to *Amansia* (Fig. 3A). The alga exhibits a deep wine-red color when living (Fig. 3B). Generally, thalli are irregularly-dichotomously branched. A single branch can extend up to 20 mm in length and 4 mm in width, including branchlets (Fig. 3C). Sawtooth-like branchlets are positioned *c.* 300 µm apart and can extend into full branches (Fig. 3D). A gelatinous layer surrounds the outermost cortical layer of apices (Fig. 3E). Blades are up to 350 µm thick in cross section, and are composed of multiple layers of small, densely packed cortical cells, and larger medullary cells (Fig. 3F). Outer cortical cells are loosely arranged, 5 µm in diameter and visible from the surface (Fig. 3G). Laterally arranged subcortical cells connected via secondary pit connections (Fig. 3H). Tightly arranged medullary cells have dimensions of 40-80 × 30-50 µm in cross section (Fig. 3I). Primary pit connections can be observed between individual medullary cells, subcortical cells, and cortical cells (Fig. 3I). No reproductive features were observed.

Distribution. — Exclusive to MCE depths of 55-104 m throughout the Hawaiian Islands, including Kapou (Lisianski), Manawai (Pearl and Hermes), Lalo (French Frigate Shoals), and Maui.

Description

Plants epiphytic on other algae or lithophytic on rubble via rhizoidal attachment or entanglement. Thallus decumbent, up to 60 mm long. Stipes appear oval to circular in cross section, holdfasts not present in collected specimens. Plants irregularly dichotomously branched, deep wine red when alive, and pale pink when dried. Vegetative axes are narrow, up to 2 mm wide excluding sawtooth branchlets, with branchlets extending up to an additional 2 mm on either side of the axis. Branchlets can extend in opposite or alternating distichous patterns. Axes are flattened except in basal regions, 300-400 µm thick, and covered in a gelatinous layer that is seemingly thin and delicate at apices to allow the cell division of loosely-arranged cortical cells. Thallus multiaxial with 1-3 layers of loosely arranged rounded outer cortical cells, 5 µm in diameter from the surface view of the thallus. No lateral secondary pit connections observed between cortical filaments. Subcortical cells appear elongated and triangular, up to 16 × 9 µm in cross section, connected via primary pit connections to the medullary and cortical cells. Laterally arranged subcortical cells connected via secondary pit connections, forming a network. Medulla cellular and compact, consisting of large hyaline cells that decrease in size toward the cortex. Medullary cells forming 5-9 layers, axially elongated, ranging in size up to 80 × 50 µm in cross-section, forming frequent pit connections to adjacent medullary cells. Gametophytic and tetrasporic reproductive structures not observed.

Gloiocladia iyoensis (Okamura) R.E.Norris
(Fig. 4A-H)

Homotypic synonym: *Gloioderma iyoense* Okamura.

TABLE 2. — Comparison of general vegetative morphology of Hawaiian species and related representatives of *Gloiocladia* J.Agardh.

Taxon	Thallus/ Branching pattern	Medullary cell description	Cortical cell description	Reference
Gloiocladia fryeana (Setchell) N.Sánchez & Rodríguez-Prieto	73 mm tall, 10 mm wide, irregularly dichotomously branching	1-3 layers, 80-150 × 70-110 µm in cross section	3-4 layers, 10 µm in diameter each	Filloramo & Saunders (2018)
G. furcata (C.Agardh) J.Agardh	85 mm tall, 50 mm wide, rounded sub-dichotomous branches	1-3 layers, 40-720 × 20-268 µm in cross section	3-5 layers, 10 µm in diameter each	Sánchez & Rodríguez-Prieto (2005)
G. iyoensis (Okamura) R.E.Norris	20 mm tall, 4 mm wide, flattened lobes, irregular pinnation	4-6 layers, 60-100 × 40-50 µm in cross section	3-5 layers, 4 µm in diameter each	This study (Fig. 4), Abbott (1999)
G. japonica (Okamura) Yoshida	60 mm tall, 10 mm wide, lobed or laciniate thallus, dichotomous pinnate, irregular branching	N/A	N/A	Yoshida (1997)
G. laciniata (J.Agardh) N.Sánchez & Rodríguez-Prieto	180 mm tall, 10 mm wide, irregularly dichotomously branching	2-3 layers, 80-200 × 90-124 µm in cross section	3-4 layers, 3 µm in diameter each	Filloramo & Saunders (2018)
G. laukuamoo K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov.	60 mm tall, 1 mm wide, irregular dichotomous branching, with opposite or alternating distichous branchlets	6-8 layers, each 40-70 × 30-50 µm in cross section	1-3 layers, 5 µm in diameter each	This study (Fig. 3)
G. media (Kylin) Filloramo & G.W.Saunders	30 mm tall, 5 mm wide irregularly dichotomously branching	2-3 layers, 130-270 × 80-130 µm in cross section	3-4 layers, 5 µm in diameter each	Filloramo & Saunders (2018)
G. microspora (Rodríguez & Femenías) Berecibar, M.J.Wynne, I.Bárbara & R.Santos	120 mm tall, compressed irregularly dichotomously branching	4-5 layers, 30-416 × 13-300 µm in cross section	3-6 layers, 8 µm in diameter each	Sánchez *et al.* (2010)
G. pelicana Gavio & Fredericq	140 mm tall, 1 cm wide, irregular to dichotomous branching lobes	1 layer, 135-220 × 200-245 µm in cross section	3-4 layers, 10 µm in diameter each	Gavio & Fredericq (2005)
G. repens (C.Agardh) N.Sánchez & Rodríguez-Prieto	250 mm tall, 6 mm wide, irregularly dichotomously branching	5-7 layers, 20-500 × 14-192 µm in cross section	5-7 layers, 5 µm in diameter each	Rodríguez-Prieto *et al.* (2007)
G. rubrispora (Searles) R.E. Norris	25 mm tall, 1 mm wide. Radial branching thalli and branchlets.	N/A	4 layers, 2-5 µm in diameter each	Searles (1984)
G. tenuissima Gavio & Fredericq	40 mm tall, 0.5 mm wide, slender terete branches, irregular	4-5 layers, 10-30 µm diameter in cross section	3-4 layers, 3-6 × 8-13 µm each	Gavio & Fredericq (2005)
G. vigeaultii Filloramo & G.W.Saunders	75 mm tall, 18 mm wide, irregularly dichotomously branching	2-3 layers, 130-300 × 70-200 µm in cross section	6-8 layers, 1-8 µm in diameter each, gradually decreasing in size	Filloramo & Saunders (2018)

ETYMOLOGY. — Laua'enohokai was established by the CWG as the Hawaiian name of this species. Laua'e refers to one of the most common ferns found in Hawai'i, *Microsorium scolopendria* (Indigenous to Australia). Nohokai, meaning sea dweller, was added to signify the ocean-land connection of the two counterparts (refer to Appendix 1 for more details of the naming process).

MATERIAL EXAMINED. — BISH 789098 (ARS 10720), BISH 789099 (ARS 11146).

HABIT AND MORPHOLOGY OF HAWAIIAN SPECIMENS. — Live specimens exhibit a variety of morphologies and are characterized by a pale pink color (Fig. 4A). The color of preserved specimens ranges from pale-red to pink and thalli can vary in shape from fan-like blades to extended branches (Fig. 4B). Flattened thalli have small sawtooth branchlets, *c.* 200 µm long, along the edge (possibly due to the incomplete growth of specimens). Branchlets spaced 100-200 µm apart (Fig. 4C). Blades are up to 150 µm thick in cross section (Fig. 4D). Cortical cells are loosely arranged, 4 µm in diameter (Fig. 4E). Subcortical cells are laterally connected via secondary pit connections (Fig. 4F). Medullary, subcortical, and cortical cells are connected via pit connections (Fig. 4G). Medullary cells, 4-6 layers in cross section, are up to 100 µm in diameter. Cortical cells in 3-4 layers are connected via pit connections, extending from elongated subcortical cells, 5 × 20 µm in size (Fig. 4H). Trichogynes observed protruding out of the thallus (Fig. 4I). Other reproductive features not observed.

DISTRIBUTION. — Two new records from MCE depths; 61 m depth from Middle Bank and 63 m depth from Lalo (French Frigate Shoals). Previous records suggested the species is present throughout the intertidal and subtidal ranges (>7 m depths) throughout the Hawaiian Islands, with only one previous collection from MCE depths (66 m depth) collected by dredging.

DISCUSSION

The description of *Gloiocladia laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. (a novel species exclusively known from MCEs) further demonstrates that Hawaiian MCEs host many unique species that do not thrive on shallow

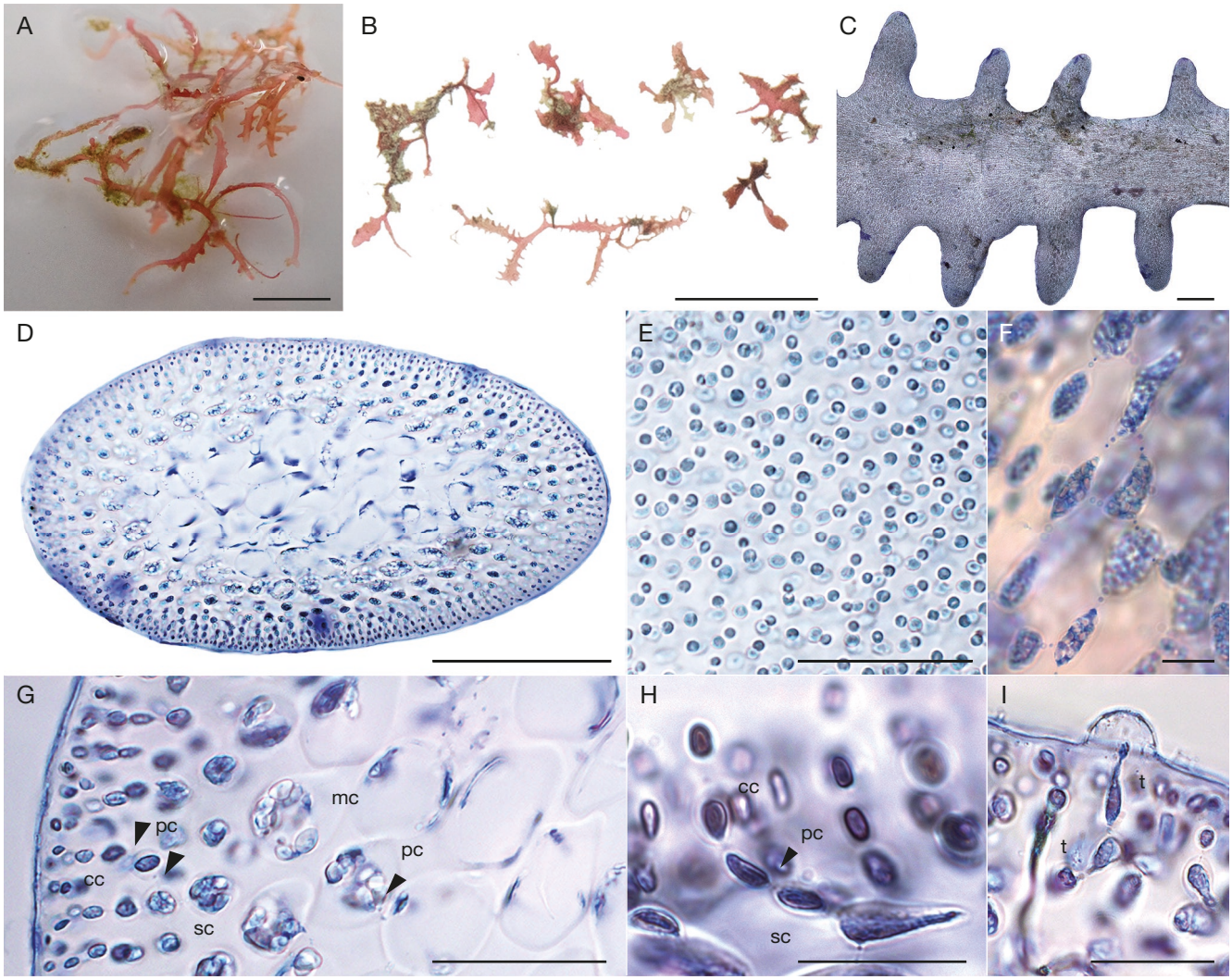

FIG. 4. — Morphology of Hawaiian mesophotic specimens of *Gloiocladia iyoensis* (Okamura) R.E.Norris: **A**, live specimens (BISH 789098, ARS 10720), showing natural coloration under laboratory light; **B**, pressed specimens (BISH 789098, ARS 10720); **C**, surface view of specimen (BISH 789099, ARS 11146) showing a blade with pinnate marginal sawtooth branchlets; **D**, cross section of medial part of plant body showing the layers of the medulla and cortex (BISH 789099, ARS 11146); **E**, surface view of cortical cells (BISH 789099, ARS 11146); **F**, top-down microscopy of subcortical cells forming lateral secondary pit connections (BISH 789098, ARS 10720); **G**, cross section showing medullary (**mc**), subcortical (**sc**), and cortical cells (**cc**) connected with pit connections (**pc**) (BISH 789099, ARS 11146); **H**, cross section showing pit connections (**pc**) between (**sc**) and (**cc**) (BISH 789099, ARS 11146); **I**, a cross section showing trichogynes (**t**) protruding out of the thallus from carpogonium (BISH 789099, ARS 11146). Scale bars: A, 5 mm; B, 10 mm; C, D, 100 µm; E, G, 50 µm; F, 10 µm; H, I, 25 µm. Photo credits: all microscopy images and pressed specimens, K. R. Allsopp; The *in situ* and live specimen images, L. Spalding, Taylor M. Williams, Randall K. Kosaki, Jason Leonard & Brian Hauk.

reefs (Paiano *et al.* 2020; Sherwood *et al.* 2020a, b; Cabrera *et al.* 2021, 2022; Alvarado *et al.* 2022). The species of *Gloiocladia* characterized in this study (*G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. and *G. iyoensis*) were collected from the mesophotic reefs throughout the Hawaiian Archipelago, from Maui to Manawai; moreover, collection records suggest that *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. has not been observed on reefs shallower than 55 m, and can inhabit locations as deep as 104 m. Previous records also suggest the presence of *G. iyoensis* throughout the Archipelago, from Hawai'i to Manawai (Abbott 1999). Thus, these two sister species have similar geographical distributions in Hawai'i. Although the depth distributions of *G. iyoensis* and *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. partially overlap (between 55-63 m depths), collections thus far suggest a habitat-related lineage divergence and that *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. is exclusive to MCEs (and is possibly endemic to the Hawaiian Islands). Additionally, an analysis of biogeographical distribution (horizontal and vertical distribution) of all previous records as well as the newly characterized specimens from this study showed that the two species are not present in the same habitats (Fig. 1). Future metagenomic studies may also allow study of these distribution and niche differentiation predictions. Environmental DNA assessments can be used to characterize MCE community structure and may allow determination of whether the two species of *Gloiocladia* ever coincide.

TABLE 3. — GenBank accessions for sequences used in phylogenetic analyses.

Name	*rbc*L	COI
Gloiocladia fryeana (Setchell) N.Sánchez & Rodríguez-Prieto GWS028557 BC	KU687880.1	KU687762.1
Gloiocladia japonica (Okamura) T.Yoshida G718 South Korea	KF547021.1	KF547029.1
Gloiocladia laciniata (J.Agardh) N.Sánchez & Rodríguez-Prieto GWS028075 BC	KU687841.1	KU687578.1
Gloiocladia media (Kylin) Filloramo & G.W.Saunders GWS021443 CA United States	KU687877.1	KM254874.1
Gloiocladia repens (C.Agardh) N.Sánchez & Rodríguez-Prieto GWS001639 Italy	KR140335.1	KR140326.1
Gloiocladia spinulosa (Okamura & Segawa) N.Sánchez & C.Rodríguez-Prieto G695 South Korea	KF547023.1	KF547031.1
Gloiocladia vigneaultii Filloramo & G.W.Saunders GWS004638 BC	KU687823.1	–
Gloioderma australe (Fr.) Pat. G0306 Australia	JX969786.1	JX969722.1
Faucheocolax attenuatus Setchell GWS001423 BC	KU687886.1	KU687787.1
Gloioderma halymenioides (Harvey) J.Agardh GWS000469 Australia	KY682904.1	HQ919528.1
Leptofauchea cocosana Filloramo & G.W.Saunders GWS037755 Australia	KR140340.1	KR140330.1
Leptofauchea nitophylloides (J.Agardh) Kylin GWS032631 Australia	KR085190.1	KR085173.1
Leptofauchea pacifica E.Y.Dawson GWS010140 BC	KR085195.1	HM916176.1
Webervanbossea sp. 1 *tasmanensis* Womersley GWS000922 Australia	KR085196.1	HM915887.1
Webervanbossea splachnoides (Harvey) G.De Toni GWS002435 Australia	KR085186.1	HM916011.1
Gloiocladia furcata (C.Agardh) J.Agardh Gfur Spain	FJ713146.1	–
Gloiocladia microspora (Rodríguez y Femenías) Berecibar, M.J.Wynne, I.Bárbara & R.Santos Gmicro2b Spain	FJ713145.1	–
Gloiocladia pelicana Gavio & Fredericq Gpeli2GF2005 GoM	FJ713144.1	–
Gloiocladia saccata (J.Agardh) R.E.Norris WES91 New Zealand	KT154694.1	–
Gloiocladia tenuissima Gavio & Fredericq GtenGF2005 GoM	FJ713141.1	–
Gloiocladia iyoensis (Okamura) R.E.Norris GiyoGF2005 Australia	FJ713142.1	–
Leptofauchea chiloensis Dalen & G.W.Saunders GWS000503 Chile	KR140338.1	–
Leptofauchea earleae Gavio & Fredericq LAF-26-5-00-1-1 GoM	HQ400570.1	–
Leptofauchea leptophylla (Segawa) Mas.Suzuki *et al.* GWS018362 South Korea	KR140339.1	KR140329.1
Leptofauchea munseomica Filloramo & G.W.Saunders GWS018532 South Korea	KR140337.1	HQ544094.1
Fryeella gardneri (Setchell) Kylin British GWS001131 Columbia	JX969776.1	JX969692.1

Species of *Gloiocladia* from other regions have also been collected from the MCE depths; *G. blomquistii* (Searles) R.E. Norris has been identified from reefs as deep as 39 m, *G. atlanticum* Searles from 40 m depth, and *G. blomquistii* (Searles) R.E. Norris from 45 m depth, based on public databases (e.g. https://www.macroalgae.org). However, collection depths are not always reported. Lack of sampling and broad-scale biodiversity assessments contribute largely to the inaccurate or incomplete representation of the natural habitat range and distribution of taxa. From published reports, there are several species of *Gloiocladia*/*Gloioderma* found in the MCEs in other parts of the world. Notably, historical records of *G. repens* (C.Agardh) N.Sánchez & Rodríguez-Prieto and *G. microspora* (Rodríguez y Femenías) Berecibar, M.J.Wynne, I.Bárbara & R.Santos suggest the adaptability of the genus in deep-water up to 120 m depth (e.g. Rodríguez-Prieto *et al.* 2007; Sánchez *et al.* 2010).

Gloiocladia laukuamoo sp. nov. can be distinguished from related species by its long, sawtooth-like axes that exhibit irregular dichotomous branching (Table 2). Other representatives of

the genus and the family tend to exhibit more regular dichotomous branching of flat, wide blades, with many projected cystocarps and/or branchlets, and only a few grow into spindly thalli. Based on the gross morphology, the two sister species (*G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. and *G. iyoensis*) are difficult to distinguish, except that *G. laukuamoo* sp. nov. displays more spindly thalli compared to the flatter and wider blades of *G. iyoensis,* based on our mesophotic specimens; though this could be dependent on each individual plant and its growth (Figs 3B; 4A). Additionally, the two species can be distinguished based on the relative sizes and number of layers of medullary and cortical cells (Table 2). *Gloiocladia rubrispora* (Searles) R.E.Norris exhibits similar gross morphology to *G. iyoensis* and *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. Although a molecular species concept is lacking for this species, morphological analyses suggest that the species can be distinguished by the pattern of branching; *G. rubrispora* branches radially while *G. iyoensis* and *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. branch complanately (Searles 1984). Until further phylogenetic analyses are performed to evaluate the synonymy of the taxa, these three species (*G. iyoensis*, *G. rubrispora*, and *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov.) should be recognized as distinct, further supporting the cryptic diversity within the genus and Rhodymeniales.

The phenomenon of highly similar gross morphology yet distinct genetic sequences with shared ancestry in algal taxa has been recognized before (e.g., Geoffroy *et al.* 2012; Saunders & Virginia Lehmkuhl 2005; Saunders 2008). However, there has not been any record of cryptic diversity and prominent correlation between shallow and deep-water species of the same geographical distribution in red algae. Phylogeographically, a single algal species can consist of multiple genetic lineages with high percent divergence. For instance, *Asparagopsis taxiformis* (Delile) Trevisan in Hawai'i consists of three distinct lineages (based on *cox*2-3 spacer and COI markers) with up to 5.3% divergence for COI, while still being considered a single species (Sherwood 2008). In the present study, Hawaiian *G. iyoensis* specimens from MCEs demonstrated 0.7-1.4% divergence in *rbc*L from the Australian sequence (FJ713142). This could be attributed to limited sample size or phylogeographic variation within the species. The new *Gloiocladia* species reported here from Hawaiian MCEs also support the biogeographical connection of algal assemblages between Hawai'i and the northwestern Pacific and Australia, as previously explored (Paiano *et al.* 2020; Sherwood *et al.* 2020a; Cabrera *et al.* 2022; Alvarado *et al.* 2022).

Based on our phylogenetic tree and morphological analyses, *Gloiocladia laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. is most closely related to *G. iyoensis*, which both thrive on Hawaiian reefs but at different depth ranges (Fig. 2). In such a three-dimensional and diverse habitat as the ocean, restriction of gene flow is still prevalent (Lessios *et al.* 2001). Moreover, ecological segregation of populations relative to their depth range has been observed as a key driver of lineage differentiation in benthic communities (Prada & Hellberg 2013). The depth differences between MCEs and shallow-water reefs may restrict gene flow, and immobile organisms such as macroalgae may evolve into distinct lineages over time. A lack of any motile life stage and limited dispersal, such as for the red algae, can directly influence the likelihood of dispersal of genetic material (Engel *et al.* 1999).

The proposal of the Deep Reef Refugia Hypothesis (or DRRH) led to exploration of population-level connectivity of shallow and mesophotic reef communities to infer whether MCEs could serve as a refuge for shallow species (Bongaerts *et al.* 2010). Sherwood *et al.* (2020b) evaluated the distributional overlap between shallow water and MCEs with specimens of another cryptic red algal genus (*Martensia*) in Hawai'i, and found five distinct lineages (i.e., species) with corresponding depth ranges and some distributional overlap at 65 m depth. While some depth-generalist or motile taxa, such as corals (Studivan & Voss 2018) and damselfish (Tenggardjaja *et al.* 2014), can be found at both shallow depths and MCEs, numerous studies have also demonstrated genetic differentiation between the two habitats and the highest level of community turnover (e.g. Bongaerts *et al.* 2017; Stefanoudis *et al.* 2019); thus support for the DRRH has been mixed at best. Our results and previous studies in the Hawaiian MCEs tend to present distinct algal assemblages and biodiversity between MCEs and shallow water ecosystems in Hawai'i and do not support the hypothesis (e.g., Paiano *et al.* 2020; Sherwood *et al.* 2020a, b; Cabrera *et al.* 2022; Alvarado *et al.* 2022).

The sister species of *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov., *G. iyoensis*, was originally described as *Gloioderma iyoense* Okamura. The primary distinction between the genera *Gloiocladia* and *Gloioderma* was the presence of *Tela arachnoidea* in the cystocarp (Norris 1991). However, these features have not been recognized in all *Gloiocladia* and *Gloioderma* species, and the phylogenetic relationships among the two genera are ambiguous; both previous and present representatives of *Gloioderma* were often placed closer to *Gloiocladia* representatives than other representatives of the same genus depending on which markers were used (e.g., Nelson & Dalen 2016; Sánchez & Rodríguez-Prieto 2005; Le Gall *et al.* 2008). Furthermore, the transfer of multiple representatives of the family Faucheaceae to *Gloiocladia* based on morphological and/or genetic comparisons was supported by other studies (Norris 1991; Rodríguez-Prieto *et al.* 2007). Although some studies employing phylogenetic analyses of the LSU, 18S, and EF2 markers (with very limited sample sizes) supported the distinction of the two genera and reinstatement of *Gloioderma* (Rodríguez-Prieto *et al.* 2007; Le Gall *et al.* 2008; Lozada-Troche *et al.* 2010), our phylogenetic analyses and other studies (Le Gall *et al.* 2008; Sánchez *et al.* 2010; Dalen & Saunders 2007) supported the synonymy of all representatives of *Gloioderma* and *Gloiocladia* based on *rbc*L, COI, and LSU markers, when performed with larger sample size. These studies resulted in the establishment of many homotypic synonyms of *Gloiocladia*/*Gloioderma* species,

creating further taxonomic confusion. Because our Hawaiian specimens did not exhibit any cystocarpic features, we were unable to investigate this in further detail. With the ambiguity of the two genera in our analyses and taxonomic priority and relevance of *Gloiocladia*, we described *G. laukuamoo* K.R.Allsopp, F.P.Cabrera & A.R.Sherwood, sp. nov. as a new species within *Gloiocladia*, rather than *Gloioderma*. The third lineage revealed by our analyses (Lineage 3) will await formal description until additional material can be examined to determine morphological and anatomical characteristics of this species.

CONCLUSION

In conclusion, this study contributes to the knowledge of the endemic and cryptic diversity of the Hawaiian MCEs and provides additional information about the depth distributions of red algae in the Hawaiian Islands. The endemic status of the species remains inconclusive until further extensive research of the MCEs in the other parts of the Pacific Ocean is conducted. While the taxonomic relationship between *Gloiocladia* and *Gloioderma* also remains inconclusive, the phylogenetic analyses further illuminate the complexities of the genera and illustrate further species diversity to be characterized from this group. The large number of specimens available from expeditions over the past two decades will support additional research on the marine biodiversity of the Hawaiian Archipelago and its mesophotic reefs, and their gradual characterization is leading to recognizing MCEs as hotspots of biodiversity.

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The scientific views and conclusions and any views or opinions expressed herein are those of the authors and do not reflect the opinions of the above organizations.

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APPENDIX

APPENDIX 1. — Hawaiian and scientific names for three Sawtooth (*Glolocladia* J.Agardh) species, available at: https://doi.org/10.5252/cryptogamie-algologie2025v46a5_s1