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Phylogenetic position of *Newhousia* (Dictyotales, Phaeophyceae) and the description of *N. sumayensis* sp. nov. from Guam

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ABSTRACT

The calcified encrusting brown algal genus *Newhousia* is reported from three new archipelagos in the Pacific: (1) Society Islands, French Polynesia; (2) Guam, Mariana Islands; and (3) Vanuatu. *Newhousia* presents a simple morphology consisting of small, rounded, two-layered calcified blades with limited interspecific variability in morphological features. Consequently, resolving cryptic diversity in *Newhousia* requires molecular phylogenetics. Bayesian and maximum likelihood phylogenetic trees, based on the concatenated *cox*1, *cox*3, *psb*A, *rbc*L and 18S rDNA sequences, supported a sister relationship of *Newhousia* with *Lobophora*/*Zonaria* clade. Analyses revealed five distinct evolutionary lineages within *Newhousia*. Genetic variation between the lineage from Guam and the two hitherto known *Newhousia* species, *N. imbricata* from Hawaii and *N. yagha* from Papua New Guinea, warrant the description of one new species, *N. sumayensis* sp. nov. The other two lineages, from the Society Islands and Vanuatu, were identified as geographically distinct populations of *N. imbricata* with limited genetic variation, rather than independent species. In the Society Islands, *N. imbricata* is common between depths of 10 - 20 m as unattached spherical structures or attached to hard substrate. In Guam, *N. sumayensis* sp. nov. grows abundantly in sciophilous habitats at depths of 10 - 21 m. We provide the first documentation of spores for this genus and of structures resembling plurilocular antheridia. Increased sampling throughout the Indo-Pacific region is required to further elucidate the distribution range and patterns of species richness in *Newhousia*.

KEYWORDS

Mariana Islands; Marine Algae; Molecular Phylogeny; New Species; Society Islands; Marine Biodiversity; Endemism

INTRODUCTION

The brown algal genus *Newhousia* (Dictyotales, Phaeophyceae) is characterized by an encrusting habit and calcified thalli. Prior to this study *Newhousia* was only known from Oahu (Hawaiian Islands; (Kraft *et al.* 2004) and Papua New Guinea (Kavieng; Vieira *et al.* 2016) (Fig. 1). Each of these two islands had their own distinct species: *N. imbricata* Kraft, G.W.Saunders, Abbott & Haroun from Oahu and *N. yagha* C.W.Vieira, De Clerck & Payri from Papua New Guinea, respectively. In addition, a paleobotanical study identified *Newhousia* fossils from post-glacial reefs deposits in Tahiti, French Polynesia (10-20 ka; Iryu 2016), and the possible occurrence of *Newhousia* at a depth of 160 m on a submerged seamount off Easter Island was reported by Easton *et al.* (2018). These reports suggest that *Newhousia* has historically been overlooked and may have a much broader biogeographical range. Because of its superficial resemblance with other brown and red encrusting algae in the Pacific (e.g., *Lobophora* and Peyssonneliales species), *Newhousia* probably has a broader distribution in the tropical Pacific as suggested by Vieira *et al.* (2016).

The phylogenetic position of *Newhousia* among the Dictyotales has not been fully resolved. Previous analyses either positioned *Newhousia* as a sister group to *Zonaria* (Kraft *et al.* 2004) or *Lobophora* (Vieira *et al.* 2016). More samples and markers are needed to resolve the phylogenetic position of *Newhousia* within the Dictyotales.

Newhousia specimens were newly reported from three archipelagos in the Pacific Ocean: the Mariana, Society, and Vanuatu Islands. The present study was undertaken with the objectives of (1) reporting new distribution records of *Newhousia* in the Pacific Ocean, (2) examining the morphology and phylogenetic identity of these new records, and (3) resolve their phylogenetic relationships with *Lobophora* and *Zonaria* by sequencing additional markers. The present study

confirms that *Newhousia* is more widespread and speciose in the tropical Pacific by the discovery of one new species, and fully resolves the phylogenetic position of the genus within the Dictyotales.

MATERIAL AND METHODS

Sampling was carried out by scuba diving using a chisel and hammer. Specimens of *Newhousia* were collected from Tahiti, Moorea, Guam, and Hawaii (Table 1; Fig. 1). Voucher specimens were preserved in silica gel and deposited in the herbaria of the University of French Polynesia (UPF), the University of Guam (GUAM), and the Bishop Museum (BISH; Honolulu, Hawaii, USA). In addition, DNA material of a specimen collected from Vanuatu was graciously provided by Gary W. Saunders (University of New Brunswick). The specimen from Vanuatu does not have a voucher specimen.

Morphological analyses

Morphological analyses followed Vieira *et al.* (2016). Photographs of the habit and anatomy were taken using a binocular stereo zoom and light microscopes (Leica MZ6 and Leica D2000; Leica Microsystems, Wetzlar, Germany), and Nikon AZ100 (Nikon, Tokyo, Japan), equipped with Canon EOS 600D and Nikon DS-FI1 digital cameras (Nikon, Tokyo, Japan).

Scanning electron micrographs (SEM) were taken using Hitachi TM3030 (Hitachi Ltd., Tokyo, Japan) and Phenom G2 Pro (Phenom-World, the Netherlands) desktop microscopes at the University of French Polynesia and the University of Guam, to observe calcified anatomical structures. Dried specimens were mounted on aluminum stubs with conductive silver paste, sputter coated with gold-palladium with the eMSCoP SC 500 sputter coater.

DNA extraction, amplification, and sequencing

Genomic DNA was extracted from tissue samples dried in silica gel with the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) and the GenCatch Blood &Tissue Genomic Mini Prep Kit (Epoch Life Science Inc., USA). Sequences were generated from the mitochondrial encoded cytochrome c oxidase subunit I (*cox*1) and III (*cox*3), the chloroplast encoded ribulose-1,5-biphosphate carboxylase large subunit (*rbc*L) and the photosystem II protein D1 (*psb*A) genes, and the nuclear-encoded small subunit 18S rRNA. Detailed amplification protocols with primers used for each marker are provided in Tables S1, S2.

Phylogenetic analyses

Specimen-level maximum likelihood (ML) and Bayesian (BI) phylogenetic trees were generated from a concatenated alignment (5,844 bp) including *cox*1 (679 bp), *cox*3 (712 bp), *psb*A (981 bp), *rbc*L (1,608 bp), and 18S rRNA (1,864 bp) sequences. The five genes sequence data was 67.5% complete for the 17-*Newhousia*-specimen matrix. For the BI analyses, we employed the best-fit model of nucleotide substitution, i.e., GTR + I + G, identified using jModelTest2 (Darriba et al. 2012). Bayesian phylogenetic inference was initiated with a random starting tree and four chains of MCMC iterations and ran simultaneously for 100 million generations, sampled every 1,000 generations. The first 25,000 (25%) trees sampled were discarded as burnin, based on the stationarity of likelihood values as assessed using Tracer version 1.7 (Rambaut *et al.* 2018). A consensus topology and posterior probability values were calculated from the remaining trees. Bayesian phylogenetic analyses were conducted using MrBayes v.3.2.2 (Ronquist and Huelsenbeck 2003). ML phylogenetic trees were reconstructed using the best fit substitution model, identified as the GTR + F + I + G4 nucleotide substitution model, and a SPR branch

swapping algorithm in PhyML v.3.0 (Guindon et al. 2010) submitted online (http://atgc.lirmm.fr/phyml/).

RESULTS

Phylogenetic results

At total of 45 sequences were generated for the five markers *cox*1 (10 sequences), *cox*3 (10), *psb*A (11), *rbc*L (8), and 18S rRNA (6) (Table S3). The BI and ML phylogenies based on the concatenation of *cox*1 + *cox*3 + *psb*A + *rbc*L + 18S rRNA positioned *Newhousia* as the sister group of *Lobophora* and *Zonaria* with full support for both phylogenies (Fig. 2). The rest of the tree is also mostly fully supported and topologically congruent with the phylogeny presented by Vieira *et al.* (2021).

The BI and ML phylogenetic trees congruently placed the *Newhousia* specimens in five distinct lineages with little or no sequence divergence within each lineage (Fig. 2). These fives lineages clustered into two separate clades. The first clade is composed of the Guamanian (*N. sumayensis* sp. nov.) and Papuan (*N. yhaga*) lineages, and the second clade of the French Polynesian, Vanuatuan, and Hawaiian (*N. imbricata*) lineages. Sequence dissimilarity among the five lineages, assessed based on the number of substitutions, ranged between 0.6 to 6.1 % in *cox*1, 1.6 to 7.5 % in *cox*3, 0.2 to 1.9 % in *psb*A, 0.5 to 4.5 % in *rbc*L, and 0.1 to 0.4 % in 18S rRNA (Table 2).

Morphological results

Thalli of the specimens from the Society Islands and Guam consisted of crusts (Figs 3-7, 18-21) composed of small, rounded, two-layered blades with limited variability in morphological

features (Figs 8-15, 22-29) and displaying a radial growth from a central point (Figs 8-10, 21-24), corresponding to the morphological features of the genus *Newhousia*. Variations in anatomical measures were negligible between the specimens from the five archipelagos (Guam, Hawaii, Papua New Guinea, Society, and Vanuatu; Table 3). Presence of randomly scattered sporangia (Figs 8, 16) was observed on specimens from Moorea, 40 to 50 µm in width, and 50 to 65 µm in height (Fig. 17). Structures resembling plurilocular antheridia were observed in one specimen from Guam (voucher GH0015686; Fig. 29).

Species observations and description

Considering the limited variations in anatomical features, species identification in *Newhousia* is based on genetic divergences. Based on the low genetic divergence between the lineages from Hawaii, French Polynesia, and Vanuatu, these lineages are regarded to be geographically distinct populations of the species *N. imbricata*. The lineage from Guam, however, is a genetically distinct species that is most closely related to *N. yhaga* from Papua New Guinea. Accordingly, we propose below the description of one new species of *Newhousia*, and we provide a diagnosis for *N. imbricata* from French Polynesia.

***Newhousia imbricata* Kraft, G.W.Saunders, Abbott & Haroun**
Figs 3-17

MORPHOLOGICAL DETAILS: Thalli forming green crusts (Figs 3-7), 20 cm in diameter and to 5 cm in thickness; either embedded onto hard substrates (Fig. 3), including bedrock or dead corals, or forming free oblate spheroidal structures (Figs 4-7) to 20 cm in diameter and 5 cm in thickness; thalli composed of imbricated rounded blades to 4 mm in diameter (Figs 8-10); blades extend peripherally from a continuous marginal meristem (Figs 9-10), 42.5 to 72.5 µm thick, bilayered (Figs 11-14), cells of the epidermal and hypodermal layers 10 to 20 µm and 32.5 to 52.5 µm thick, respectively; epidermal cells rectilinear in surface view and cross section (Figs 11-15), 4.3 to 10.9 µm in width by 12.8 to 21.5 µm in length; hypodermal cells cuboidal in cross-section and rectilinear in long section (Figs 11-15), 17.5 to 27.5 µm in width by 50 to 60 µm in length; oogonia and antheridia unknown; spores (Figs 16, 17) without stalk cell; randomly

scattered sporangia 40 to 50 µm wide and 50 to 65 µm long were observed on the thallus on specimens from Moorea.

Newhousia sumayensis Schils & C.W.Vieira, sp. nov.

Figs 18-29

DESCRIPTION: Thalli forming mustard brown colored crusts (Figs 18-21) to 6 mm in thickness; thalli composed of imbricated, round blades (Figs 22-24) to 6 mm in diameter; blades extend at their margins from a continuous marginal meristem, 35 to 90 µm thick, bilayered, cells of the epidermal and hypodermal layers 6 to 25 µm and 15 to 65 µm thick, respectively; epidermal cells semi-cuboidal (Figs 25-29), 8 to 15 µm in width by 10 to 20 µm in length; hypodermal cells rectilinear (Figs 25-29), 15 to 25 µm in width by 25 to 42 µm in length; oogonia and sporangia are unknown; presumed plurilocular antheridia were observed buried in an old blade covered by a stack of younger blades (Fig. 29); mitochondrial-encoded *cox*1 (GenBank accession MZ577048 from the Holotype) and *cox*3 (GenBank accession MW585093 from the Holotype) sequences; chloroplast-encoded *rbc*L (GenBank accession MW585104 from the Holotype) and *psb*A (GenBank accession MW585103 from the Holotype) sequences; nuclear-encoded 18S rRNA sequence (GenBank accession MW797066 from the Holotype).

DIAGNOSIS: Differing from other *Newhousia* species and lineages by (1) its distinct mustard brown color underwater and (2) considerable genetic divergences [GH0015686, GH0015687, GH0015689] for each of the five studied markers: *cox*1 5.5-6.1%; *cox*3 (4.7-7.5%); *psb*A (0.9-1.5%); *rbc*L (1.5-3.4%); and 18S rDNA (0.2-0.4%).

ETYMOLOGY: The specific epithet *sumayensis* refers to the type locality of this species, which is close to the historic village of Sumay (Apra Harbor, Guam, Mariana Islands). Prior to World War II, Sumay was a thriving CHamoru fishing village on the southern shores of Apra Harbor, where the holotype was collected.

HOLOTYPE: GH0015686 Gab Gab Reef, Apra Harbor, Guam; coll. T. Schils, 24.xii.2019; deposited in the University of Guam Herbarium (GUAM).

ISOTYPES: GH0015687 and GH0015689; Gab Gab Reef, Apra Harbor, Guam; coll. T. Schils, 24.xii.2019; deposited in the University of Guam Herbarium (GUAM).

PARATYPES: GH0013143 (29.v. 2012), GH0015576 (22.v. 2019), GH0015578 (22.v. 2019) and GH0015595 (22.v. 2019); Western Shoals, Apra Harbor, Guam; coll. T. Schils; deposited in the University of Guam Herbarium (GUAM).

TYPE LOCALITY: 13.443728 N, 144.641062 E; 21.1 m depth; Gab Gab Reef, Apra Harbor, Guam.

GEOGRAPHIC DISTRIBUTION: So far, endemic to Guam in the Mariana Islands.

HABITAT: Large patches of crustose thalli (up to 0.25 m^2 in size) occur in sciophilous habitats of sheltered reefs in Apra Harbor, especially underneath the extensive colonies of plate-and-pillar

coral (*Porites rus* Forskål). Smaller crusts grow on coral rubble (some developing into phaeoliths) and bare reef in low-light environments.

DISCUSSION

In this study we report the occurrence of the calcified encrusting brown algal genus *Newhousia* from three new archipelagos in the Pacific: Guam in the Mariana Islands, the Society Islands in French Polynesia, and Vanuatu (Fig. 1).

Diversity and geography

In the 17 years since its discovery in Hawaii, the enigmatic genus *Newhousia* has now been recorded from five disjunct island areas in the Pacific Ocean (Hawaii, Mariana Islands, Papua New Guinea, Society Islands, and Vanuatu), each between ~2000 to ~8000 km apart. The recent findings of *Newhousia* throughout the Pacific Ocean strongly suggest that the genus is far more widespread in the tropical (Indo-)Pacific.

Each of the five island areas for which *Newhousia* has been reported contains its own unique genetic lineage. While the lineage from Guam represents a distinct species, the specimens from the Hawaiian (Lehua and O'ahu), Society (Moorea and Tahiti), and Vanuatu (Efate) Islands contain little genetic variation based on the markers used in this study, and were therefore considered to be distinct geographical populations of *N. imbricata*. Despite dedicated search efforts in various habitats down to 20 m depth in the Society Islands, *Newhousia* was only found at two high islands (Tahiti and Moorea). *Newhousia* was not found in the atoll of Rangiroa in the Tuamotu Islands (lacking any high volcanic islands), making of the Society Islands the easternmost known limit of *Newhousia* distribution. The current pattern of geographic diversity in *Newhousia* (i.e., one genetic lineage per archipelago) could indicate that the genus is more genetically diverse at an oceanic scale. Increased sampling throughout the Indo-Pacific oceans is

required to better understand the distribution range and patterns of genetic diversity of *Newhousia*.

Phylogeny and evolution

Our molecular analyses resolved the phylogenetic position of *Newhousia* within the Dictyotales. The BI and ML phylogenies fully supported *Newhousia* as a sister group to the *Lobophora*/*Zonaria* clade. The tree was rooted on *Lobophora*/*Newhousia*/*Zonaria* according to Vieira *et al.* (2021). This relationship was also fully supported in the phylogenetic analyses of Vieira *et al.* (2021). With respect to morphology, the placement of *Newhousia* in a sister position to *Lobophora*/*Zonaria* suggests that the encrusting form – characteristic for *Newhousia* and found in one of the sub-clades of *Lobophora* (Vieira *et al.* 2014, Vieira *et al.* 2017) – appeared independently in these two genera (i.e., homoplasy of crustose habits).

The phylogenetic trees revealed five distinct evolutionary lineages, which corresponded to *N. sumayensis* sp. nov., *N. yhaga*, and three geographically distinct populations of *N. imbricata*,. The sister relationship between the Guamanian (*N. sumayensis*) and Papua New Guinean (*N. yhaga*) species was well-supported.

Compared to *Lobophora*, the rather small sequence divergences between *Newhousia* lineages indicate that: (1) these are recent diversification events, and/or (2) diversification rates are considerably lower in *Newhousia*. Because of the relatively young geological ages of the current Hawaiian high islands, 0-5.1 Myr (Price and Clague 2002), and the Society Islands, 0-4.5 Myr (Duncan and McDougall 1976), the *N. imbricata* lineages from these two island groups might represent early stages of speciation. The pattern of genetic divergence is consistent with geographical isolation and limited dispersal (Bittner *et al.* 2010). The limited morphological variability between *Newhousia* lineages suggests that their morphology has remained stable over

time and might reflect the limited genetic variation. In contrast, *Lobophora*, an evolutionary younger group (Vieira *et al.* 2021), is characterized by a large interspecific morphological variation and greater genetic diversity (Vieira *et al.* 2017).

According to Vieira *et al.* (2021), *Newhousia* originated during the lower Cretaceous, 136 Ma [108-164 Ma], within the Central Indo-Pacific where the sister species *N. sumayensis* and *N. yhaga* occur. From the Central Indo-Pacific, the genus extended its distribution range in an eastward direction toward Polynesia. Two dispersal scenarios could explain the presence of *N. imbricata* in both hemispheres: either the ancestral lineage of *N. imbricata* colonized (1) both the northern (Hawaii) and southern (French Polynesia, Vanuatu) Polynesian islands from the Central Indo-Pacific, or (2) sequentially from one Polynesian island group to another hereby crossing hemispheres. While hemisphere-crossing has been well documented in floating algae, capable of long distance dispersal through drifting (e.g., kelp; Bolton 2010), it is less well-known in non-buoyant algae (Van Oppen *et al.* 1993, van Oppen *et al.* 1994).

Ecology

In the Society Islands, *N. imbricata* typically grows among corals, adjacent to crustose coralline algae, and they mutually overgrow each other. *Newhousia imbricata* adopts two habits: (1) a free form, forming spherical sessile structures (phaeoliths), and (2) embedded to hard substrates such as bedrock and dead corals, similarly to crustose calcifying red algae. *Newhousia imbricata* is common from 10 to at least 20 m depth and can cover large surfaces of more than 1 m^2 in its encrusting form or is scattered across the seafloor as phaeoliths. While the deepest samples were collected at a depth of 20 m (in Tahiti), fossil records suggest that *N. imbricata* might or did occur deeper on Pleistocene reefs in Tahiti (Iryu 2016). In Guam, *N. sumayensis* is a common alga in sciophilous environments of sheltered habitats in Apra Harbor, particularly underneath

the extensive coral colonies of the plate-and-pillar coral, *Porites rus*, but also on coral rubble and bare reef substrate. *Newhousia sumayensis* covers large patches on these reefs alongside *Peyssonnelia* spp. and various species of sponges. The alga is abundant in the 5 to 25 m depth range. The studied specimen of *N. imbricata* from Hawaii was collected from Lehua Island at 76 m depth. The discovery of *N. imbricata* at these depths renders the occurrence of *Newhousia* on mesophotic reefs of the Pukao seamount at 160 m depth plausible (Easton *et al.* 2018), but would require morphological or molecular confirmation.

Newhousia shares similar ecological traits with other reef calcifiers, like limestone accretion and cementing substrates together. The role of extant *Newhousia* species as reef calcifiers may be most important between 10 to at least 20 m depth, where it is most common, and possibly in deeper waters (Easton *et al.* 2018). Other ecological roles remain to be investigated.

As a calcifying organism composed of aragonite (ca. 97 % weight) and calcite (ca. 3 %) (Kraft *et al.* 2004), *Newhousia* might also be subject to changes in the oceans' carbonate chemistry (Hofmann and Bischof 2014). As a primarily aragonite calcifier, it could be more prone to the effects of ocean acidification similar to most hermatypic corals (Mollica *et al.* 2018). Other aragonite-depositing algae [e.g., *Peyssonnelia squamaria* (S.G.Gmelin) Decaisne ex J.Agardh], however, have been documented to thrive under lower pH levels induced by CO_2 through increased photosynthesis and growth rates (Yıldız 2018). More research is needed to assess the effects of ocean acidification on *Newhousia*'s calcification and growth rates.

Fossil records

Due to their generally soft-bodied nature, the occurrence of Phaeophyceae as fossils is rare in the geological record and their occurrence in the fossil record is debated (Silberfeld *et al.* 2013).

Fossils are nonetheless crucial for calibrating evolutionary trees. At present reconstructions of genetic timescales for the Phaeophyceae are based on a limited number of fossils (Silberfeld *et al.* 2013). The only two genera of the class Phaeophyceae that exhibit thallus calcification are *Padina* and *Newhousia*. However, *Padina* fossils in the geological record can be underrepresented because of their habit (i.e., erect to recumbent fan-like fronds) and mineralogy (i.e., deposition of aragonite on the thallus surface; (Iryu 2016). Calcification in *Newhousia* (i.e., an encrusting algae with extra- and intra-cellular calcium carbonate deposition) is more favorable for fossilization. *Newhousia* fossils were identified for the first time in post-glacial reef deposits in Tahiti, French Polynesia (Iryu 2016) based on their characteristic morphological features. While these fossils are too young for time calibrations of phaeophyceaen phylogenies, it confirms that the genus is capable of fossilization. Evolutionary studies of Phaeophyceae could, therefore, benefit from future discoveries of older *Newhousia* fossils.

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TABLES

Table 1. Collection information of *Newhousia* specimens from this study and previous publications (Kraft *et al*. 2004, Vieira *et al*. 2015).

Species	Voucher	Locality	Country	Latitude	Longitude	Collector	Depth (m)	Date
N. imbricata	PF766[A]	Vallée Blanche, Tahiti	FP	-17.580627	-149.628601	C. Vieira	20	26 Apr 201
N. imbricata	PF1228[B]	Moorea	FP	-17.47927	-149.85097	C. Vieira	10-13	25 Jun 201
N. imbricata	PF1229[B]	Moorea	FP	-17.47927	-149.85097	C. Vieira	10-13	25 Jun 201
N. imbricata	PF1388[B]	Moorea	FP	-17.47807	-149.84012	M. Zubia	0-2	27 Jun 201
N. imbricata	PF1421[B]	Moorea	FP	-17.47055	-149.77754	C. Vieira	10-12	28 Jun 201
N. sumayensis	GH0013143[C]	Western Shoals, Apra Harbor	Guam	13.452211	144.654282	T. Schils	~10	29 May 20
N. sumayensis	GH0015576[C]	Western Shoals, Apra Harbor	Guam	13.452211	144.654282	T. Schils	10.5	22 May 20
N. sumayensis	GH0015578[C]	Western Shoals, Apra Harbor	Guam	13.452211	144.654282	T. Schils	12.8	22 May 20
N. sumayensis	GH0015595[C]	Western Shoals, Apra Harbor	Guam	13.452211	144.654282	T. Schils	13.6	22 May 20
N. sumayensis	GH0015686[A]	Gab Gab Reef, Apra Harbor	Guam	13.443728	144.641062	T. Schils	21.1	24 Jul 201
N. sumayensis	GH0015687[B]	Gab Gab Reef, Apra Harbor	Guam	13.443728	144.641062	T. Schils	20.0	24 Jul 201
N. sumayensis	GH0015689[B]	Gab Gab Reef, Apra Harbor	Guam	13.443728	144.641062	T. Schils	13.6	24 Jul 201
N. yhaga	IRD11128[A] (PC0063019)	Paeowa Island	PNG	-5.154500	145.833000	C. Payri	10	13 Nov 20
N. yhaga	IRD11129	Malamal Anchorage	PNG	-5.119950	145.823000	C. Payri	10	18 Nov 20
N. imbricata	GWS001638[A]	O'ahu	Hawaii	21.273817	-157.721420	G.T. Kraft	10-17	16 Mar 20

N. imbricata	ARS09591 (BISH 783322)	Lehua	Hawaii	22.01942	-160.10277	J. Leonard	76	14 Sep 201
N. imbricata	GWS022466	Bonza, Hideaway Island	Vanuatu	-17.698	168.26	K. Dixon, E. McQualter	-	01 Nov 20

FP: French Polynesia; PNG: Papua New Guinea. [A] Holotype. [B] Isotype. [C] Paratype.

Table 2. Pair-wise sequence dissimilarity matrix (%), based on the number of substitutions between the five *Newhousia* lineages for five genes (*cox*1, *cox*3, *psb*A, *rbc*L, and 18S RNA).

***cox*1**					
	***N. imbricata* (FP)**	***N. imbricata* (HI)**	***N. imbricata* (VU)**	***N. sumayensis***	***N. yhaga***
***N. imbricata* FP**	0 - 0.3	-	-	-	-
***N. imbricata* HI**	0.9 - 1.3	0	-	-	-
***N. imbricata* VU**	1.4 - 1.6	0.6	0	-	-
N. sumayensis	5.5 - 6.1	5.7 - 5.9	5.7 - 5.9	0	-
N. yhaga	N/A	N/A	N/A	N/A	N/A
***cox*3**					
	***N. imbricata* (FP)**	***N. imbricata* (HI)**	***N. imbricata* (VU)**	***N. sumayensis***	***N. yhaga***
***N. imbricata* FP**	0 - 0.2	-	-	-	-
***N. imbricata* HI**	1.7 - 1.9	0	-	-	-
***N. imbricata* VU**	1.9 - 2.1	1.6	0	-	-
N. sumayensis	6.7 - 7.5	6.1 – 6.7	7.0 - 7.5	0	-
N. yhaga	6.4 - 6.7	5.8	6.3	4.7 - 4.9	0
***psb*A**					
	***N. imbricata* (FP)**	***N. imbricata* (HI)**	***N. imbricata* (VU)**	***N. sumayensis***	***N. yhaga***
***N. imbricata* FP**	0	-	-	-	-
***N. imbricata* HI**	0.2 - 0.3	0	-	-	-
***N. imbricata* VU**	0.2	0.5	0	-	-
N. sumayensis	1 - 1.5	1 - 1.5	1.0 - 1.3	0 - 0.3	-
N. yhaga	1.2 - 1.4	1.5	1.3	0.9 - 1.5	0
***rbc*L**					
	***N. imbricata* (FP)**	***N. imbricata* (HI)**	***N. imbricata* (VU)**	***N. sumayensis***	***N. yhaga***
***N. imbricata* FP**	0 - 0.8	-	-	-	-
***N. imbricata* HI**	1.7 - 2.3	0	-	-	-
***N. imbricata* VU**	0.5 - 1.3	0.5 - 1.1	0	-	-
N. sumayensis	1.5 - 2.2	3.0 - 3.4	2.65 - 2.67	0	-
N. yhaga	3.4 - 4.0	4.5	3.7 - 4.1	2.8 - 2.9	0
18S rDNA					
	***N. imbricata* (FP)**	***N. imbricata* (HI)**	***N. imbricata* (VU)**	***N. sumayensis***	***N. yhaga***
***N. imbricata* FP**	0 - 0.2	-	-	-	
***N. imbricata* HI**	0.1 - 0.3	0	-	-	-
***N. imbricata* VU**	N/A	N/A	N/A	-	-
N. sumayensis	0.2 - 0.4	0.2	N/A	0 - 0.1	
N. yhaga	N/A	N/A	N/A	N/A	N/A

N/A, non-available data. FP. French Polynesia. HI. Hawaii. VU. Vanuatu.

Table 3. **Anatomical features of *Newhousia* species (Dictyotales, Phaeophyceae). Anatomical measurements are in µm.**

	N. imbricata French Polynesia	*N. imbricata* Hawaii	*N. imbricata* Fossil Tahiti	*N. sumayensis* Guam	*N. yagha* PNG[1]
Blade thickness					
Average ± SD	54.7 ± 7.3	N/A	N/A	35.3 ± 5.1	45.7 ± 5.1
Min-Max	42.5 - 72.5	45 - 90	N/A	35 - 91	40 - 52
Epidermal cell length					
Average ± SD	15.9 ± 3.6	N/A	N/A	15.4 ± 3.9	26.7 ± 7.2
Min-Max	12.8 - 21.5	7 - 25	N/A	10 - 20	20.4 - 36.4
Epidermal cell width					
Average ± SD	7.1 ± 2.5	N/A	N/A	10.7 ± 2.1	14.9 ± 1.1
Min-Max	4.3 - 10.9	10 - 15	N/A	8 - 15	13.3 - 16.2
Epidermal cell height					
Average ± SD	16.5 ± 2.9	N/A	N/A	11.5 ± 2	11.3 ± 2.4
Min-Max	10 - 20	14 - 17	8 - 15	6 - 23	8 - 14
Hypodermal cell length					
Average ± SD	53.9 ± 5.2	N/A	N/A	33.7 ± 6.1	59.7 ± 3.9
Min-Max	50 - 62	30 - 55	N/A	25 - 42	20.4 - 36.4
Hypodermal cell width					
Average ± SD	23.0 ± 3.3	N/A	N/A	20.3 ± 3.2	32.3 ± 3.2
Min-Max	17.5 - 27.5	9 - 36	N/A	15 - 25	28 - 36
Hypodermal cell height					
Average ± SD	38.1 ± 5.3	N/A	N/A	24.4 ± 5.2	34.3 ± 3.9
Min-Max	32.5 - 52.5	32 - 58	25 - 40	15 - 60	30 - 40
Reference	This Study	Kraft et al. (2004)	Iryu (2016)	This study	Vieira et al. (2016)

[1]PNG, Papua New Guinea (Vieira et al. 2016); SD, standard deviation based on twenty measures for each character.

FIGURES LEGENDS

Fig. 1. Geographical distribution of the brown algal genus *Newhousia* (Dictyotales, Phaeophyceae) and sampling localities in the Mariana, Melanesian, Hawaiian, and Society Islands.

Fig. 2. Phylogenetic tree of the brown algal genus *Newhousia* (Dictyotales, Phaeophyceae). Specimen-level maximum likelihood phylogenies based on a concatenated alignment of *cox*1 + *cox*3 + *psb*A + *rbc*L + 18S rRNA sequences (5,844 bp), obtained from PhyML analyses. Numbers at nodes indicate bootstrap values (left numbers) and Bayesian posterior probabilities

(right numbers) obtained from a MrBayes analysis. Black semi-circle indicates full support in the maximum likelihood (left semi-circle) and Bayesian (right semi-circle) analyses.

Figs 3-17. *Newhousia imbricata*: habit, morphological and anatomical features, and structure of spores.

Figs 3, 4. Habit of *N. imbricata* in Moorea, French Polynesia; attached to bedrock (Fig. 3) or forming unattached spherical structures (phaeoliths; Fig. 4).

Figs 5-7. External morphology of *N. imbricata*: Fig. 5, *N. imbricata* from Tahiti (PF766), and Figs 6, 7, *N. imbricata* from Moorea (PF1228); Fig.7, fractured phaeolith structure showing new thalli of *N. imbricata* growing on top of the limestone remains of former thalli forming the crust and phaeolith structures. Scale bar = 1 cm.

Figs 8, 9. Surface blades of *N. imbricata*: Fig. 8, showing scattered spores (PF1215), scale bar = 1 mm; Fig. 9, microscopic and Fig. 10, scanning electron micrographs showing a blade radial growth (PF766), scale bar = 1 mm.

Fig. 11. Cross section of a blade of *N. imbricata* (PF766). Scale bar = 40 µm.

Fig. 12. Longitudinal section of a blade of *N. imbricata* (PF766). Scale bar = 40 µm.

Figs 13, 14. Scanning electron micrograph *N. imbricata* cross section (PF766): Fig. 13, scale bar = 100 µm; Fig. 14, scale bar = 50 µm.

Fig. 15. Scanning electron micrograph of a *N. imbricata* blade surface with epidermal tissue partially removed showing hypodermal cell structures in surface view (PF766). Scale bar = 200 µm.

Fig. 16. Spores on a surface fragment of *N. imbricata* (PF1215). Scale bar = 500 µm.

Fig. 17. Spore of *N. imbricata* developing without a stalk cell (PF1215). Scale bar = 50 µm.

Figs 18-29. *Newhousia sumayensis* sp. nov.: habit, morphological, and anatomical features.

Figs 18, 19. Habit of *N. sumayensis* in Apra Harbor, Guam: Fig. 18, GH0015578; Fig. 19, GH0015595.

Fig. 20. Holotype of *N. sumayensis* from Guam (GH0015686; Fig. 5). Scale bar = 2 cm.

Figs 21-23. Surface blades of *N. sumayensis* (GH0015868): Fig. 21, scale bar = 2 mm; Figs 22-23, scale bar = 100 µm.

Fig. 24. Scanning electron micrograph of *N. sumayensis* blades (GH0015686). Scale bar = 1 mm.

Fig. 25. Cross section of a blade of *N. sumayensis* (GH0015868). Scale bar = 40 µm.

Fig. 26. Longitudinal section of blade of *N. sumayensis* (GH0015868). Scale bar = 40 µm.

Fig. 27. Section of several layers of *Newhousia* blades growing on top of a dead coral skeleton. Scale bar = 2 mm.

Fig. 28. Scanning electron micrograph of a section of *N. sumayensis* (GH0015578). Scale bar = 50 µm.

Fig. 29. Scanning electron micrograph of a section of *N. sumayensis* (GH0015686). Arrowheads indicate structures that resemble plurilocular antheridia like those found in *Zonaria turneriana* J. Agardh (see Phillips & Clayton 1997). Scale bar = 100 µm.

SUPPLEMENTARY MATERIALS

Table S1. DNA sequences of primers used for amplification of *cox*1, *cox*3, *psb*A, *rbc*L, and 18S rDNA in this study.

Marker	Primer	Sequence
*cox*1	cox1F	TCAACAAATCATAAAGATATTGG
	cox1F_DIC	AACCCTATATTTGTTATTCGGTGG
	cox1R	ACTTCTGGATGTCCAAAAAAYCA
*cox*3	cox3 44F	CATCGCCACCCATTTCAT
	cox3 739R	CATCGACAAAATGCCAATACCA
*psb*A	psbAF	ATGACTGCTACTTTAGAAAGACG
	psb1R1	GCTAAATCTARWGGGAAGTTGTG
*rbc*L	68F	TGCCWAAATGGGRWAYTGGGATGC
	R708	TTAAGNTAWGAACCYTTAACTTC
	543F	CCWAAATTAGGTCTTTCWGGWAAAAA
	1391R	TCNAANGTAATATCTTTCCATA
18S rDNA	P2(F)	CTGGTTGATTCTGCCAGT
	P4(R)	TGATCCTTCYGCAGGTTCAC
	P12(R)	CGGCCATGCACCACC
	P14(F)	CGGTAATTCCAGCTCC

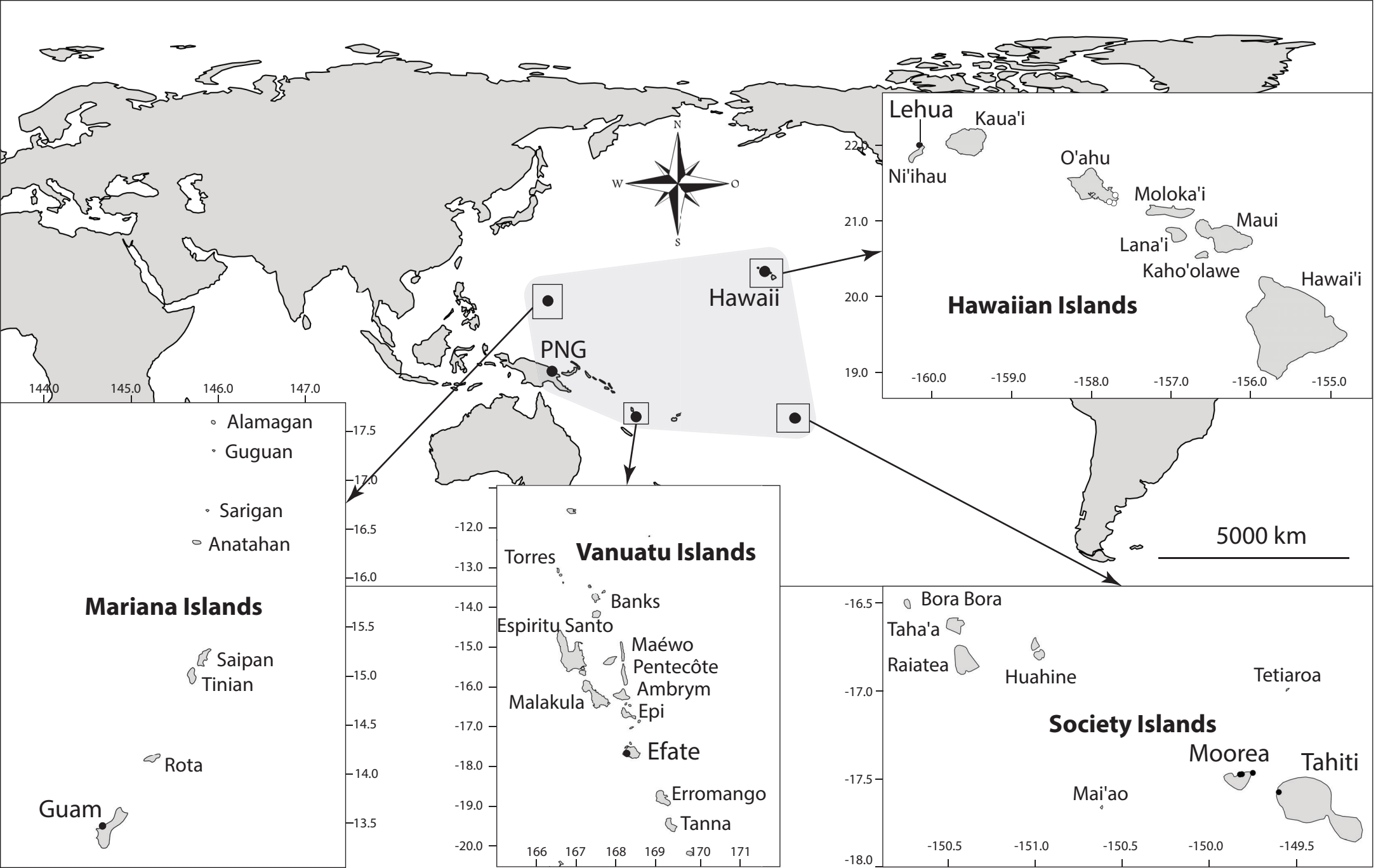
Table S2. Amplification profiles.

	***cox*1**		***cox*3**		***psb*A**		***rbc*L**		**18S rDNA**	
	T°C	**Time**	**T°C**	**Time**	**T°C**	**Time**	**T°C**	**Time**	**T°C**	**Time**
Initial Denaturation step	94°C	3 min	94°C	3 min	94°C	3 min	94°C	3 min	94°C	7 min
Denaturation	94°C	45 s	94°C	1 min	94°C	1 min	94°C	45 s	94°C	1 min
Annealing	52°C	45 s	46°C	1 min	46°C	1 min	52°C	45 s	55°C	1 min
Number of cycles	40x		35x		35x		40x		40x	
Elongation	72°C	1 min	72°C	2 min	72°C	2 min	72°C	1 min	72°C	1 min 30 sec
Final Elongation step	72°C	6 min	72°C	10 min	72°C	10 min	72°C	6 min	72°C	10 min

Table S3. GenBank accession numbers of specimens used in this study. In bold, sequences of *Newhousia* specimens generated for this study.

11.	Voucher	*cox*1	*cox*3	*psb*A	*rbc*L	18S rDNA
Newhousia imbricata	PF766	**MZ577049**	-	-	**MW585107**	**MW797069**
N. imbricata	PF1228	**MZ577053**	**MW585089**	-	-	-
N. imbricata	PF1229	**MZ577050**	**MW585090**	**MW585099**	**MW585109**	**MW797070**
N. imbricata	PF1388	**MZ577052**	**MW585091**	**MW585098**	**MW585110**	**MW797067**
N. imbricata	PF1421	**MZ577051**	**MW585088**	**MW585097**	**MW585108**	**MW797068**
N. sumayensis	GH0013143	**MW590249**	-	-	-	-
N. sumayensis	GH0015576	-	-	**MW585095**	-	-
N. sumayensis	GH0015578	-	-	**MW585096**	-	-
N. sumayensis	GH0015595	-	-	**MW585100**	-	-
N. sumayensis	GH0015686	**MZ577048**	**MW585093**	**MW585103**	**MW585104**	**MW797066**
N. sumayensis	GH0015687	**MZ577046**	**MW585094**	**MW585102**	**MW585105**	-
N. sumayensis	GH0015689	**MZ577047**	**MW585092**	**MW585101**	**MW585106**	**MW797065**
N. yhaga	IRD11128	-	KU249203	KU249195	KU249201	-
N. yhaga	IRD11129	-	MZ577054	-	KU249202	-
N. imbricata	GWS001638	-	-	-	EF990240	AY423547
N. imbricata	GWS022466	HQ919456	**OL411838**	**OL411839**	MZ050393	-
N. imbricata	ARS09591	**MZ577055**	**MZ577056**	**MZ577057**	**MZ577058**	**MZ576553**
Dichotoma robustus2	GWS025008, D1702	MW127576	MK516762	KU249197	KU249200	-
Dic. dichotoma	D338, D3389, JALee01, IK2	MW223880	MW223459	AY748319	AY422654	-
Distromium decumbens	IK76, SZKIZ059	-	-	AY422645	AY422683	AB087117
Dis. didymothrix	FRA0361	-	-	-	EU579948	-
Homoeostrichus formosana	TAHL39	-	DQ866952	-	DQ866931	DQ866938
H. sinclairii	HV2045, HV2194, SL17	MW224302	MW223520	DQ866953	DQ866934	-
Lobophora abaculusa	CV3250, IRD277	-	KM487896	KM488036	KM488179	-
L. abscondita	CV3088, IRD11057, IRD7919	-	KM487773	KM488068	KM488129	-
L. australis	SAP109517, SALee36	-	AB665369	DQ866944	DQ866924	-
L. gibbera	IRD11058, IRD275	-	KM487795	KM488069	KM488139	-

L. hederacea	IRD10191, CV3234, IRD7880	-	KM487822	KM488055	KM488165	-
L. nigrescens2	GWS025025, HV03610, IRD10195, IRD10214	MW127646	KU353374	KM488025	KM488122	-
L. obscura2	IRD10187	-	KM487780	KM488072	KM488140	-
L. pachyventera2	IRD7881, CV3095	-	KM487803	KM488058	KM488126	-
L. rosacea	CV3072, IRD7913, IRD10209, CV3249	MW224328	KM487936	KM488009	KM488111	-
L. undulata	CV3078, CV3182, CV3059	-	KM487847	KM488039	KM488148	-
Padina arborescens	PCAB11325, IK65, HV1622, SZKIZ065	-	JQ363941	AY430357	JQ364049	AB090392
P. australis	ODC1420, ODC1459, KUd3208	-	JQ363945	MW225745	AB690272	MF661900
P. crassa	BW00676, LBC0086, KL4, SMNOK074	MW224362	JQ363960	AY422643	AB358909	AB095297
Zonaria angustata	SALee, SAL61	-	-	DQ866946	DQ866932	-
Z. crenata	KUd356, SALee58, SAL16, 10M	-	AB665391	DQ866945	DQ866933	AF350234
Z. diesingiana	KUd7720, KUd1071	-	AB665390	AB899260	AB899284	DQ866937
Z. tournefortii	ODC2170, LLG2439, LBC112	MW224393	JQ364041	-	EU579973	-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Lehua
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Hawai'i
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Guguan
Sarigan
Anatahan
Mariana Islands
Saipan
Tinian
Rota
Guam
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16.5
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15.0
14.5
14.0
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Torres
Vanuatu Islands
Banks
Espiritu Santo
Maéwo
Pentecôte
Ambrym
Malakula
Epi
Efate
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Tanna
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Moorea
Tahiti
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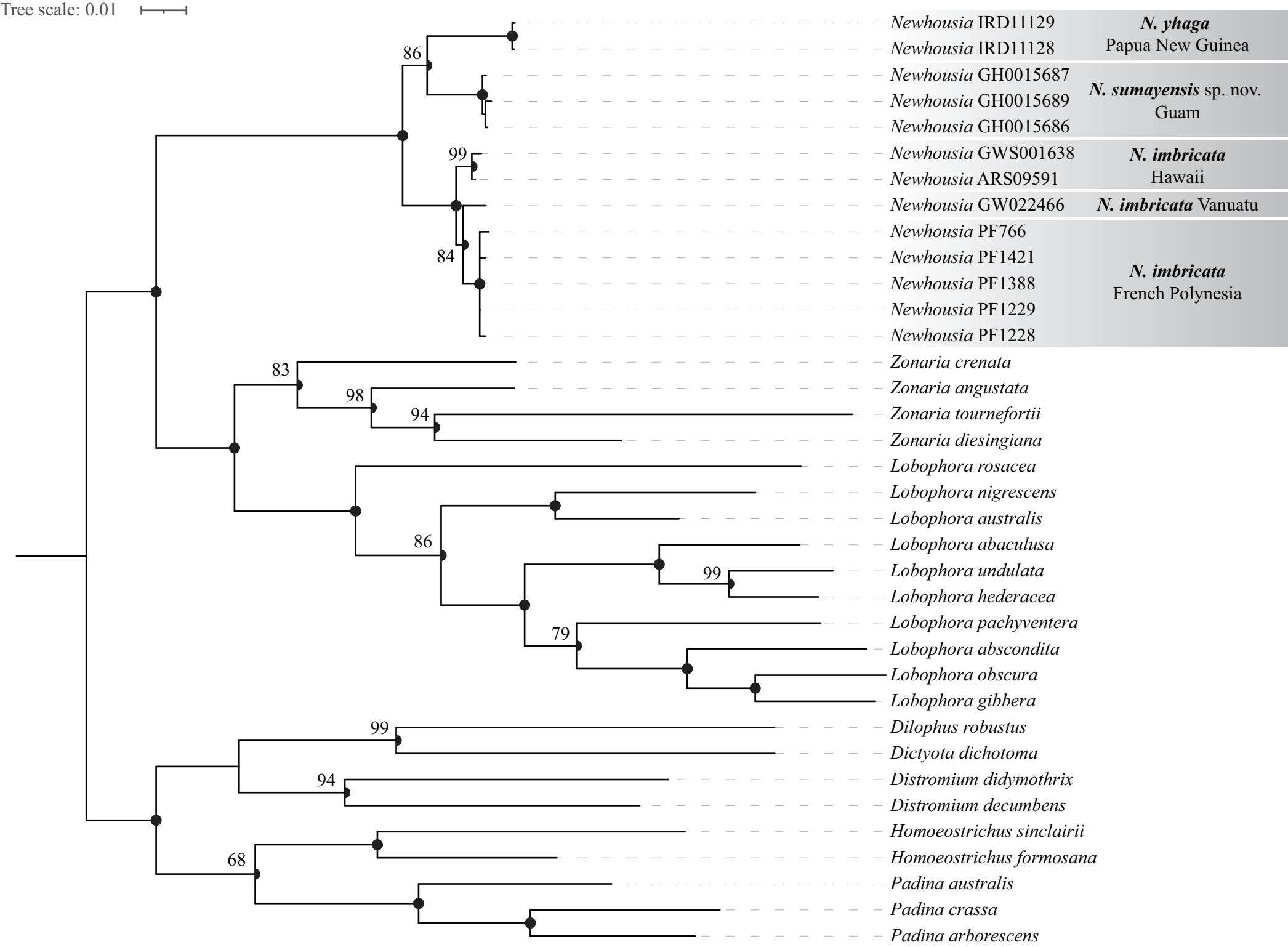
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Newhousia IRD11128
N. yhaga
Papua New Guinea
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Newhousia GH0015689
Newhousia GH0015686
N. sumayensis sp. nov.
Guam
Newhousia GWS001638
Newhousia ARS09591
N. imbricata
Hawaii
Newhousia GW022466
N. imbricata Vanuatu
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Newhousia PF1388
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Zonaria angustata
Zonaria tournefortii
Zonaria diesingiana
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Lobophora nigrescens
Lobophora australis
Lobophora abaculusa
Lobophora undulata
Lobophora hederacea
Lobophora pachyventera
Lobophora abscondita
Lobophora obscura
Lobophora gibbera
Dilophus robustus
Dictyota dichotoma
Distromium didymothrix
Distromium decumbens
Homoeostrichus sinclairii
Homoeostrichus formosana
Padina australis
Padina crassa
Padina arborescens
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