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The genus *Lobariella* (Ascomycota: *Lobariaceae*) in Hawaii: late colonization, high inferred endemism and three new species resulting from "micro-radiation"

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Abstract: We assessed the taxonomy and phylogenetic relationships of Hawaiian species of the neotropical genus *Lobariella*. A single species was previously reported from the archipelago, the widespread neotropical *L. crenulata*. We targeted three loci of the mitochondrial and nuclear ribosomal rDNA gene cistron (mtSSU, nuLSU, ITS) and also performed a molecular clock analysis. Our results show that *L. crenulata* s. str. is seemingly present in the archipelago based on older herbarium collections. However, Hawaiian *Lobariella* includes three additional, presumably endemic, species unrelated to *L. crenulata* and new to science: *L. flynniana* Lücking, Moncada & C. W. Sm., with richly branched marginal phyllidia giving the thallus a fruticose appearance; *L. robusta* Lücking, Moncada & C. W. Sm., with a rather thick thallus and abundant, large, laminal phyllidia; and *L. sandwicensis* Lücking, Moncada & C. W. Sm., with a delicate thallus producing apothecia. *Lobariella flynniana* represents a novel morphotype within the genus, thus far known only from Hawaii. All three species are very closely related, forming a well-supported, monophyletic clade in spite of their morphological differences, suggesting local micro-radiation. Molecular clock analysis indicates that this clade colonized the islands between 1–8 mya and diverged between 0–2 mya. We interpret recent colonization as one of the main reasons why this clade has not diversified further.

Key words: Kokee State Park, lichen, Neotropics, *Pseudocyphellaria*, taxonomy, Waikamoi Reserve, Waimea District

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Introduction

The concept of the evolution of life is linked to Darwin's visit to the Galapagos Islands (Sulloway 1982; Weiner 1994; Grant & Estes 2009). However, the true laboratory of evolution is found in the Hawaiian archipelago, arguably the most remote place on Earth, being over 4000 km to the closest continental land mass (Wagner & Funk 1995; Fleischer *et al.* 1998). Notably, Darwin himself wrote in a letter to Joseph Dalton Hooker in 1850: "Of all places in the world I would like to see a good flora of the Sandwich Islands. I would subscribe 50 pounds to any collector to go there and work at these islands." (Burkhardt & Smith 1984; Kay 1997). Hawaii is home to some of the most striking evolutionary radiations in vascular plants, such as the Hawaiian lobeliads in the family *Campanulaceae*, with 126 species in six genera having evolved from a single colonization event *c.* 13 mya (Givnish *et al.* 2009), and the silversword alliance in the family *Asteraceae* (Baldwin *et al.* 1991; Baldwin & Sanderson 1998; Barrier *et al.* 2001; Carlquist *et al.* 2003). Island biota also often evolved unique forms. Thus, endemic species of *Geranium* L., a genus elsewhere known only as herbaceous, form woody stems in Hawaii (Fosberg 1936; Pax *et al.* 1997; Kidd 2005). The two native raspberry species (*Rubus hawaiensis* A. Gray and *R. macraei* A. Gray) lack defensive thorns (Morden *et al.* 2003), and endemic species of the mint family lost the characteristic scent based on oily

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substances (Morden & Loeffler 1999), possibly due to the absence of native herbivores.

Unfortunately, this unique environment has been almost overwhelmed by human influence, including land use change and a large number of invasive species (Kirch 1982; Olson & James 1982; Stone *et al.* 1992; Asquith 1995; Pratt *et al.* 2009). The 1386 native plant species (Imada 2012) are opposed by close to 10 000 introduced taxa, with some, such as the Kahili Ginger (*Hedychium gardnerianum* Griff.) and Strawberry Guava (*Psidium cattleianum* Sabine), threatening to take over entire forests (Department of Land and Natural Resources 2007). Such human-induced alteration of island floras is a global phenomenon (Castro *et al.* 2010). In Hawaii, major efforts are directed at trying to contain the impact of alien influences while stabilizing and restoring native elements, particularly those close to extirpation (Stone & Scott 1985). Nearly 40% of the original native Hawaiian flora is extinct or threatened with extinction (Sakai *et al.* 2002; Wood 2007, 2012; US Fish and Wildlife Service 2010).

In contrast to vascular plants, Hawaiian bryophytes, lichens and fungi are believed to include mostly widespread species. While estimates of endemism reach 80% for vascular plants (Wagner *et al.* 1999; Wagner & Herbst 2002; Evenhuis & Eldredge 2002*a*, *b*), they are substantially lower for cryptogams. Among bryophytes, two genera (1%) and 178 species are listed as endemic (Staples *et al.* 2004; Staples & Imada 2006). Of the 880 lichens (Smith 2013), up to 30% are considered endemic (Eldredge & Miller 1995). Compared to vascular plants, Hawaiian lichens have generally received less attention (Smith 1993). Only a small number of new taxa have been described in the past few decades (Esslinger 1978; Kalb & Vězda 1980; McCarthy 1993; Moon *et al.* 2001; Kashiwadani *et al.* 2002; Aptroot *et al.* 2012). Modern treatments have covered foliicolous taxa (Smith 1977; Smith *et al.* 1997; Sérusiaux & Lücking 2007), alectorioid and umbilicarioid lichens (Smith 1984, 2001), and parmelioid species (Smith 1993). The last study in particular supported the view that Hawaiian lichens are generally widespread, a view expressed by other workers (Wirth 1997; Marbach 2000; Smith 2001; Inoue 2002; Sérusiaux & Lücking 2007). In contrast, a biogeographical analysis of *Cladoniaceae* suggested 40% of species in that family are endemic (Stenroos & Smith 1993). Smith (1995) provided an analysis of ascospore features of Hawaiian lichens and found a higher proportion of species with pigmented and/or large ascospores.

The Hawaiian biota is also notable for its biogeographical relationships and inferred dispersal routes. Most native vascular plants, such as forest trees of the genera *Acacia* Mill. (*Fabaceae*), *Cheirodendron* Nutt. ex Seem. (*Araliaceae*) and *Metrosideros* Banks ex Gaertn. (*Myrtaceae*), have Indopacific-Australasian relationships (Mueller-Dombois 1987; Wright *et al.* 2001; Percy *et al.* 2008; Brown *et al.* 2012; Mitchell *et al.* 2012), explained by the northern subtropical jet stream being the predominant dispersal agent (Geiger *et al.* 2007). Biogeographical relationships with North, Central and South America are less common; for example, the closest relative of the Hawaiian silverswords (genera *Argyroxiphium* DC., *Dubautia* Gaudich. and *Wilkesia* A. Gray) are the North American tarweeds (Baldwin *et al.* 1991; Carlquist *et al.* 2003). As so far studied, lichenized fungi, for example in the family *Cladoniaceae* (Stenroos & Smith 1993) and the genus *Pannaria*, mostly have Australasian affinities, whereas few are linked to the neotropical realm. This was first supported with molecular data for the genus *Pseudocyphellaria* Vain. s. lat. (*Lobariaceae*), in which all Hawaiian species are related to palaeotropical taxa, with the exception of *P. hawaiiensis* H. Magn. (Moncada *et al.* 2014).

The genus *Lobariella* Yoshim. is entirely restricted to the Neotropics, with the notable exception of *L. crenulata* (Hook.) Yoshim. reported from Hawaii (Yoshimura 1984, 1998; Yoshimura & Arvidsson 1994). The genus was recently revised using molecular data (Moncada *et al.* 2013), showing that it is much more speciose than previously assumed and that secondary chemistry, previously thought to vary within species (Yoshimura 1984; Yoshimura & Arvidsson 1994), is an important systematic character. For that study, we had revised material of *L. crenulata* at the US National Herbarium, collected in Hawaii by the late Mason Hale, and concluded that it represented at least two different species, based on morphology and chemistry: *L. crenulata* s. str. and *L. subcrenulata* Moncada & Lücking. Since these represented two unrelated lineages within the genus (Moncada *et al.* 2013), this suggested that Hawaii was colonized at least two times independently from the Neotropics. In order to test this hypothesis, we obtained fresh material of *Lobariella* from Hawaii during a field trip in June 2013 and additional fieldwork in September 2016 and sequenced three loci of the nuclear and mitochondrial ribosomal DNA. We also revised numerous herbarium specimens. Much to our surprise, the material studied turned out to represent three species new to science, all closely related but morphologically disparate and including a phenotype never before observed in the genus, forming a well-supported clade different from the species believed to occur in Hawaii.

Material and Methods

Herbarium material of *Lobariella* originating from Hawaii was revised at the US National Herbarium, the herbarium of the University of Hawaii at Manoa (HAW) and the herbarium of the National Tropical Botanical Garden on Kauai (PTBG). We performed thin-layer chromatography in solvent C to determine the chemical constituents of each sample (Orange *et al.* 2010).

New fresh material of *Lobariella* was collected in Hawaii by all authors during fieldwork in June 2013 and by the third author in September 2016. We obtained 42 new sequences of the nuclear ITS barcoding locus, including 16 specimens from Hawaii and the remainder from Colombia and Costa Rica, 12 new sequences of the nuclear large subunit (nuLSU), including two from Hawaii, and 15 new sequences of the mitochondrial small subunit (mtSSU) ribosomal DNA, including two from Hawaii. DNA was extracted using the QIAGEN DNeasy Plant Mini Kit. Dilutions of 10:1 were used for PCR amplifications, with the primer pairs ITS1F and ITS4 for the ITS (White *et al.* 1990; Gardes & Bruns 1993), mrSSU1 and MSU7 for the mtSSU (Zoller *et al.* 1999; Zhou & Stanosz 2001), and AL2R and LR6 for the nuLSU (Vilgalys & Hester 1990; Mangold *et al.* 2008). The 25 µl PCR reactions contained 2·5 µl buffer, 2·5 µl dNTP mix, 1 µl of each primer (10 µM), 5 µl BSA, 2 µl Taq, 2 µl genomic DNA extract and 9 µl distilled water. The thermal cycling parameters were set as follows: initial denaturation for 3 min at 95 °C followed by 30 cycles of 1 min at 95 °C, 1 min at 52 °C, 1 min at 73 °C, and a final elongation for 7 min at 73 °C. Amplification products were mounted on 1% agarose gels stained with ethidium bromide and, after cutting of the target bands, purified using the QIAGEN QIAquick PCR Purification Kit or NucleoSpin DNA purification kit (Macherey-Nagel). Fragments were sequenced using the BigDye Terminator reaction kit (ABI PRISM, Applied Biosystems). Sequencing and PCR amplifications were performed using the same sets of primers. Cycle sequencing was executed with the following setting: 25 cycles of 95 °C for 30 s, 48 °C for 15 s and 60 °C for 4 min. Sequenced products were precipitated with 10 µl of sterile dH_2O, 2 µl of 3 M NaPA (sodium phenylacetate) and 50 µl of 95% EtOH, and subsequently loaded on an ABI 3100 (Applied Biosystems) automatic sequencer. Sequence fragments obtained were assembled with DNASTAR SeqMan 4.03, manually inspected and adjusted and, after quality control within the context of multiple alignments for each locus, submitted to GenBank (Table 1).

The sequences obtained were aligned with a previous data set analyzed by Moncada *et al.* (2013), using selected sequences of *Lobariaceae* from GenBank (Table 1). Alignments for each locus were assembled separately in BioEdit 7.0.9 (Hall 1999) and automatically pre-aligned using ClustalW2 (Thompson *et al.* 1994) to detect potentially problematic sequences. Final alignments were made with MAFFT 6.850b (Katoh *et al.* 2002, 2009) using the "–auto" option and subsequent manual inspection. The individual alignments were subjected to analysis of ambiguously aligned regions using the GUIDANCE webserver (Penn *et al.* 2010*a*, *b*) and introns and regions aligned with low confidence (below 0·90) were removed. This resulted in an alignment length of 554 sites for the ITS, 999 for the nuLSU, and 831 for the mtSSU partition. The separate gene trees were tested for topological conflict using tree-branch comparison at a bootstrap support threshold of 70% (Mason-Gamer & Kellogg 1996; Miadlikowska & Lutzoni 2000; Kauff & Lutzoni 2002), and three single- or multilocus data sets were generated: 1) a 3-locus data set of 18 species (one sample per species) of *Lobariella*, with *Lobaria pulmonaria* as outgroup, to determine the closest relative of the Hawaiian taxa; 2) a single-locus ITS data set of 65 samples of *Lobariella*, with three species of *Yoshimuriella* as outgroup, to assess species delimitations; and 3) a single-locus nuLSU data set of representative species of *Lobariaceae*, including 10 of the 12 currently recognized genera (Moncada *et al.* 2013; Lücking *et al.* 2017), with *Nephroma parile* as outgroup, to perform a molecular clock analysis. Phylogenetic analyses were performed on each locus and the combined data set using maximum likelihood in RAxML 7.2.6 (Stamatakis 2006), with parametric bootstrapping using 500 replicates under the GTRGAMMA model. Trees were visualized in FigTree v.1.4.0 (Drummond & Rambaut 2007).

A relaxed, uncorrelated lognormal molecular clock model was employed to date the evolutionary origin of the Hawaiian *Lobariella* clade, using data set (3). The program BEAST v.1.7.5 (Drummond & Rambaut 2007)

TABLE 1. *Newly generated sequences (in* ***bold****) and sequences downloaded from GenBank used in this study. Specimens marked with an asterisk* are those used for the 3-locus and for the nuLSU molecular clock analysis.*

		GenBank Accession number					
Taxon	No.	ITS	nuLSU	mtSSU	Country	Collector	Number
*Lobaria pulmonaria**			AF183934	AF069541			
*Nephroma parile**		AY340557					
Yoshimuriella dissecta		AF524920					
Y. fendleri		AF524915					
Y. subdissecta		KC011029			Colombia	*Moncada*	3152
Lobariella angustata	(1)	KC011030			Colombia	*Vargas*	310a
L. angustata	(2)	KC011031			Colombia	*Vargas*	281a
L. angustata	(3)	**KY769437**			Colombia	*Lücking*	35322
L. auriculata	(1)	**KY769449**			Colombia	*Moncada*	7553
L. auriculata	(2)	**KY769451**			Colombia	*Moncada*	7549
L. auriculata	(3)	**KY769456**			Colombia	*Pelaez*	121
*L. botryoides**	(1)	KC011033	**KY769418**	**KY769403**	Colombia	*Moncada*	s.n.
L. botryoides	(2)	**KY769439**			Colombia	*Moncada*	6450
L. botryoides	(3)	**KY769460**			Colombia	*Barbosa*	79
*L. crenulata**	(1)	KC011034	**KY769421**	**KY769408**	Colombia	*Diaz*	L9
L. crenulata	(2)	**KY769453**			Colombia	*Moncada*	7559
L. crenulata	(3)	**KY769454**			Colombia	*Moncada*	7522
*L. ecorticata**		KC011035		**KY769406**	Colombia	*Moncada*	3156
*L. flavomedullosa**		KC011037	**KY769420**	**KY769405**	Colombia	*Moncada*	s.n.
L. flavomedullosa	(1)	**KY769440**			Colombia	*Moncada*	6640
L. flavomedullosa	(2)	**KY769441**			Colombia	*Moncada*	6645
L. flavomedullosa	(3)	**KY769442**			Colombia	*Moncada*	6666
*L. flynniana**	(1)	**KY769446**	**KY769428**	**KY769416**	Hawaii	*Moncada*	7028a
L. flynniana	(2)	**KY769447**			Hawaii	*Moncada*	7028b
*L. isidiata**		KC011038	**KY769422**	**KY769409**	Colombia	*Diaz*	L12
*L. nashii**		AF524902	EU558770	EU558804	Mexico	*Nash*	42486
*L. pallida**		HQ650695	DQ883796	DQ912296	Costa Rica	*AFTOL310*	47518
L. pallida	(1)	KC011039			Colombia	*Lücking*	33379
L. pallida	(2)	KC011040			Colombia	*Lücking*	33311b
L. pallida	(3)	KC011042			Colombia	*Moncada*	5354
*L. pallidocrenulata**		KC011051	KC011023	**KY769407**	Colombia	*Lücking*	33371a
L. pallidocrenulata	(1)	KC011047			Colombia	*Lücking*	33371c
L. pallidocrenulata	(2)	KC011052			Colombia	*Lücking*	33371b
L. pallidocrenulata	(3)	KC011054			Colombia	*Lücking*	33354
L. parmelioides	(1)	KC011056			Colombia	*Moncada*	5351
L. parmelioides	(2)	KC011057			Colombia	*Moncada*	5356
*L. parmelioides**	(3)	KC011060	**KY769423**	**KY769410**	Colombia	*Moncada*	5355
L. pseudocrenulata	(1)	KC011061			Colombia	*Vargas*	309b
*L. pseudocrenulata**	(2)	**KY769436**	**KY769424**	**KY769412**	Colombia	*Lücking*	35323
L. pseudocrenulata	(3)	**KY769443**			Colombia	*Lücking*	35840
L. reticulata	(1)	KC011062			Colombia	*Lücking*	34104
*L. reticulata**	(2)	KC011063	KC011024	**KY769411**	Colombia	*Moncada*	4982
L. reticulata	(3)	**KY769458**			Colombia	*Lücking*	39430
L. robusta	(1)	**KY769461**			Hawaii	*Smith*	CWS05a
L. robusta	(2)	**KY769462**			Hawaii	*Smith*	CWS05b
L. robusta	(3)	**KY769463**			Hawaii	*Smith*	CWS06a
L. robusta	(4)	**KY769464**			Hawaii	*Smith*	CWS06b
L. robusta	(5)	**KY769465**			Hawaii	*Smith*	CWS07
L. robusta	(6)	**KY769466**			Hawaii	*Smith*	CWS08
L. robusta	(7)	**KY769467**			Hawaii	*Smith*	CWS09
L. robusta	(8)	**KY769468**			Hawaii	*Smith*	CWS10a
L. robusta	(9)	**KY769469**			Hawaii	*Smith*	CWS10b
L. robusta	(10)	**KY769470**			Hawaii	*Smith*	CWS12
L. robusta	(11)	**KY769471**			Hawaii	*Smith*	CWS11

Table 1 (*continued*).

Taxon	No.	GenBank Accession number			Country	Collector	Number
		ITS	nuLSU	mtSSU			
Lobariella rugulosa	(1)	**KY769432**			Costa Rica	*Moncada*	5728
L. rugulosa★	(2)	**KY769433**	**KY769427**	**KY769415**	Costa Rica	*Moncada*	5755
L. rugulosa	(3)	**KY769438**			Costa Rica	*Lücking*	34631
L. sandwicensis	(1)	**KY769444**			Hawaii	*Moncada*	6940
L. sandwicensis	(2)	**KY769445**			Hawaii	*Moncada*	7027
L. sandwicensis★	(3)	**KY769448**	**KY769429**	**KY769417**	Hawaii	*Moncada*	7029
L. sipmanii	(1)	KC011064			Colombia	*Moncada*	s.n.
L. sipmanii	(2)	KC011065			Colombia	*Moncada*	s.n.
L. sipmanii	(3)	KC011066			Colombia	*Diaz*	L11
L. soredians★	(1)	KC011067	**KY769419**	**KY769404**	Colombia	*Moncada*	s.n.
L. soredians	(2)	**KY769434**			Colombia	*Fonseca*	152
L. soredians	(3)	**KY769435**			Colombia	*Fonseca*	65
L. spathulifera★		**KY777441**	**KY769425**	**KY769413**	Colombia	*Lücking*	35225
L. spathulifera	(1)	**KY769450**			Colombia	*Moncada*	7531
L. spathulifera	(2)	**KY769452**			Colombia	*Moncada*	7512
L. spathulifera	(3)	**KY769455**			Colombia	*Moncada*	7162
L. stenroosiae	(1)	AF524922			Brazil	*Stenroos*	5088
L. stenroosiae★	(2)	**KY769430**	**KY769426**	**KY769414**	Costa Rica	*Moncada*	5725
L. stenroosiae	(3)	**KY769431**			Costa Rica	*Moncada*	5752
L. subcrenulata★	(1)	HQ650696	DQ883797	DQ912297	Costa Rica	*AFTOL314*	47520
L. subcrenulata	(2)	**KY769457**			Colombia	*Moncada*	9044
L. subcrenulata	(3)	**KY769459**			Colombia	*Lücking*	39482

was used for this purpose, with the following specifications: 1) GTR substitution model with base frequencies estimated and Gamma and invariant sites with six Gamma categories; 2) speciation through a Yule process with the 'yule.birthRate' prior set to an exponential distribution with 0·7 as mean; 3) the 'ucld.mean' prior (mean substitution rate) set to an exponential distribution with 0·001 as mean; and 4) the 'ucld.stdev' prior (mean substitution rate) set to an exponential distribution with 0·6 as mean. All other priors except 'tmrca' and 'treemodel.rootheight' (see below) were held to default values. Estimation of priors was approximated by first running a strict clock and using the 'meanRate' posterior estimate as prior for a subsequent run applying a relaxed, lognormal, uncorrelated clock, with all other priors set to default values, and then further runs in an iterative manner, using the obtained posterior estimates as priors, until no substantial change was observed in the posteriors. The obtained final priors were: ac: shape = 0·05, scale = 10·0, offset = 0·0; ag: shape = 0·05, scale = 20·0, offset = 0·0; at: shape = 0·05, scale = 10·0, offset = 0·0; cg: shape = 0·05, scale = 10·0, offset = 0·0; gt: shape = 0·05, scale = 10·0, offset = 0·0; frequencies: uniform, lower = 0·0, upper = 1·0; alpha: exponential, mean = 0·5, offset = 0·0; pInv: uniform, lower = 0·0, upper = 1·0; ucld.stdev: exponential, mean = 0·7, offset = 0·0; ucld.mean: exponential, mean = 0·001, offset = 0·0; treeModel.rootHeight: normal, mean = 85·0, stdev = 10·0; tmrca(Ingroup): normal, mean = 62·0, stdev = 10·0; yule.birthRate: 0·7, offset = 0·0. All runs were performed with 50 million generations each and analyses were performed on the CIPRES Science Gateway server (Miller *et al.* 2010). The time to the most recent ancestor ('tmrca') for the ingroup node of *Lobariaceae* was calibrated at 62 mya, using a normal prior distribution with the standard deviation set to 10 my; in addition, the 'treemodel.rootheight' (*Nephroma* divergence) was calibrated at 85 mya, using a normal prior distribution with the standard deviation set to 10 my. Both values followed Rivas Plata (2011: 21), who performed an analysis across all Ascomycota using ten fungal fossils (Rivas Plata 2011: 15). Notably, Rivas Plata (2011) estimated the stem node age of *Peltigerales* at 186 mya, very similar to Amo de Paz *et al.* (2011) and Prieto & Wedin (2013) with 185 mya and 184 mya, respectively. The latter two did not contain the *Nephroma* divergence for comparison; however, the very similar stem node estimates for *Peltigerales* across these studies support our selection for the two external calibration points. To test the resulting chronogram, we fitted *a posteriori* the age estimate of a fossil species of *Lobaria* similar in morphology to *L. pulmonaria*, estimated at 12–24 mya (Peterson 2000). The molecular clock trees were estimated using a constrained topology based on a previous multigene study (Moncada *et al.* 2013). For that purpose, data set (3) was analyzed in RAxML with a constrained multifurcate tree and the resulting fully-resolved best tree was used as constraint for the molecular clock analysis. This was done by removing the tree swapping operators 'subtreeSlide', 'narrowExchange', 'wideExchange' and 'wilsonBalding' (Drummond & Rambaut 2007).

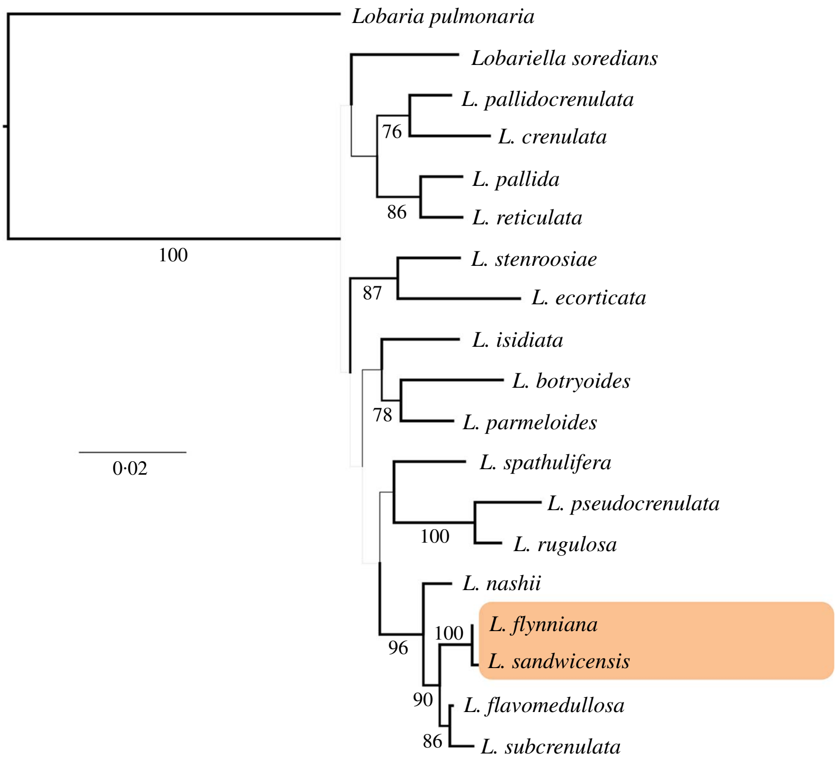


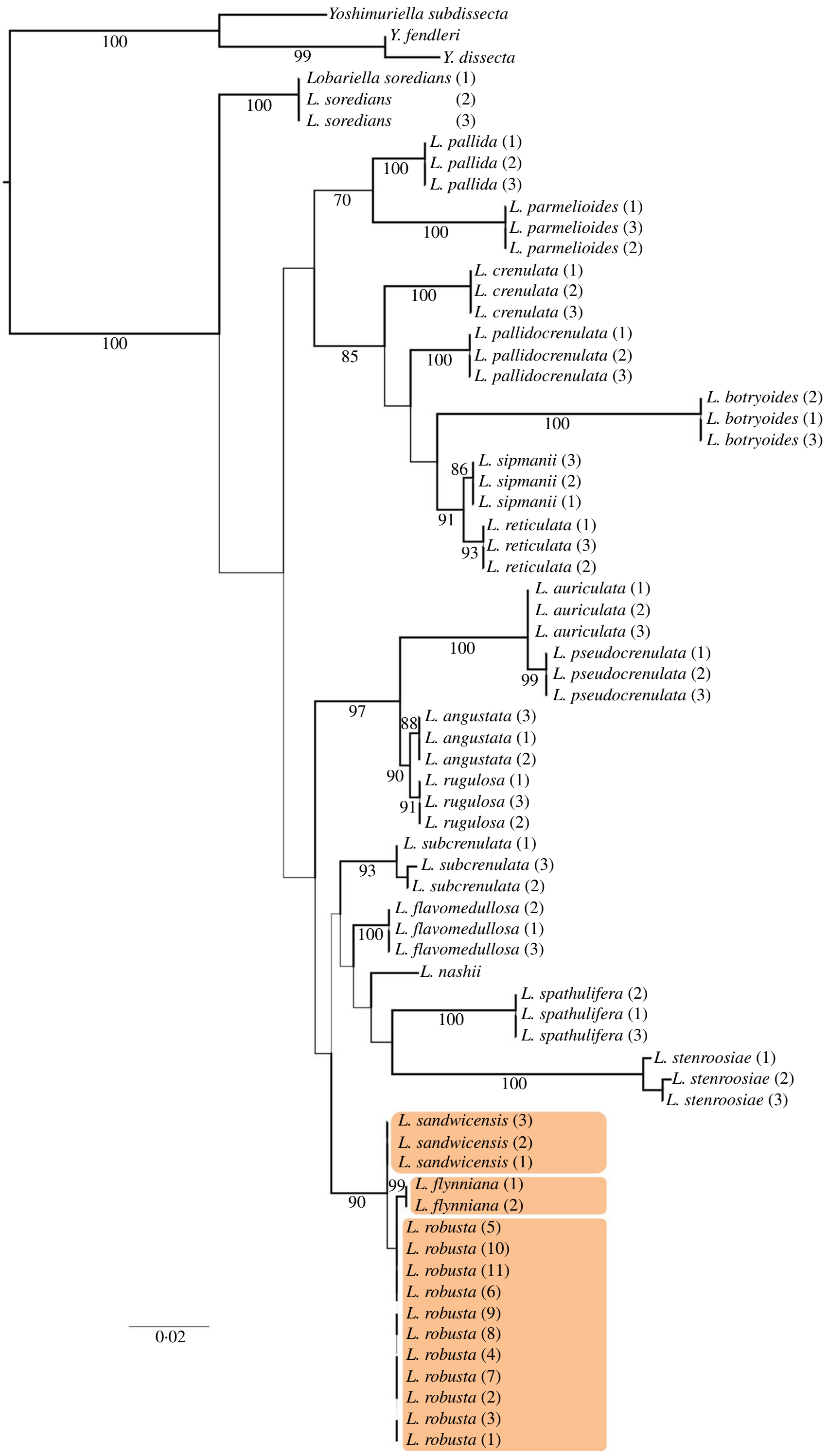
FIG. 1. Best-scoring maximum likelihood tree based on a 3-locus combined data set (mtSSU, nuLSU, ITS) of *Lobariella* highlighting the position of the Hawaiian species. Branch thickness is proportional to bootstrap support and bootstrap values of ≥70% are indicated below branches. *Lobaria pulmonaria* as the outgroup. For voucher information see Table 1.

Results

In the 3-loci analysis, the genus *Lobariella* emerged as a long branch relative to the outgroup, *Lobaria pulmonaria*, but with comparatively short branches leading to the individual species and a lack of backbone support (Fig. 1). The following sister group relationships were supported: *Lobariella crenulata* vs. *L. pallidocrenulata*, *L. pallida* vs. *L. reticulata*, *L. ecorticata* vs. *L. stenroosiae*, *L. botryoides* vs. *L. parmelioides* and *L. pseudocrenulata* vs. *L. rugulosa*. In addition, we found strong support for a clade of five species, including two Hawaiian taxa, with *L. nashii* sister to a clade of four species in which *L. flavomedullosa* plus *L. subcrenulata* are supported as sister clade to the Hawaiian *L. flynniana* and *L. sandwicensis*, two of the three new species described below.

The expanded taxon set of the single-locus ITS analysis (Fig. 2) recovered the *L. pseudocrenulata*-*rugulosa* clade, further including *L. angustata* and *L. auriculata*. The six species *L. botryoides*, *L. crenulata*, *L. pallida*, *L. pallidocrenulata*, *L. parmelioides* and *L. reticulata*, forming three supported sister clades in the 3-loci analysis, clustered in an unsupported clade in the ITS analysis,

FIG. 2. Best-scoring maximum likelihood tree based on an expanded, single-locus ITS data set of *Lobariella* highlighting the position of the Hawaiian species. Branch thickness is proportional to bootstrap support and bootstrap values of ≥70% are indicated below branches. For voucher information see Table 1.


Yoshimuriella subdissecta
Y. fendleri
Y. dissecta
100
99
Lobariella soredians (1)
L. soredians (2)
L. soredians (3)
100
L. pallida (1)
L. pallida (2)
L. pallida (3)
100
70
L. parmelioides (1)
L. parmelioides (3)
L. parmelioides (2)
100
L. crenulata (1)
L. crenulata (2)
L. crenulata (3)
100
100
85
L. pallidocrenulata (1)
L. pallidocrenulata (2)
L. pallidocrenulata (3)
100
L. botryoides (2)
L. botryoides (1)
L. botryoides (3)
100
L. sipmanii (3)
L. sipmanii (2)
L. sipmanii (1)
86
91
L. reticulata (1)
L. reticulata (3)
L. reticulata (2)
93
L. auriculata (1)
L. auriculata (2)
L. auriculata (3)
100
L. pseudocrenulata (1)
L. pseudocrenulata (2)
L. pseudocrenulata (3)
99
97
L. angustata (3)
L. angustata (1)
L. angustata (2)
88
90
L. rugulosa (1)
L. rugulosa (3)
L. rugulosa (2)
91
L. subcrenulata (1)
L. subcrenulata (3)
L. subcrenulata (2)
93
L. flavomedullosa (2)
L. flavomedullosa (1)
L. flavomedullosa (3)
100
L. nashii
L. spathulifera (2)
L. spathulifera (1)
L. spathulifera (3)
100
L. stenroosiae (1)
L. stenroosiae (2)
L. stenroosiae (3)
100
L. sandwicensis (3)
L. sandwicensis (2)
L. sandwicensis (1)
99
90
L. flynniana (1)
L. flynniana (2)
L. robusta (5)
L. robusta (10)
L. robusta (11)
L. robusta (6)
L. robusta (9)
L. robusta (8)
L. robusta (4)
L. robusta (7)
L. robusta (2)
L. robusta (3)
L. robusta (1)
0·02

with the addition of *L. sipmanii* as strongly supported sister to *L. reticulata*. The clade of five species with *L. nashii* in a basal position and comprising the two Hawaiian species was recovered in the ITS analysis but did not have support; this clade further included *L. spathulifera* and *L. stenroosiae*. In both the 3-locus tree and the ITS tree, the sequenced Hawaiian taxa formed a well-supported, monophyletic clade.

The relaxed, uncorrelated, lognormal molecular clock analysis estimated the stem node age of the genus *Lobariella* versus its sister genus, *Yoshimuriella*, at (18–)26(–42) mya, and the crown node age at (11–)17(–28) mya (Fig. 3). In this analysis, the Hawaiian *L. flynniana-sandwicensis* clade diverged from the neotropical *L. flavomedullosa-subcrenulata* clade (1–)8 mya, and the two Hawaiian species *L. flynniana* and *L. sandwicensis* separated from each other (0–)2(–6) mya.

Discussion

For a long time, the neotropical genus *Lobariella* was believed to contain just five species, with only one of them, *L. crenulata*, occurring outside the Neotropics on the Hawaiian Islands (Yoshimura 1984, 1998; Yoshimura & Arvidsson 1994). Molecular phylogenetic revision, in combination with a revised morphological and chemical concept, revealed the existence of more than 25 species in the Neotropics, a five-fold increase (Lumbsch *et al.* 2011; Moncada *et al.* 2013).

Based on this new concept, material reported from Hawaii under the name *Lobariella crenulata* seemed to represent two species, *L. crenulata* s. str. and *L. subcrenulata*, suggesting that the archipelago had been colonized at least twice independently from the Neotropics, with the trade winds as the likely dispersal agent (Geiger *et al.* 2007). However, apart from unsequenced herbarium collections fitting the concept of *L. crenulata sensu* Moncada *et al.* (2013), the present study revealed three species new to science for Hawaii, namely *L. flynniana*, *L. robusta* and *L. sandwicensis* (see below). These three species form a well-supported clade of closely related taxa, with a comparatively long stem branch, suggesting 'micro-radiation' after initial colonization by an ancestor within the group formed by the neotropical species *L. flavomedullosa*, *L. nashii*, *L. subcrenulata* and relatives.

The molecular clock analysis suggests that initial colonization leading to this clade took place between 1–8 mya, with crown divergence at around 2 mya, much later than, for example, in the vascular plant family *Campanulaceae*, estimated at *c.* 13 mya (Givnish *et al.* 2009). The close relationship between other Hawaiian taxa of *Lobariaceae*, in the genera *Crocodia*, *Podostictina* and *Pseudocyphellaria*, and lineages from the Palaeotropics (Moncada *et al.* 2014) supports the notion that colonization of the archipelago by these macrolichens occurred comparatively late, which might explain the absence of large radiations as observed for vascular plant lineages. The Hawaiian lobeliads, with 126 species evolving from a single colonization *c.* 13 mya, display a diversification rate of 0·37 species per million years (calculated from Givnish *et al.* 2009); this rate would produce two species within two million years, suggesting that the diversification rate in Hawaiian *Lobariella* is comparable to that of vascular plants. This view is supported by a recent study of the related genus *Sticta* in Madagascar and the Masquarenes, with a radiation into more than a dozen to *c.* 30 species dating back to the Late Miocene, *c.* 11–5 mya (Simon *et al.* 2016). Hence time of colonization, more than evolutionary constraints, might determine the level of radiation in these lichen fungi. Apart from the fact that successful establishment of epiphytic lichens depends on the prior development of woody vegetation, the reason for late colonization of Hawaii by *Lobariella* and other *Lobariaceae* could be the relatively young age of these lineages: the crown node age estimate for *Lobariella*, with a mean value of 17 mya, is rather close to the initial colonization by Hawaiian lobeliads (13 mya). Thus, at the time when *Lobariella* diversified in the Neotropics, the Hawaiian lobeliads had already colonized the archipelago.

The younger evolutionary age of lichenized lineages could also be a reason why

FIG. 3. Relaxed log-normal molecular clock tree of *Lobariaceae* showing origin and diversification of *Lobariella* including two Hawaiian species. Bars indicate 95% posterior density intervals of the node age estimates. The relative placement of the *Lobaria* fossil (Peterson 2000) is indicated. For voucher information see Table 1.

lichen fungi are much less diverse than vascular plants in general. There are 15 131 species currently recognized in the class Lecanoromycetes (Lücking *et al.* 2017) compared to 335 498 species of vascular plants (Roskov *et al.* 2016), a ratio of 22:1. However, while Lecanoromycetes date back to *c.* (283–) 320(–353) mya (Lücking *et al.* 2009; Amo de Paz *et al.* 2011; Rivas Plata 2011; Prieto & Wedin 2013; Beimforde *et al.* 2014;

Pérez-Ortega *et al.* 2016), vascular plants date back to between 433–513 mya based on the fossil record and molecular clock studies (Edwards & Feehan 1980; Lücking *et al.* 2009; Willis & McElwain 2014; Silvestro *et al.* 2015), an age difference of *c.* 50%. Under such a time difference, comparable diversification rates would partially explain the extant species richness ratio of 22:1. On the other hand, global differences in species richness do not seem to hold at a smaller scale. Thus, while 1386 native vascular plant species are known from Hawaii, our recent phylogenetic studies suggest that the current number of 880 lichenized species listed for the archipelago (Smith 2013) may be a substantial underestimation and the total might well be comparable to that of vascular plants; in *Pseudocyphellaria* the number of species recognized for Hawaii has increased by 70% (Moncada *et al.* 2014), and now in *Lobariella* by 300%. It therefore appears that such comparable species richness in vascular plants and lichens in the archipelago is the result of different evolutionary processes: early and infrequent colonization by vascular plant lineages, with strongly isolated evolutionary histories leading to substantial radiations, versus later and more frequent colonization by lichen fungal lineages, with subsequent divergence but lower levels of radiation. Notably, this was recently shown for Galapagos basidiolichens, which are now recognized as ten endemic species, each derived from an independent, comparatively recent colonization event (Dal Forno *et al.* 2017).

Of the three Hawaiian species of *Lobariella* described as new below, the most remarkable is *L. flynniana*. It forms numerous lateral, much branched and ascending lobules, giving the species a fruticose rather than foliose appearance. Such a phenotype is unknown in any other species of the genus. A comparable situation is found in the Hawaiian *Phaeophyscia laciniata* Essl. (Esslinger 1978) and in the supposedly endemic genus *Ramalinopsis* (Follmann 1974) which represents a foliose species nested within the fruticose genus, *Ramalina*. The phenomenon of developing novel morphotypes on islands is well documented for vascular plants, including the aforementioned genus *Geranium* (Fosberg 1936; Pax *et al.* 1997; Kidd 2005). The very close relationship between the three sequenced Hawaiian *Lobariella* species, in spite of their morphological differences, is also in line with findings for vascular plants. For instance, the species of the silversword alliance, although recognized in three separate genera, are all closely related genetically with differences that, in continental taxa, are usually found within populations of a single species (Baldwin *et al.* 1991; Baldwin & Sanderson 1998; Carlquist *et al.* 2003). Thus, not only evolutionary rates but also other evolutionary phenomena found in vascular plant island biota appear to be expressed in lichen fungi, including levels of endemism.

Comparison of the newly collected and sequenced samples with specimens revised from the US National Herbarium (US), the University of Hawaii at Manoa (HAW), and the National Tropical Botanical Garden (PTBG) revealed that the material we had first identified as *Lobariella subcrenulata* represents the newly described *L. sandwicensis*. Thus, it is questionable whether the material currently identified as *L. crenulata*, which is characterized by a different medullary chemistry dominated by gyrophoric acid (Moncada *et al.* 2013), actually represents that species since morphological similarity in the absence of molecular data can be misleading. If future data show that it is an undescribed species, the different chemistry suggests that this taxon is not related to the *L. flynniana* clade (Moncada *et al.* 2013), which indicates a second, independent colonization of the islands by *Lobariella*. At present, inferred endemism for Hawaiian *Lobariella* is estimated at 75%, compared to zero based on previous, traditional taxonomy. This percentage is exactly the same as inferred for *Pseudocyphellaria* s. lat. (Moncada *et al.* 2014) and is in the same range as for vascular plants (Wagner *et al.* 1999; Eldredge & Evenhuis & 2002; Wagner & Herbst 2002).

Currently, *Lobariella* appears to be a rare genus in Hawaii. In spite of an intensive search, during our fieldwork in 2013 we were able to collect only five specimens during eight days at 14 sites on three of the four largest islands, whereas for *Pseudocyphellaria* s. lat. and *Sticta* we gathered close to 200 samples (Moncada *et al.* 2014). On the Big Island (Hawaii), *L. robusta* has so far been found only at the type locality. It appears that the mostly cyanobacterial species in *Pseudocyphellaria* and *Sticta* can cope better with habitat threats than the green-algal *Lobariella* species, which is supported by the rarity of other green-algal *Lobariaceae* in Hawaii (Magnusson & Zahlbruckner 1943). One of these reported taxa, *Pseudocyphellaria dissimulata*, in reality represents *L. sandwicensis* (see below). Whether the rarity of green-algal, lobarioid lichens is a recent trend or goes further back is difficult to assess. In herbarium collections of *Lobariaceae* from Hawaii revised by us in HAW, PTBG and US, the proportion of cyanobacterial *Pseudocyphellaria* and *Sticta* specimens (193) was also substantially higher than *Lobariella* (13) but field observations from the late 1970s suggest that *Lobariella* was more abundant at that time. In the light of the results presented here, it appears necessary to raise awareness of Hawaiian cryptogams in terms of conservation. If we assume that many other lichen groups show similar evolutionary histories, with high inferred endemism, conservation of Hawaiian lichens (Smith 1991) takes on an entirely new dimension. Much research is needed to understand the evolution of Hawaiian cryptogams so the rare and endemic species can be conserved where necessary.

Taxonomic Treatment

Lobariella crenulata (Hook. f.) Yoshim.

Notes. This species was reported from Hawaii by Yoshimura (1984, 1998) and Yoshimura & Arvidsson (1994) but many collections revised by us belong to the newly described *Lobariella sandwicensis* (see below). Only five collections have the morphology and chemistry characteristic of *L. crenulata* (Moncada *et al.* 2013) but fresh material is required to confirm this identification with molecular data. Given that *L. sandwicensis* is similar to the neotropical *L. subcrenulata* in morphology and chemistry, but represents a phylogenetically distinct species, it is not unlikely that the Hawaiian material of *L. crenulata* represents a distinct lineage as well.

Specimens examined. **USA:** *Hawaii*: Hawaii, Waimea, Keck Observation Office, roadside tree, 30 ix 2008, *C. W. Smith* s. n. (HAW); Kauai, Kokee Park, Kalalau Lookout area, 1200 m, dry upland scrub forest, 1965, *M. E. Hale* 31684 (US); Kauai, Waimea, Na Pali-Kona Forest Reserve, Koaie Canyon, 900 m, mixed forest, on exfoliating bark of *Dodonaea*, 1996, *T. Flynn et al.* 5933 (PTBG); Kauai, Waimea, Kokee State Park, Kalalau Valley, *T. Flynn* 3890 (PTBG); Maui, East Maui, Makawao Forest Reserve, below Puu Nianiau, 1800 m, over moss on *Myrsine* trunk, 1975, *C. W. Smith* 1962 (HAW).

Lobariella flynniana Lücking, Moncada & C. W. Sm. sp. nov.

MycoBank No.: MB 820526

ITS barcoding sequence: KY769446, KY769447 (isotype)

Differing from *Lobariella subcrenulata* in the delicate thallus with numerous, richly branched, lateral lobules.

Type: USA, Hawaii, Kauai, West Kauai, western slopes of Mount Waialeale, Kokee State Park, 20 km ENE of Waimea and 35 km NW of Lihue, at end of Kokee Road, Pihea Trail, 22°08'51"N, 159°37'53"E, 1250–1350 m, mostly undisturbed montane mesic forest, 15 June 2013, *B. Moncada, R. Lücking & T. Flynn* 7028 (F—holotype; PTBG—isotype).

(Fig. 4A–C)

Thallus growing on tree branches, up to 5 cm diam., except for the primary lobes loosely attached and ascending, appearing subfruticose; *photobiont* green (presumably *Dictyochloropsis* s. lat. clade 2 according to Dal Grande *et al.* (2014)). *Primary lobes* up to 1 cm long, with irregular, crenulate to incised apices, 1–3 mm wide, much branched laterally and dividing into numerous, ascending, irregularly oriented lobules 0·2–0·5 mm wide giving the thallus a subfruticose appearance. *Upper surface* light green when hydrated, pale green-grey to yellowish grey when dry, smooth; maculae

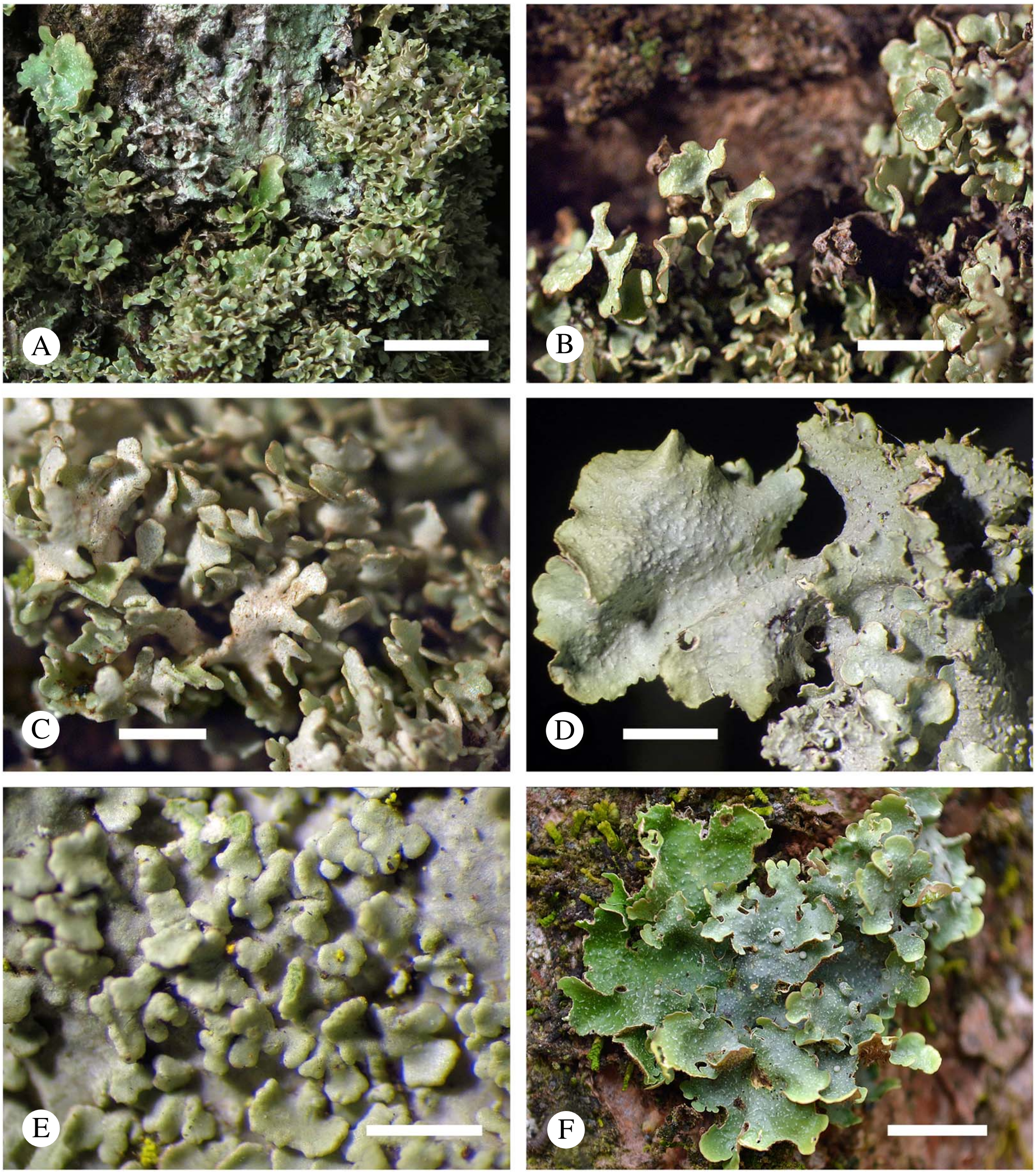


FIG. 4. A–C, *Lobariella flynniana* (holotype); A, thallus *in situ*; B & C, marginal lobules enlarged. D & E, *L. robusta* (holotype); D, thallus lobes; E, phyllidia enlarged. F, *L. sandwicensis*, thallus *in situ*. Scales: A & D = 5 mm; B, C & E = 1 mm; F = 10 mm. In colour online.

absent; *pseudocyphellae* present, initially (at lobe margins) visible as irregular, white lines or dots up to 0·10 × 0·05 mm in size, becoming elongate-linear up to 0·3 × 0·1 mm. Genuine *isidia* or *phyllidia* absent, except for the much branched, ascending lateral lobules. *Lower surface* cream-coloured to white; primary lobes except near the margin with a short, dense, cream-coloured tomentum formed of up to 20 µm long hyphae composed of globose cells up to 5 µm diam., and discrete, up to 0·5 mm long and

0·1 mm wide, cream-coloured rhizines composed of strongly agglutinated, parallel hyphae; *rhizines* unbranched to sparsely branched at the tip and covered with tomentum in the thallus centre; lower surface of lateral lobules glabrous or with short, white tomentum formed of up to 15 µm long hyphae composed of globose cells up to 5 µm diam. *Upper cortex* paraplectenchymatous, 15–20 µm thick with 3–5 µm thick epicortex, formed of 2–3 cell layers; algal layer 15–20 µm thick; *medulla* 50–80 µm thick; lower cortex paraplectenchymatous, 7–10 µm thick, formed of 2–3 cell layers.

Apothecia and *pycnidia* not observed.

Secondary chemistry. Chemosyndrome B (according to Moncada *et al.* 2013): cortex with pseudocyphellarin A (minor to trace), K+ yellow; medulla with *Lobariella* unidentified 3 (major), 4-*O*-methyl-gyrophoric acid (major), gyrophoric acid (minor or trace), and *Lobariella* unidentified 2 (minor), K+ emerald green to sordid yellow, C−.

Etymology. With great pleasure, we dedicate this new species to Timothy Flynn, Herbarium Collections Manager at the National Tropical Botanical Garden on Kauai, for his invaluable assistance and his keen eye in finding the rarest Hawaiian lichens.

Ecology. *Lobariella flynniana* is thus far known only from the type collection in montane mesic forest on West Kauai. It was found growing exposed to frequent fog on the stem of a small tree in a semi-exposed situation.

Notes. This species is readily distinguished from all other species of the genus by the small, delicate thallus producing numerous, richly branched, lateral lobules giving the lichen a subfruticose appearance, a unique morphology among *Lobariella* species.

Lobariella robusta Lücking, Moncada & C. W. Sm. sp. nov.

MycoBank No.: MB 820527

ITS barcoding sequences: KY769461, KY769462 (isotype)

Differing from *Lobariella nashii* and *L. stenroosiae* in the broad, squamiform, mostly unbranched phyllidia and the robust, rather thick thallus.

Type: USA, Hawaii, Hawaii, Waimea, Keck Observation Headquarters, 20°01'25"N, 155°39'55"E, 822 m, corticolous on *Metrosideros polymorpha*, 27 September 2016, *C. W. Smith* CWS05 (HAW—holotype; B, F—isotypes).

(Fig. 4D & E)

Thallus growing on tree trunks, up to 5 cm diam., rather closely attached; *photobiont* green (presumably *Dictyochloropsis* s. lat. clade 2 according to Dal Grande *et al.* (2014)). *Primary lobes* up to 2 cm long, with rounded, incised apices, 5–10 mm wide. *Upper surface* light green when hydrated, pale green-grey to yellowish grey when dry, smooth; maculae absent; *pseudocyphellae* present, initially (at lobe margins) visible as irregular, white lines or dots up to 0·10 × 0·05 mm in size, becoming elongate-linear up to 0·5 × 0·1 mm. *Phyllidia* present and abundant, laminal, squamiform, obliquely arranged or bent down to the surface in more or less the same direction, dorsiventral, with both sides corticate but the underside darker, 0·3–1·0 mm long and broad, rounded to flabellate or fan-shaped when larger, unbranched or apically crenulate or shallowly branched. *Lower surface* cream-coloured to light brown; primary lobes with a short, dense, cream-coloured tomentum formed of up to 30 µm long hyphae composed of globose cells up to 5 µm diam., and discrete, up to 1 mm long and 0·15 mm wide, white to cream-coloured rhizines composed of strongly agglutinated, parallel hyphae; *rhizines* unbranched to sparsely branched at the tip and covered with tomentum in the thallus centre. *Upper cortex* paraplectenchymatous, 15–25 µm thick with 3–5 µm thick epicortex, formed of 2–3 cell layers; algal layer 20–30 µm thick; *medulla* 50–100 µm thick; lower cortex paraplectenchymatous, 10–15 µm thick, formed of 2–3 cell layers.

Apothecia frequent, cup-shaped, up to 2 mm diam., with thick, strongly prominent, lobulate, grey to cream-coloured margins; lobules 5–10 per apothecium, more or less regular with rounded or rarely bifurcate tips; *disc* concave, dark red-brown. *Excipulum* composed of more or less parallel, partly branched hyphae with wide lumina resembling a paraplectenchyma, 30–40 µm wide, hyaline; *hypothecium* formed of densely intricate hyphae partially resembling a paraplectenchyma, 15–25 µm high, pale yellowish. *Hymenium* 100–120 µm high, clear, with orange, strongly conglutinated, 10–20 µm high epithecium; *asci* narrowly clavate, 100–120 × 10–13 µm. *Ascospores* narrowly fusiform, 70–80 × 3–4 µm, 7-septate, hyaline.

Pycnidia not observed.

Secondary chemistry. Chemosyndrome B (according to Moncada *et al.* 2013): cortex with pseudocyphellarin A (minor to trace), K+ yellow; medulla with *Lobariella* unidentified 3 (major), 4-*O*-methyl-gyrophoric acid (major), gyrophoric acid (minor or trace) and *Lobariella* unidentified 2 (minor), K+ emerald green, C−.

Etymology. The epithet refers to the rather robust, leathery thallus of this species.

Ecology. This species is known from a single, well-developed population on the island of Hawaii, in mesic, open-landscaped parkland where it grows together with *Lobariella crenulata*.

Notes. *Lobariella robusta* agrees with the neotropical, related species *L. nashii* and *L. stenroosiae* (Moncada *et al.* 2013) in producing dorsiventral phyllidia and in the secondary chemistry. However, in the last two species the phyllidia are laciniate and sparsely to frequently branched, whereas in *L. robusta* they are broadly squamiform and mostly unbranched. Also, the thallus is more robust and leathery in *L. robusta*. In spite of the morphological differences, the species is very closely related to the marginally lobed *L. flynniana*, differing only in two consistent indels in the ITS.

Additional specimens examined. **USA:** *Hawaii*: Hawaii, Waimea, Keck Observation Office, roadside tree, 30 ix 2008, *C. W. Smith* s. n. (F, HAW); Hawaii, Waimea, Keck Observation Headquarters, 20°01'25"N, 155°39'55"E, 822 m, corticolous on *Metrosideros polymorpha*, 2016, *C. W. Smith* CWS06, CWS10 (B, HAW), CWS07, CWS08, CWS09, CWS11, CWS12 (B).

Lobariella sandwicensis Lücking, Moncada & C. W. Sm. sp. nov.

MycoBank No.: MB 820528

ITS barcoding sequence: KY769448 (isotype)

Differing from *Lobariella subcrenulata* in the smaller thallus with narrower lobes.

Type: USA, Hawaii, Kauai, West Kauai, western slopes of Mount Waialeale, Kokee State Park, 20 km ENE of Waimea and 35 km NW of Lihue, at end of Kokee Road, Pihea Trail, 22°08'51"N, 159°37'53"E, 1250–1350 m, mostly undisturbed montane mesic forest, 15 June 2013, *B. Moncada, R. Lücking & T. Flynn* 7029 (F—holotype; PTBG—isotype).

(Fig. 4F)

Thallus growing on tree trunks, up to 10 cm diam., more or less closely attached; *photobiont* green (presumably *Dictyochloropsis* s. lat. clade 2 according to Dal Grande *et al.* (2014)). *Individual lobes* up to 5 cm long, with irregular to almost rounded apices and irregular to crenate-lobate margins, 3–8 mm wide, irregularly branched, forming more or less rounded thallus rosettes. *Upper surface* bright green when hydrated, pale green-grey when dry, smooth except for the erumpent pseudocyphellae; maculae absent; *pseudocyphellae* present, initially (at lobe margins) visible as irregular, white lines or dots up to 0·10 × 0·05 mm in size, becoming elongate-linear up to 0·5 × 0·1 mm. *Isidia* or *phyllidia* absent. *Lower surface* cream-coloured, becoming grey-brown towards the centre, with a short, dense, cream-coloured to pale brown tomentum formed of up to 30 µm long hyphae composed of globose cells up to 5 µm diam., and discrete, up to 1 mm long and 0·1 mm wide, cream-coloured to pale brown rhizines composed of strongly agglutinated, parallel hyphae; *rhizines* unbranched to sparsely branched at the tip and covered with tomentum in the thallus centre. *Upper cortex* paraplectenchymatous, 15–25 µm thick with a 3–5 µm thick epicortex, formed of 3–4 cell layers; algal layer 15–25 µm thick; *medulla* 60–100 µm thick; lower cortex paraplectenchymatous, 7–15 µm thick, formed of 2–3 cell layers.

Apothecia rare, cup-shaped, up to 3 mm diam., with thick, strongly prominent, lobulate, grey to cream-coloured margins; lobules 5–10 per apothecium, more or less regular with rounded or rarely bifurcate tips; *disc* concave, orange-brown. *Excipulum* composed of more or less parallel, partly branched hyphae with wide lumina resembling a paraplectenchyma, 30–50 µm wide, hyaline; *hypothecium* formed of densely intricate hyphae partially resembling a paraplectenchyma, 15–25 µm high, pale yellowish. *Hymenium* 100–120 µm high, clear, with a yellow-orange, strongly conglutinated, 10–20 µm high epithecium; *asci* narrowly clavate, 100–120 × 10–13 µm. *Ascospores* narrowly fusiform, 50–70 × 3·5–4·5 µm, 7-septate, hyaline.

Pycnidia not observed.

Secondary chemistry. Chemosyndrome B (according to Moncada *et al.* 2013): cortex with pseudocyphellarin A (major to trace), K+ yellow; medulla with *Lobariella* unidentified 3 (major), 4-*O*-methyl-gyrophoric acid (major), gyrophoric acid (minor or trace) and *Lobariella* unidentified 2 (minor), K+ emerald green, C−.

Etymology. The epithet points out the inferred endemism of this new species, using the historical name of the Sandwich Islands for Hawaii.

Ecology. *Lobariella sandwicensis* appears to be the most common species of the genus in Hawaii. It occurs in mesic montane forest in shaded to semi-exposed situations and is known, at least based on earlier and historical collections, from the islands of Kauai, Maui and Oahu. It has not been found on the island of Hawaii, where *L. robusta* occurs.

Notes. *Lobariella sandwicensis* is very similar in morphology to the neotropical, related species *L. subcrenulata* and it shares the same chemistry. It tends to produce smaller thalli with narrower lobes but without molecular data such a difference would be considered infraspecific or ontogenetic variation. While both species belong in the same clade within the genus, the differences in the ITS barcoding locus are substantial, as shown by the long branch leading to the Hawaiian *Lobariella* clade (Fig. 2).

Additional specimens examined. **USA:** *Hawaii*: unknown locality, *H. Mann & W. T. Brigham* s. n. (US); Kauai, on ridge W of Hanapepe River, 1895, *A. A. Heller* 2754 (US); Kauai, boundary of Hanalei and Waimea, Awaawapuhi Trail, 1200 m, *T. Flynn* 4774b (PTBG); Kauai, Waimea, 1905, *Hochreutiner* 3514 (G; as *Sticta dissimulata* Nyl.); Kauai, Waimea, Kokee State Park, Ditch Trail, 1100 m, summer dry forest, epiphytic on small branches of *Dodonaea viscosa*, 1991, *T. Flynn & M. Chapin* 4640 (PTBG); Kauai, Waimea District, Kokee State Park, from the yard of John H. R. Plews, Mohilhi Road, 1109 m, epiphytic on dead stems of *Dubautia latifolia*, 1996, *T. Flynn, M. Thom & J. H. R. Plews* 5971 (PTBG); Kauai, West Kauai, western slopes of Mount Waialeale, Kokee State Park, 20 km ENE of Waimea and 35 km NW of Lihue, at end of Kokee Road, Pihea Trail, 22°08'51"N, 159°37'53"E, 1250–1350 m, mostly undisturbed montane mesic forest, 2013, *B. Moncada, R. Lücking & T. Flynn* 7027 (F); Kauai, West Kauai, western slopes of Mount Waialeale, Kokee State Park, Awaawapuhi Trail, bottom of trail, corticolous on *Dodonaea*, 1981, *C. W. Smith* 6188 (HAW); Kauai, Waimea District, Na Pali-Kona Forest Reserve, "Pig Ridge", SE of Waialae Stream, 3300–3600 ft., *Acacia koa* forest with *Metrosideros*, *Panicum*, *Bidens*, badly damaged by pig rooting, epiphytic on *Metrosideros polymorpha*, 1993, *T. Flynn & G. Kawakami* 5456, 5456a (PTBG); Kauai, Waimea, Na Pali-Kona Forest Reserve, Kohua Ridge, 1140 m, *Metrosideros* dominated forest, with *Cheirodendron*, *Melicope*, *Myrsine*, *Elaeocarpus*, *Dianella*, *Dryopteris*, *Athyrium*, and *Asplenium*, on *Vaccinium calycinum*, 1995, *T. Flynn et al.* 5695 (PTBG); Maui, East Maui, Haleakalā Volcano, Lower Waikamoi Preserve (The Nature Conservancy), 5 km SE of Pulakani and 18 km SE of Kahului, lower access trail to preserve off Olinda Road, 20°48'23"N, 156°15'19"E, 1200–1300 m, disturbed primary forest dominated by *Acacia koa* and *Campanulaceae*, with invasive *Hedychium gardnerianum* in lower portions, 2013, *B. Moncada, R. Lücking & P. Bily* 6940a (F); Maui, East Maui, Haleakalā Volcano, Haleakalā Crater, Paliku, 2120 m, on *Sophora chrysophylla*, *C. W. Smith* 2971 (HAW); Maui, West Maui, Pu'u Kukui, trail from cabin to summit, 1300–1700 m, mossy forest to alpine bog, 1965, *M. E. Hale* 31259, 31287, 31290 (US); Oahu, Waianae Range, Land of 10 000 Snails, just about "snail jail", 730 m, on *Pisonia*, 30 vi 2011, *C. W. Smith* s. n. (HAW); Oahu, Waianae Range, Pu'u Kaua, on *Schinus terebinthifolius*, *C. W. Smith* 1559 (HAW); Oahu, unknown locality, *E. Bailey* s. n. (US); Oahu, unknown locality, *H. Mann & W. T. Brigham* s. n. (US).

Key to Hawaiian species of *Lobariella*

1 Thallus proliferating with numerous, much-branched marginal lobules, making the thallus appear subfruticose; chemosyndrome B according to Moncada *et al.* (2013), medulla C−, K+ emerald green; Kauai . . . . **L. flynniana**
Thallus regularly foliose; chemistry and distribution variable 2

2(1) Thallus with numerous laminal, squamiform phyllidia; chemosyndrome B, medulla C−, K+ emerald green; Hawaii (Big Island) . . . . **L. robusta**
Thallus lacking phyllidia; chemistry and distribution variable 3

3(2) Secondary chemistry of chemosyndrome A according to Moncada *et al.* (2013), medulla C+ distinctly pink-red, K+ yellow; thallus rather robust; widespread . . . . **L. crenulata**
Secondary chemistry of chemosyndrome B, medulla C−, K+ emerald green; thallus rather delicate; Kauai, Maui, Oahu (not known from Hawaii). . . . . **L. sandwicensis**

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