
The *Sticta filix* morphodeme (Ascomycota: Lobariaceae) in New Zealand with the newly recognized species *S. dendroides* and *S. menziesii*: indicators of forest health in a threatened island biota?

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Abstract: We present a phylogenetic revision of the *Sticta filix* morphodeme in New Zealand. This non-monophyletic group of early diverging clades in the genus *Sticta* is characterized by a stalked thallus with a green primary photobiont and the frequent formation of a dendriscocauloid cyanomorph. Traditionally, three species have been distinguished in New Zealand: *S. filix* (Sw.) Nyl., *S. lacera* (Hook. f. & Taylor) Müll. Arg. and *S. latifrons* A. Rich., with two cyanomorphs separated under the names *Dendriscocaulon dendriothamnodes* Dughi ex D. J. Galloway (traditionally associated with *S. latifrons*) and *D. dendroides* (Nyl.) R. Sant. ex H. Magn. (traditionally associated with *S. filix*). *Sticta lacera* was not included in the present study due to the lack of authentic material (all specimens originally identified under that name and sequenced clustered with *S. filix*); *S. filix* was confirmed as a distinct species whereas *S. latifrons* s. lat. was shown to represent two unrelated species, *S. latifrons* s. str. and the reinstated *S. menziesii* Hook. f. & Taylor. The cyanomorphs of *S. filix* and *S. latifrons* are not conspecific with the types of the names *D. dendriothamnodes* and *D. dendroides*, respectively; the *D. dendriothamnodes* cyanomorph belongs to the Australian taxon *Sticta stipitata* C. Knight ex F. Wilson, which is not present in New Zealand, whereas the *D. dendroides* cyanomorph corresponds to a previously unrecognized species with unknown chloromorph, recombined here as *Sticta dendroides* (Nyl.) Moncada, Lücking & de Lange. Thus, instead of three species (*S. filix*, *S. lacera*, *S. latifrons*) with their corresponding cyanomorphs, five species are now distinguished in this guild in New Zealand: *S. dendroides* (cyanomorph only), *S. filix* (chloro- and cyanomorph), *S. lacera* (chloromorph only), *S. latifrons* (chloro- and cyanomorph) and *S. menziesii* (chloro- and cyanomorph). A key is presented for identification of the chloromorphs and the dendriscocauloid cyanomorphs of all species. Semi-quantitative analysis suggests that species in this guild are good indicators of intact forest ecosystems in New Zealand and that the two newly recognized species, *S. dendroides* and *S. menziesii*, appear to perform particularly well in this respect. The use of lichens as bioindicators of environmental health is not yet established in New Zealand and so, based on our results, we make the case to develop this approach more thoroughly.

Key words: Australia, ITS barcoding locus, lichens, photosymbiodemes, species recognition

Accepted for publication 19 July 2017

Introduction

Lobariaceae species are among the most conspicuous macrolichens (Galloway 1985,

2007; Brodo *et al.* 2001; Wirth *et al.* 2013; Stenroos *et al.* 2016). They are usually found in wet, temperate to tropical ecosystems. Currently, 466 species are accepted in 12

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genera (Galloway & Elix 2013; Moncada *et al.* 2013a; Galloway 2015; Jaklitsch *et al.* 2016; Lücking *et al.* 2017). Except for tropical species of *Sticta* (Schreb.) Ach., the family is richest in the Southern Hemisphere (Galloway *et al.* 1995; Galloway 2001) and has been particularly well studied in New Zealand with 66 species currently accepted (Galloway 2007). These correspond to ten genera under the current genus concept, two of them (*Ricasolia* De Not. and *Yoshimuriella* Moncada & Lücking) requiring confirmation (see below) and two, namely *Dendricosticta* Moncada & Lücking and *Lobariella* Yoshim., being absent from the country (Moncada *et al.* 2016). Additional species have been reported from oceanic possessions of New Zealand (de Lange & Galloway 2015).

Lichens have long been used as bioindicators and species in *Lobariaceae* are excellent indicators of forest health (Rose 1974, 1976, 1992; Selva 1994, 1996; Zedda 2002). A prime example is *Lobaria pulmonaria* (L.) Hoffm., which has been extensively studied in this respect in Europe and North America (Søchting & Christensen 1989; Gauslaa 1994; McCune 2000; Campbell & Fredeen 2004; Kalwij *et al.* 2005; Jüriado & Liira 2009; Scheidegger 2009; Nascimbene *et al.* 2010; Gustafsson *et al.* 2013; Cansaran-Duman *et al.* 2015; Giorgio *et al.* 2015). Other *Lobariaceae* considered rare and threatened by land use change in the Northern Hemisphere, including *Sticta fuliginosa* (Dicks.) Ach., *S. limbata* (Sm.) Ach. and *S. sylvatica* (Huds.) Ach. (Hodkinson *et al.* 2014; Magain & Sérusiaux 2015), offer similar potential for bioindication of ecological continuity. Recent phylogenetic studies have shown that species concepts in these taxa require critical revision (Moncada *et al.* 2014a; Magain & Sérusiaux 2015), which will have an influence on their use as bioindicators.

In the tropics and the Southern Hemisphere, *Lobariaceae* have been used or mentioned as potential bioindicators of forest health based on studies in Cuba (Rosabal *et al.* 2010), Colombia (Simijaca-Salcedo *et al.* 2014; Ramírez-Morán *et al.* 2016), French Guiana (Normann *et al.* 2010), Chile (Galloway 1992) and Thailand (Wolseley *et al.* 1994). Despite a wealth of literature dealing with *Lobariaceae*

(Galloway 1985, 1988, 2007; de Lange *et al.* 2012; de Lange & Galloway 2015), New Zealand lags behind in using lichens (and especially *Lobariaceae*) for conservation monitoring (Galloway 2008; de Lange *et al.* 2012). This is all the more remarkable considering that New Zealand's native ecosystems, like many other island biotas, have been and continue to be severely affected by humans and invasive plants and animals (Atkinson 1989; Holdaway 1989; King 1990; Anderson 2002; Worthy & Holdaway 2002; Tennyson & Martinson 2006; Prebble & Wilmshurst 2009; de Lange *et al.* 2010; Brown *et al.* 2015).

Hutcheson *et al.* (1999) provided a summary of the use of bioindicators in New Zealand as a means of determining ecosystem health, pointing out the general lack of studies and near absence of work with lichens; observations confirmed by Galloway (2008). De Lange *et al.* (2012) published the first ever threat assessment for the New Zealand lichen biota, including their lichenicolous fungi, noting that for lichens assessed as 'threatened' or 'at risk', ecosystem degradation and habitat loss were significant factors in causing their decline. The majority of New Zealand's lichen biota listed by de Lange *et al.* (2012) were assessed as 'data deficient', one of the issues being the correct application of names, especially of presumably cosmopolitan or predominantly Northern Hemisphere lichens thought to occur in New Zealand, including those in *Lobariaceae*.

Only a small number of studies have so far addressed the problem of species recognition in lichen fungi in New Zealand with molecular techniques (Summerfield *et al.* 2002; Thomas *et al.* 2002; Parnmen *et al.* 2012, 2013; Buckley *et al.* 2014; Hayward *et al.* 2014; Myles 2014; Pino-Bodas *et al.* 2015). Multi-locus approaches or studies using the ITS barcoding locus (Schoch *et al.* 2012) have shown that species delimitation in *Lobariaceae* is complex and that names globally applied to certain morphotypes, such as *Pseudocyphellaria crocata* (L.) Vain., *Sticta dichotoma* Bory and *S. fuliginosa*, represent numerous lineages (Magain *et al.* 2012; Moncada *et al.* 2014a, b; Magain & Sérusiaux 2015). As *Lobariaceae* are

conspicuous lichens within the majority of New Zealand's ecosystems and have tremendous potential for use as bioindicators, testing current species delimitations (Galloway 1985, 1988, 1997, 2007) using molecular data is critically needed, enabling accurate quantitative studies to establish monitoring protocols with these lichens.

Here we focus on the *Sticta filix* morphodeme, pedunculate species of *Sticta* that associate with green-algal primary photobionts but often form dendriscocauloid photomorphs with cyanobacterial secondary photobionts. This enigmatic *Sticta-Dendriscocaulon* morphodeme is restricted to the Southern Hemisphere, being replaced in the tropics and the Northern Hemisphere by other genera with morphologically similar cyanobionts, such as *Dendriscosticta*, *Ricasolia* and *Yoshimuriella* (Tønsberg & Goward 2001; Stenroos *et al.* 2003; Takahashi *et al.* 2006; Moncada *et al.* 2013a; Tønsberg *et al.* 2016). Although *Ricasolia* (with *R. adscripta* (Nyl.) Nyl.) and *Yoshimuriella* (with *Lobaria dictyophora* (Müll. Arg.) D. J. Galloway) are possibly present in New Zealand (Moncada *et al.* 2016), they do not form dendriscocauloid cyanomorphs; *L. dictyophora* has been suggested to be included in the *L. peltigera* group (= *Yoshimuriella*; Moncada *et al.* 2013a) by Galloway (2007), but differs in its primary cyanobacterial photobiont (which is why it would not be expected to form a dendriscocauloid cyanomorph) and its chemistry, lacking gyrophoric acid (Galloway 1985, 2007).

In New Zealand, the *S. filix* morphodeme is found in temperate rainforests, mostly in shaded microhabitats growing near the base or on the lower part of large trees among bryophytes, small ferns and other small, shade-tolerant plants. Galloway (1985, 1988, 1997, 2007) listed three species of this 'guild' for New Zealand: *S. filix* (Sw.) Nyl., *S. lacera* (Hook. f. & Taylor) Müll. Arg. and *S. latifrons* A. Rich. Of these, *S. filix* and *S. latifrons* form large, conspicuous lichens whereas *S. lacera* is comparatively small and easily overlooked or mistaken for *Pseudocyphellaria multifida* with which it often co-occurs. *Sticta lacera* is presumed to be endemic for New Zealand while the other

two species have been reported from (south-) eastern Australia (Galloway 2001). To provide a solid base for the use of this guild and its photomorphs as bioindicators, we assessed its phylogenetic relationships and species delimitation using a combination of molecular (ITS barcoding locus) and morphological data.

Materials and Methods

Fieldwork was undertaken by BM, RL and PDL, accompanied in part by D. Blanchon, in February 2015 on New Zealand's North Island, visiting a total of 33 sites (Table 1, Fig. 1). 1084 specimens were collected, 745 of which were *Lobariaceae*; all specimens were photographed *in situ* and then curated for voucher documentation with small pieces of medulla used for DNA extraction. Specimens were deposited in AK and UNITEC, with duplicates in B and F. At the Field Museum, dried *Lobariaceae* specimens were scanned by HR, both upper and lower side, yielding 1374 high resolution images (352 for *Sticta*), for assessment of morphometric characters such as lobe width, internode length, cyphellae diameter, as well as other morphological features. Additional images, particularly of dendriscocauloid morphs, were taken at the Botanic Garden and Botanical Museum (BGBM) with a SONY Cybershot G digital camera attached to a Zeiss Zoom 2000 dissecting microscope. Morphological and anatomical characters were further assessed using Leica MS5 and Motic K400 dissecting microscopes and Zeiss Axioscop 2 VistaVision VWR V036 compound microscopes. Material representing the *Sticta filix* morphodeme was initially identified with the five names provided by Galloway (2007), namely the chloromorphs as *S. filix*, *S. lacera* and *S. latifrons*, and the cyanomorphs as *Dendriscocaulon dendriothamnodes* and *D. dendroides*.

DNA extraction and sequencing were performed by BM at the Pritzker Laboratory for Molecular Systematics and Evolution at the Field Museum. Sequences of the internal transcribed spacer (ITS) were targeted for all specimens of the *Sticta filix* morphodeme and 52 new sequences were generated for this study. DNA was extracted using the SIGMA REDEExtract-N-Amp Plant PCR Kit (St. Louis, Missouri, USA). Dilutions of 10:1 up to 10:2 were used for PCR amplifications with the primer pairs ITS1F and ITS4 (Gardes & Bruns 1993; White *et al.* 1990). 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 each at 95 °C, 52 °C and 73 °C with 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

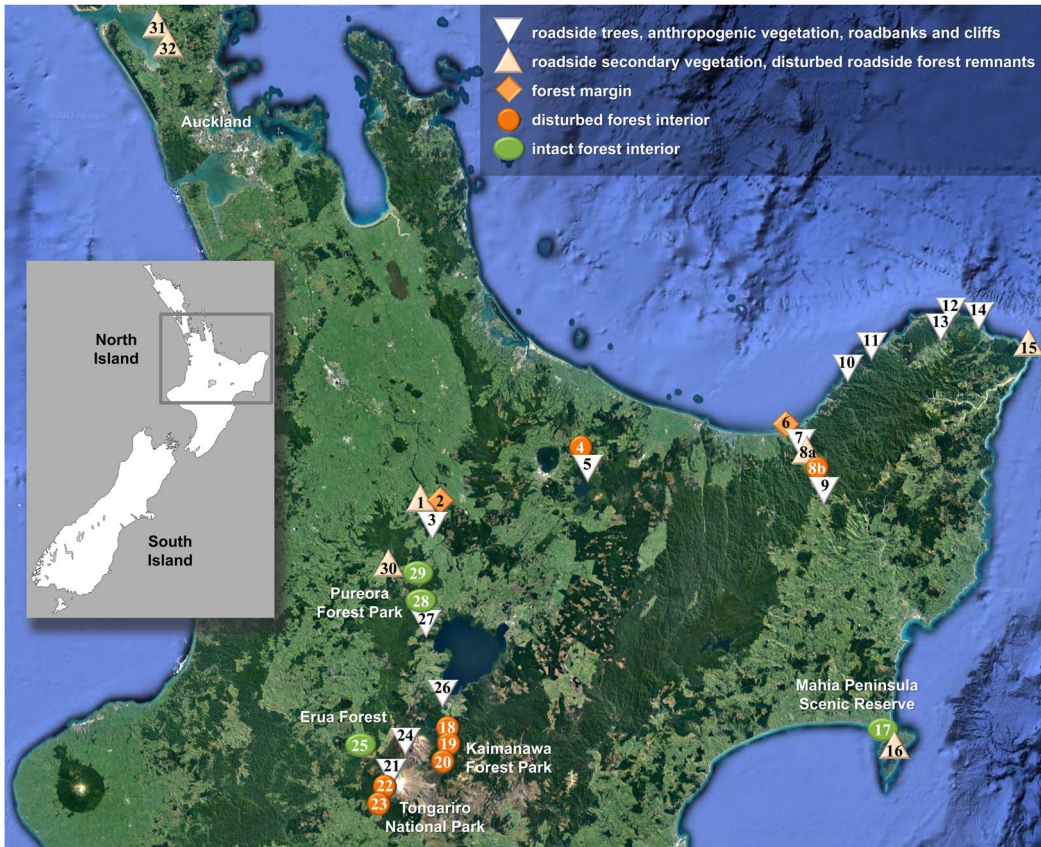


FIG. 1. Map showing location of sites visited for this study on New Zealand's North Island plotted on a Google Earth satellite map depicting forest cover (<https://www.google.com/earth/>; ©Nasa, TerraMetrics). Symbols correspond to conservation status categories as indicated in legend. The site numbers correspond to those in Table 1. In colour online.

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 dH₂O, 2 µl of 3 M Napa 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 submitted to GenBank (Table 2).

The obtained sequences were aligned with 16 additional sequences of related *Sticta* species from GenBank (Table 2), using the *S. caliginosa* D. J. Galloway-*S. marginifera* Mont. clade as outgroup (Moncada *et al.* 2014a). The alignment was assembled in BioEdit 7.2.5 (Hall 1999) and the final alignment was made with MAFFT 7.244 (Katoh *et al.* 2002, 2009) using the [-auto] option. The final alignment included 67 ingroup

OTUs and was 626 bases long. Sequences obtained from specimens originally identified as *S. lacera* were shown to be conspecific with *S. filix* and the only available sequence in GenBank labelled with that name also clustered with *S. filix*. Hence, our dataset for this morphodeme presumably represented only two species, *S. filix* and *S. latifrons*, with their corresponding cyanomorphs whereas *S. lacera* might not be a good species but instead a depauperate ecomorph of *S. filix*. Phylogenetic analysis was performed using maximum likelihood in RAxML 8.2.8 (Stamatakis 2015) applying the GTR-Gamma model and 1000 bootstrap replicates. The resulting trees were visualized in FigTree 1.4.2 (Drummond & Rambaut 2007).

Based on structural and floristic characteristics (closed forest cover, tree composition, extension, proximity to roads or urban areas), the 33 sites were classified into five conservation status categories (Table 1, Fig. 2): strongly disturbed (category 1), moderately disturbed (2), intermediate (3), slightly disturbed (4) and intact (5). For each

TABLE 1. Sites visited for this study on New Zealand's North Island, including coordinates (Lat., Long.), altitude, vegetation type and habitat, conservation status (Stat), and number of lichen specimens (Spec) collected at each site. The site numbers correspond to those in Fig. 1.

No.	Region	Site name	Lat.	Long.	Altitude (m)	Vegetation type	Habitat	Stat	Spec
1	Waikato	Waipapa Road at W. River bridge	-38-28	175-68	180–190	<i>Phyllocladus trichomanoides</i> - <i>Kunzea robusta</i> forest	disturbed forest edge	2	42
2	Waikato	Waipapa Road at W. River bridge	-38-28	175-68	185	<i>Phyllocladus trichomanoides</i> - <i>Kunzea robusta</i> forest	disturbed forest edge	3	3
3	Waikato	Lake Maraetai at Waipapa Dam, above Waikato River	-38-29	175-68	195	Whakamaru Ignimbrite Cliffs	open roadbank running along exposed cliff	1	11
4	Bay of Plenty	Lake Okataina Road	-38-08	176-41	140	<i>Dacrydium cupressinum</i> - <i>Beilschmiedia tawa</i> forest	shady forest edge	4	29
5	Bay of Plenty	Lake Okataina Foreshore, Tauranganui Bay	-38-10	176-43	320	seral vegetation dominated by <i>Weinmannia racemosa</i> and <i>Cordyline australis</i>	exposed, planted trees along beach near lodge	1	31
6	Bay of Plenty	Toatoa to Motu Road	-38-04	177-44	80–90	podocarp forest dominated by <i>Podocarpus totara</i> , <i>Prumnopitys taxifolia</i> and <i>Dacrycarpus dacrydioides</i>	shady forest edge along road	3	22
7	Bay of Plenty	Toatoa to Motu Road	-38-05	177-45	85	fractured greywacke (siltstone facies) supporting dense bryophyte mats and seedlings	open roadbank	1	10
8a	Bay of Plenty	Toatoa to Motu Road	-38-06	177-46	85	<i>Dacrydium cupressinum</i> - <i>Beilschmiedia tawa</i> forest	roadside open forest	2	17
8b	Bay of Plenty	Toatoa to Motu Road	-38-06	177-46	85	<i>Dacrydium cupressinum</i> - <i>Beilschmiedia tawa</i> - <i>Fuscospora truncata</i> forest	shady forest edge along road and shady roadbank	4	20
9	Bay of Plenty	Toatoa to Motu Road	-38-09	177-49	450	fractured greywacke (siltstone facies) supporting dense bryophyte and lichen mats and seedlings	scrub with rocky outcrops	1	9
10	Bay of Plenty	State Highway 35 near Omaio Bay	-37-77	177-68	0–10	<i>Metrosideros excelsa</i> coastal forest	<i>Metrosideros</i> trees above coastal rocks	1	2
11	Bay of Plenty	State Highway 35 near Papatea Bay	-37-68	177-79	10	<i>Vitex lucens</i> roadside forest remnant	exposed <i>V. lucens</i> trees	1	11
12	Gisborne	Lottin Point Road of Te Araroa Road, Bay	-37-55	178-16	0–10	<i>Metrosideros excelsa</i> coastal forest	<i>Metrosideros</i> trees above coastal rocks	1	28
13	Gisborne	Lottin Point Road of Te Araroa Road, Bay	-37-56	178-16	10	<i>Metrosideros excelsa</i> coastal forest	exposed roadside trees	1	4
14	Gisborne	Hicks Bay, Wharf Road	-37-57	178-30	0–5	fractured basaltic conglomerate, supporting dense lichen field	coastal rock cliff	1	1
15	Gisborne	East Cape Road, East Cape Lighthouse	-37-69	178-55	20–50	<i>Kunzea robusta</i> - <i>Cordyline australis</i> successional forest	slightly disturbed successional forest	2	44
16	Hawke's Bay	Mahia Peninsula, Mahia East Coast Road	-39-18	177-91	300	<i>Beilschmiedia tawa</i> - <i>Hedycarya arborea</i> - <i>Melicytus ramiflorus</i> forest remnant	disturbed roadside forest remnant	2	47
17	Hawke's Bay	Mahia Peninsula, Kinikini Road, Mahia Peninsula Scenic Reserve	-39-12	177-87	150–200	<i>Dysoxylum spectabile</i> - <i>Rhopalostylis sapida</i> - <i>Beilschmiedia tawa</i> forest transitioning into riparian podocarp forest	well-preserved forest	5	162

TABLE 1 (continued).

No.	Region	Site name	Lat.	Long.	Altitude (m)	Vegetation type	Habitat	Stat	Spec
18	Waikato	Tongariro National Park, Tree Trunk Gorge Road	-39-17	175-80	745	<i>Fuscospora cliffortioides</i> - <i>Kunzea serotina</i> forest	margin of well-preserved forest	4	59
19	Waikato	Kaimanawa Forest Park, Tree Trunk Gorge Road	-39-18	175-81	725	<i>Fuscospora cliffortioides</i> - <i>Lophozonia menziesii</i> - <i>Fuscospora fusca</i> forest	margin of well-preserved forest	4	20
20	Waikato	Kaimanawa Forest Park, Rangipo Intake Road	-39-21	175-78	720-730	<i>Fuscospora cliffortioides</i> - <i>Lophozonia menziesii</i> - <i>Fuscospora fusca</i> forest	margin of well-preserved forest	4	9
21	Manawatu-Manganui	Tongariro National Park, Mount Ruapehu, Turoa Ski Area	-39-31	175-53	1620	alpine flush dominated by <i>Chionochoira pallens</i> , <i>Epilobium macropus</i> , <i>Schoenus pauciflorus</i>	disturbed fragment adjacent to parking lot	1	4
22	Manawatu-Manganui	Tongariro National Park, Mount Ruapehu, Okahune Mountain Road	-39-32	175-51	1375	<i>Fuscospora cliffortioides</i> - <i>Phyllocladus alpinus</i> - <i>Halocarpus bififormis</i> forest	margin of well-preserved forest	4	2
23	Manawatu-Manganui	Tongariro National Park, Mount Ruapehu, Okahune Mountain Road	-39-33	175-49	1130	<i>Fuscospora cliffortioides</i> - <i>Phyllocladus alpinus</i> - <i>Halocarpus bififormis</i> forest	margin of well-preserved forest	4	18
24	Manawatu-Manganui	Tongariro National Park, Mount Ngauruhoe, Mangatepopo Road	-39-14	175-58	1130	<i>Chionochoira rubra</i> grassland with <i>Hebe venustula</i> , <i>H. tetragona</i> , <i>Olearia nummulariifolia</i> shrubs	margin of grassland near parking lot	1	10
25	Manawatu-Manganui	Erua Forest, Fishers Road	-39-17	175-38	800-900	podocarp forest dominated by <i>Podocarpus totara</i> and <i>Prumnopitys ferruginea</i>	well-preserved forest	5	245
26	Waikato	Tokaanu Geothermal Reserve	-38-97	175-76	365	<i>Kunzea tenuicaulis</i> tree-shrubland with <i>Leptospermum scoparium</i> agg.	disturbed vegetation along trail	1	7
27	Waikato	Western Bay Road, Great Lake Trail Waihaha Link at Waihaha River	-38-70	175-68	480	riparian secondary regrowth dominated by <i>Salix cinerea</i> , <i>Pittosporum tenuifolium</i> , <i>Pseudopanax arboreus</i> and <i>Kunzea robusta</i>	disturbed vegetation adjacent to parking lot	1	13
28	Manawatu-Manganui	Hauhangaroa Range, Pureora Forest Park, Waihora Lagoon	-38-65	175-66	550-560	dense podocarp forest dominated by <i>Dacrydium cupressinum</i> , <i>Prumnopitys taxifolia</i> , <i>P. ferruginea</i> , <i>Dacrycarpus dacrydioides</i> and <i>Podocarpus totara</i>	well-preserved forest	5	54
29	Waikato	Pureora Forest Park, Link Road Saddle, Link Track to Mount Pureora at Forestry Road	-38-54	175-65	800-820	dense podocarp forest dominated by <i>Dacrydium cupressinum</i> , <i>Prumnopitys taxifolia</i> , <i>P. ferruginea</i> , <i>Dacrycarpus dacrydioides</i> and <i>Podocarpus totara</i>	well-preserved forest	5	17
30	Waikato	Pureora Forest Park, junction of Maraeroa Road with State Highway 30 at Waimihia Stream	-38-51	175-53	530	riparian secondary regrowth	disturbed roadside vegetation and secondary forest	2	9
31	Auckland	Mataia Bay area W of Kaipara Coast Highway	-36-49	174-42	0-80	regenerating <i>Kunzea robusta</i> -dominated forest with pockets of <i>Agathis australis</i> - <i>Phyllocladus trichomanoides</i> forest	regenerating forest and mangrove	2	105
32	Auckland	Omeru Waterfall Scenic Reserve E of Kaipara Coast Highway	-36-56	174-48	60	riparian podocarp forest dominated by <i>Podocarpus totara</i>	disturbed forest remnants	2	19

TABLE 2. GenBank Accession numbers and voucher information for the ITS sequences used in this study. Newly generated sequences are in bold.

Taxon	GenBank Accession no.	Extract	Country	Voucher
<i>Dendriscoaulon</i> aff. <i>dendroides</i>	AF350303		New Zealand	
<i>Dendriscoaulon</i> aff. <i>dendriothamnodes</i> 1 (= <i>S. latifrons</i>)	MF373800	MON3876	New Zealand	Lücking et al. 38815 (AK, F)
<i>Dendriscoaulon</i> aff. <i>dendriothamnodes</i> 1 (= <i>S. latifrons</i>)	MF373802	MON3878	New Zealand	Lücking et al. 38019 (AK, F)
<i>Dendriscoaulon</i> aff. <i>dendriothamnodes</i> 2 (= <i>S. menziesii</i>)	MF373801	MON3877	New Zealand	Lücking et al. 38195 (F)
<i>Dendriscoaulon</i> aff. <i>dendriothamnodes</i> 2 (= <i>S. menziesii</i>)	MF373806	MON3882	New Zealand	Lücking et al. 39004 (F)
<i>Dendriscoaulon</i> sp. (= <i>S. dendroides</i>)	MF373799	MON3875	New Zealand	Lücking et al. 38734 (F)
<i>Dendriscoaulon</i> sp. (= <i>S. dendroides</i>)	MF373803	MON3879	New Zealand	Lücking et al. 38039 (F)
<i>Dendriscoaulon</i> sp. (= <i>S. dendroides</i>)	MF373804	MON3880	New Zealand	Lücking et al. 38053 (F)
<i>Dendriscoaulon</i> sp. (= <i>S. dendroides</i>)	MF373805	MON3881	New Zealand	Lücking et al. 39007 (F)
<i>Sticta ainoae</i>	EU558731		Argentina	
<i>S. babingtonii</i>	MF373808	MON4282	New Zealand	de Lange 12640 (F)
<i>S. babingtonii</i>	MF373809	MON4284	New Zealand	de Lange 12631b (F)
<i>S. caliginosa</i>	MF373760	MON3507	New Zealand	Lücking et al. 39060a (F)
<i>S. caliginosa</i>	MF373767	MON3782	New Zealand	Lücking et al. 39038 (F)
<i>S. caliginosa</i>	MF373768	MON3783	New Zealand	Lücking et al. 39002 (F)
<i>S. caulescens</i>	EU558737		Argentina	
<i>S. cinereoglauca</i>	AF350309		New Zealand	
<i>S. cinereoglauca</i>	MF373794	MON3835	New Zealand	Lücking et al. 38776 (AK, F, UNITEC)
<i>S. cinereoglauca</i>	MF373798	MON3863	New Zealand	Lücking et al. 38646 (AK, F, UNITEC)
<i>S. filix</i>	AF350304		New Zealand	
<i>S. filix</i>	AF350305		New Zealand	
<i>S. filix</i>	MF373759	MON2974	New Zealand	de Lange 12284 (F)
<i>S. filix</i>	MF373766	MON3779	New Zealand	Lücking et al. 39034 (F)
<i>S. filix</i>	MF373769	MON3784	New Zealand	Lücking et al. 38844b (AK, F, UNITEC)
<i>S. filix</i>	MF373770	MON3785	New Zealand	Lücking et al. 38864 (AK, F, UNITEC)
<i>S. filix</i>	MF373771	MON3786	New Zealand	Lücking et al. 38159 (AK, F)
<i>S. filix</i>	MF373772	MON3787	New Zealand	Lücking et al. 38090 (F)
<i>S. filix</i>	MF373773	MON3788	New Zealand	Lücking et al. 38156 (F)
<i>S. filix</i>	MF373774	MON3789	New Zealand	Lücking et al. 38125 (AK, F)
<i>S. filix</i>	MF373775	MON3790	New Zealand	Lücking et al. 38190 (F)
<i>S. filix</i>	MF373776	MON3791	New Zealand	Lücking et al. 39016 (F)
<i>S. filix</i>	MF373777	MON3792	New Zealand	Lücking et al. 39003 (AK, F, UNITEC)
<i>S. filix</i>	MF373779	MON3817	New Zealand	Lücking et al. 38850a (F)
<i>S. filix</i>	MF373780	MON3819	New Zealand	Lücking et al. 38028a (AK, F, UNITEC)
<i>S. gaudichaldia</i>	EU558734		Argentina	
<i>S. gaudichaldia</i>	EU558736		Argentina	
<i>S. hypochra</i>	EU558714		Argentina	
<i>S. hypochra</i>	EU558733		Argentina	
<i>S. hypochra</i>	EU558735		Argentina	
<i>S. latifrons</i> 1	AF350307		New Zealand	
<i>S. latifrons</i> 1	MF373763	MON3538	New Zealand	de Lange 2517 (F)
<i>S. latifrons</i> 1	MF373764	MON3719	New Zealand	Lücking et al. 38767b (F)
<i>S. latifrons</i> 1	MF373765	MON3720	New Zealand	Lücking et al. 38696c (AK, F, UNITEC)

TABLE 2 (continued).

Taxon	GenBank Accession no.	Extract	Country	Voucher
<i>Sticta latifrons</i> 1	MF373781	MON3822	New Zealand	Lücking et al. 38327 (AK, F)
<i>S. latifrons</i> 1	MF373782	MON3823	New Zealand	Lücking et al. 38310 (AK, F)
<i>S. latifrons</i> 1	MF373783	MON3824	New Zealand	Lücking et al. 38441 (F)
<i>S. latifrons</i> 1	MF373784	MON3825	New Zealand	Lücking et al. 38446 (AK, F, UNITEC)
<i>S. latifrons</i> 1	MF373785	MON3826	New Zealand	Lücking et al. 38657 (F)
<i>S. latifrons</i> 1	MF373786	MON3827	New Zealand	Lücking et al. 38763 (F)
<i>S. latifrons</i> 2 (= <i>S. menziesii</i>)	MF373761	MON3522	New Zealand	Lücking et al. 39050 (AK, F, UNITEC)
<i>S. latifrons</i> 2 (= <i>S. menziesii</i>)	MF373787	MON3828	New Zealand	Lücking et al. 38008 (AK, F)
<i>S. latifrons</i> 2 (= <i>S. menziesii</i>)	MF373788	MON3829	New Zealand	Lücking et al. 39001 (F)
<i>S. latifrons</i> 2 (= <i>S. menziesii</i>)	MF373789	MON3830	New Zealand	Lücking et al. 38782 (F)
<i>S. latifrons</i> 2 (= <i>S. menziesii</i>)	MF373790	MON3831	New Zealand	Lücking et al. 38194 (F)
<i>S. latifrons</i> 2 (= <i>S. menziesii</i>)	MF373791	MON3832	New Zealand	Lücking et al. 38178 (AK, F)
<i>S. latifrons</i> 2 (= <i>S. menziesii</i>)	MF373792	MON3833	New Zealand	Lücking et al. 38009 (F)
<i>S. latifrons</i> 2 (= <i>S. menziesii</i>)	MF373793	MON3834	New Zealand	Lücking et al. 39010 (AK, F, UNITEC)
<i>S. latifrons</i> 2 (= <i>S. menziesii</i>)	MF373795	MON3848	New Zealand	Lücking et al. 38029 (AK, F, UNITEC)
<i>S. marginifera</i>	AB245116		Japan	
<i>S. martinii</i>	AF350306		New Zealand	
<i>S. martinii</i>	AF351155		New Zealand	
<i>S. martinii</i>	MF373778	MON3816	New Zealand	Lücking et al. 38807 (AK, F)
<i>S. squamata</i>	MF373762	MON3534	New Zealand	Lücking et al. 39157 (F, UNITEC)
<i>S. squamata</i>	MF373796	MON3854	New Zealand	Lücking et al. 38673 (F)
<i>S. squamata</i>	MF373807	MON4263	New Zealand	Knight s. n. (F, OTA)
<i>S. subcaperata</i>	AF350308		New Zealand	
<i>S. subcaperata</i>	MF373758	MON2922	New Zealand	de Lange 12088 (F)
<i>S. subcaperata</i>	MF373797	MON3859	New Zealand	Lücking et al. 38155 (AK, F)

taxon delimited from the phylogenetic analysis, we computed the proportion of specimens among all collected lichen specimens per site and subsequently the average proportion per conservation category over all sites pertaining to a given category. None of the newly delimited taxa occurred in site classes 1–3. In order to test whether a given species was found more frequently in intact (site class 5) as opposed to slightly disturbed forest (site class 4), we compared the frequency values using a one-tailed Wilcoxon-Mann-Whitney U-test (Marx et al. 2016; <https://ccb-compute2.cs.uni-saarland.de/wttest>). While this approach is not based on thorough quantitative sampling, it gives an estimate of the relative frequency of each taxon in relation to site conservation status that can be used as a hypothesis for more detailed studies.

Results

The *Sticta filix* morphodeme does not form a monophyletic clade; instead, the target samples are dispersed over several early diverging clades of the *Sticta* tree following Moncada et al. (2014a: 218, fig. 3). Within this

assemblage interspecies relationships are, with a small number of exceptions, not supported (Fig. 2). Next to the outgroup, two basal clades are formed by *S. cinereoglauca* Hook. f. & Taylor, *S. squamata* D. J. Galloway and *S. babingtonii* D. J. Galloway, all from New Zealand and the last two for the first time provided with ITS sequence data. The 43 specimens of the target taxa are found within a larger, unsupported clade and form four clades, three of them well supported, instead of the two expected clades (*filix* and *latifrons*). *Sticta filix* is monophyletic but in this analysis the clade is not supported. A second clade is formed by South American taxa: *S. ainoae* D. J. Galloway & J. Pickering, *S. gaudichaldia* Delise, *S. hypochra* Vain. and *S. caulescens* De Not. A third, larger subclade contains the samples identified as *S. latifrons* and an additional clade composed only of a

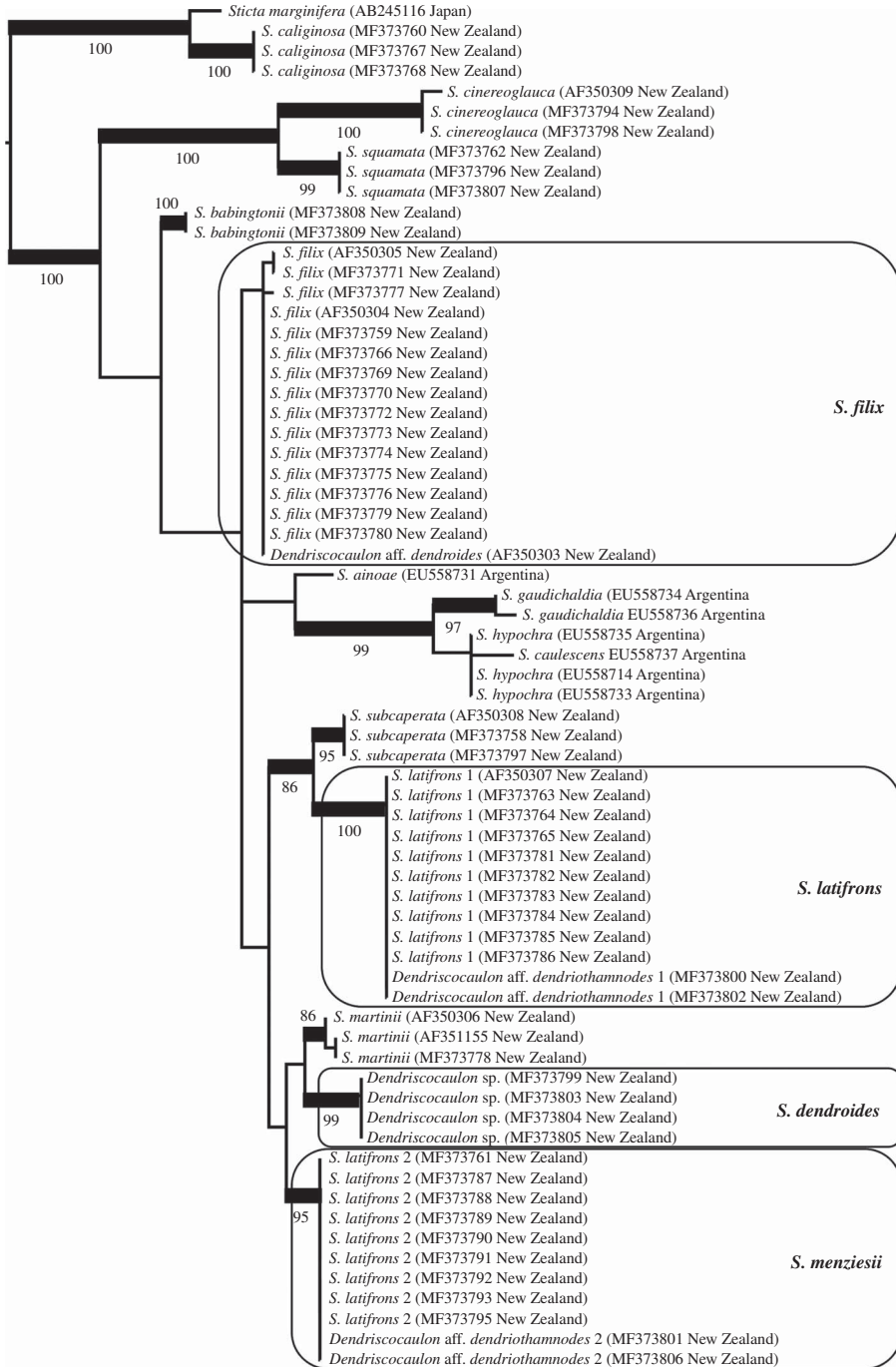


FIG. 2. Best-scoring maximum likelihood tree based on phylogenetic analysis of *Sticta* species using the ITS barcoding locus, focusing on the *S. filix* guild and other, mostly New Zealand taxa found basally in the *Sticta* phylogeny (see Moncada *et al.* 2014a: 218, fig. 3, for a broader context). Supported clades are thickened and bootstrap values indicated. The clades of interest are marked in boxes and final names applied to each clade are given.

dendriscoauloid cyanomorph. Here, *S. latifrons* s. lat. falls into two distinct, distantly related clades, *S. latifrons* 1 and *S. latifrons* 2. The latter is more closely related (though unsupported) to the dendriscoauloid clade plus *S. martinii* D. J. Galloway, whereas *S. latifrons* 1 is supported sister to *S. subcaperata* (Nyl.) Nyl. *Sticta latifrons* 1 and *S. latifrons* 2 each have two dendriscoauloid cyanomorphs, whereas a fourth cyanomorph clustered with *S. filix*. The cyanomorph related to *S. latifrons* 2 and *S. martinii* does not represent any of the other known green species of *Sticta* from New Zealand, viz. *S. babingtonii*, *S. caperata*, *S. cinereoglauca*, *S. livida* Kremp., *S. martinii*, *S. squamata* and *S. subcaperata* (all sequenced except *S. livida* and none conspecific with the

cyanomorph clade). A possible exception is *S. lacera*, which has not yet been sequenced but is a doubtful taxon (see above in Material and Methods) from which no cyanomorph has been reported (Galloway 1985, 1997, 2007).

Comparison with type material revealed that the *Sticta latifrons* 1 clade corresponds to *S. latifrons* s. str. whereas the *S. latifrons* 2 clade agrees with the type of *S. menziesii*, thus far subsumed under synonymy with *S. latifrons* (Fig. 2). *Sticta menziesii* is therefore reinstated below. High-resolution digital scanning of the sequenced samples and careful qualitative and quantitative analysis of features such as lobe configuration, pigmentation and cyphellae size revealed that the three phylogenetically recognized, green-algal morphs can be distinguished as follows:

- 1 Thallus branches dendroid, with the main branches usually forming a darker, vein-like pattern throughout the underside; lamina at least marginally, sometimes completely, dissected into fine lobules 0.5–2.0 mm broad; cyphellae usually diminutive and inconspicuous, 0.1–0.5 mm diam., very rarely up to 1 mm along the veins (Fig. 3) ***Sticta filix*** (chloromorph)
- Thallus branches flabellate to truncate, without vein-like pattern except at the base; lamina with irregular to sinuose margins or forming (3–)5–10 mm broad lobules; cyphellae conspicuous, (0.3–)0.5–3.0 mm diam. (Figs 4 & 5) 2
- 2(1) Lobes more or less truncate, often with irregular margins, main lobes 20–80 mm broad; underside cream-coloured to pale brown throughout, rarely darker brown; cyphellae of irregular size but large cyphellae rather abundant, 1–3 mm diam., often irregular to angular in outline (Fig. 4) ***Sticta latifrons*** (chloromorph)
- Lobes more or less flabellate to ligulate, with regularly sinuose margins, main lobes (5–)10–30 mm broad; underside medium to dark brown, rarely pale brown; cyphellae of regular size, 0.3–1.0 mm diam., regularly rounded (Fig. 5) ***Sticta menziesii*** (chloromorph)

Whereas the conspicuous, vein-like pattern of the underside and the strongly and finely dissected lobes readily distinguish *Sticta filix* from the other two species, we found that the best character to separate morphologically intermediate forms of *S. menziesii* and *S. latifrons* from each other is the disposition, size and shape of the cyphellae, a character that also separates *S. filix* from the other two species, further underlining the potential use of cyphellae

morphology for species delimitation in *Sticta* (Moncada *et al.* 2013b).

Regarding the cyanomorphs and the two available names, *Dendriscoaulon dendroides* and *D. dendriothammodes*, the type of the latter is from Australia and associated with *Sticta stipitata* C. Knight ex F. Wilson (Galloway 1983, 2007), a species of the *S. filix* morphodeme not occurring in New Zealand. Hence, *D. dendriothammodes* becomes a synonym of *S. stipitata* and the name must be

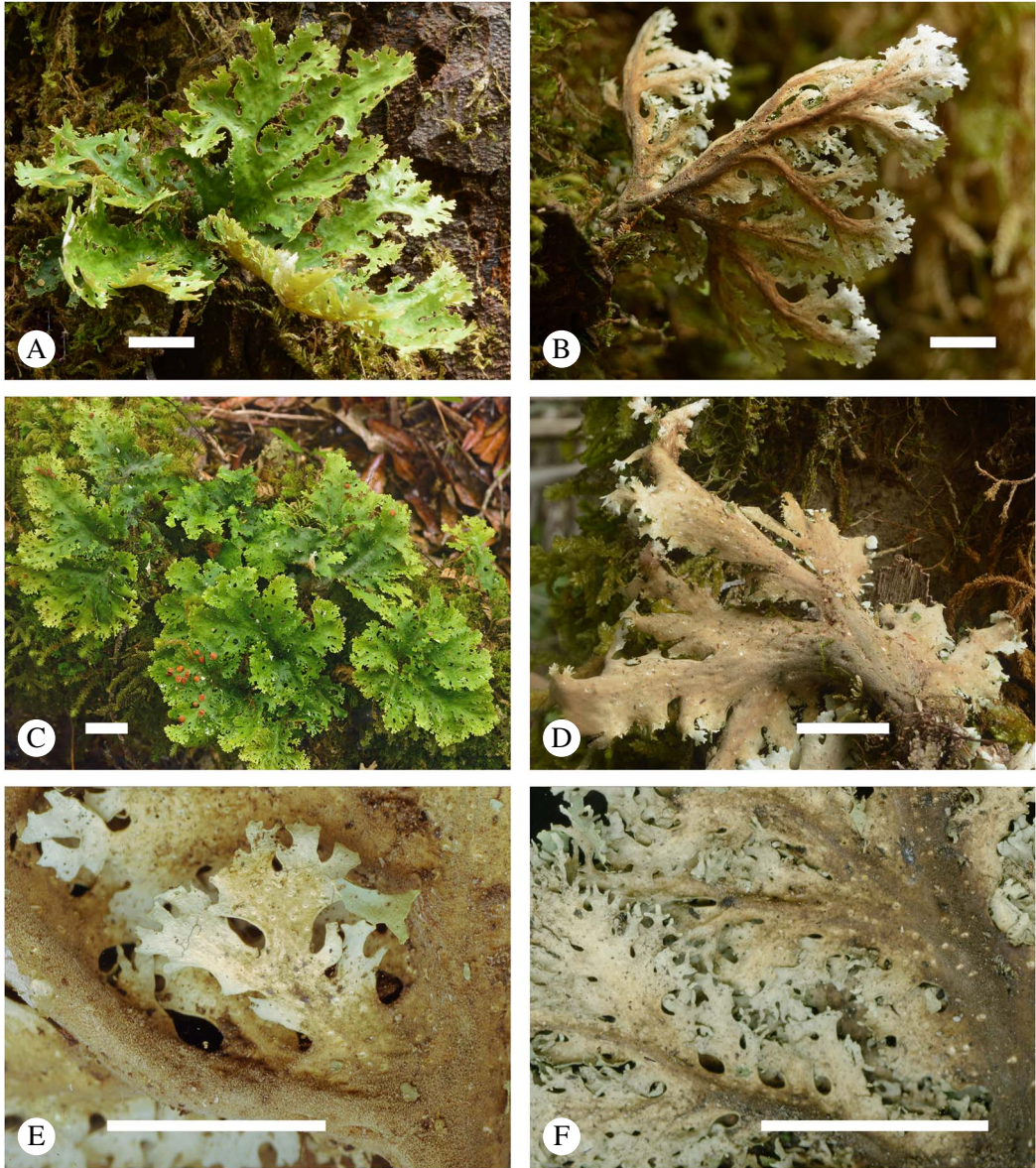


FIG. 3. *Sticta filix*, general habit and morphological details of the chloromorph. A & C, upper side; B & D, lower side; E & F, lower side enlarged showing cyphellae (A & B, Lücking et al. 39036; C & E, Lücking et al. 38159; D, Lücking et al. 38156; F, Lücking et al. 39016). Scales = 10 mm. In colour online.

excluded from the New Zealand biota. A morphologically similar cyanomorph is associated with *S. latifrons* (James & Henssen 1976; Galloway 2007) which was confirmed here with molecular data; in spite of its

similarity, this cyanomorph is not conspecific with the type of *D. dendrothamnodes* and its correct name is *S. latifrons*. A third, also similar cyanomorph was found associated with *S. menziesii* and consequently must bear

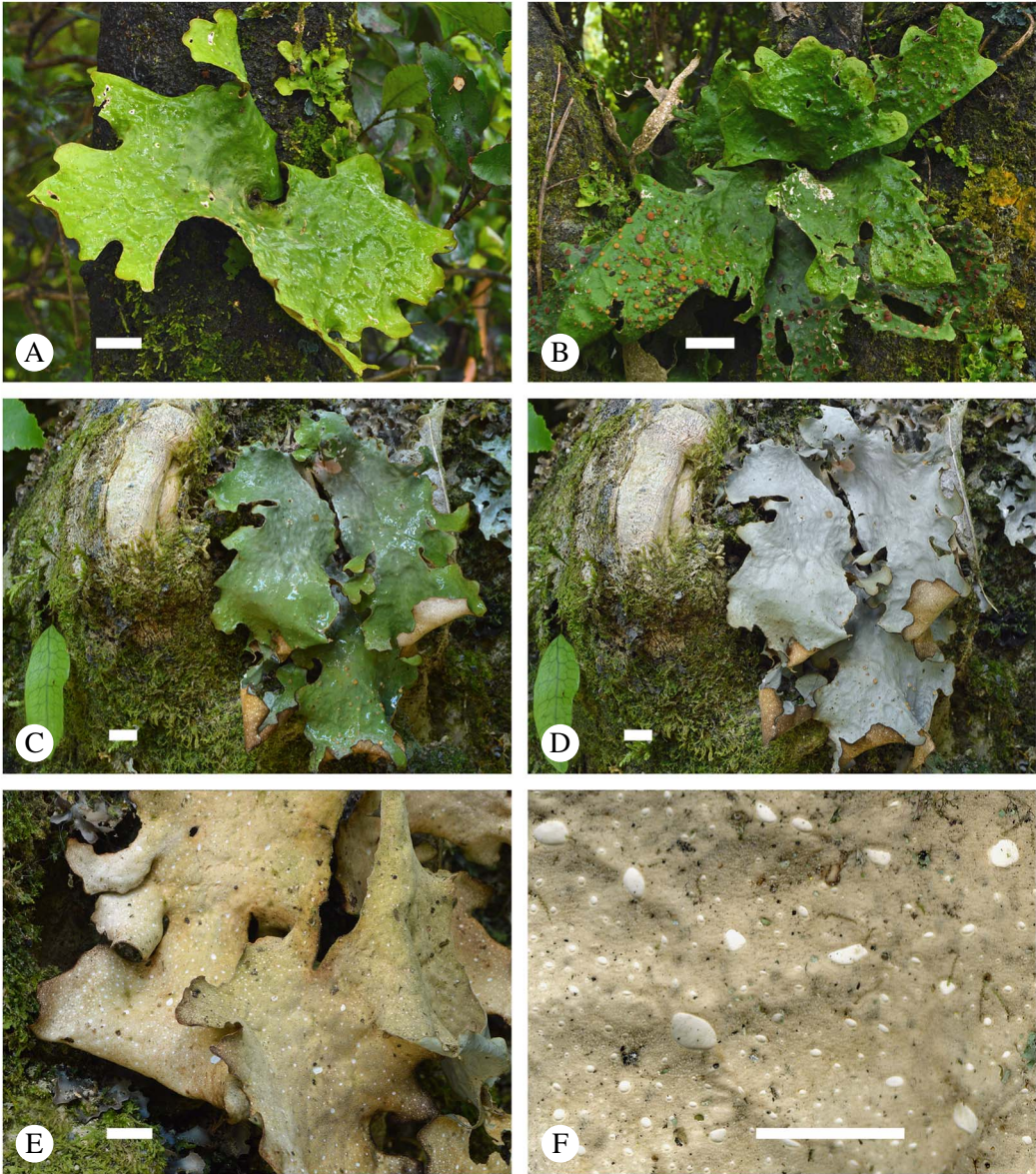


FIG. 4. *Sticta latifrons* s. str., general habit and morphological details of the chloromorph. A–D, upper side (in D dried); E, lower side; F, lower side enlarged showing cyphellae (A & F, *Lücking et al.* 38441; B, *Lücking et al.* 38446; C–E, *Lücking et al.* 38110). Scales = 10 mm. In colour online.

that name. A problem then arises with the cyanomorph associated with *S. filix* and the one forming a separate clade without a known chloromorph (Fig. 2). We were unable to obtain the sequenced material of

the *Sticta filix* cyanomorph for study; however, according to James (in Mark *et al.* 1964), James & Henssen (1976), Thomas *et al.* (2002) and Galloway (2007), this cyanomorph corresponds to the morphology of

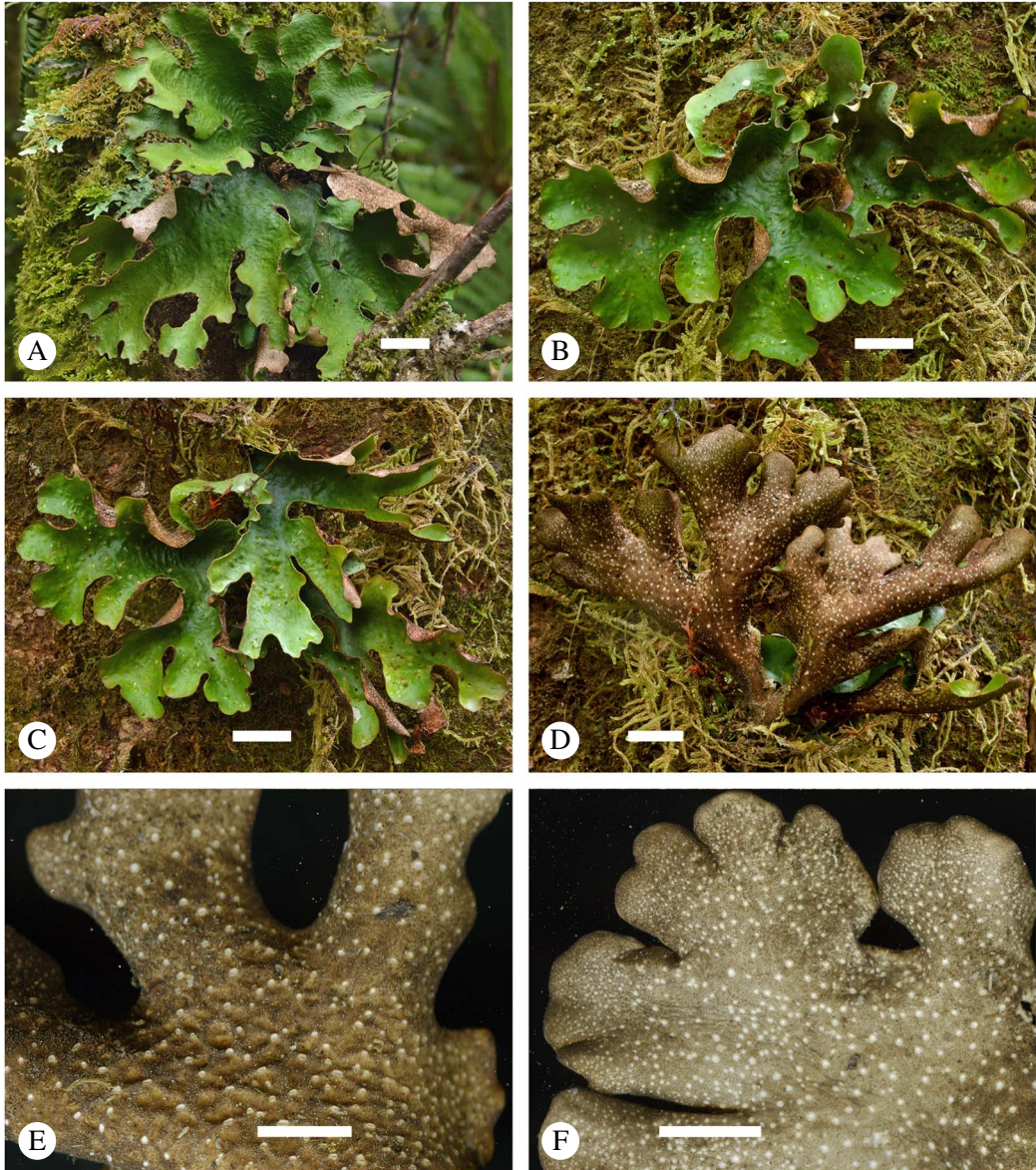


FIG. 5. *Sticta menziesii*, general habit and morphological details of the chloromorph. A–C, upper side; D, lower side; E & F, lower side enlarged showing cyphellae (A, Lücking *et al.* 38029; B–D, Lücking *et al.* 38178; E, Lücking *et al.* 38009; F, Lücking *et al.* 38194). Scales = 10 mm. In colour online.

D. dendroides but also to that of the additional cyanomorph forming a separate clade, sister to *S. menziesii*. Unfortunately, the type of *D. dendroides* is very depauperate and cannot be unambiguously assigned to either the

S. filix cyanomorph or the cyanomorph forming a separate clade, so we epitypify *D. dendroides* with a specimen of the latter following recent recommendations (Ariyawansa *et al.* 2014), making the epithet

dendroides available for that clade (as *Sticta dendroides*; see below) rather than describing a new species for it (Fig. 2). The possibility still exists that this cyanomorph is associated with *S. lacera*; if that turns out to be the case, then *S. dendroides* becomes a synonym of *S. lacera* without further nomenclatural disruptions. However, as noted under Material and Methods, because sequenced specimens originally identified as *S. lacera*, including one forming part of a previous study (AF350305; Thomas *et al.* 2002), turned out to be conspecific with *S. filix*, the possibility

must be considered that *S. lacera* is a depauperate form or ecomorph of *S. filix*.

As a consequence, the four dendriscocauloid cyanomorphs now known from New Zealand have the following names: *S. dendroides*, *S. filix* (= *D. aff. dendroides*), *S. latifrons* (= *D. aff. dendriothamnodes* 1) and *S. menziesii* (= *D. aff. dendriothamnodes* 2). Aside from the *S. filix* cyanomorph, which we did not obtain for study, the other three cyanomorphs present morphological and anatomical features that make their distinction readily possible:

- 1 Thallus up to 5(–10) cm long, main branches flattened, dorsiventral, *c.* 1 mm broad, with the upper side bluish grey with cream-coloured maculae and the lower side cream-coloured; branch surface glabrous to sparsely pilose (*Dendriscocaulon dendroides*) (Fig. 6) **Sticta dendroides** (cyanomorph)
- Thallus up to 3 cm long, main branches cylindrical, *c.* 0.25–0.50 mm broad, cream-coloured all around; branch surface densely pilose (*Dendriscocaulon aff. dendriothamnodes*) (Figs 7 & 8) 2

- 2(1) Secondary branches forming a rather perpendicular angle with the main branch (pointing sideways); apical branchlets branching mostly trichotomously, with uneven sides or slightly swollen after the branching point (best seen under a compound microscope); cortical cells of main branches rectangular in section, arranged in radiating rows; hairs numerous but not dense, formed on every second to fifth cell per layer in cross-section, 35–60 µm long (Fig. 7) **Sticta menziesii** (cyanomorph)
- Secondary branches forming an oblique angle with the main branch (pointing upwards); apical branchlets branching mostly dichotomously, with parallel sides (best seen under a microscope); cortical cells of main branches honeycomb-shaped in section, arranged in parenchymatic pattern; hairs dense, formed on every or every second cell per layer in cross-section, 20–35 µm long (Fig. 8) **Sticta latifrons** (cyanomorph)

Since *Sticta menziesii* was previously synonymized under *S. latifrons* (Galloway 1985, 1997, 2007), their cyanomorphs were also not separated and instead considered a single entity, *Dendriscocaulon dendriothamnodes* (Galloway 1983, 1985, 2007); however, this is the cyanomorph of an Australian species, *S. stipitata* (Galloway 2001, 2007). The macroscopic and microscopic differences found between the sequenced cyanomorphs further support the separation of *S. menziesii* from *S. latifrons*. Other than imagery, we were unable to investigate the type of *Dendriscocaulon*

dendriothamnodes from Australia, so we are unable to state at present how this *S. stipitata* cyanomorph differs in morphological and anatomical features from the cyanomorphs of *S. latifrons* and *S. menziesii*.

Of the 33 sites visited during our fieldwork in 2015, 13 classify as strongly disturbed (1), seven as rather strongly disturbed (2), two as intermediate (3), seven as slightly disturbed (4), and four as intact (5). All four of the above species were found only at sites corresponding to categories 4 and 5, being absent from intermediate to strongly disturbed sites

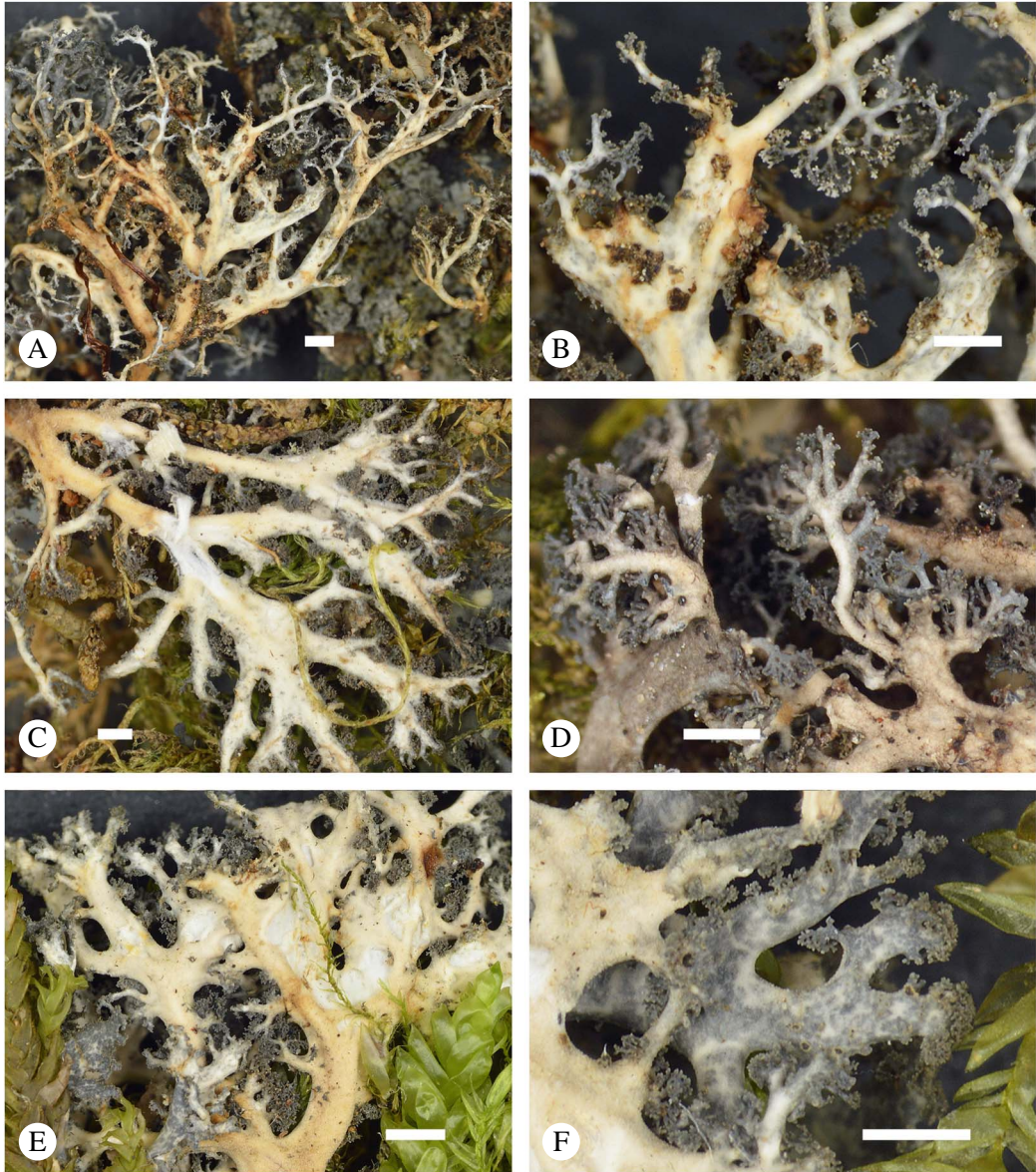


FIG. 6. *Sticta dendroides*, general habit and morphological details of the cyanomorph. A, C & E, lower side; B & D, lower side and tips enlarged; F, upper side and tips enlarged (A & B, Lücking et al. 38317; C, Lücking et al. 38053; D, Lücking et al. 38734; E & F, Lücking et al. 38039). Scales = 1 mm. In colour online.

(categories 1–3). Notably, the four species exhibit two different patterns (Fig. 9): *Sticta filix* and *S. latifrons* were both found in slightly disturbed and intact sites but were relatively more common in slightly disturbed sites, whereas the previously

unrecognized *S. dendroides* and *S. menziesii* were almost entirely restricted to intact sites. This difference is significant for both *S. dendroides* (one-tailed Mann-Whitney U-test, $P = 0.0121$) and *S. menziesii* (Mann-Whitney U-test, $P = 0.0242$).

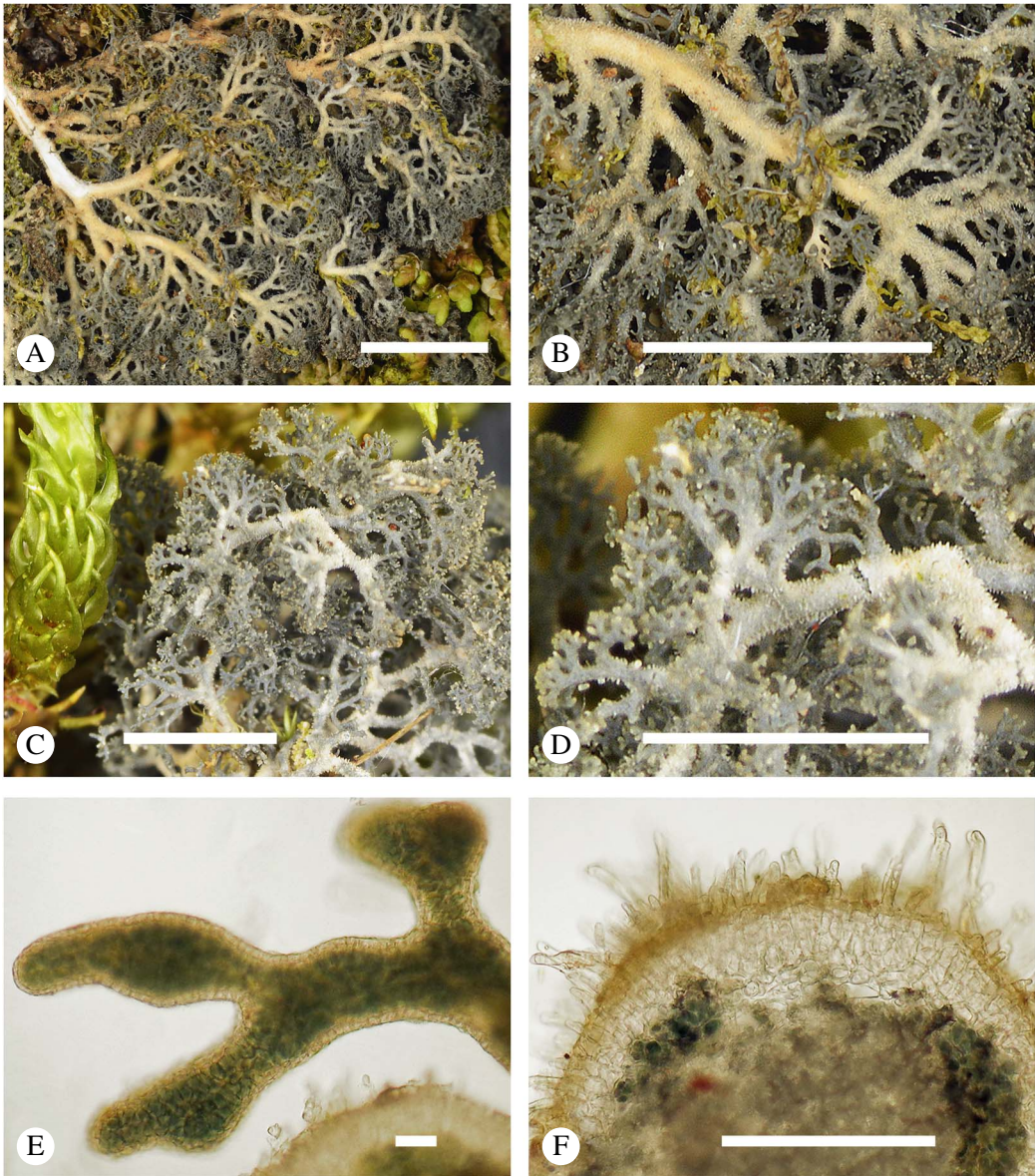


FIG. 7. *Sticta menziesii*, general habit and morphological details of the cyanomorph. A, thallus; B, thallus enlarged; C & D, tips enlarged; E, apical branches in microscope view; F, section through main stem showing cortical layers and hairs (A, B & F, *Lücking et al.* 38195; C–E, *Lücking et al.* 39004). Scales: A & B = 1 mm; C & D = 0.5 mm; E & F = 100 µm. In colour online.

Discussion

The results of our molecular phylogenetic study of the *Sticta filix* morphodeme in New Zealand, focusing on the two large species of

this ‘guild’, *S. filix* and *S. latifrons*, and their cyanobacterial photomorphs, revealed the presence of a third large species which agrees morphologically with the type material of *S. menziesii* Hook. f. & Taylor, previously

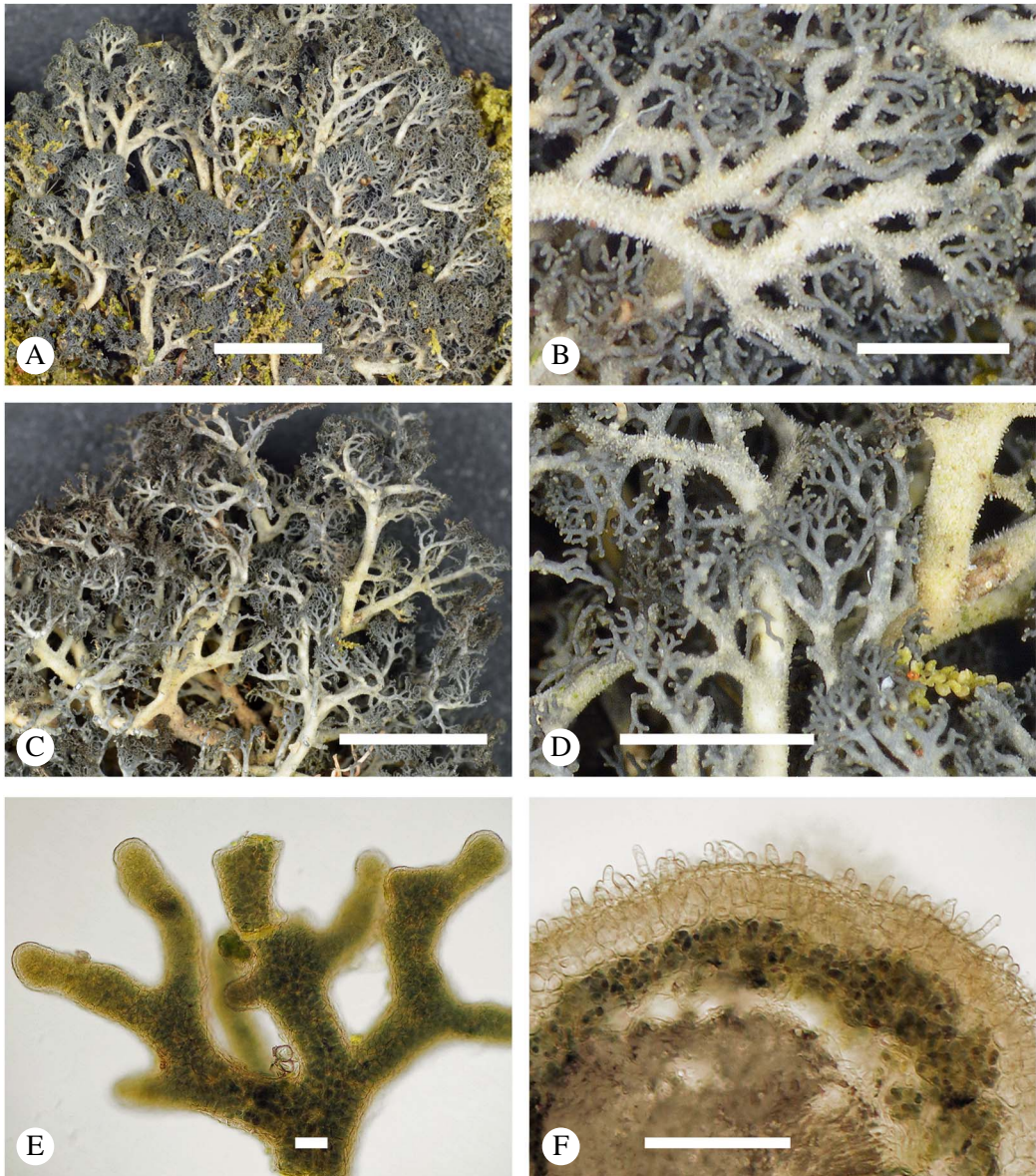


FIG. 8. *Sticta latifrons*, general habit and morphological details of the cyanomorph. A & C, thallus; B & D, thallus enlarged; E, apical branches in microscope view; F, section through main stem showing cortical layers and hairs (A, B & F, *Lücking et al.* 39011; C–E, *Lücking et al.* 38815). Scales: A = 1 mm; B, C & D = 0.5 mm; E & F = 100 μ m. In colour online.

treated as a synonym of *S. latifrons* (Galloway 1985, 1997, 2007). Accordingly, we reinstate *S. menziesii* formally below. Ecologically, the species has a preference for dense, humid forests, growing on the lower trunks of trees

and associated shrubs and saplings within the understorey and shrub layers, and being virtually absent from even only slightly disturbed sites. This sets it aside from *S. latifrons* s. str., which has broader habitat

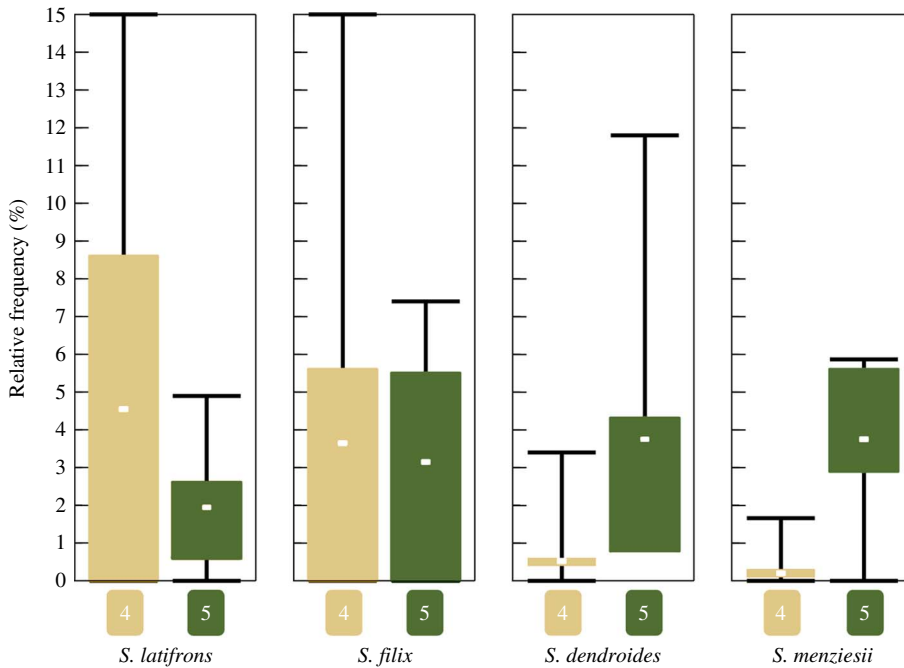


FIG. 9. Boxplot showing mean relative frequency of the four recognized *Sticta* species in intact (conservation status category 5) and slightly disturbed (category 4) forest sites (all four species are absent from sites corresponding to categories 1–3). Relative frequency is the number specimens of a species found at a site expressed as a percentage of the total number of specimens recorded at the same site. Whiskers indicate min/max, boxes indicate 25th and 75th percentiles; $n = 7$ for slightly disturbed sites, $n = 4$ for intact sites. In colour online.

preferences and can be found on exposed trunks and canopy branches in lowland or riparian forest remnants, especially in places where cool, moisture-laden air ponds. Under such conditions, *S. latifrons* can be locally common even in somewhat degraded forest remnants. The reinstatement of *Sticta menziesii* not only clarifies an apparent morphological discrepancy and adds a further, potentially endemic, taxon to New Zealand's lichen biota, but because of its observed ecological preferences it also recognizes a species with the capacity to be an excellent bioindicator of forest health in New Zealand.

Based on the results of our phylogenetic study, we also recognize four different dendriscocauloid photomorphs, one conspecific with each of *Sticta filix*, *S. latifrons* and *S. menziesii*, and a fourth one epitypified to represent the existing name *Dendriscocaulon dendroides* (Nyl.) R. Sant. ex H. Magn.,

below recombined in the genus *Sticta* as *S. dendroides*. The newly recognized taxon, *S. dendroides*, also discriminates between well-conserved and somewhat degraded forest. In our semi-quantitative analysis, *S. dendroides* is the only one of the four taxa exclusively represented by its cyanomorph, whereas both morphs were included for *S. latifrons* and *S. menziesii* and chloromorphs only for *S. filix*. In *S. latifrons*, the cyanomorphs behave in a similar way as the chloromorphs, being found in both well-conserved and somewhat degraded forest, whereas in *S. menziesii* the cyanomorphs were exclusively found in intact forests. Thus, the cyanomorphs also discriminate between conservation status and could theoretically be used as bioindicators in addition to the chloromorphs, although their morphological distinction might prove challenging in the field.

The present work underlines the importance of a polyphasic species delimitation approach, taking into consideration both macroscopic and microscopic phenotype characters and molecular data. The need for thorough taxonomic re-evaluation, even of taxa generally believed to be well understood, is particularly obvious when using lichens as bioindicators to assess ecosystem health. The two species *S. dendroides* and *S. menziesii* had not been properly recognized before and therefore their discrimination of intact versus disturbed forest had not been perceived either, as they appear to be better indicators of well-conserved, native forest than the two previously recognized taxa, *S. filix* and *S. latifrons*; the latter two not only seem to tolerate certain levels of disturbance but appear to thrive better under these circumstances.

New Zealand has a very rich assembly of *Lobariaceae* macrolichens, a family that has been identified as containing potentially excellent bioindicators of forest health (Rose 1974, 1976, 1992; Galloway 1985, 1988, 1992, 2007, 2009; Søchting & Christensen 1989; Gauslaa 1994; Selva 1994, 1996; Wolseley *et al.* 1994; McCune 2000; Zedda 2002; Campbell & Fredeen 2004; Kalwij *et al.* 2005; Juriado & Liira 2009; Scheidegger 2009; Nascimbene *et al.* 2010; Gustafsson *et al.* 2013; Simijaca-Salcedo *et al.* 2014; Cansaran-Duman *et al.* 2015; Giorgio *et al.* 2015; Ramírez-Morán *et al.* 2016). However, despite the fact that New Zealand is currently regarded as the best studied area when it comes to the taxonomy of *Lobariaceae* (Galloway 2009), our results show that species delimitations are far from settled, which has implications for our understanding of species-level ecology. The past treatment of *Sticta menziesii* as part of the natural variation exhibited by *S. latifrons* meant that its potential as a bioindicator of intact forest was not recognized. The preference of *S. menziesii* for intact forests could also make it a useful visual aid to monitor invasive browsing animals such as deer (including *Cervus elaphus scoticus*, *C. nippon*, *C. unicolor*, *Dama dama* and *Odocoileus virginianus*) and possum (*Trichosurus vulpecula*), all deliberately introduced and now widespread in New Zealand (Atkinson 1989; King 1990;

Anderson 2002; Worthy & Holdaway 2002; Prebble & Wilmshurst 2009; Brown *et al.* 2015). While these animals do not necessarily feed on this lichen, their impact is likely to affect its presence and abundance through secondary effects of changes in vegetation structure and microclimate.

The four *Sticta* species recognized here can be readily recognized in the field, although tools such as a hand lens are required for proper recognition, particularly of the cyanomorphs. This makes these lichens good candidates for use in rapid field assessments of the ecological integrity and vegetation health of forest ecosystems. Considering the rather limited use of lichens as bioindicators in New Zealand (Hutcheson *et al.* 1999; Galloway 2008; de Lange *et al.* 2012), we recommend that their potential for use in the New Zealand-wide monitoring of indigenous vegetation health should be further explored through quantitative assessments, and to this end we designed a field guide to aid in the critical identification of the species of interest (see Supplementary Material Figure S1, available online).

Taxonomic Novelties

***Sticta dendroides* (Nyl.) Moncada, Lücking & de Lange comb. nov.**

Mycobank No.: MB 821871

Leptogium dendroides Nyl., *Flora* 50: 438 (1867); *Dendriscoaulon dendroides* (Nyl.) R. Sant. ex H. Magn., *Tilläggs och Ändringar till Förteckning över Skandinavians Växter* 4, *Lavar*: 9 (1950); *Dendriscoaulon filicinellum* Nyl., *Lichenes Novae Zelandiae (Paris)*: 10 (1888) [nom. illeg., ICN Art. 52.1]; type: New Zealand, *Lyall* s. n. (H-NYL 41030—lectotype!, Galloway 1985: 154); New Zealand, North Island, Erua Forest, *Lücking et al.* 38053 (F—epitype!, designated here; MBT 377561).

Diagnostic characters. Photobiont cyanobacterial (*Nostoc*). Thallus corticolous, often between bryophytes, microfruticulose, 3–5 (–10) cm high, dendroid with distinct main stems and obliquely inserted lateral branches. Main branches flattened, dorsiventral, with the upper side bluish grey with cream-coloured maculae and the lower side cream-coloured. Stem and branch surface glabrous to sparsely pilose.

Notes. After its original description in the genus *Leptogium*, Nylander (1888) realized that the species should belong in *Dendrisocaulon* but renamed it *D. filicinellum*, creating an illegitimate name. This dendrisocauloid cyanomorph was usually associated with the chloromorph *Sticta filix* (Galloway 1985, 2007), even in the protologue (Nylander 1867). However, in the type material there is no evidence for a direct connection with that particular species. Unfortunately, we could not locate the sequenced specimen of the cyanomorph that clusters with *S. filix* (Thomas *et al.* 2002: AF350303), but based on the description given by Galloway (1985, 2007) it is expected to be quite similar to the clade of the unique cyanomorph found here. Since the type of *Leptogium dendroides* is very depauperate, we decided to epitypify the name with a specimen from this clade. Thus, instead of making *Leptogium dendroides* a synonym of *S. filix*, this epitypification makes the name available for the separate clade and avoids the description of a new species.

Specimens examined. **New Zealand:** *North Island:* Hawke's Bay, Mahia Peninsula, Kinikini Road, Mahia Peninsula Scenic Reserve, 56 km SSW of Gisborne, trail through reserve, 39°07'28"S, 177°52'27"E, 150–200 m, kohekohe (*Dysoxylum spectabile*), nikau (*Rhopalostylis sapida*) and tawa (*Beilschmiedia tawa*) forest transitioning into riparian podocarp forest dominated by kahikatea (*Dacrycarpus dacrydioides*), matai (*Prumnopitys taxifolia*) and totara (*Podocarpus totara* var. *totara*), with an understorey of mahoe (*Melicactus ramiflorus* subsp. *ramiflorus*), kotukutuku (*Fuchsia excorticata*), horoeka (*Pseudopanax crassifolius*) and kaikomako (*Pennantia corymbosa*), well-preserved forest, on *Schefflera*, 2015, R. Lücking, B. Moncada & P. de Lange 38734 (F); Manawatu-Manganui, Erua Forest, Fishers Road, 1 km W to 5 km SW of National Park village, Tupapakura Waterfall Track, 39°10'19"S, 175°22'35"E, 800–900 m, podocarp tree land dominated by totara (*Podocarpus totara* var. *totara*) and miro (*Prumnopitys ferruginea*), with an understorey of kamahi (*Weinmannia racemosa*), well-preserved forest, on *Weinmannia*, 2015, R. Lücking, B. Moncada & P. de Lange 38039 (F); *ibid.*, on *Cyathea*, 38053 (F); Manawatu-Manganui, Hauhangaroa Range, Pureora Forest Park, Waihora Lagoon, 39 km WNW of Taupo, trail from Waihora Lagoon car park to lagoon, 38°38'46"S, 175°39'37"E, 550–560 m, dense podocarp forest dominated by rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*), miro (*P. ferruginea*), kahikatea (*Dacrycarpus dacrydioides*) and totara (*Podocarpus totara* var. *totara*) with an understorey of

mahoe (*Melicactus ramiflorus* subsp. *ramiflorus*), pate (*Schefflera digitata*), kotukutuku (*Fuchsia excorticata*) and kaikomako (*Pennantia corymbosa*), well-preserved forest, on *Melicactus lanceolatus*, 2015, R. Lücking, B. Moncada & P. de Lange 39007a (F).

***Sticta menziesii* Hook. f. & Taylor**

Mycobank No.: MB 406297

Sticta menziesii Hook. f. & Taylor in Hooker, *The Botany of the Antarctic Voyage of H. M. Discovery Ships Erebus and Terror 1839–1843* 1: 198 (1844); *Sticta latifrons* var. *menziesii* (Hook. f. & Taylor) Bab. in Hooker, *The Botany of the Antarctic Voyage of H. M. Discovery Ships Erebus and Terror 1839–1843* 2: 277 (1855); type: New Zealand, Dusky Bay, *Menzies* s. n. (BM—lectotype!, Galloway 1997: 143).

Diagnostic characters (chloromorph). *Photobiont* green (*Dictyochloropsis*). *Thallus* corticolous, macrofoliose, distinctly stalked, up to 10 cm high. *Lobes* flabellate to ligulate, with sinuose margins, (5–)10–30 mm broad; underside medium to dark brown, rarely pale brown; cyphellae of regular size, 0.3–1.0 mm diam., regularly rounded. For diagnostic characters of the cyanomorph, see key above.

Notes. This species is reinstated here from prior synonymy with *Sticta latifrons* based on the results from the molecular phylogenetic analysis and the morphological differences with the latter, outlined in the key above. The type specimen, shown in a photograph in Galloway (1997: 144) and beautifully illustrated by Babington in Hooker (1855: plate CXXII; Fig. 10), is a typical representative of this taxon, agreeing perfectly with well-developed specimens sequenced here.

All other synonyms listed under *Sticta latifrons* in Galloway (1985, 1997, 2007) represent *S. latifrons* s. str. This also applies to the names *Sticta menziesii* var. *dissecta* Kremp. and *S. menziesii* var. *palmata* Kremp., as well as *S. menziesii* var. *ochroleuca* (C. Bab.) Kremp.

Specimens examined (chloromorphs). **New Zealand:** *North Island:* Manawatu-Manganui, Erua Forest, Fishers Road, 1 km W to 5 km SW of National Park village, Tupapakura Waterfall Track, 39°10'19"S, 175°22'35"E, 800–900 m, podocarp forest dominated by



FIG. 10. Illustration of the type material of *Sticta menziesii* by Babington in Hooker (1855), clearly showing the typical features of the species. In colour online.

totara (*Podocarpus totara* var. *totara*) and miro (*Prumnopitys ferruginea*), with an understorey of kamahi (*Weinmannia racemosa*), well-preserved forest, 2015, R. Lücking, B. Moncada & P. de Lange 38008 (AK, F), 38009 (F), 38029 (AK, F, UNITEC), 38048 (AK, F, UNITEC), 38194 (F), 38202 (F), 38941 (F); *ibid.*, on *Weinmannia*, 38178 (AK, F); Manawatu-Manganui, Hauhangaroa Range, Pureora Forest Park, Waihora Lagoon, 39 km WNW of Taupo, trail from Waihora Lagoon car park to lagoon, 38°38'46"S, 175°39'37"E, 550–560 m, dense podocarp forest dominated by rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*),

miro (*P. ferruginea*), kahikatea (*Dacrycarpus dacrydioides*) and totara (*Podocarpus totara* var. *totara*) with an understorey of mahoe (*Meliclytus ramiflorus* subsp. *ramiflorus*), pate (*Schefflera digitata*), kotukutuku (*Fuchsia excorticata*) and kaikomako (*Penmanthia corymbosa*), well-preserved forest, on *Dacrycarpus dacrydioides*, 2015, R. Lücking, B. Moncada & P. de Lange 39010 (AK, F, UNITEC); *ibid.*, on *Prumnopitys ferruginea*; 39001 (F); Waikato, Pureora Forest Park, Link Road Saddle, Link Track to Mount Pureora at Forestry Road, 42 km NW of Taupo, Link Road Pureora Track car park to base of Mount Pureora, 38°32'11"S, 175°38'44"E, 800–820 m, dense

podocarp forest dominated by rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*), miro (*P. ferruginea*), kahikatea (*Dacrycarpus dacrydioides*) and totara (*Podocarpus totara* var. *totara*) with an understorey of mahoe (*Melicytus ramiflorus* subsp. *ramiflorus*), pate (*Schefflera digitata*), kotukutuku (*Fuchsia excorticata*) and kaikomako (*Pennantia corymbosa*), well-preserved forest, 2015, R. Lücking, B. Moncada & P. de Lange 39050 (AK, F, UNITEC); Waikato, Tongariro National Park, Tree Trunk Gorge Road, 38 km E of National Park village, roadside, 39°09'56"S, 175°48'11"E, 745 m, mountain beech (*Fuscospora cliffortioides*) forest with makahikatoa (*Kunzea serotina*), margin of well-preserved forest along road, 2015, R. Lücking, B. Moncada & P. de Lange 38782 (F).

Specimens examined (cyanomorphs). **New Zealand:** *North Island:* Manawatu-Manganui, Erua Forest, Fishers Road, 1 km W to 5 km SW of National Park village, Tupapakura Waterfall Track, 39°10'19"S, 175°22'35"E, 800–900 m, podocarp forest dominated by totara (*Podocarpus totara* var. *totara*) and miro (*Prumnopitys ferruginea*), with an understorey of kamahi (*Weinmannia racemosa*), well-preserved forest, 2015, R. Lücking, B. Moncada & P. de Lange 38195 (F); Manawatu-Manganui, Hauhangaroa Range, Pureora Forest Park, Waihora Lagoon, 39 km WNW of Taupo, trail from Waihora Lagoon car park to lagoon, 38°38'46"S, 175°39'37"E, 550–560 m, dense podocarp forest dominated by rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*), miro (*P. ferruginea*), kahikatea (*Dacrycarpus dacrydioides*) and totara (*Podocarpus totara* var. *totara*) with an understorey of mahoe (*Melicytus ramiflorus* subsp. *ramiflorus*), pate (*Schefflera digitata*), kotukutuku (*Fuchsia excorticata*) and kaikomako (*Pennantia corymbosa*), well-preserved forest, 2015, R. Lücking, B. Moncada & P. de Lange 39004 (F).

Specimens of Sticta filix examined. **New Zealand:** *North Island:* Manawatu-Manganui, Erua Forest, Fishers Road, 1 km W to 5 km SW of National Park village, Tupapakura Waterfall Track, 39°10'19"S, 175°22'35"E, 800–900 m, podocarp forest dominated by totara (*Podocarpus totara* var. *totara*) and miro (*Prumnopitys ferruginea*), with an understorey of kamahi (*Weinmannia racemosa*), well-preserved forest, 2015, R. Lücking, B. Moncada & P. de Lange 38024a (F), 38028a (AK, F, UNITEC), 38090 (F), 38112 (F), 38149 (AK, F); *ibid.*, on *Coprosma grandifolia*, 38094 (AK, F); *ibid.*, on *Pseudowintera*, 38125 (AK, F); *ibid.*, on *Weinmannia*, 38107 (AK, F, UNITEC), 38148 (AK, F); Manawatu-Manganui, Erua Forest, Fishers Road, 1 km W to 5 km SW of National Park village, Tupapakura Waterfall Track, 39°10'19"S, 175°22'35"E, 800–900 m, podocarp forest dominated by totara (*Podocarpus totara* var. *totara*) and miro (*Prumnopitys ferruginea*), with an understorey of kamahi (*Weinmannia racemosa*), well-preserved forest, 2015, R. Lücking, B. Moncada & P. de Lange 38156 (F), 38159 (AK, F), 38190 (F); Manawatu-Manganui, Hauhangaroa Range, Pureora Forest Park, Waihora Lagoon, 39 km WNW of Taupo, trail from Waihora Lagoon car park to lagoon,

38°38'46"S, 175°39'37"E, 550–560 m, dense podocarp forest dominated by rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*), miro (*P. ferruginea*), kahikatea (*Dacrycarpus dacrydioides*) and totara (*Podocarpus totara* var. *totara*) with an understorey of mahoe (*Melicytus ramiflorus* subsp. *ramiflorus*), pate (*Schefflera digitata*), kotukutuku (*Fuchsia excorticata*) and kaikomako (*Pennantia corymbosa*), well-preserved forest, 2015, R. Lücking, B. Moncada & P. de Lange 39016 (F), 39034 (F), 39036 (F); *ibid.*, on *Dacrycarpus dacrydioides*, 39009 (F); *ibid.*, on *Prumnopitys ferruginea*, 39003 (AK, F, UNITEC); Waikato, Kaimanawa Forest Park adjacent to Tongariro National Park, Tree Trunk Gorge Road, 39 km E of National Park village, roadside, 39°10'31"S, 175°48'33"E, 725 m, mountain beech (*Fuscospora cliffortioides*), silver beech (*Lophozonia menziesii*) and red beech (*Fuscospora fusca*) forest, margin of well-preserved forest along road, 2015, R. Lücking, B. Moncada & P. de Lange 38844b (AK, F, UNITEC), 38850a (F), 38851 (AK, F, UNITEC); Waikato, Kaimanawa Forest Park, Rangipo Intake Road, 36 km ESE of National Park village, road head at hydroelectric dam of Tongariro River, 39°12'38"S, 175°46'48"E, 720–730 m, mountain beech (*Fuscospora cliffortioides*), silver beech (*Lophozonia menziesii*) and red beech (*Fuscospora fusca*) forest, margin of well-preserved forest along road, 2015, R. Lücking, B. Moncada & P. de Lange 38864 (AK, F, UNITEC).

Specimens of Sticta latifrons examined (chloromorph). **New Zealand:** *North Island:* Bay of Plenty, Lake Okataina Foreshore, Tauranganui Bay, 18 km ENE of Rotorua, parking lot facing lake near Lakes Lodge, 38°06'02"S, 176°25'49"E, 320 m, seral vegetation dominated by kamahi (*Weinmannia racemosa*) and ti kouka or cabbage tree (*Cordylina australis*), with pohutukawa (*Metrosideros excelsa*), exposed, planted trees along the beach near the lodge, with gully tree fern (*Cyathea cunninghamii*) and mamaku (*C. medullaris*), on *Cordylina australis*, 2016, R. Lücking, B. Moncada & P. de Lange 38357 (F); Bay of Plenty, Lake Okataina Road, 18 km NE of Rotorua, roadside along main road, 38°04'36"S, 176°24'51"E, 140 m, rimu (*Dacrydium cupressinum*) and tawa (*Beilschmiedia tawa*) forest, with a dense mahoe (*Melicytus ramiflorus* subsp. *ramiflorus*), pate (*Schefflera digitata*) and tree fern (*Dicksonia fibrosa* and *D. squarrosa*) understorey, shady forest edge along road, 2016, R. Lücking, B. Moncada & P. de Lange 38303 (F), 38310 (AK, F), 38318 (AK, F, UNITEC), 38327 (AK, F); Bay of Plenty, Toatoa to Motu Road, 17 km ESE of Opotiki, roadside along main road, 38°03'30"S, 177°27'46"E, 85 m, rimu (*Dacrydium cupressinum*), tawa (*Beilschmiedia tawa*) and hard beech (*Fuscospora truncata*) forest, with a dense mahoe (*Melicytus ramiflorus* subsp. *ramiflorus*), pate (*Schefflera digitata*) and tree fern (*Dicksonia fibrosa* and *D. squarrosa*) understorey, shady forest edge along road and shady roadbank, 2015, R. Lücking, B. Moncada & P. de Lange 38441 (F), 38446 (AK, F, UNITEC), 38447 (F); Hawke's Bay, Mahia Peninsula, Kinikini Road, Mahia Peninsula Scenic Reserve, 56 km SSW of Gisborne, trail through reserve, 39°07'28"S, 177°52'27"E, 150–200 m, kohekohe (*Dysoxylum*

spectabile), nikau (*Rhopalostylis sapida*) and tawa (*Beilschmiedia tawa*) forest transitioning into riparian podocarp forest dominated by kahikatea (*Dacrydium dactyloides*), matai (*Prumnopitys taxifolia*) and totara (*Podocarpus totara* var. *totara*), with an understorey of mahoe (*Melicactus ramiflorus* subsp. *ramiflorus*), kotukutuku (*Fuchsia excorticata*), horoeka (*Pseudopanax crassifolius*) and kaikomako (*Pennantia corymbosa*), well-preserved forest, 2015, R. Lücking, B. Moncada & P. de Lange 38657 (F), 38696c (AK, F, UNITEC), 38763 (F); *ibid.*, on *Beilschmiedia tarairi*, 38767b (F); *ibid.*, on *Kunzea robusta*, 38669 (AK, F); *ibid.*, on *Kunzea*, 38773a (F), 38774 (F); *ibid.*, on *Melicactus ramiflorus*, 38662 (AK, F); Manawatu-Manganui, Erua Forest, Fishers Road, 1 km W to 5 km SW of National Park village, Tupapakukura Waterfall Track, 39°10'19"S, 175°22'35"E, 800–900 m, podocarp tree-land dominated by totara (*Podocarpus totara* var. *totara*) and miro (*Prumnopitys ferruginea*), with an understorey of kamahi (*Weinmannia racemosa*), well-preserved forest, on *Carpodetus serratus*, 2015, R. Lücking, B. Moncada & P. de Lange 38111 (F); Waikato, Tongariro National Park, Tree Trunk Gorge Road, 38 km E of National Park village, roadside, 39°09'56"S, 175°48'11"E, 745 m, mountain beech (*Fuscospora cliffortioides*) forest with makahikatoa (*Kunzea serotina*), margin of well-preserved forest along road, 2015, R. Lücking, B. Moncada & P. de Lange 38835 (F).

Specimens of Sticta latifrons examined (cyanomorph). **New Zealand:** North Island: Manawatu-Manganui, Erua Forest, Fishers Road, 1 km W to 5 km SW of National Park village, Tupapakukura Waterfall Track, 39°10'19"S, 175°22'35"E, 800–900 m, podocarp forest dominated by totara (*Podocarpus totara* var. *totara*) and miro (*Prumnopitys ferruginea*), with an understorey of kamahi (*Weinmannia racemosa*), well-preserved forest, 2015, R. Lücking, B. Moncada & P. de Lange 38019 (AK, F); Waikato, Tongariro National Park, Tree Trunk Gorge Road, 38 km E of National Park village, roadside, 39°09'56"S, 175°48'11"E, 745 m, mountain beech (*Fuscospora cliffortioides*) forest with makahikatoa (*Kunzea serotina*), margin of well-preserved forest along road, 2015, R. Lücking, B. Moncada & P. de Lange 38815 (AK, F).

Funding for field and laboratory work for this study was provided by a grant from the National Science Foundation (NSF) to The Field Museum: DEB-1354884 'Collaborative Research: Evolution, Diversification, and Conservation of a Megadiverse Flagship Lichen Genus' (PI HTL, CoPI RL). The Field Museum's Prince Fund supported the internship of HR as part of this research project. The Department of Conservation in Auckland, New Zealand, is warmly thanked for logistic support and for making possible the participation of PJDL in the fieldwork. Unitec Institute of Technology (Auckland) and Dan Blanchon kindly provided assistance for organizing a workshop on the use of *Lobariaceae* as bioindicators of environmental health. Dan Blanchon also participated in part of the fieldwork and Allison Knight provided additional material and helped trace voucher specimens from previous phylogenetic studies deposited in OTA. Dhahara Ranatunga of the Auckland Museum

kindly helped with the logistics of depositing voucher specimens at AK and sending material to F. Konstanze Bensch assisted with MycoBank registration of the nomenclatural novelties and the GenBank Direct Submission staff promptly provided the GenBank Accession numbers.

SUPPLEMENTARY MATERIAL

For supplementary material accompanying this paper visit <https://doi.org/10.1017/S0024282917000706>

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