**Plant and Fungal Systematics** 71(1): 164–191, 2026
DOI: https://doi.org/10.35535/pfsyst-2026-0013

ISSN 2544-7459 (print)
ISSN 2657-5000 (online)

# The *Pseudocyphellaria hookeri* clade (*Peltigerales*): a species pair-photosymbiodeme speciation complex?

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**Article info**

Received: 16 Apr. 2026
Revision received: 6 Jul. 2026
Accepted: 6 Jul. 2026
Published: 31 Jul. 2026

**Associate Editor**

Marcela Cáceres

**Abstract**. We present an integrative taxonomic revision of the *Pseudocyphellaria hookeri* group in Aotearoa | New Zealand. Molecular data of the fungal ITS barcoding marker resolve the group as monophyletic, in a strongly supported clade on a long stem branch, related to the *P. crocata* group. Our study confirms the three species previously assigned to this group, *P. hookeri*, *P. durietzii*, and *P. montagnei*, as part of this clade. In addition, a fourth species was detected and is formally described here, namely *P. coralloidea* sp. nov. It is characterized by a cyanobacterial photobiont and coralloid clusters of stout, robust isidia partially eroding into soralia-like structures. Given that the *P. hookeri* clade contains four different combinations of photobionts and reproductive structures (*durietzii*: green, apothecia; *montagnei*: green, phyllidia; *hookeri*: cyanobacterial, apothecia; *coralloidea*: cyanobacterial: isidia), we hypothesized that this clade evolved from a polymorphic ancestor representing both a photosymbiodeme and a species pair. Indeed, both cases are well documented in other taxa of *Pseudocyphellaria*. However, our results do not support such a conclusion, but rather indicate step-wise transitions between photobionts and/or reproductive strategy. We also found that *P. durietzii* and *P. hookeri* are not photomorphs sharing the same mycobiont, as previously suggested. All four species of the *P. hookeri* group are described and illustrated and their taxonomy is discussed, including a dichotomous key. We also provide information about their distribution, ecology, and conservation status. We introduce the term "soredisidia" for reproductive structures that represent a transition between genuine soralia and true isidia. This contribution is dedicated to our esteemed colleague, André Aptroot, on the occasion of his 65th birthday.

**Key words**: *Lobaria asperula*, *Lobarioideae*, *Peltigeraceae*, *Podostictina pickeringii*, *Sticta squamata*, temporal banding

## Introduction

*Pseudocyphellaria* Vain. is one of the most diverse genera of macrolichens, with about 120 species currently recognized, but many more are predicted based on preliminary molecular data, with most of the known and predicted species occurring in the Southern Hemisphere (Galloway 1985, 1986, 1988, 1992, 1994, 2007; Moncada et al. 2014; Lücking et al. 2017a). The genus is recognized by its often large, leathery thalli with mostly punctiform pseudocyphellae on the lobe underside, rarely also the upper side. Molecular phylogenetic studies have shown that pseudocyphellate *Lobariaceae* (or *Peltigeraceae* subfamily *Lobarioideae*) do not form a monophyletic group. Three smaller genera, *Crocodia* Link (including *Parmostictina* Nyl.), *Podostictina* Clem., and *Yarrumia* D.J. Galloway, were segregated from *Pseudocyphellaria*, and two further species, for a short time segregated in the genus *Anomalobaria* B. Moncada & Lücking, were eventually included in *Lobaria* s.str. (Galloway & Elix 2013; Moncada et al. 2013a; McCune et al. 2014; Miądlikowska et al. 2014; Galloway 2015). Molecular data also show a substantial level of unrecognized, hidden

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diversity within *Pseudocyphellaria*. Thus, the core group of the genus, centered around the type species, *P. crocata* (L.) Vain., comprises dozens of species corresponding to a broadly defined *P. crocata* morphodeme (Moncada et al. 2014; Lücking et al. 2017b).

*Pseudocyphellaria*, as other genera in *Lobariaceae*, includes several examples of species pairs and photosymbiodemes (Galloway 1985, 1988, 1992, 1994, 2007; Messuti et al. 2016; Widhelm et al. 2021a, 2023). Species pairs are morphologically similar or identical forms that differ in their reproductive strategy, either sexual via ascospores or vegetative via soredia or isidia (Du Rietz 1924; Poelt 1970; Tehler 1982; Mattson & Lumbsch 1989; Lücking et al. 2021). Molecular studies demonstrated that species pairs are taxonomically complex, ranging from demonstrably conspecific forms with alternative reproductive strategies, such as *Porina mirabilis* Lücking & Vězda vs. *Phyllophiale alba* R. Sant., to cases in which genetically identical forms differ in reproductive strategy and ecology, such as *Physcia aipolia* (Ehrh. ex Humb.) Fürnr. vs. *P. caesia* (Hoffm.) Fürnr., to species complexes in which different lineages can reproduce either sexually, vegetatively, or both, as in the *Letharia vulpina* (Nyl.) Hue complex or in the genus *Porpidia* Körb. (Lücking & Vězda 1998; Kroken & Taylor 2001; Myllys et al. 2001; Lücking 2004; Baloch & Grube 2006; Buschbom & Mueller 2006; Crespo & Pérez-Ortega 2009; Altermann et al. 2016; Grewe et al. 2018; Lagostina et al. 2018; Widhelm et al. 2021a, 2023). In Aotearoa | New Zealand (henceforth New Zealand), presumed species pairs in *Pseudocyphellaria* are represented by *P. cinnamomea* (A. Rich.) Vain. (apotheciate) vs. *P. dissimilis* (Nyl.) D.J. Galloway & P. James (isidiate-phyllidiate) or *P. homoeophylla* (Nyl.) C.W. Dodge (apotheciate) vs. *P. glabra* (Hook. f. & Taylor) C.W. Dodge (isidiate). An example from southern South America is *P. pilosella* Malme (apotheciate) vs. *P. piloselloides* (Räsänen) H. Magn. (sorediate; Messuti et al. 2016).

Photosymbiodemes constitute instances where the same fungus associates with two different photobionts, either green algae or cyanobacteria, often forming strikingly different morphologies as part of the same lichen or in separate thalli (Ott 1988; Armaleo & Clerc 1991; Green et al. 1993; Sanders 2001; Honegger 2009; Moncada et al. 2013b). Presumed photosymbiodemes are also frequent in New Zealand, e.g., in *P. coriacea* (Hook. f. & Taylor) D.J. Galloway & P. James (green) vs. *P. allanii* D.J. Galloway (cyanobacterial), *P. lividofusca* (Kremp.) D.J. Galloway & P. James (green) vs. *P. knightii* D.J. Galloway (cyanobacterial), and *P. rufovirescens* (C. Bab.) D.J. Galloway (green) vs. *P. murrayi* D.J. Galloway (cyanobacterial). In these cases, the alternative names for the cyanobacterial forms are now considered synonyms (Galloway 2007).

The evolutionary mechanisms generating and maintaining such polymorphisms are not known, but it is conceivable that originally polymorphic taxa (Fig. 1A) in the course of time, through loss mutations and lineage sorting, give rise to distinctive lineages with only one type of reproduction and one type of photobiont (Fig. 1C). As a result, on the way from (A) to (C), one would postulate the existence of transitional forms representing different

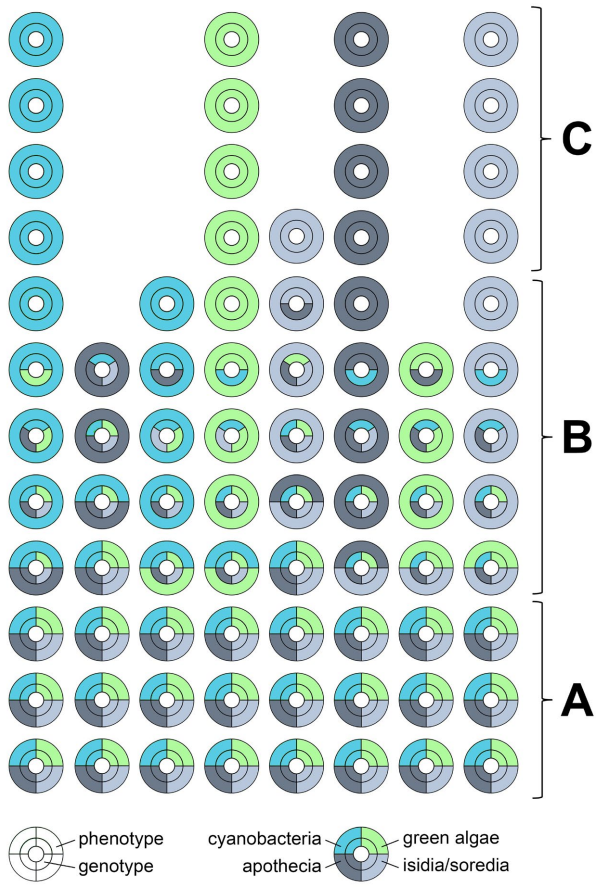


**Figure 1**. Simplified schematic representation of a polymorphic ancestral lineage (A), with two photobionts and two types of reproduction present in each individuum, evolving into separate, distinct lineages, each representing a uniform genotype and phenotype (C). The timeline undergoes a period of lineage sorting containing mixed genotypes and phenotypes and often only one or two of the genotypes expressed (B).

combinations of reproductive strategies and photobiont types (Fig. 1B). As part of a molecular phylogenetic revision of the genus *Pseudocyphellaria* in New Zealand, we identified such a potential clade, containing three known species, *P. durietzii* D.J. Galloway (green, apothecia), *P. hookeri* (C. Bab.) D.J. Galloway & P. James (cyanobacterial or rarely green, apothecia), and *P. montagnei* (C. Bab.) D.J. Galloway & P. James (green, phyllidia and sometimes apothecia), and an unnamed taxon with cyanobacteria bearing isidia. The clade is an early diverging lineage in one of two large subclades within *Pseudocyphellaria*, the subclade comprising *P. crocata* and its relatives, and appears to be a good case study to test the above hypothesis.

Here, we characterize the *Pseudocyphellaria hookeri* clade, formally introducing one new species. We use this group as a model clade to test possible evolutionary mechanisms leading to morphologically distinctive species, emerging from a putative polymorphic lineage representing a species pair-photosymbiodeme complex.

## Material and methods

Material of *Pseudocyphellaria* and other *Lobariaceae* was collected by four of the authors (BM, RL, PdL, DB) during a two-week field trip in New Zealand's North

Island in 2015. The collected material was carefully dried and prepared for molecular analysis. All specimens were documented with photographs *in situ* in the field, using a NIKON D3200 digital camera with a NIKKOR 150 mm 2.8 VR macro lens. Morphological and anatomical assessments were carried out at the Field Museum, Chicago, and at the Botanischer Garten Berlin, Freie Universität Berlin, using LEICA MS5, MOTIC K400, and LEICA ZOOM 2000 dissecting microscopes, as well as ZEISS Axioscop 2, OLYMPUS BH-2, and VISTAVISION VWR V036 compound microscopes. In addition, the dried specimens were scanned (both upper and lower side) at high resolution by co-author HR, using a flatbed scanner, as part of an intern project (for details of this project, see Ranft et al. 2018). Preliminary identifications were carried out using the keys provided by Galloway (1985, 1988, 2007). The material is deposited at AK, with duplicates in B, F and UNITEC (herbarium acronyms following Thiers 2008). For spot tests, we used commercial bleach (C) and 10% potassium hydroxide solution (K). Thin-layer chromatography was performed following Orange et al. (2010), using Supelco TLC Silica Gel 60 F254 20 × 20 cm glass plates in solvent C (toluene:acetic acid = 170:30).

We used the location data of the collected and studied specimens, as well as published literature, to infer the habitat ecology of each of the taxa. To explore the full range of available data, we also surveyed iNaturalist (Mason et al. 2025; Wang et al. 2025) for reliably identifiable individuals belonging to taxa in the target clade (File S1).

We targeted the fungal ITS barcoding marker for sequencing, as it provides good resolution to distinguish most taxa in this genus (Moncada et al. 2014; Messuti et al. 2016; Lücking et al. 2017b), although cases are known in *Pseudocyphellaria* where population-genetic markers, such as RADseq, give a more fine-scaled differentiation (Widhelm et al. 2021a, 2023). Molecular work was performed at the Field Museum's Pritzker DNA lab. For DNA extraction, we used the QIAGEN DNeasy Plant Mini Kit, with dilutions of 10:1 for PCR amplifications, employing the primer pairs ITS1F and ITS4 (Gardes & Bruns 1993; White et al. 1990). Each of 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. Thermal cycling parameters were: 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 final elongation for 7 min at 73°C. The amplification products were mounted on 1% agarose gels stained with ethidium bromide. After cutting, the target bands were purified using the QIAGEN QIAquick PCR Purification Kit or Nucleo Spin DNA purification kit (Macherey-Nagel). Fragments were sequenced at the Pritzker DNA lab using the Big Dye Terminator reaction kit (ABI PRISM, Applied Biosystems), with the same sets of primers for sequencing and PCR amplifications. Cycle sequencing was executed with the following setting: 25 cycles of 95°C for 30 sec, 48°C for 15 sec, 60°C for 4 min. Sequencing products were precipitated with 10 µl of sterile $dH_2O$, 2 µl of 3 M Napa, and 50 µl of 95% EtOH and subsequently loaded on an ABI 3100 (Applied Biosystems) automatic sequencer. The obtained sequence reads were checked in NCBI MegaBlast (Morgulis et al. 2008), assembled with DNASTAR SeqMan 4.03, manually inspected and adjusted and, after quality control within the context of a multiple alignment, submitted to GenBank (Table 1).

The obtained sequences were aligned with all available ITS sequences of *Pseudocyphellaria* from GenBank (Table 1). The overall alignment was assembled in BIOEDIT 7.0.9 (Hall 1999, 2011) and then automatically aligned using MAFFT 7 with the auto option (Katoh & Standley 2013), with subsequent manual inspection

**Table 1**. GenBank accessions for the terminals used in the phylogenetic analysis, including voucher information for newly generated sequences (accessions in bold). The photomorph is only indicated in cases a taxon had two different photomorphs in the same clade. Collectors and collector number are only given for newly generated sequences.

| Name of taxa | Photomorph | ITS Accession | Sample | Collectors | Number |
|---|---|---|---|---|---|
| *Pseudocyphellaria allanii* | – | AF351138 | – | – | – |
| *Pseudocyphellaria argyracea* | – | **PZ600660** | MON3614 | Lücking et al. | 38501 |
| *Pseudocyphellaria argyracea* | – | **PZ600661** | MON3541 | Lücking et al. | 38723 |
| *Pseudocyphellaria argyracea* | – | **PZ600662** | MON3659 | Lücking et al. | 38505 |
| *Pseudocyphellaria bartlettii* | – | **PZ600663** | MON3443 | Lücking et al. | 38552 |
| *Pseudocyphellaria bartlettii* | – | **PZ600664** | MON3613 | Lücking et al. | 38481 |
| *Pseudocyphellaria bartlettii* | – | **PZ600665** | MON3442 | Lücking et al. | 38536 |
| *Pseudocyphellaria biliana* | – | KJ523062 | – | – | – |
| *Pseudocyphellaria biliana* | – | KJ523063 | – | – | – |
| *Pseudocyphellaria biliana* | – | KJ523064 | – | – | – |
| *Pseudocyphellaria billiarderii* | – | **PZ600674** | MON3566 | Lücking et al. | 38917 |
| *Pseudocyphellaria billiarderii* | – | **PZ600675** | MON3575 | Lücking et al. | 38824 |
| *Pseudocyphellaria billiarderii* | – | **PZ600676** | MON3564 | Lücking et al. | 38798 |
| *Pseudocyphellaria carpoloma* | – | **PZ600666** | MON3617 | Lücking et al. | 38414 |
| *Pseudocyphellaria carpoloma* | – | **PZ600667** | MON3618 | Lücking et al. | 38477 |
| *Pseudocyphellaria carpoloma* | – | **PZ600668** | MON3449 | Lücking et al. | 39177 |
| *Pseudocyphellaria cinnamomea* | – | AF351139 | – | – | – |
| *Pseudocyphellaria citrina* | – | MN272295 | – | – | – |
| *Pseudocyphellaria citrina* | – | OQ922979 | – | – | – |

**Table 1**. Continued.

| Name of taxa | Photomorph | ITS Accession | Sample | Collectors | Number |
|---|---|---|---|---|---|
| *Pseudocyphellaria citrina* | – | PQ168919 | – | – | – |
| *Pseudocyphellaria confusa* | – | KJ523104 | – | – | – |
| *Pseudocyphellaria confusa* | – | KJ523107 | – | – | – |
| *Pseudocyphellaria coralloidea* | – | **PZ600680** | MON3539 | Lücking et al. | 38809 |
| *Pseudocyphellaria corbettii* | – | AF351150 | – | – | – |
| *Pseudocyphellaria corbettii* | – | KJ523039 | – | – | – |
| *Pseudocyphellaria coriacea* | – | AF351149 | – | – | – |
| *Pseudocyphellaria coriacea* | – | **PZ600636** | MON3553 | Lücking et al. | 39026 |
| *Pseudocyphellaria coriacea* | – | **PZ600637** | MON3610 | Lücking et al. | 38620 |
| *Pseudocyphellaria coriacea* | – | **PZ600650** | MON3611 | Lücking et al. | 38610 |
| *Pseudocyphellaria coriacea* | – | **PZ600651** | MON3608 | Lücking et al. | 38475 |
| *Pseudocyphellaria coriacea* | – | **PZ600652** | MON3454 | Lücking et al. | 39160 |
| *Pseudocyphellaria coriifolia* | – | EU558706 | – | – | – |
| *Pseudocyphellaria coriifolia* | – | EU558709 | – | – | – |
| *Pseudocyphellaria crocata* | – | EU558699 | – | – | – |
| *Pseudocyphellaria dissimilis* | – | AF351151 | – | – | – |
| *Pseudocyphellaria dissimilis* | – | **PZ600638** | MON3598 | Lücking et al. | 38032 |
| *Pseudocyphellaria dissimilis* | – | **PZ600639** | MON3726 | Lücking et al. | 38056 |
| *Pseudocyphellaria durietzii* | – | **PZ600681** | MON3434 | Lücking et al. | 39191 |
| *Pseudocyphellaria durietzii* | – | **PZ600682** | MON3545 | Lücking et al. | 38761 |
| *Pseudocyphellaria durietzii* | – | **PZ600683** | MON3697 | Lücking et al. | 38667 |
| *Pseudocyphellaria durietzii* | – | **PZ600684** | MON3695 | Lücking et al. | 38619 |
| *Pseudocyphellaria durietzii* | – | **PZ600685** | MON3549 | Lücking et al. | 38756b |
| *Pseudocyphellaria durietzii* | – | **PZ600686** | MON3485 | Lücking et al. | 39199 |
| *Pseudocyphellaria durietzii* | – | PZ600687 | MON3696 | Lücking et al. | 38666 |
| *Pseudocyphellaria durietzii* | – | **PZ600688** | MON3698 | Lücking et al. | 38758 |
| *Pseudocyphellaria durietzii* | – | **PZ600689** | MON3897 | Lücking et al. | 38722 |
| *Pseudocyphellaria episticta* | – | AF351152 | – | – | – |
| *Pseudocyphellaria episticta* | – | **PZ600656** | MON3671 | Lücking et al. | 38826 |
| *Pseudocyphellaria episticta* | – | **PZ600657** | MON3673 | Lücking et al. | 38843 |
| *Pseudocyphellaria faveolata* | – | PZ600671 | MON3579 | Lücking et al. | 39032 |
| *Pseudocyphellaria faveolata* | – | **PZ600672** | MON3577 | Lücking et al. | 38181 |
| *Pseudocyphellaria faveolata* | – | **PZ600673** | MON3578 | Lücking et al. | 38999 |
| *Pseudocyphellaria fimbriata* | – | **PZ600653** | MON3706 | Lücking et al. | 38124 |
| *Pseudocyphellaria fimbriata* | – | **PZ600654** | MON3704 | Lücking et al. | 38209 |
| *Pseudocyphellaria fimbriata* | – | **PZ600655** | MON3705 | Lücking et al. | 38175 |
| *Pseudocyphellaria freycinetii* | – | AF257184 | – | – | – |
| *Pseudocyphellaria freycinetii* | – | EU558717 | – | – | – |
| *Pseudocyphellaria freycinetii* | – | EU558724 | – | – | – |
| *Pseudocyphellaria glabra* | – | AF351144 | – | – | – |
| *Pseudocyphellaria glabra* | – | MT376226 | – | – | – |
| *Pseudocyphellaria glabra* | – | MT376237 | – | – | – |
| *Pseudocyphellaria granulata* | – | AF350313 | – | – | – |
| *Pseudocyphellaria granulata* | – | **PZ600669** | MON3759 | Lücking et al. | 38065 |
| *Pseudocyphellaria granulata* | – | **PZ600670** | MON3574 | Lücking et al. | 38801 |
| *Pseudocyphellaria hawaiiensis* | – | KJ523078 | – | – | – |
| *Pseudocyphellaria hawaiiensis* | – | KJ523085 | – | – | – |
| *Pseudocyphellaria hawaiiensis* | – | MN272293 | – | – | – |
| *Pseudocyphellaria homoeophylla* | – | AF351145 | – | – | – |
| *Pseudocyphellaria homoeophylla* | – | **PZ600658** | MON3601 | Lücking et al. | 38165 |
| *Pseudocyphellaria homoeophylla* | – | **PZ600659** | MON3602 | Lücking et al. | 38169 |
| *Pseudocyphellaria hookeri* | – | AF350315 | – | | |
| *Pseudocyphellaria hookeri* | – | **PZ600677** | MON3691 | Lücking et al. | 38769 |
| *Pseudocyphellaria hookeri* | – | **PZ600678** | MON3692 | Lücking et al. | 38768 |
| *Pseudocyphellaria hookeri* | – | **PZ600679** | MON3694 | Lücking et al. | 38977 |
| *Pseudocyphellaria intricata* | – | MH295161 | – | – | – |
| *Pseudocyphellaria intricata* | – | MH295187 | – | – | – |
| *Pseudocyphellaria intricata* | – | MH295199 | – | – | – |
| *Pseudocyphellaria lacerata* | – | MH295154 | – | – | – |
| *Pseudocyphellaria lacerata* | – | MH295231 | – | – | – |
| *Pseudocyphellaria lacerata* | – | MH295233 | – | – | – |

**Table 1**. Continued.

| Name of taxa | Photomorph | ITS Accession | Sample | Collectors | Number |
|---|---|---|---|---|---|
| *Pseudocyphellaria lechleri* | – | EU558716 | – | – | – |
| *Pseudocyphellaria lechleri* | – | MF970444 | – | – | – |
| *Pseudocyphellaria lechleri* | – | MF970446 | – | – | – |
| *Pseudocyphellaria lividofusca* | (chloro) | AF351153 | – | – | – |
| *Pseudocyphellaria lividofusca* | (chloro) | **PZ600649** | MON3708 | Lücking et al. | 38102b |
| *Pseudocyphellaria lividofusca* | (cyano: *knightii*) | AF351140 | – | – | – |
| *Pseudocyphellaria lividofusca* | (cyano: *knightii*) | KJ523043 | – | – | – |
| *Pseudocyphellaria lividofusca* | (cyano: *knightii*) | **PZ600648** | MON3707 | Lücking et al. | 38102a |
| *Pseudocyphellaria macroisidiata* | – | KJ523057 | – | – | – |
| *Pseudocyphellaria macroisidiata* | – | KJ523060 | – | – | – |
| *Pseudocyphellaria macroisidiata* | – | KJ523097 | – | – | – |
| *Pseudocyphellaria maculata* | – | AF351147 | – | – | – |
| *Pseudocyphellaria montagnei* | – | **PZ600690** | MON3562 | Lücking et al. | 38513 |
| *Pseudocyphellaria montagnei* | – | **PZ600691** | MON3703 | Lücking et al. | 38649 |
| *Pseudocyphellaria montagnei* | – | **PZ600692** | MON3503 | Lücking et al. | 39133 |
| *Pseudocyphellaria montagnei* | – | **PZ600693** | MON3502 | Lücking et al. | 39143 |
| *Pseudocyphellaria montagnei* | – | **PZ600694** | MON3501 | Lücking et al. | 39109 |
| *Pseudocyphellaria multifida* | (chloro) | AF351146 | – | – | – |
| *Pseudocyphellaria multifida* | (chloro) | **PZ600644** | MON3774 | Lücking et al. | 38047 |
| *Pseudocyphellaria multifida* | (chloro) | **PZ600645** | MON3820 | Lücking et al. | 39031 |
| *Pseudocyphellaria multifida* | (cyano) | **PZ600646** | MON3723 | Lücking et al. | 38006 |
| *Pseudocyphellaria multifida* | (cyano) | **PZ600647** | MON3712 | Lücking et al. | 38196 |
| *Pseudocyphellaria neglecta* | – | AF351141 | – | – | – |
| *Pseudocyphellaria neglecta* | – | AJ437687 | – | – | – |
| *Pseudocyphellaria neglecta* | – | AJ888211 | – | – | – |
| *Pseudocyphellaria norvegica* | – | MH295214 | – | – | – |
| *Pseudocyphellaria norvegica* | – | MH295217 | – | – | – |
| *Pseudocyphellaria norvegica* | – | MH295226 | – | – | – |
| *Pseudocyphellaria pilosella* | – | KT722796 | – | – | – |
| *Pseudocyphellaria pilosella* | – | KT861464 | – | – | – |
| *Pseudocyphellaria pilosella* | – | KT861466 | – | – | – |
| *Pseudocyphellaria piloselloides* | – | KT722799 | – | – | – |
| *Pseudocyphellaria piloselloides* | – | KT861461 | – | – | – |
| *Pseudocyphellaria piloselloides* | – | KT861462 | – | – | – |
| *Pseudocyphellaria pomaikaiana* | – | KJ523098 | – | – | – |
| *Pseudocyphellaria pomaikaiana* | – | KJ523100 | – | – | – |
| *Pseudocyphellaria pomaikaiana* | – | KJ523101 | – | – | – |
| *Pseudocyphellaria rufovirescens* | (chloro) | AF351142 | – | – | – |
| *Pseudocyphellaria rufovirescens* | (chloro) | **PZ600641** | MON3584 | Lücking et al. | 38700 |
| *Pseudocyphellaria rufovirescens* | (chloro) | **PZ600643** | MON3587 | Lücking et al. | 38995 |
| *Pseudocyphellaria rufovirescens* | (cyano: *murrayi*) | AF350316 | – | – | – |
| *Pseudocyphellaria rufovirescens* | (cyano: *murrayi*) | **PZ600640** | MON3710 | Lücking et al. | 38117b |
| *Pseudocyphellaria rufovirescens* | (cyano: *murrayi*) | **PZ600642** | MON3715 | Lücking et al. | 39017a |
| *Pseudocyphellaria xanthosticta* | – | MF537268 | – | – | – |
| *Pseudocyphellaria xanthosticta* | – | MF537269 | – | – | – |
| *Pseudocyphellaria xanthosticta* | – | MF537293 | – | – | – |

(File S2). Phylogenetic analysis was performed using maximum likelihood in RAxML 8 (Stamatakis 2014), with non-parametric bootstrapping using 1,000 replicates under the GTRGAMMA model (File S3). Trees were visualized in FIGTREE 1.4.4 (Drummond & Rambaut 2007).

## Results

Molecular phylogenetic analysis of the fungal ITS barcoding marker placed *Pseudocyphellaria hookeri* and its relatives in a fully supported clade (BS = 100) on a long stem branch, as an early diverging lineage in a larger subclade (Clade I) including *P. billardierei* (Delise) Räsanen and the *P. crocata* clade (Figs 2, 3). This larger subclade was sister to another large subclade (Clade II) including all other species of the genus from New Zealand, such as *P. dissimilis*, *P. glabra*, *P. haywardiorum* D.J. Galloway, *P. multifida* (Laurer ex Nyl.) D.J. Galloway & P. James, and *P. rufovirescens*, among others.

Clade II included several examples of confirmed species pairs, in some instances combined with photosymbiodemes, such as *P. homoeophylla* (green, apotheciate) vs. *P. glabra* (green, isidiate) or *P. rufovirescens* (green) vs. *P. murrayi* D.J. Galloway (cyanobacterial),

now a synonym of *P. rufovirescens* (Galloway 2007). A remarkable case of a combined species pair-photosymbiodeme complex in Clade I is *P. carpoloma* (Delise) Vain. (green, apotheciate), which has an undescribed sorediate counterpart with soredia and yellow pigment corresponding to the *P. crocata* morphodeme (to be treated in a forthcoming paper).

In the *Pseudocyphellaria hookeri* clade, situated on a long and fully supported (BS = 100) stem branch, *P. montagnei* (green, phyllidiate) was recovered as the earliest emerging clade, sister to a weakly supported clade (BS = 66) including *P. hookeri*, *P. durietzii*, and one undescribed taxon. In that clade, *P. durietzii* was recovered as sister to a fully supported clade (BS = 100) including *P. hookeri* (cyanobacterial, apotheciate) and the

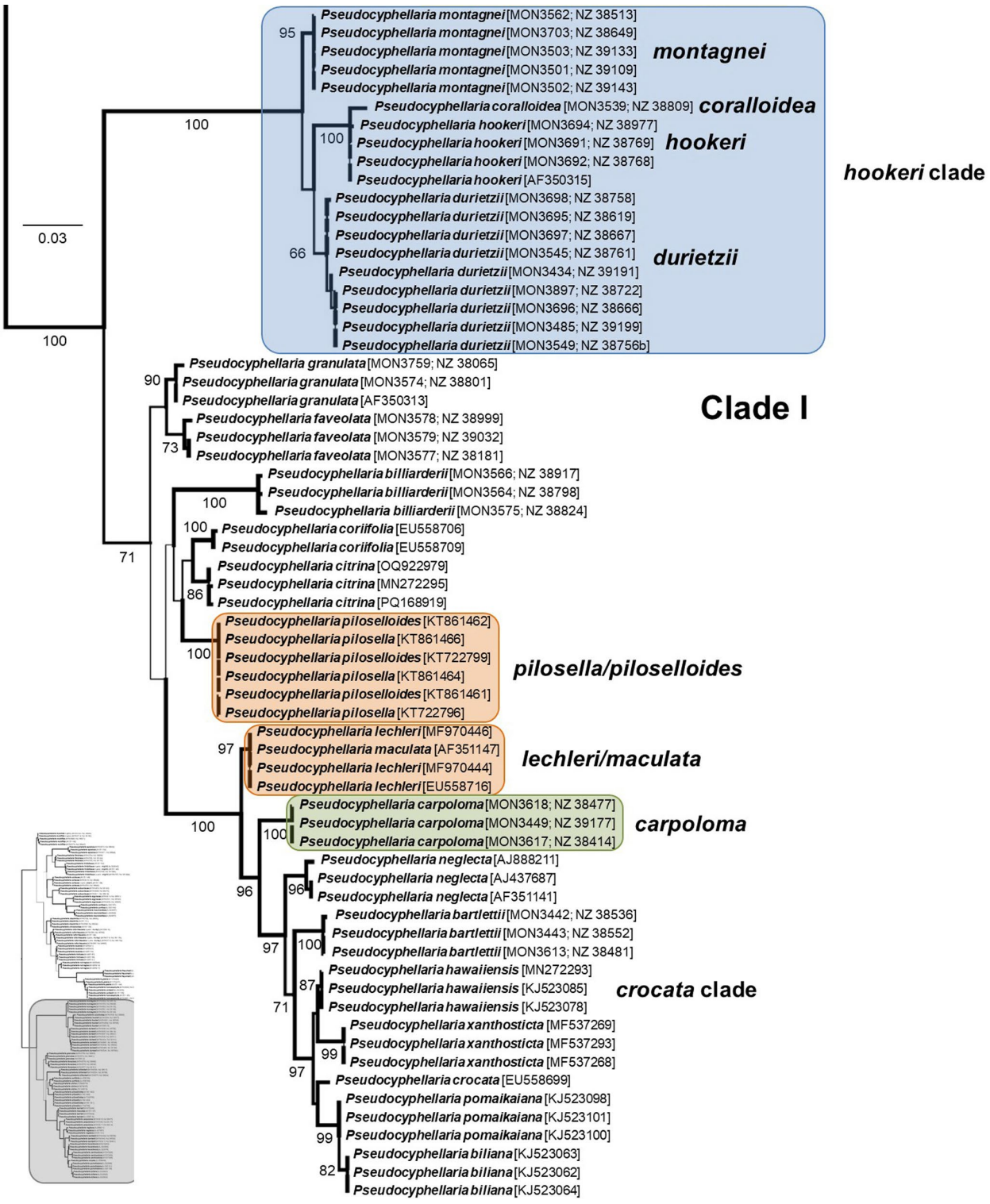


**Figure 2**. Best-scoring maximum likelihood tree of *Pseudocyphellaria* based on the fungal ITS barcoding marker, showing Clade I. Bootstrap support values of 70 or greater are indicated below branches. In blue the highlighted *P. hookeri* clade; clades highlighted in beige include species pairs, clades highlighted in green refer to photosymbiodemes. For continuation (Clade II), see Fig. 3.

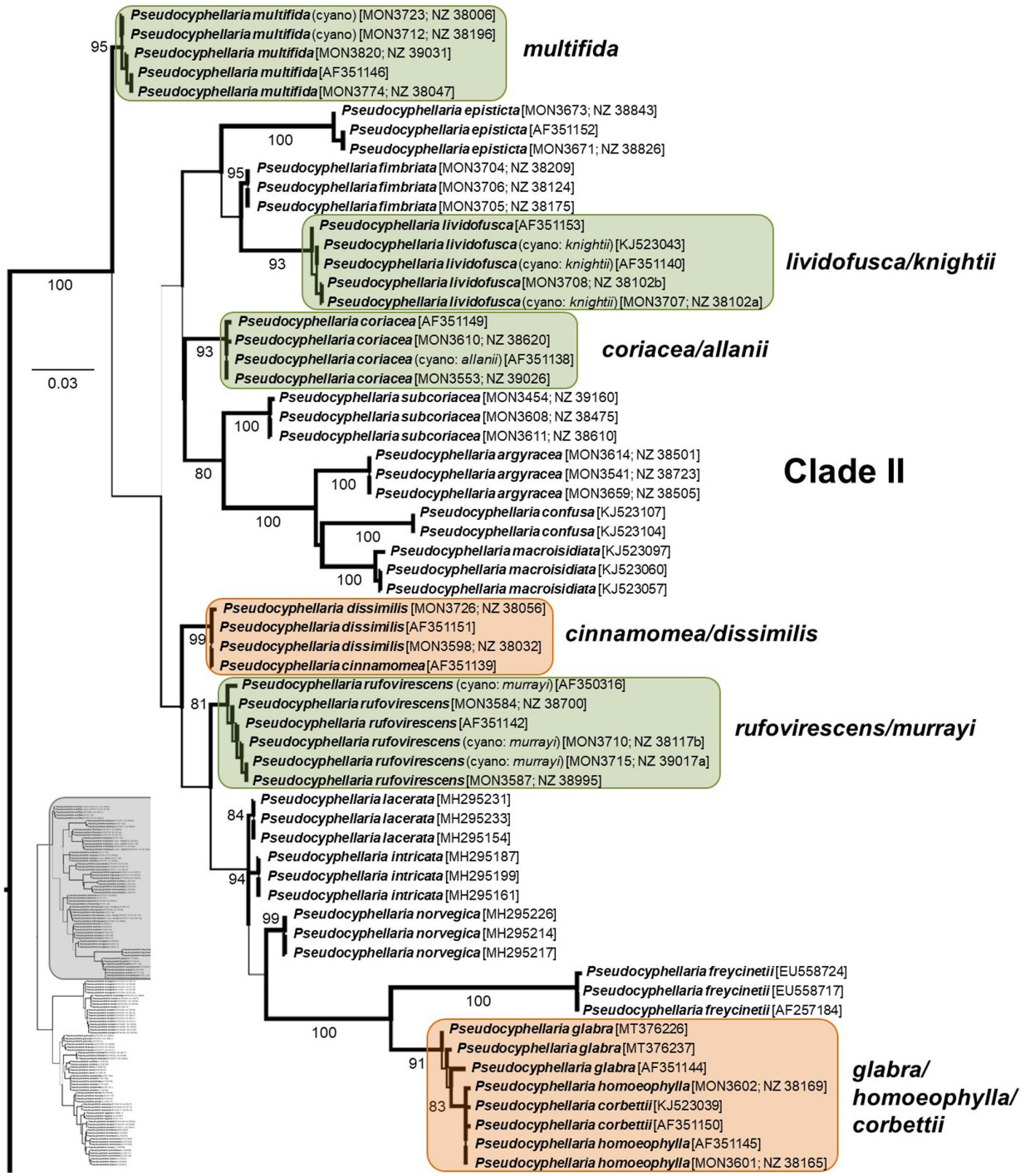


**Figure 3**. Best-scoring maximum likelihood tree of *Pseudocyphellaria* based on the fungal ITS barcoding marker, showing Clade II. Bootstrap support values of 70 or greater are indicated below branches. Clades highlighted in beige include species pairs, clades highlighted in green refer to photosymbiodemes. For continuation (Clade I), see Fig. 2.

undescribed taxon with cyanobacteria and isidia. *Pseudocyphellaria durietzii* differs from *P. montagnei* in seven substitutions and three indels (98% similarity), *P. hookeri* differs from *P. durietzii* in 11 substitutions (98% similarity), and *P. coralloidea* differs from *P. hookeri* in three substitutions (99.5% similarity).

Manual ancestral character state reconstruction indicates the hypothetical ancestral lineage of the *P. hookeri* clade as likely associated with green algae and with sexual reproduction (Fig. 4), consistent with the fact that the phyllidiate *P. montagnei* often also produces

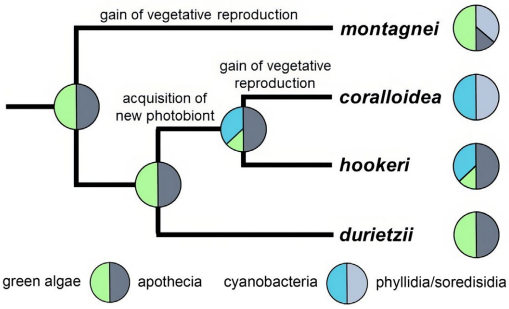


**Figure 4**. Manual reconstruction of the most likely ancestral character states in the *Pseudocyphellaria hookeri* clade.

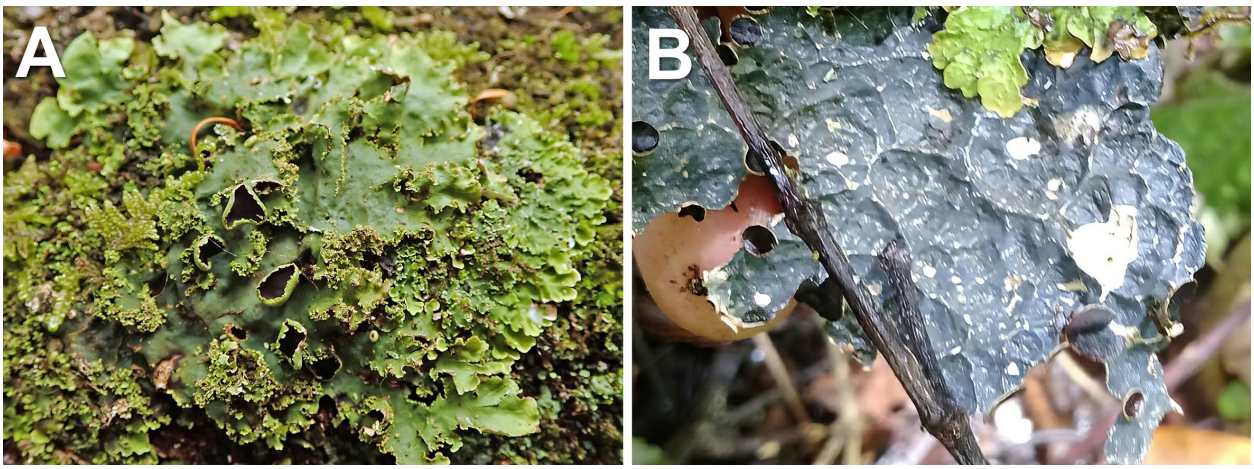


**Figure 5**. A – Field image of an individual of *Pseudocyphellaria montagnei* with phyllidia and apothecia [Marley Ford; https://www.inaturalist.org/observations/38788756; https://creativecommons.org/licenses/by-nc/4.0/deed.en]; B – field image of an individual of *P. hookeri* with green-algal lobes attached to a cyanobacterial thallus [Marley Ford; https://www.inaturalist.org/observations/9750022; https://creativecommons.org/licenses/by-nc/4.0/deed.en].

apothecia. Apparently, there was a single acquisition of a cyanobacterial photobiont, leading to the clade including *P. hookeri* and its closely related, isidiate sister taxon. Since we consider it unlikely that vegetative reproduction, once gained, is subsequently lost (as it provides a clear evolutionary advantage especially in combination with persistent sexual reproduction), we presume two separate, independent gains of vegetative reproduction in the *P. hookeri* clade. This is supported by the fact that the phyllidia found in *P. montagnei* and the isidia present in *P. coralloidea* are of a profoundly different nature and so likely did not evolve from a shared ancestral structure.

Revision of numerous specimens and surveying iNaturalist records supported the following cases of genuine polymorphism: *P. montagnei* typically produces phyllidia, but rather often also scattered to abundant apothecia on otherwise phyllidiate thalli, as seen in several instances on iNaturalist [e.g., https://www.inaturalist.org/observations/38788756] (Fig. 5A). At least one instance of a photosymbiodeme between the cyanobacterial *P. hookeri* and attached green-algal lobes was found in iNaturalist [e.g., https://www.inaturalist.org/observations/9750022] (Fig. 5B). No photosymbiodemes were found in connection with *P. durietzii* and *P. montagnei*, and no confirmed specimen of *P. durietzii* was found to produce genuine phyllidia, although scattered adventive lobules are sometimes present. The newly described species with a cyanobacterial photobiont and isidia is only known from a single collection with sequence data and a few additional specimens lacking sequence data, and no apothecia or associated green-algal lobes were observed.

## Discussion

### The *Pseudocyphellaria hookeri* clade as a model of polymorphic ancestry?

Hitherto, most cases of putative species pairs or photosymbiodemes in lichen-forming fungi have either revealed complexes of closely related lineages or unresolved clades, indicating either early stages of speciation or extant polymorphism (Lücking & Vězda 1998; Kroken & Taylor 2001; Myllys et al. 2001; Lücking 2004; Baloch & Grube 2006; Buschbom & Mueller 2006; Crespo & Pérez-Ortega 2009; Altermann et al. 2016; Grewe et al. 2018; Lagostina et al. 2018; Widhelm et al. 2021a, 2023). The *Pseudocyphellaria hookeri* clade, endemic to New Zealand, seems to be the first known example of a well-defined clade that diversified into distinct lineages, each representing one of four possible reproductive mode / photobiont combinations.

Our study, however, indicates that the four taxa recognized in this clade did not evolve from a single, polymorphic ancestor, as hypothesized at the onset of this study. Rather, it appears that the ancestral lineage was phenotypically uniform, representing an apotheciate green algal lichen. Subsequently, there was a single acquisition of cyanobacteria as the main photobiont along the branch leading to the *P. hookeri*/*coralloidea* clade. Notably, while *P. hookeri* is mostly only found with a cyanobacterial photobiont, rare cases of photosymbiodemes with green-algal lobes have been reported and partly documented (Fig. 5B). Thus, it appears that at least some individuals in this species maintain the genetic makeup to associate with green algae. Notably, while the green algal lobes closely resemble those of *P. durietzii*, they must be phylogenetically distinct from the latter if formed by the mycobiont of *P. hookeri*.

We postulate that the ancestral lineage first split into two lineages, differing in overall morphology, but each retaining sexual reproduction by means of apothecia and one (*P. montagnei*) gaining vegetative reproduction through phyllidia. The alternative interpretation of the ancestral lineage featuring both modes of reproduction and vegetative reproduction being lost in the second lineage is not likely, as vegetative reproduction represents an evolutionary advantage, especially if combined with persisting sexual reproduction. This means that vegetative reproduction by means of isidia in the lineage leading to *P. coralloidea* is to be interpreted as a second, independent gain of this mode of reproduction in this clade, which

is supported by the different morphology of the isidia compared to the phyllidia of *P. montagnei*. The isidia found in *P. coralloidea* are thus not homologous with the phyllidia of *P. montagnei*, rejecting the hypothesis that a reproductively polymorphic ancestor gave rise to a green algal and a cyanobacteria lineage with vegetative propagules.

The different thallus morphology of the four taxa, together with their phylogenetic distinctiveness, does not allow us to consider the corresponding counterparts species pairs (e.g., *P. durietzii* vs. *P. montagnei*; *P. hookeri* vs. *P. coralloidea*) or photosymbiodemes (*P. montagnei* vs. *P. coralloidea*). Seemingly an exception is the pair *P. durietzii* vs. *P. hookeri*, which both agree in thallus configuration and the scrobiculate to faveolate lobe surface and so appear to form a photosymbiodeme. However, both represent phylogenetically clearly separate lineages. The number of between three and eleven substitutions and indels between the four lineages, resulting a genetic similarity (based on the ITS barcoding marker) between 98% and 99.5%, indicates that these lineages diverged relatively recently. This likely happened in the late Miocene and into the Pliocene, corresponding to a phase of tectonic uplifting and mountain building in the region, known as the Kaikoura Orogeny, from a previously largely submerged Te Riu-a-Māui | Zealandia (Wallis & Trewick 2009; Trewick & Bland 2012; Bull et al. 2019).

### Revisiting the taxonomy of *Lobariaceae*

A study employing the temporal banding approach (Kraichak et al. 2018) proposed to merge *Lobariaceae* and *Nephromataceae* with *Peltigeraceae*, given the relatively recent splits between these three monophyletic lineages. This proposal was accepted, as the lichens formed by the fungi in these three clades are morphologically and ecologically quite similar and diagnostic differences, such as the position of the apothecia, ascospore types, the configuration of the thallus underside, and the absence or presence of veins and pores (cyphellae, pseudocyphellae) are found at the genus, rather than the family level (Lücking 2019). The three previously separate families were then recognized at subfamily level (Lumbsch & Leavitt 2019) and the new classification was subsequently implemented in various papers (Simon et al. 2020; Moncada et al. 2020, 2021; Torres et al. 2021; Widhelm et al. 2021b; Lücking et al. 2022).

However, previous works had shown notable differences in ascus types and ascoma development between each of the three clades (Letrouit-Galinou 1971; Henssen & Jahns 1973; Keuck 1977; Honegger 1978; Henssen et al. 1981; Wiklund & Wedin 2003; Spribille & Muggia 2013). As part of a new book project presenting all accepted families of lichenized fungi (Moncada & Lücking 2027), we restudied the ascus types of representatives of the above three families and could confirm the rather striking differences in ascus types: *Peltigeraceae* (*Peltigera*, *Solorina*) display a conspicuous, plug-shaped, amyloid ring in the tholus directly above the ocular chamber, *Nephromataceae* (*Nephroma*) lacks an amyloid apparatus, and the genera of *Lobariaceae* exhibit a variously layered amyloid cap in the dome of the tholus. Given these differences, it seems prudent to keep the three families separate, even if their inferred age is lower than the range accepted for most other families of lichen-forming fungi. It should be noted that in an earlier paper focusing on *Parmeliaceae* (Kraichak et al. 2017), the family-level temporal band was delimited between 102 and 113 mya (107.5 mya ± 5%), whereas in the expanded study on *Lecanoromycetes*, it was set to between 117 and 129 mya (123 mya ± 5%). In the latter study, the stem age of the three families was reconstructed at 107 mya (*Peltigeraceae*) and 103 mya (*Lobariaceae*, *Nephromataceae*), respectively. While these ages are distinctly between the minimum age set in the 2018 study, they fall well within the range for family rank set in the 2017 study, underlining the potential issues with the temporal banding approach when used as exclusive criterion and without consistency across analyses and taxa. The continued separation at family level is also in line with the long stem branches leading to the crown nodes in each of the three lineages in phylogenomic approaches (Widhelm et al. 2021b), indicating a long time of evolution in isolation. In any case, for those who prefer otherwise, the classification at subfamily level is available (Lücking 2019; Lumbsch & Leavitt 2019).

## Key to the species of the *Pseudocyphellaria hookeri* group

1 Photobiont green; apothecia and/or phyllidia present . . . 2
Photobiont cyanobacterial; apothecia or soredisidia present. . . . . 4

2(1) Marginal and partly laminal phyllidia abundant; apothecia often present but not usually abundant; thallus regularly radiating, with narrow lobes with more or less even surface . . . . . ***P. montagnei***
[if medulla and pseudocyphellae yellow, check *Podostictina pickeringii*; if pseudocyphellae absent and apothecial disc red-brown, check *Lobaria asperula*]

Distinct phyllidia absent, at best some adventive lobules present but rare; apothecia usually present . . . . . 3

3(2) Thallus distinctly faveolate, the sharp ridges usually lacking pycnidia; lobes more or less linear . . . . . ***P. durietzii*** (typical form)
Thallus uneven to at best scrobiculate, the shallow ridges often furnished with pycnidia arranged in dense rows; lobes irregular, often broadened . . . . . ***P. durietzii*** (“chlorohookeri” form)

4(1) Clusters of short, thickened isidia present along the margins and partly on the surface, when breaking off leaving white, soredia-like structures (soredisidia); apothecia not observed; lobes more or less rounded, with uneven surface and indistinct maculae . . . . . ***P. coralloidea***
Isidia absent; apothecia often present; lobes broadened, somewhat truncate, typically scrobiculate with pycnidia lining the shallow ridges, with distinct maculae . . . . . ***P. hookeri***

## Taxonomy

***Pseudocyphellaria coralloidea*** B. Moncada, de Lange, Blanchon & Lücking, sp. nov. (Figs 6, 7)

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Diagnosis: Differing from *Pseudocyphellaria hookeri* in the comparatively small thallus with rounded lobes and uneven to at best finely scrobiculate surface and the formation of clusters of stout, partly eroding isidia; from *P. intricata* in the initial formation of isidia that only later partly erode to resemble soredia (reversed in the latter).

Type: New Zealand, North Island, Waikato: Tongariro National Park, Tree Trunk Gorge Road, 38 km E of National Park village, roadside; 39.1656°S, 175.8031°E, 745 m; mountain beech (*Fuscospora cliffortioides*) forest with makahikatoa (*Kunzea serotina*), margin of well-preserved forest along road; February 20, 2015, R. Lücking, B. Moncada & P.J. de Lange 38809 (AK – holotype!; F-C0265522F – isotype!; DNA voucher: MON3539).

**Etymology**. The epithet refers to the coralloid clusters of isidia.

**Description**. Primary photobiont a cyanobacterium (*Nostoc*). Thallus irregular to forming suborbicular rosettes, up to 7 cm diam., sparsely branched, with 2–3 branching points per 5 cm radius, branching mostly anisotomous; lobes more or less rounded, horizontal,

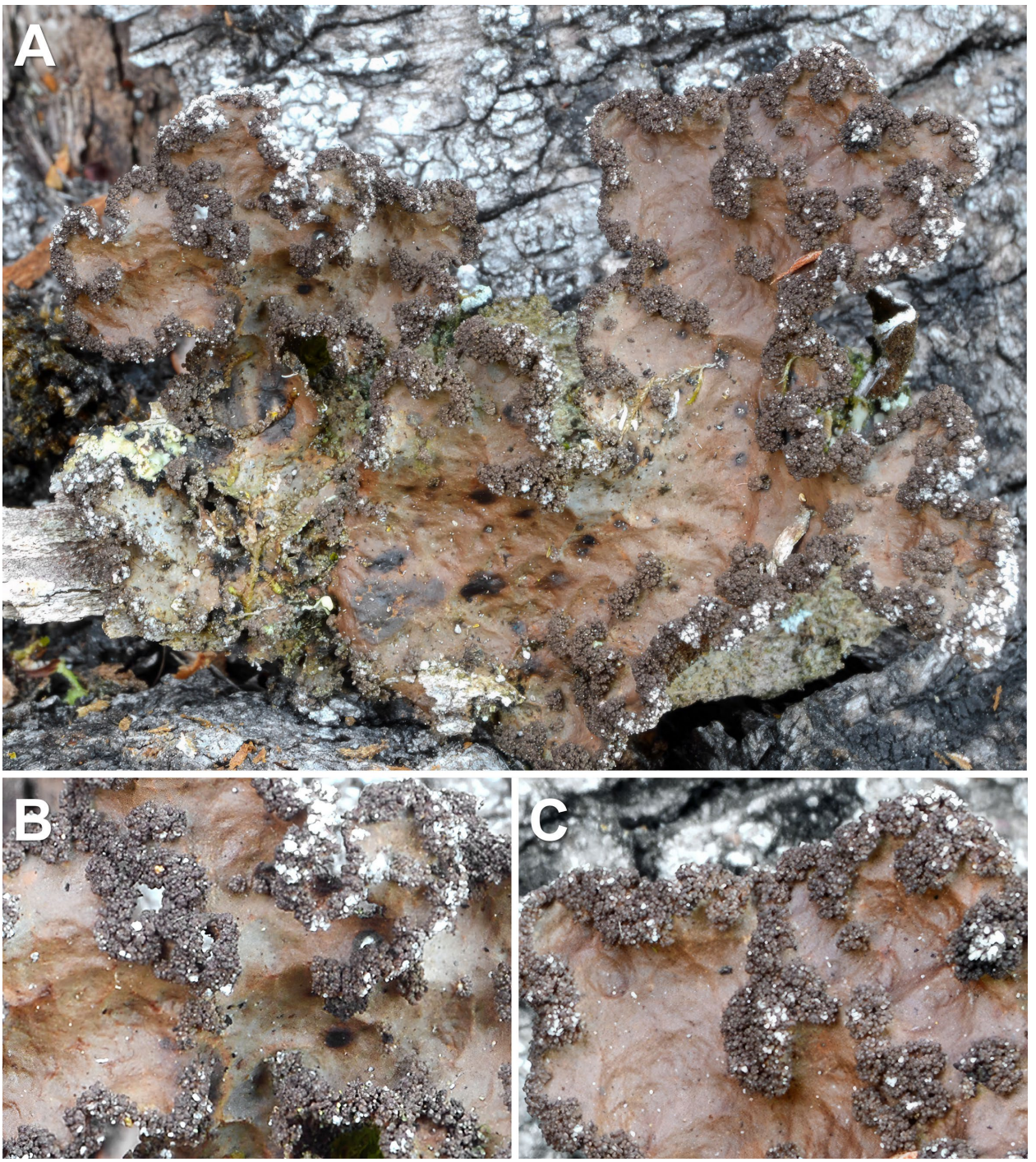


**Figure 6**. Field images of *Pseudocyphellaria coralloidea* (type) on *Manoao colensoi* (*Podocarpaceae*). A – thallus with soredisidia; B, C – detail showing clusters of soredisidia.

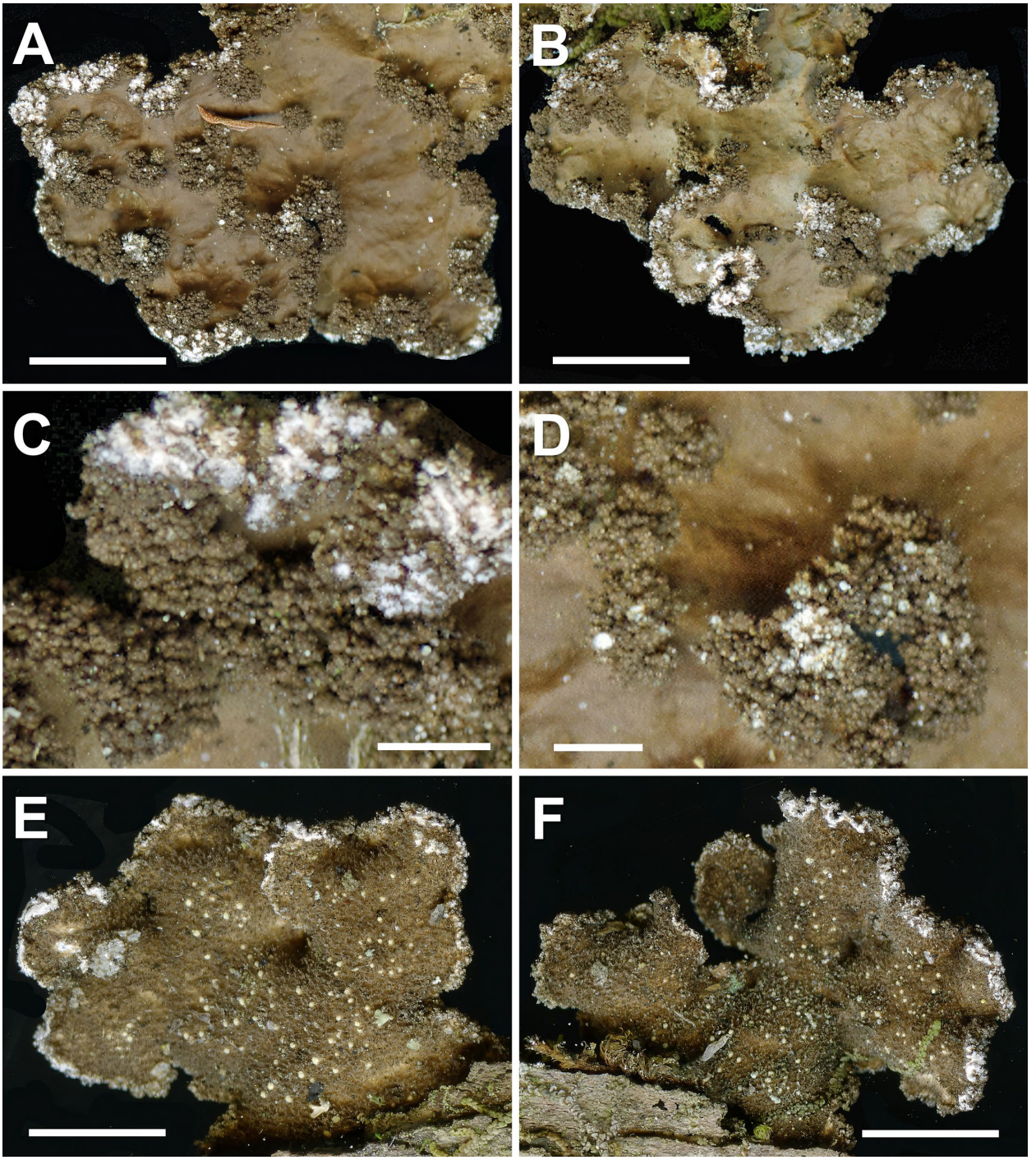


**Figure 7**. *Pseudocyphellaria coralloidea* (type). A, B – dried specimen (upper side); C, E – detail showing clusters of isidia; E, F – underside with pale yellow pseudocyphellae. Scales: A, B, E, F = 5 mm; C, D = 1 mm.

adjacent, margins entire to irregular, slightly thickened; lobe internodes 3–8 mm long, 5–15 mm broad, subcoriaceous. Upper surface uneven to finely scrobiculate towards the margins, shallowly pitted towards the center, grey-brown when fresh, brown in the herbarium, opaque; upper surface glabrous, without papillae, without pruina, without maculae. Thallus especially along the margins and in part on the lamina furnished with dense clusters of stout, coralloid, brown isidia; individual isidia knob-shaped, 0.1–0.2 mm broad, emerging from a compact, strongly branching base, the clusters up to 1.5 mm high; isidia partly eroding and leaving behind white, soralia-like structures. Medulla white. Lower surface undulate, mid to darker brown throughout; tomentum dark brown, dense up to the margins, rather sharply delimited by the margins appearing patchy white and irregularly sorediate. Rhizines not observed. Pseudocyphellae abundant except for a marginal zone, dispersed, distinctly protruding, punctiform, 0.1–0.3 mm diam., whitish to mostly pale yellow. Thallus in section 100–150 µm thick. Upper cortex 10–15 µm thick, pale yellowish, cells isodiametric, lumina 2–3 µm diam. Photobiont layer 20–40 µm thick, the *Nostoc* cells organized in clusters surrounded by fungal hyphae; cells greenish blue, 4–5 µm diam. Medulla 70–90 µm thick, colorless, hyphae 3–4 µm diam., strongly encrusted with colorless, granular, hydrophobic crystals. Lower cortex

8–12 µm thick, pale yellowish, cells isodiametric, lumina 2–4 µm diam. Tomentum hairs septate, unbranched to apically branched, densely conglutinate in fascicles, pale yellowish, becoming brown, 4–5 µm thick, to 100 µm long. Apothecia and pycnidia not observed.

**Secondary chemistry**. Tenuiorin, methyl lecanorate (tr.), methyl gyrophorate, hopane-6α,7β,22-triol, 6α-acetoxyhopan-7β,22-diol (tr.), norstictic (tr.), stictic acid, hypostictic acid (tr.), cryptostictic acid, constictic acid, pseudocyphellae with pulvinic acid (tr.), pulvinic dilactone (tr.), calycin (tr.); surface C+ pink-red, K+ yellow, medulla C+ pink-red, K+ yellow-orange or turning red, P+ orange (Fig. 8).

**Distribution and ecology**. This new species, presumably endemic to New Zealand, is thus far known from the following locations in Te Ika-a-Maui | North Island (the Kaimanawa Ranges at Tree Trunk Gorge (39.1656°S, 175.8105°E, 745 m a.s.l.), Mahia Peninsula (39.1529°S, 177.8931°E) at the northern end of Te Matau a Maui | Hawke's Bay, and from the Waihora Stream, Aorangi Range, southern Wairarapa (41.3097°S, 75.2867°E, 43 m a.s.l.), as well as one site in Te Waipounamu | South Island (North West Nelson, Golden Bay, Whahariki–Puponga Farm Park, Pillar Light Bush, 40.5091°S, 172.7800°E, 77 m a.s.l.) and from one location in the southern tablelands of Rekohu | Wharekauri | Chatham Island (44.0478°S, 176.3959°W, 128 m a.s.l.), the largest island in the Chatham Islands group. Our searches of iNaturalist NZ [https://www.inaturalist.nz] observations of the superficially similar *P. cinnamomea* (A. Rich.) Vain., *P. dissimilis* (Nyl.) D.J. Galloway & P. James, and *P. intricata sensu* Galloway (1988) located a few additional observations which may also be this species. However, none of the images and information provided are sufficiently clear for us to be certain of a species level identification.

As a newly described species known from less than ten collections, characterization of its ecology is fraught. At the type locality, the species is known from roadside vegetation traversing a mountain beech (*Nothofagus* (*Fuscospora*) *cliffortioides* (Hook.f.) Oerst.) forest, the specimen came from the ecotone between the forest and a frost flat, growing on the trunk of *Manoao colensoi* (Hook.) Molloy. At this location it has also been seen on the lower and mid trunk sections of *Kunzea serotina* de Lange & Toelken. At Mahia Peninsula specimens were collected from a scenic reserve in riparian forest dominated by *Beilschmiedia tawa* (A. Cunn.) Kirk, *Didymocheton spectabilis* (G. Forst.) Mabb. & Holzmeyer and *Rhopalostylis sapida* H. Wendl. & Drude, and from a roadside remnant dominated by *Beilschmiedia tawa*, *Hedycarya arborea* J.R. Forst. & G. Forst, *Pennantia corymbosa* J.R. Forst. & G. Forst. and two species of *Myoporum* Banks & Sol. ex G. Forst. In Te Waipounamu | South Island, specimens were sampled from the upper trunk of *Kunzea amathicola* de Lange & Toelken in regenerating coastal forest. On the Chatham Islands, plants were collected admixed with *Parmotrema* A. Massal. on the trunk of *Coprosma chathamica* Cockayne in dense *Dracophyllum arboreum* Cockayne / *Myrsine chathamica* F. Muell. forest. Associated lobarioid lichens are not well known, though at Tree Trunk Gorge the species was collected with *Crocodia rubella* (Hook.f. & Taylor) Trevis, *Lobaria adscripta* (Nyl.) Hue, *Lobarina scrobiculata* (Scop.) Nyl, *Podostictina ardesiaca* (D.J. Galloway) Moncada & Lücking, *Pseudocyphellaria*

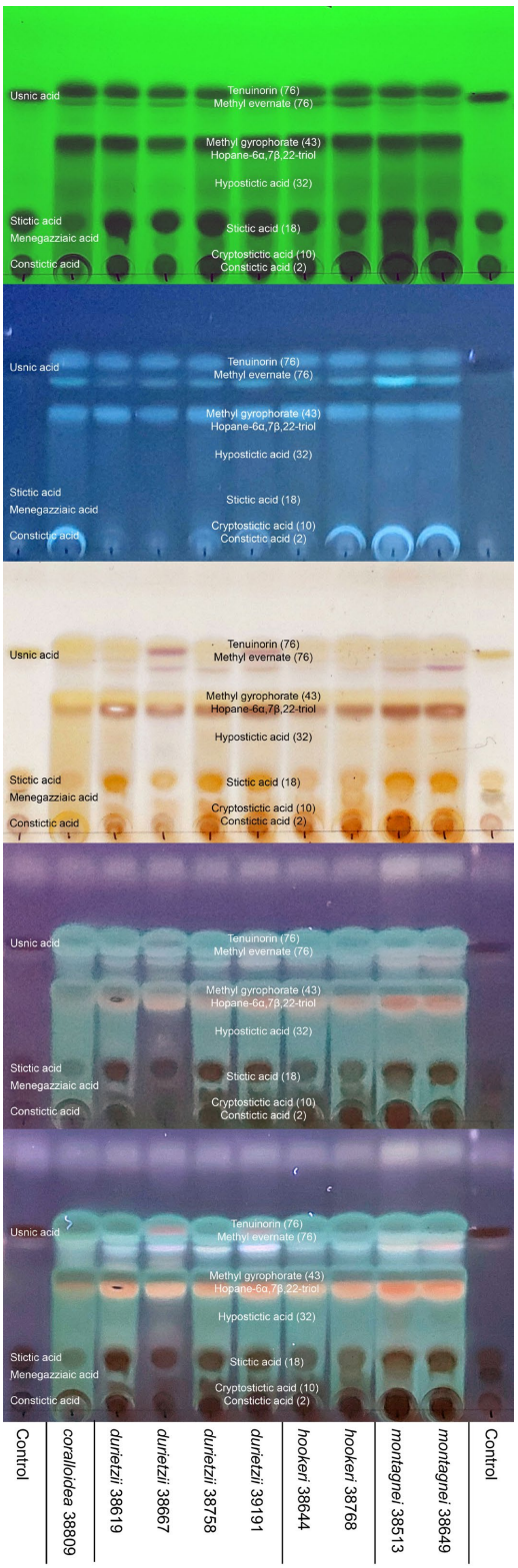


**Figure 8**. TLC plates showing the chemistry of species of the *Pseudocyphellaria hookeri* clade in solvent C. From above to below: Before charring UV 254 nm; before charring UV 365 nm; after charring; after charring UV 254 nm; after charring UV 365 nm.

*crassa* D.J. Galloway, *P. intricata sensu* Galloway (1988), *P. glabra* (Hook.f. & Taylor) C.W. Dodge, *P. gretae* D.J. Galloway, *Yarrumia colensoi* (C. Bab.) D.J. Galloway, and *Y. coronata* (Müll.Arg.) D.J. Galloway, as associates. These are quite different habitats and span an altitudinal range of 82–745 m a.s.l. from riparian and coastal-influenced forest to montane beech (*Nothofagus* Blume) forest.

**Conservation status**. As this new species is still very poorly known to Aotearoa | New Zealand lichenologists, we suggest that it should be listed as 'Data Deficient' using the New Zealand Threat List Classification Criteria (Rolfe et al. 2022).

**Remarks**. The sequenced material of this new species was initially identified on morphological grounds as an aberrant specimen of *Pseudocyphellaria argyracea* (Delise) Vain. The latter agrees in the cyanobacterial photobiont, the grey-brown color, and the brown isidia eroding into soralia-like structures. However, other, more typical New Zealand material of *P. argyracea* turned out to be phylogenetically unrelated (Figs 2, 3) and was found to differ, first and foremost, in the presence of whitish pseudocyphellae on the upper lobe surface, best seen near the margins. These soon develop into soralia-like structures from which loosely corticate, grey-brown pseudoisidia arise in clusters. Also, the lobe surface is reticulately ridged rather than scrobiculate (Fig. 9A, B). Chemically, in contrast to *P. coralloidea*, *P. argyracea* lacks the stictic/norstictic acid chemosyndrome (Galloway 1988, 2007), a further difference with the new taxon.

Another species similar to *Pseudocyphellaria coralloidea* is *P. intricata* (Delise) Vain. It agrees with the new species in the absence of upper pseudocyphellae and the uneven surface, but does not produce isidia from the soralia (Fig. 9D) and is not closely related (Figs 2, 3). It also has narrower, often marginally undulate lobes, and characteristically sparse, larger, and usually irregularly shaped pseudocyphellae on the thallus underside, and lacks the stictic acid chemosyndrome (Galloway 1985, 1988, 2007). *Pseudocyphellaria bartlettii* D.J. Galloway agrees with *P. coralloidea* in chemistry and the partly pale yellow lower pseudocyphellae, but like *P. argyracea*, it has a reticulately ridged surface and produces only delicate pseudoisidia from the soralia (Fig. 9C). The main diagnostic feature of the new species is thus the well-developed, robust, clearly corticate, brown isidia that produce soralia-like, whitish structures by eroding (mnemonics: "first brown, then white"), whereas in the other three species, the white-grey soralia or soralia-like structures are prior to forming brownish isidia or no isidia at all (mnemonics: "first white, then brown").

Phylogenetically, *Pseudocyphellaria coralloidea* is closely related to *P. hookeri*, with which it shares the cyanobacterial photobiont. Otherwise, its aspect as

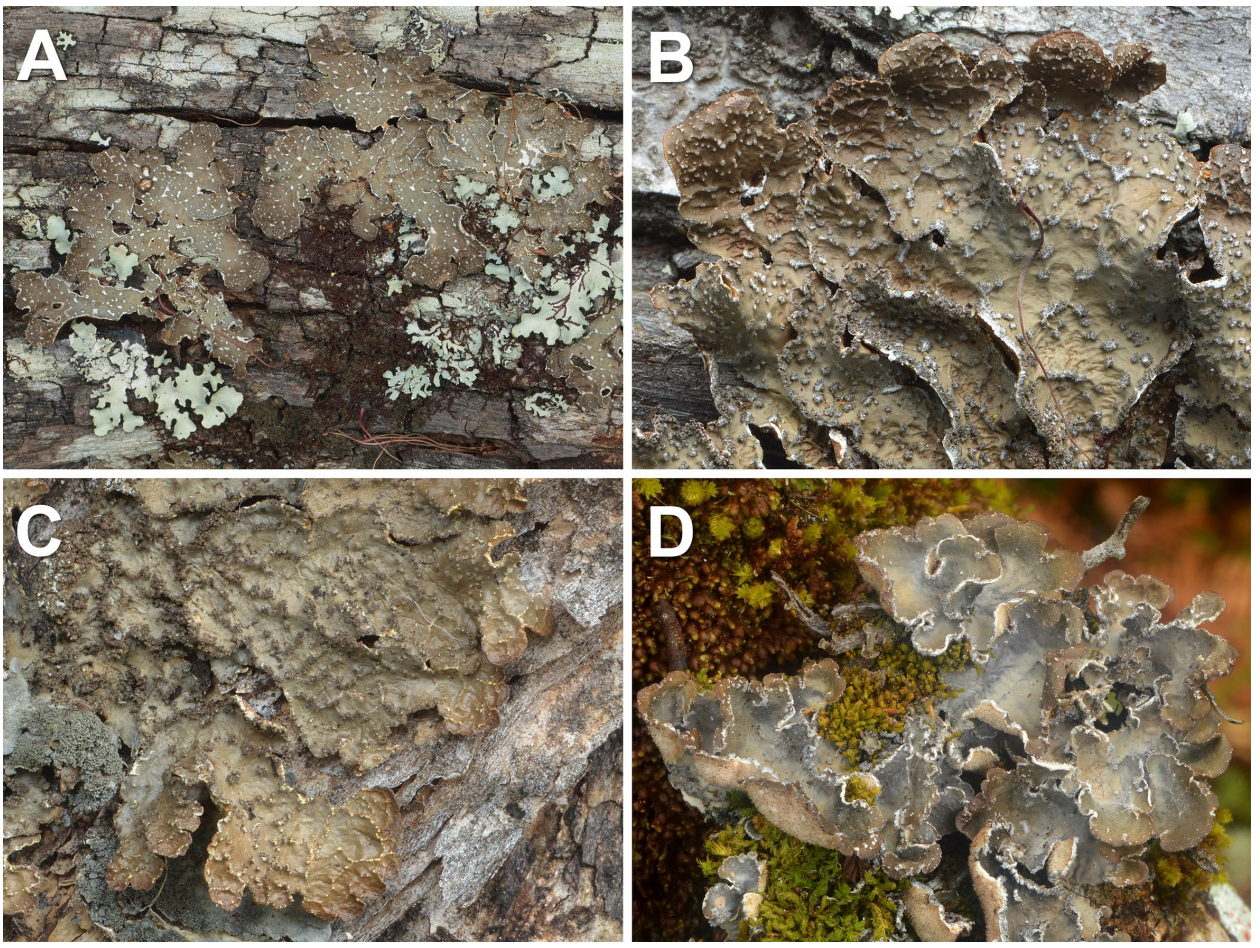


**Figure 9**. Field images of species of *Pseudocyphellaria* occurring in New Zealand potentially to be confused with *P. coralloidea*. A, B – *P. argyracea* (A: Lücking et al. 38501; B: Lücking et al. 38505). C – *P. bartlettii* (Lücking et al. 38536); D – *P. intricata* (Lücking et al. 38153).

a rather small lichen, not clearly scrobiculate-faveolate and with numerous marginal and laminal isidia, is quite distinctive. It therefore cannot be considered a species pair of *P. hookeri*.

We propose the new term "soredisidia" for vegetative propagules that intergrade between genuine soralia and true isidia. In *Pseudocyphellaria*, this appears to be a common phenomenon, also seen in the *P. neglecta* (Müll. Arg.) H. Magn. complex (Lücking et al. 2017b).

**Additional Specimens examined**. NEW ZEALAND. North Island: Northern Hawke Bay (near Wairoa), Mahia Peninsula, Kinikini Road; 20 Jan. 2013, P.J. de Lange s.n. (UNITEC 6109; F). Central Volcanic Plateau, Kaimanawa Forest Park, Tree Trunk Gorge Road; 20 Feb. 2015, P.J. de Lange 12542 (AK 356821). Southern Wairarapa, Aorangi Range, Waihora Stream; 25 Feb. 2014, P.J. de Lange 12039 (UNITEC 6157). South Island: North West Nelson, Golden Bay, Whararikі–Puponga Farm Park, Pillar Light Bush, 30 Nov. 2019, P.J. de Lange 14818 & T.J.P.J. de Lange (UNITEC 128182). Chatham Islands: Rekohu (Chatham Island), Southern Tablelands, Alfred Preece's Farm; 30 Jul. 2015, P.J. de Lange CH2555 & A. Baird (UNITEC 7730).

***Pseudocyphellaria durietzii*** D.J. Galloway in Galloway et al., The Lichenologist 15(2): 142. 1983. (Figs 10–12)

**Brief description**. Primary photobiont a green alga (*Symbiochloris*). Thallus irregular to forming suborbicular rosettes, rather loosely attached, much branched, lobes laciniate to broadened, horizontal, partly imbricate, more or less truncated. Upper surface typically deeply faveolate with sharp ridges, sometimes only scrobiculate with shallow ridges, bright green when fresh, yellowish gray in the herbarium, glabrous, without maculae. Medulla white. Lower surface appearing bullate owing to the faveolate upper surface, pale brown to beige, shortly tomentose, becoming whitish and glabrous towards the margins. Pseudocyphellae whitish, small and punctate, scattered. Soralia, isidia and phyllidia absent but sometimes with scattered adventive lobules. Apothecia often abundant, laminal to submarginal, often along the ridges, sessile and constricted below, up to 4 mm in diam.; thalline margin distinct, somewhat prominent, entire to crenulate; disc black, non-pruinose. Ascospores 8 per ascus, more or less biseriate, fusiform, 1-septate, 20–25 × 6.5–8.5 µm, brown. Pycnidia abundant, typically in dense lines along the ridges. Conidia bacillar.

**Secondary chemistry**. Tenuinorun, methyl gyrophorate, methyl evernate (tr.), methyl lecanorate (tr.), evernic acid (tr.), gyrophoric acid (tr.), hopane-7β,22-diol (tr.), hopane-6α,7β,22-triol (tr.), 7β-acetoxyhopan-6α,22-diol (tr.), 6α-acetoxyhopan-7β,22-diol (tr.), norstictic (tr.), stictic acid, hypostictic acid (tr.), cryptostictic acid (tr.), constictic acid; surface C+ pink-red, K+ yellow, medulla C+ pink-red, K+ yellow-orange or turning red, P+ orange (according to Galloway et al. 1983; Galloway 1985) (Fig. 8).

**Distribution and ecology**. Galloway (1985, 1988, 2007) noted that *Pseudocyphellaria durietzii* is present in the three main islands of Aotearoa| New Zealand, Te Ika-a-Maui | North, Te Wai Pounamu | South and Rakiura | Stewart Islands. Our field work has extended this range ~835 km east to the Chatham Islands, where the species is locally present on Rekohu | Wharekauri | Chatham and Rangihaute | Rangiauria | Pitt Islands. For Te Ika-a-Maui | North Island, Galloway (2007) gave a mostly montane distribution for the species from Mt Hikurangi (37.9167°S, 178.0595°E, 1,752 m a.s.l.), the highest point in the Raukumara Range, as well as Tairawhiti | East Cape south to near Te Rawhiti (41.2947°S, 174.6195°E, 20 m a.s.l.), west of Wellington City. Our field work in Te Ika-a-Maui | North Island has increased this range north to Unuwhao, Te Paki, (34.4373°S, 172.8908°E, 211 m a.s.l.), Te Aupouri | Far North.

Galloway (1988), based on an analysis of 30 specimens, considered *P. durietzii* a species of lowland forest and scrub with a preference for shaded sites with high humidity and rainfall. However, he also noted its occurrence in subalpine scrub on Mt Hikurangi – evidently an unusual habitat for it. His treatment noted that the main phorophytes were the podocarps *Dacrycarpus dacrydioides* (A. Rich.) de Laub., *Dacrydium cupressinum* Sol. ex Lamb., *Podocarpus totara* G. Benn. ex D. Don and *Pectinopitys ferruginea* (G. Benn. ex D. Don) C.N. Page [recorded as *Prumnopitys ferruginea* (G. Benn. ex D. Don) de Laub.]. Other common phorophytes included *Coprosma rhamnoides* A. Cunn., *Ixerba brexioides* A. Cunn., *Metrosideros umbellata* Cav. and *Pterophylla racemosa* (L.f.) Pillon & H.C. Hopkins (as *Weinmannia racemosa* L.f.). Our field work has discovered this species in a range of habitats either poorly collected or not explored by David Galloway; these include coastal forest and shrubland, and regenerating forest dominated by *Kunzea* Rchb. and *Leptospermum* J.R. Forst. & G. Forst. Common phorophytes in these habitats include *Kunzea amathicola* de Lange & Toelken, *K. linearis* (Kirk) de Lange & Toelken, *K. robusta* de Lange & Toelken, *Leptospermum hoipolloi* L.M.H. Schmid & de Lange f. *hoipolloi*, *L. scoparium* J.R. Forst. & G. Forst., *L. tairawhitiense* G.J. Atkins, de Lange & M.A.M. Renner, *Metrosideros excelsa* Sol. ex Gaertn. In these northern locations, and around Tairawhiti | East Cape and Te Matau a Maui | Hawke's Bay, *P. durietzii* was also commonly collected from lowland forest dominated *Beilschmiedia tawa*, *Didymocheton spectabilis*, *Hedycarya arborea*, *Myoporum laetum* G. Forst. and *Rhopalostylis sapida*. A common phorophyte in these locations is *Cordyline australis* (G. Forst.) Endl. In these habitats associated lobariaceous lichens often include *Crocodia aurata* (Ach.) Link, *Crocodia poculifera* (Müll. Arg.) D.J. Galloway & Elix, *Pseudocyphellaria carpoloma* (Delise) Vain., *P. chloroleuca* (Hook.f. & Taylor) Du Rietz, *P. coriacea* (Hook.f. & Taylor) D.J. Galloway & P. James, *P. episticta* (Nyl.) Vain., *P. dissimilis* (Nyl.) D.J. Galloway & P. James, *P. montagnei*, *Sticta fuliginosa*, *S. martinii* D.J. Galloway, *S. subcaperata* (Nyl.) Nyl., and *Yarrumia coronata*.

**Conservation status**. *Pseudocyphellaria durietzii* has been assessed as 'Not Threatened' by the New Zealand Lichen Threat Listing Panel over two iterations (de Lange et al. 2012, 2018). Since those assessments, our

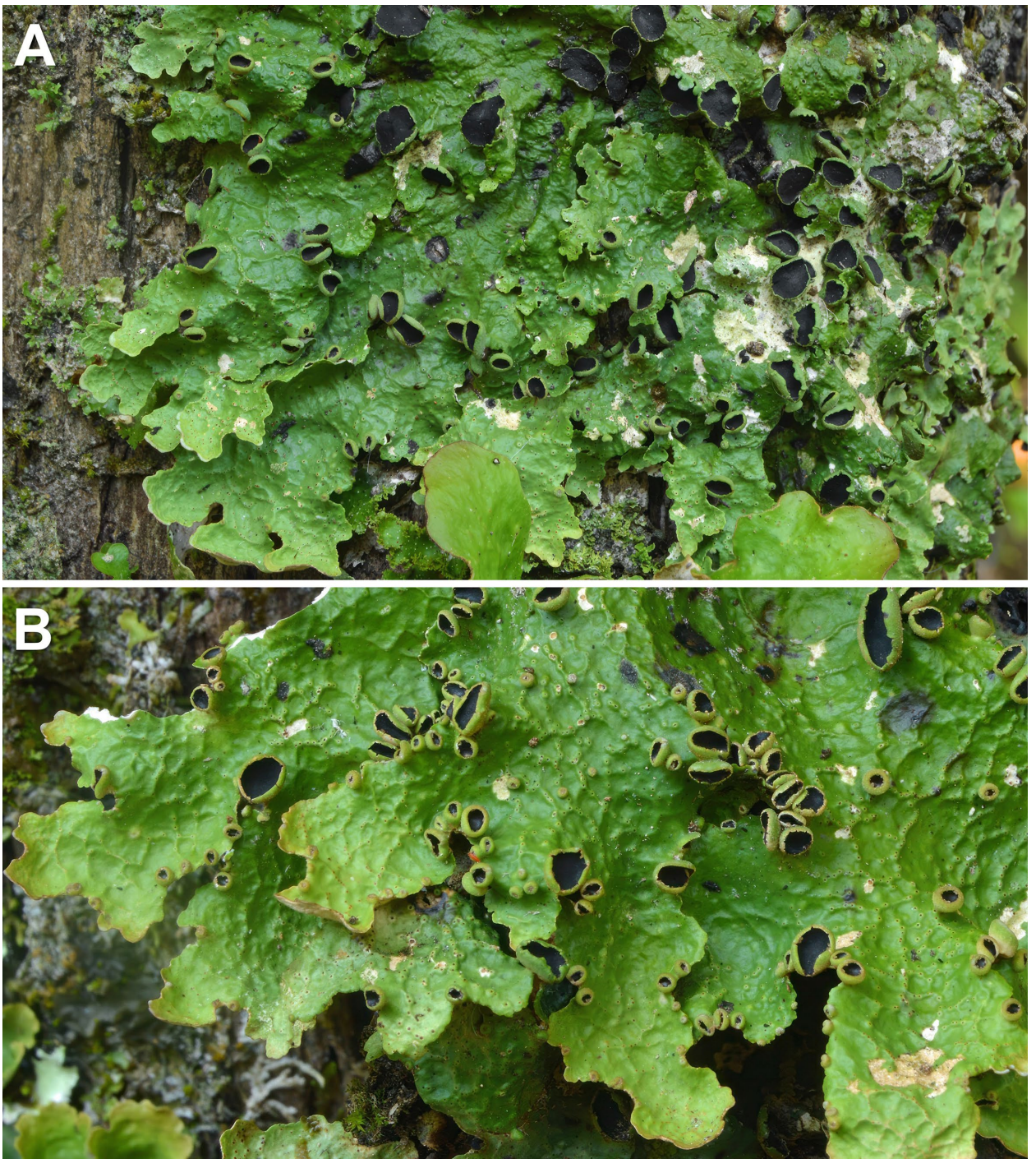


**Figure 10**. Field images of *Pseudocyphellaria durietzii* ("chlorohookeri"). A, B – specimens in situ (Lücking et al. 38666, 38667), with abundant apothecia.

knowledge of its range and ecological preferences has increased considerably. However, it is notable that the species still remains poorly known to the lichenological and the wider botanical community. For example, until the preparation of this manuscript, there were no observations explicitly identified as *P. durietzii* on iNaturalist NZ (https://www.inaturalist.nz). Instead, almost all instances that we have now identified as this species based on morphology (12 as of 27 Mar. 2026; see File S1) had previously been named *P. montagnei*, a species that typically features abundant phyllidia and more rarely additional apothecia. In the observations now re-identified as *P. durietzii*, based on characters such as scrobiculate to faveolate lobes, observers often commented that phyllidia were absent, poorly developed or not convincing. It seems that the occasional development of adventive lobules, interpreted as phyllidia, had confused observers, given that the presence of phyllidia has been stressed as an important difference in keys (e.g., Galloway 1988, 2007), resulting in erroneous placement of specimens of *P. durietzii* within *P. montagnei*. Following on from this recognition, we see no reason to change the current threat status of *P. durietzii*, beyond making the recommendation that the species is qualified 'DPR' [Data Poor Recognition] (see Rolfe et al. 2022), as so few people have to date correctly identified it.

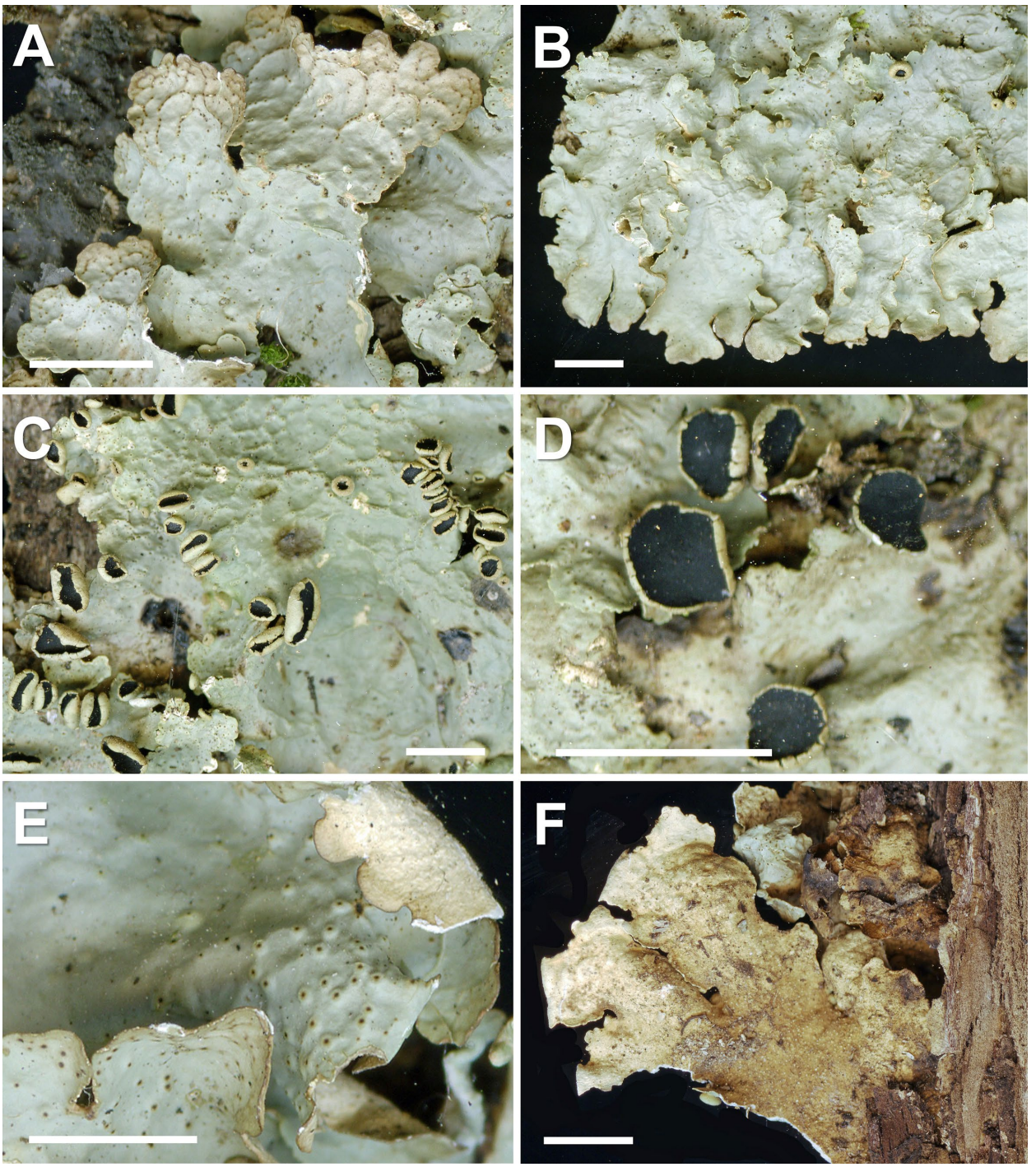


**Figure 11**. *Pseudocyphellaria durietzii* ("chlorohookeri" morph). A, B – dried specimens (upper side; A: Lücking et al. 38758; B: Lücking et al. 39191); C, D – lobes with apothecia (C: Lücking et al. 38666; D: Lücking et al. 38667); E – detail showing pycnidia (Lücking et al. 38650); F – underside (Lücking et al. 38666). Scale = 5 mm.

**Remarks**. Contrary to many historical names in the genus, *Pseudocyphellaria durietzii* is a more recently described species (Galloway et al. 1983), characterized by a green photobiont, a typically faveolate thallus (Fig. 12) lacking vegetative propagules, and apothecia with black disc (Galloway et al. 1983; Galloway 1985, 1988, 2007). It was initially considered to be a green algal morph of *P. hookeri*; putative photosymbiodemes, with both morphs presumably connected to each other, have been reported (Galloway 1985, 1988).

Curiously, all specimens studied here from North Island, including those represented by sequence data, deviate from typical *P. durietzii* in the scrobiculate rather than faveolate thallus, with shallow ridges often lined with numerous pycnidia (Figs 10, 11, 12D). In surface structure, they are thus similar to most of the studied and sequenced material of *P. hookeri* from North Island in the scrobiculate, rather than faveolate, thalli (described as "deeply faveolate" for *P. durietzii* by Galloway 1985). Examination of additional herbarium collections and occurrence records in iNaturalist (Figs 14, 15) demonstrated that the surface structure in *P. hookeri* varies, with individuals intergrading between faveolate and scrobiculate. In *P. durietzii*, on the other hand, no intermediate

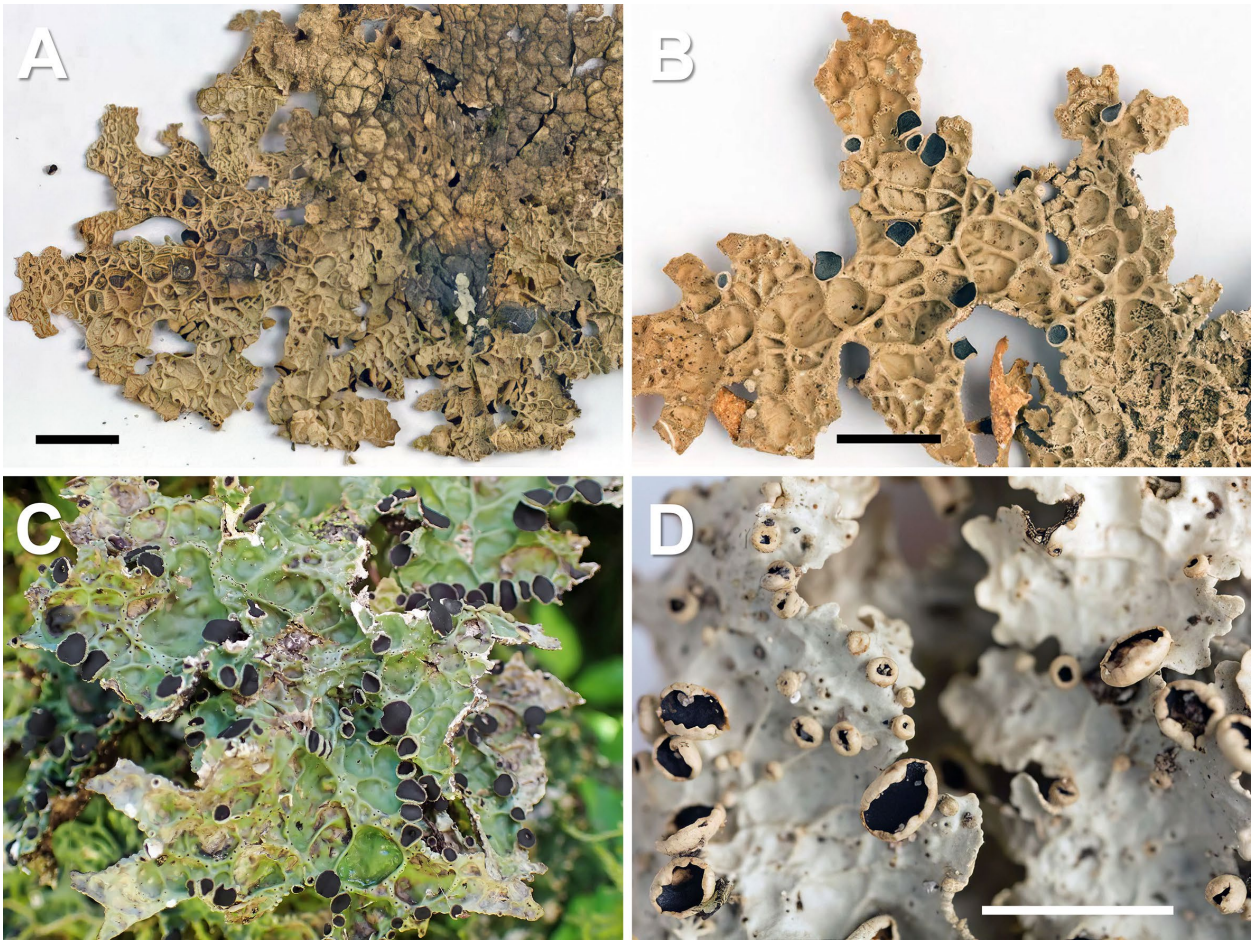


**Figure 12**. *Pseudocyphellaria durietzii*. A, B – dried specimens showing faveolate morph [A: the type; Wilton 2026; https://scd.landcareresearch.co.nz/Specimen/CHR_375960; https://creativecommons.org/licenses/by-nc/4.0/deed.en; B: de Lange 7392; https://www.aucklandmuseum.com/discover/collections/record/670710; https://creativecommons.org/licenses/by-nc/4.0/deed.en; C – specimen in situ from iNaturalist [Dr. C.R. Schack; https://www.inaturalist.org/observations/198548773; https://creativecommons.org/licenses/by-nc/4.0/deed.en; D – herbarium specimen representing the "chlorohookeri" morph [Ranatunga & Hoane 2006; https://www.aucklandmuseum.com/discover/collections/record/670711; https://creativecommons.org/licenses/by-nc/4.0/deed.en]. Scales: A, B = 10 mm; D = 5 mm.

forms were found, and the examined individuals could always be assigned to either the faveolate or the scrobiculate form. We label the latter "chlorohookeri" form, as we initially considered with a distinct species. However, since sequence data from faveolate specimens are lacking, for the time being we consider them the same taxon.

Notably, while *Pseudocyphellaria durietzii* and *P. hookeri* belong in the same, strongly supported clade, they are phylogenetically distinct and do not represent the same species (Fig. 3). We did not observe any photosymbiodemes with cyanobacterial lobes attached to a green algal thallus, but based on one of our own collections (Lücking et al. 38767a) and one iNaturalist record [https://www.inaturalist.org/observations/9750022], we could confirm the existence of green algal lobes directly attached to a cyanobacterial thallus; in another record, two separate lichens, one *P. durietzii*, the other *P. hookeri*, may be growing intermingled [https://www.inaturalist.org/observations/59081753]. If indeed the same fungus is involved in the aforementioned cases, it means that those green algal lobes do not represent *P. durietzii*; in any case, given their phylogenetic distinctiveness, the two taxa (*P. durietzii*, *P. hookeri*) cannot be considered part of a photosymbiodeme.

*Pseudocyphellaria durietzii* is easily confused with other similar, yet unrelated (Fig. 13) species, as also shown by some iNaturalist records [https://www.inaturalist.org/observations/198548773]. Scrobiculate forms resemble *P. rufovirescens* (C. Bab.) D.J. Galloway, which agrees in the pale, thinly tomentose underside, but differs in the broader surface ridges and has red-brown apothecial discs (Fig. 13A), at best pale brownish ascospores. Also, its chemistry is different, with the surface and medulla reacting C– due to the absence of gyrophoric acid (Galloway 1985, 1988, 2007). Faveolate forms can be mistaken for *P. faveolata* (Delise) Malme and *P. billardierei* (Delise) Räsänen (Fig. 13C, D). Both differ in the usually thicker, darker lower tomentum. In addition, *P. faveolata* typically features verruciform pseudocyphellae projecting from the lobe margins and the black apothecial disc is often pruinose, especially when young; its ascospores are larger (23–35 × 10–14 µm). Its chemistry is also different, containing physciosporin instead of tenuinorin and gyrophoric acid derivates (Galloway 1985, 1988, 2007). *Pseudocyphellaria billardierei* is less readily separated from *P. durietzii*. Although not closely related (Fig. 3), its chemistry is quite similar to that of *P. durietzii*, the apothecial disc varies from red-brown to black, and the

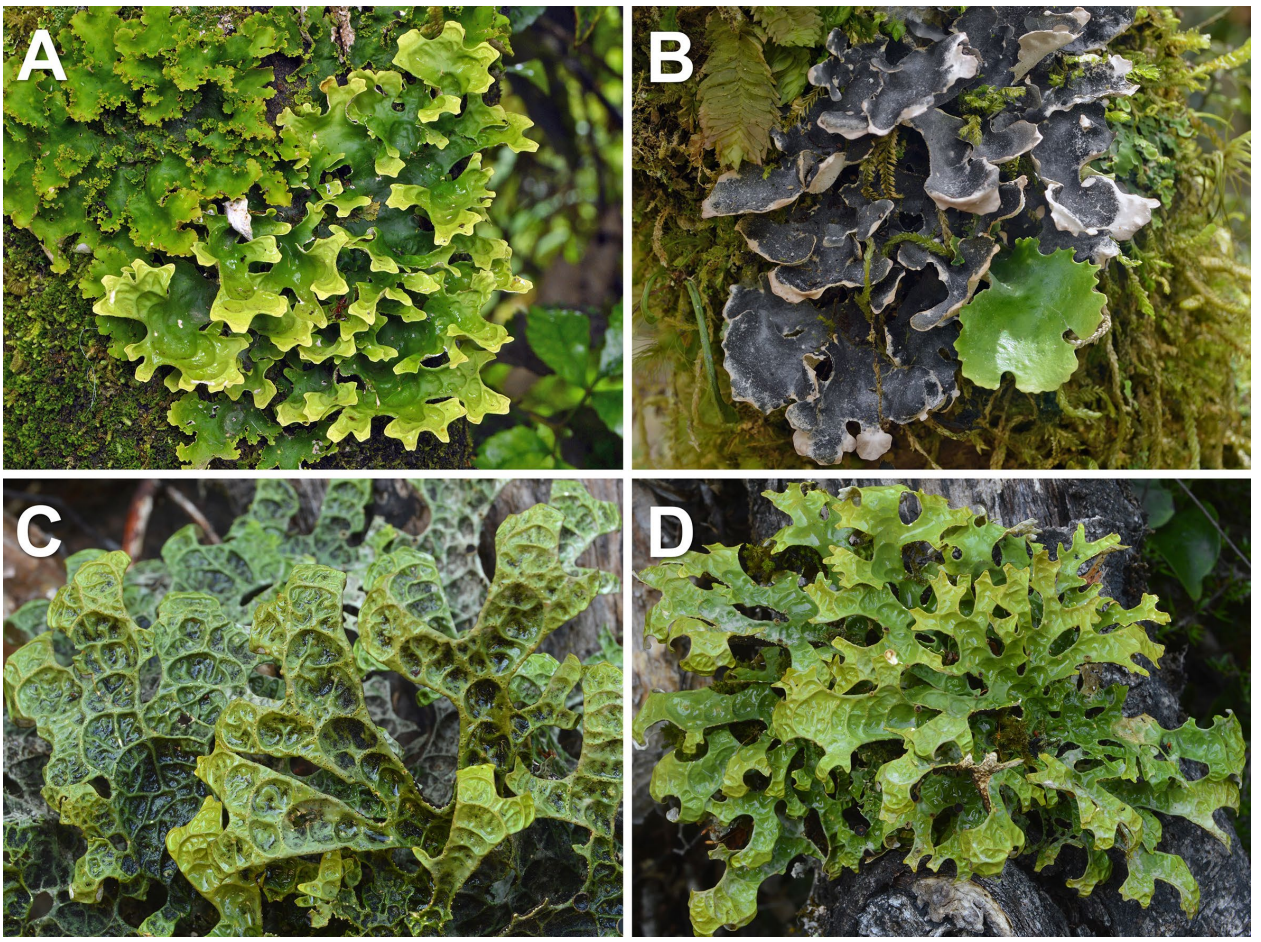


**Figure 13**. Field images of species of *Pseudocyphellaria* present in New Zealand potentially to be confused with *P. durietzii* and *P. hookeri*. A, B – *P. rufovirescens*, in B the cyanobacterial phase, previously named *P. murrayi* (A: Lücking et al. 38442; Lücking et al. 38196); C – *P. faveolata* (Lücking et al. 38822); D – *P. billardierei* (Lücking et al. 38824).

tomentum, usually keyed out as thick and dark, is more broadly described as pale and often thin to lacking towards the margins; its ascospores are only slightly larger than those of *P. durietzii*. Notably, given the similarities, Galloway et al. (1983) and Galloway (1985, 1988) never discussed the taxonomy of both species comparatively. In our sequenced specimens of *P. billardierei*, the lobes are rather regularly linear, the apothecial disc is rather dark brown, and the underside is whitish and thinly tomentose towards the margins, but dark brown and thickly tomentose towards the center. A further difference towards *P. durietzii* appear to be the mostly marginally formed apothecia.

**Specimens examined**. NEW ZEALAND. North Island, Hawke's Bay: Mahia Peninsula, Mahia East Coast Road, 61 km S of Gisborne, roadside forest remnant; 39.1792°S, 177.9083°E, 300 m; tawa (*Beilschmiedia tawa*) / porokaiwhiri (*Hedycarya arborea*) with mahoe (*Melicytus ramiflorus*) forest remnant and kaikomako (*Pennantia corymbosa*) / ti kouka or cabbage tree (*Cordyline australis*) with mahoe (*Melicytus ramiflorus*) and ngaio (*Myoporum laetum* and *M. semotum*) forest remnant, disturbed roadside forest remnant, on *Cordyline australis*; February 18, 2015, R. Lücking, B. Moncada & P.J. de Lange 38619 (AK, UNITEC, B, F-C0265556F; DNA voucher: MON3695). North Island, Hawke's Bay: Mahia Peninsula, Kinikini Road, Mahia Peninsula Scenic Reserve, 56 km SSW of Gisborne, trail through reserve; 39.1244°S, 177.8742°E, 150–200 m; kohekohe (*Dysoxylum spectabile*) / nikau (*Rhopalostylis sapida*) with tawa (*Beilschmiedia tawa*) forest transitioning into riparian podocarp forest dominated by kahikatea (*Dacrycarpus dacrydioides*), matai (*Pruminopitys taxifolia*) and totara (*Podocarpus totara* var. *totara*) with an understorey of mahoe (*Melicytus ramiflorus* subsp. *ramiflorus*), kotukutuku (*Fuchsia excorticata*), horoeka (*Pseudopanax crassifolius*) and kaikomako (*Pennantia corymbosa*), well-preserved forest; February 19, 2015, R. Lücking, B. Moncada & P.J. de Lange 38650 (B, F-C0265557F), 38659 (AK, UNITEC, B, F-C0265559F), 38756b (B, F-C0266929F; DNA voucher: MON3548), 38758 (B, F-C0265563F; DNA voucher: MON3698), 38761 (AK, B, F-C0265564F; DNA voucher: MON3545); ibid., on *Kunzea robusta*; February 19, 2015, R. Lücking, B. Moncada & P.J. de Lange 38655 (AK, B, F-C0265558F), 38666 (AK, B, F-C0265560F; DNA voucher: MON3696), 38667 (AK, UNITEC, B, F-C0265561F; DNA voucher: MON3697), 38722 (AK, B, F-C0265562F; DNA voucher: MON3897). North Island, Auckland: Omeru Waterfall Scenic Reserve E of Kaipara Coast Highway, 14 km NNE of Helensville, first part of trail from parking lot to reserve; 36.5586°S, 174.4753°E, 60 m; riparian podocarp forest dominated by totara (*Podocarpus totara* var. *totara*), disturbed forest remnants with tarata (*Pittosporum eugenioides*) and houhere (*Hoheria populnea*); February 26, 2015, R. Lücking, B. Moncada & P.J. de Lange 39191 (B, F-C0265565F; DNA voucher: MON3434); ibid., on *Kunzea robusta*; February 26, 2015, R. Lücking, B. Moncada & P.J. de Lange 39199 (B, F-C0265474F; DNA voucher: MON3485). Northland, Hokianga, Oue; 6 Feb. 2018, M. Ford s.n. (UNITEC 9783). Northland, Whangarei, Mair Park; 1 Apr. 2020, P. Bell-Butler s.n. (UNITEC 11593). Aotea | Great Barrier Island, Motukaikoura, Ngati

Rehua Track; 10 Jun. 2008, A.J. Marshall s.n., & I. Ennis (UNITEC 3388). North Auckland, Rodney District, Dome Track; 4 Apr. 2003, A.J. Marshall s.n. (UNITEC 374). Kaipara, Mataia, Mataia Farm, 'Cabbage Tree Swamp'; 30 May 2021, A.J. Marshall s.n. & E. Thom (UNITEC 12826). Rodney District, Ararimu Valley Road, Ernest Morgan Reserve; 16 May 2008, P.J. de Lange 7392 (AK 302314). Western Waikato, South Kawhia, Awaroa Valley, Awaroa Scenic Reserve; 11 Feb. 2022, P.J. de Lange 15303 (UNITEC 13165). Northern Hawke Bay (near Wairoa), Mahia Peninsula, Kinikini Road; 20 Jan. 2013, P.J. de Lange s.n. (UNITEC 6107). Wellington, Hutt Valley, Kaitoki Regional Park; 12 Nov. 1989, A.E. Wright 9436 (AK 187534). South Island: North West Nelson, Golden Bay, Whatariki–Puponga Farm Park, Pillar Light Bush; 30 Nov. 2019, P.J. de Lange 14558 & T.J.P.J. de Lange (UNITEC 11296). Marlborough, D'Urville Island, Mount Maud; 2 Jan. 1988, B.W. & G.C. Hayward s.n. (AK 181582). Westland, Haast Pass; 17 Feb. 1992, D.J. Blanchon 9218 (AK 310313).

***Pseudocyphellaria hookeri*** (C. Bab.) D.J. Galloway & P. James, The Lichenologist 12(3): 299. 1980.
(Figs 14, 15)

**Brief description**. Primary photobiont a cyanobacterium (*Nostoc*). Thallus irregular to forming suborbicular rosettes, rather loosely attached, much branched, lobes laciniate to broadened, horizontal, partly imbricate, rounded to more or less truncated. Upper surface scrobiculate to faveolate with shallow to sharp ridges, bluish grey when fresh, brownish gray in the herbarium, glabrous, with numerous whitish maculae. Medulla white. Lower surface uneven to bullate owing to the scrobiculate to faveolate upper surface, pale to dark brown, shortly tomentose, becoming whitish and glabrous towards the margins. Pseudocyphellae whitish or partly pale yellow, small and punctate, dispersed. Soralia, isidia and phyllidia absent. Apothecia sparse to abundant, laminal to submarginal, often along the ridges, sessile and constricted below, up to 8 mm in diam.; thalline margin distinct, prominent, crenulate; disc black, non-pruinose. Ascospores 8 per ascus, more or less biseriate, fusiform, 1-septate, 20–30 × 8–11 µm, brown. Pycnidia abundant, typically in dense lines along the ridges. Conidia bacillar.

**Secondary chemistry**. Tenuiorin, methyl evernate, methyl lecanorate, methyl gyrophorate, evernic acid (tr.), gyrophoric acid (tr.), hopane-6α,7β,22-triol, 7ß-acetoxyhopan-6α,22-diol (tr.), 6α-acetoxyhopan-7β,22-diol (tr.), norstictic (tr.), stictic acid, hypostictic acid (tr.), cryptostictic acid, onstictic acid, sometimes (pseudocyphellae) pulvinic acid (tr.), pulvinic dilactone (tr.), calycin (tr.); surface C+ pink-red, K+ yellow, medulla C+ pink-red, K+ yellow-orange or turning red, P+ orange (according to Galloway et al. 1983; Galloway 1985) (Fig. 8).

**Distribution and ecology**. *Pseudocyphellaria hookeri* has been collected from the two larger islands of Aotearoa | New Zealand, Te Ika-a-Maui | North Island, and Te Wai Pounamu | South Islands, as well as from the Chatham Islands (Rangihaute | Rangiauria | Pitt Island). Galloway (1988, p. 169) considered the species to be a "mainly a northern species in North I. [sic] ... rare in South I. [sic] (north-west Nelson and Jackson Bay)". Despite more collections and observations becoming available since then, this assessment remains largely correct; for example, as of 27 Mar. 2026, there are no observations of the species from Te Wai Pounamu | South Island on iNaturalist NZ (https://www.inaturalist.nz). The species is indeed most commonly encountered from the Waikato Region north through Te Tai Tokerau | Northland, with outlying populations in Te Paki, at Unuwhao (34.4374°S, 172.8911°E).

Galloway (1988, p. 169) considered *Pseudocyphellaria hookeri* "characteristic of cool, moist, humid habitats (gullies, streams sides, on successional shrubs or in standing forest or forest remnants) in moderate to deep shade". In our experience, this is still largely correct. The species is characteristic of the wetter, westerly 'cloud forests' of Te Tai Tokerau | Northland, though we have noted that it does seem to also favor sites where cool air ponds, such as those caused by temperature inversion zones, i.e., places where evening cold air ponds like in dolines and sinkholes within dense forest, along the ecotone of frost flats, or near valley floors in steep hill country. In these places it is often found on the twigs and trunks of saplings and shrubs such as *Carpodetus serratus* J.R. Forst. & G. Forst., *Coprosma areolata* Cheeseman, *C. rigida* Cheeseman, *C. rotundifolia* A. Cunn., *Melicytus lanceolatus* Hook.f., *Myrsine salicina* (Hook.f.) Heward ex Hook.f., *Leptospermum hoipolloi* f. *hoipolloi*, *L. scoparium*, *Pennantia corymbosa*, *Pseudopanax crassifolius* (Sol. ex A. Cunn.) K. Koch, *Pterophylla sylvicola* (Sol. ex A. Cunn.) Pillon & Hopkins, and *Quintinia serrata* A. Cunn. Galloway (1988) also noted a marked preference for the branches of *Dacrycarpus dacrydioides*. In Te Paki, the species has been found on *Cordyline australis* and *Kunzea linearis*. In these habitats *P. hookeri* usually grows in isolation from other lobariaceous species, but it has been found in association with *Crocodia rubella*, *Pseudocyphellaria dissimilis*, *P. glabra*, *P. gretae*, *P. lividofusca* (Kremp.) D.J. Galloway & P. James, *Sticta caliginosa* D.J. Galloway, *S. fuliginosa* (Hoffm.) Ach., *S. latifrons* A. Rich., *S. menziesii* Hook.f. & Taylor, *Yarrumia colensoi*, and *Y. coronata*.

**Conservation status**. *Pseudocyphellaria hookeri* has been assessed as 'At Risk / Naturally Uncommon' qualified 'Sp' [Sparse] by the New Zealand Lichen Threat Listing Panel over two iterations (de Lange et al. 2012, 2018). Since those assessments, our knowledge of its range and ecological preferences has changed little, the species remains a biologically sparse, mostly uncommon, though at times locally common, component of New Zealand forests.

**Remarks**. *Pseudocyphellaria hookeri* is rather readily recognized by the cyanobacterial thallus with scrobiculate-faveolate surface and the apothecia with black disc. The only similar lichen is the cyanobacterial phase of *P. rufovirescens*, previously named *P. murrayi* D.J. Galloway (Renner & Galloway 1982; Galloway 1985, 1988, 2007). It differs from *P. hookeri* in the same way as the green phase of *P. rufovirescens* from *P. durietzii*, namely in the scrobiculate to only shallowly faveolate

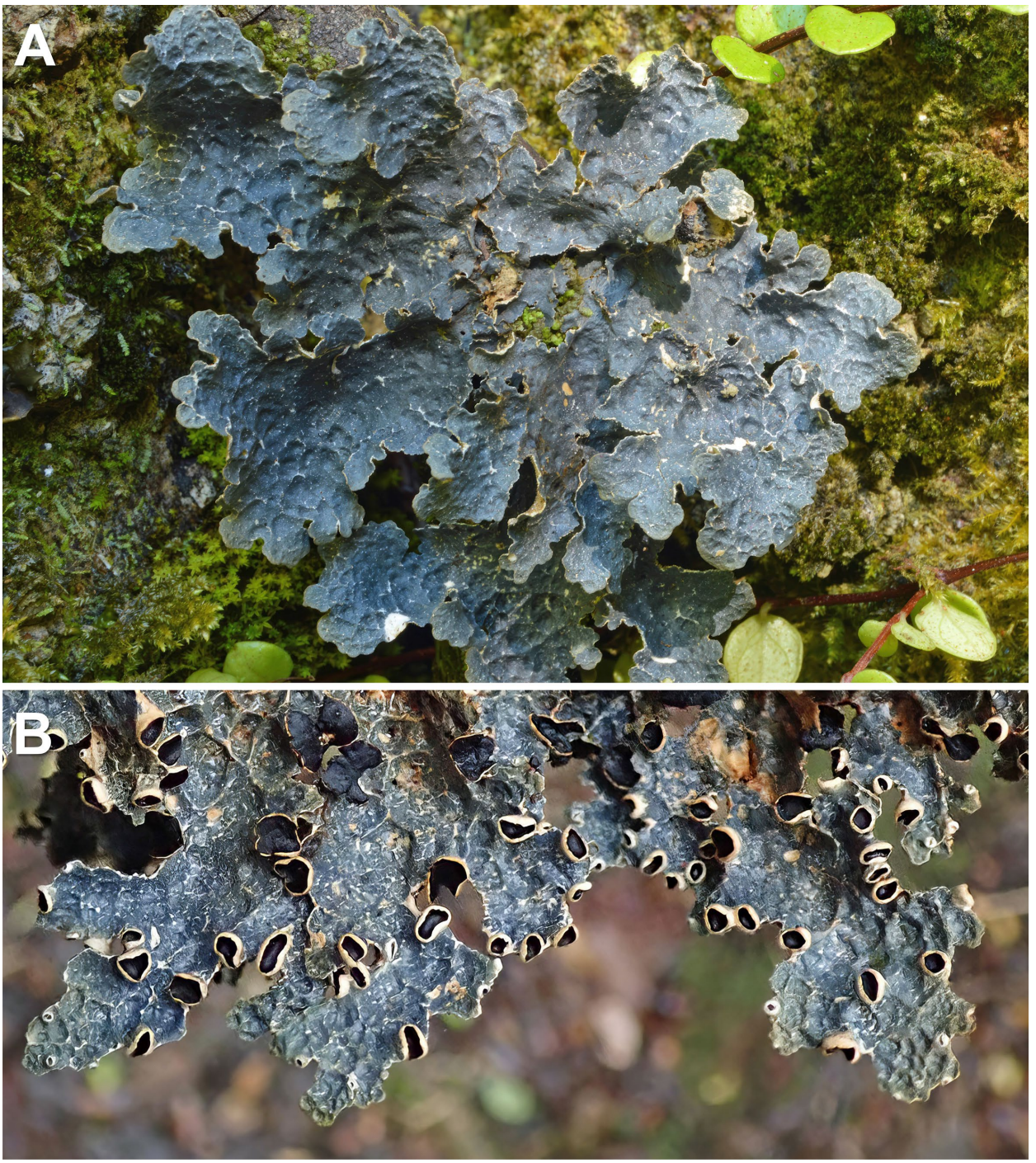


**Figure 14**. Field images of *Pseudocyphellaria hookeri*. A, B – thallus, in B with apothecia [A: Lücking et al. 38769; B: from iNaturalist; Marley Ford; https://www.inaturalist.org/observations/26733755; https://creativecommons.org/licenses/by-nc/4.0/deed.en]. Scale = 1 mm.

surface with broad ridges (Fig. 13B) and in the chemistry, the surface and medulla reacting C– due to the absence of gyrophoric acid. Notably, while *P. hookeri* and *P. durietzii* are distinct species, *P. rufovirescens* and the cyanobacterial phase named *P. murrayi* represent a genuine photosymbiodeme of the same mycobiont (Figs 2, 3) and are often observed together on the same thallus (Fig. 13B).

**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; 39.1244°S, 177.8742°E, 150–200 m; kohekohe (*Dysoxylum spectabile*) / nikau (*Rhopalostylis sapida*) with tawa (*Beilschmiedia tawa*) forest transitioning into riparian podocarp forest dominated by kahikatea (*Dacrycarpus dacrydioides*), matai (*Pruminopitys taxifolia*) and totara (*Podocarpus totara* var. *totara*) with an understorey of mahoe (*Melicytus ramiflorus* subsp. *ramiflorus*), kotukutuku (*Fuchsia excorticata*), horoeka (*Pseudopanax crassifolius*) and kaikomako (*Pennantia corymbosa*), well-preserved forest, on *Beilschmiedia tarairi*; February 19, 2015, R. Lücking, B. Moncada & P.J. de Lange 38644 (AK, UNITEC, B, F-C0265834F; DNA voucher: MON3693), 38768 (AK, B, F-C0265835F; DNA voucher: MON3692), 38769 (B, F-C0265836F; DNA voucher: MON3691). North Island, Waikato: Western Bay Road, Great Lake Trail Waihaha Link at Waihaha River, 36 km W of Taupo, trail head at parking lot off the road (Bike Trail Car Park); 38.7008°S, 175.6842°E, 480 m;

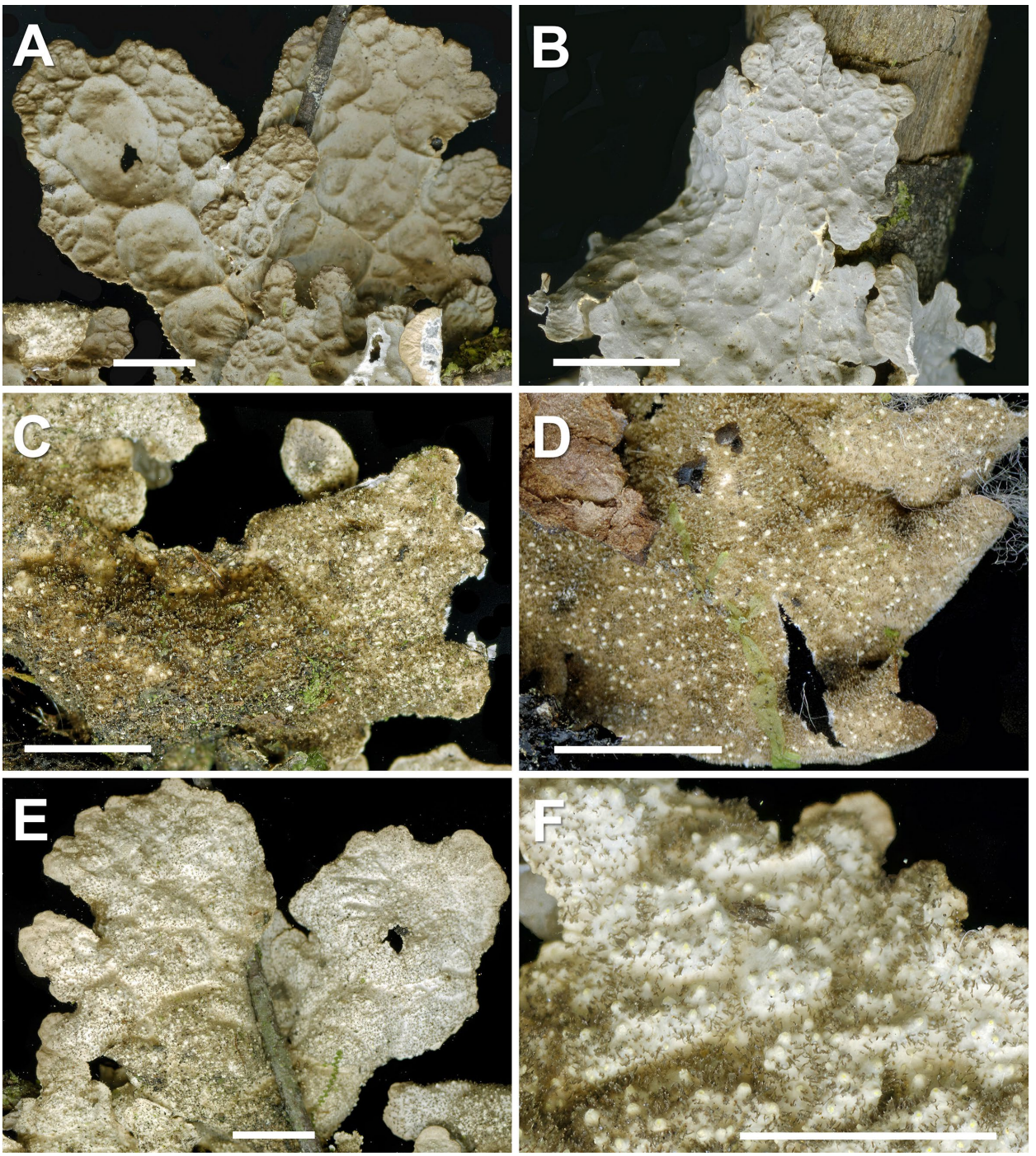


**Figure 15**. *Pseudocyphellaria hookeri*. A, B – dried specimens (upper side; A: Lücking et al. 38768; B: Lücking et al. 38769); C–F – underside showing thin tomentum and pseudocyphellae (C: Lücking et al. 38644; D: Lücking et al. 38977; E: Lücking et al. 38678; F: Lücking et al. 38768). Scale = 5 mm.

riparian secondary regrowth dominated by grey willow (*Salix cinerea*), kohuhu (*Pittosporum tenuifolium* subsp. *colensoi*), whauwhaupaku (*Pseudopanax arboreus*) and rawirinui (*Kunzea robusta*), disturbed vegetation adjacent to parking lot, on *Salix cinerea*; February 22, 2015, R. Lücking, B. Moncada & P.J. de Lange 38977 (B, F-C0265837F; DNA voucher: MON3694). [Photosymbiodeme:] North Island, Hawke's Bay: Mahia Peninsula, Kinikini Road, Mahia Peninsula Scenic Reserve, 56 km SSW of Gisborne, trail through reserve; 39.1244°S, 177.8742°E, 150–200 m; kohekohe (*Dysoxylum spectabile*) / nikau (*Rhopalostylis sapida*) with 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 (*Melicytus ramiflorus* subsp. *ramiflorus*), kotukutuku (*Fuchsia excorticata*), horoeka (*Pseudopanax crassifolius*) and kaikomako (*Pennantia corymbosa*), well-preserved forest, on *Beilschmiedia tarairi*; February 19, 2015, R. Lücking, B. Moncada & P.J. de Lange 38767a (B, F-C0266915F; DNA voucher: MON3718). Te Paki, Unuwhao, near Unuwhao Pa; 12 Apr. 2015, P.J. de Lange 12646 (UNITEC 7187). Northland, Puketi Forest, Onekura Bluffs; 9 Dec. 1987, A.E. Wright 7916 (AK 178753). Western Northland, Waipoua Forest, Old Coach Road; 6 Nov. 2014, P.J. de Lange 12372 (UNITEC 7374). Western Northland, Marlborough Forest; 6 Nov. 2014, P.J. de Lange 12357 (UNITEC 7375). Auckland, Waitakere Ranges, Cascades Kauri Park; 31 Jul. 1992, J.E. Braggins & M.L. Fromont s.n. (AK 210082). South Auckland, Hunua Range,

Mine Road, 30 Nov. 2018, P.J. de Lange 14342 & T.J.P.J. de Lange (UNITEC 10550). Waikato, Hamilton Basin, Marychurch Kahikatea Forest; 27 Nov. 2011, P.J. de Lange 10293, T.J. de Lange & F.J.T. de Lange (AK 329719). South Auckland, Pureora, Waimihia Stream, opposite Maraeroa Rd; 13 Apr. 2015, P.J. de Lange 12621 (UNITEC 7190). Wanganui, Wanganui River, Tawhata; Apr 1949, E.H. Bunn 6 (AK 310283). South Island: Nelson, Motueka, Aniseed Valley; Sep 1978, J.K. Bartlett s.n. (AK 204215). Chatham Islands: Rangiauria (Pitt) Island, North Head, Orchard Bush; 29 May 2008, P.J. de Lange CH1302 & P.B. Heenan (AK 302701).

***Pseudocyphellaria montagnei*** (C. Bab.) D.J. Galloway & P. James, The Lichenologist 12(3): 300. 1980. (Figs 16, 17)

**Brief description**. Primary photobiont a green alga (*Symbiochloris*). Thallus usually forming regularly rosettes, rather closely attached, much branched, lobes laciniate to flabellate, horizontal, partly imbricate, more or less rounded and sometimes canaliculate. Upper surface uneven, rarely finely scrobiculate, bright green to brownish green when fresh, yellowish to brownish gray in the herbarium, glabrous, without maculae. Medulla white. Lower surface uneven, pale brown to beige, shortly tomentose, becoming whitish and glabrous towards the margins and darker towards the center. Pseudocyphellae whitish, rarely yellowish, small and punctate, scattered. Phyllidia abundant, predominantly formed along the lobe margins, of rounded, partly imbricate squamules in several layers. Apothecia often abundant, laminal to submarginal, often along the ridges, sessile and constricted below, up to 5 mm in diam.; thalline margin distinct, somewhat prominent, entire to crenulate or becoming phyllidiate; disc black, non-pruinose. Ascospores 8 per ascus, more or less biseriate, fusiform, 1-septate, 24–31 × 7–10 µm, brown. Pycnidia often present, typically in dense lines along the ridges. Conidia bacillar.

**Secondary chemistry**. Tenuiorin, methyl evernate, methyl gyrophorate, evernic acid (tr.), hopane-6α,7β,22-triol, norstictic (tr.), stictic acid, hypostictic acid (trace), cryptostictic acid, constictic acid; surface C+ pink-red, K+ yellow, medulla C+ pink-red, K+ yellow-orange or turning red, P+ orange (according to Galloway 1985, 1988, 2007) (Fig. 8).

**Distribution and ecology**. Galloway (1988) documented this species as present in the two main islands of Aotearoa | New Zealand, Te Ika-a-Maui | North Island and Te Wai Pounamu | South Islands, noting that it is also present on Manawa Tawhi | Three Kings Islands, 53 km north of the northern tip of Te Ika-a-Maui | North Island, Te Paki. In Te Wai Pounamu | South Island, the species is uncommon, occurring only in the northwest, whereas in Te Ika-a-Maui | North Island, *Pseudocyphellaria montagnei* is a very common, mostly northern, and generally coastal and lowland species. Our recent field work confirms this distribution.

A common photophilous species of northern coastal forest and associated shrubland, in these associations it most commonly collected from *Avicennia marina* subsp. *australasica* (Walp.) J. Everett, *Beilschmiedia taraire* (A. Cunn.) Kirk, *Cordyline australis*, *Corynocarpus laevigatus* J.R. Forst. & G. Forst., *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Didymocheton spectabilis*, *Kunzea amathicola*, *K. ericoides* (A. Rich.) Joy Thomps., *K. linearis*, *Leptospermum hoipolloi*, *L. scoparium*, *Melicytus ramiflorus* J.R. Forst. & G. Forst. subsp. *ramiflorus*, *Metrosideros excelsa*, *Podocarpus totara* var. *totara*, *Rhopalostylis sapida* and *Vitex lucens* Kirk. Associated lobarioid lichens include a range of photophilous species but especially *Crocodia aurata*, *C. poculifera*, *Lobaria asperula* (Stirt.) Yoshim., *Podostictina pickeringii* (Tuck.) B. Moncada & Lücking, *Pseudocyphellaria bartlettii* D.J. Galloway, *P. carpoloma*, *P. chloroleuca*, *P. coriacea*, *P. haywardiorum* D.J. Galloway, *Sticta babingtonii* D.J. Galloway, and *S. squamata* D.J. Galloway.

**Conservation status**. *Pseudocyphellaria montagnei* has been assessed as 'Not Threatened' by the New Zealand Lichen Threat Listing Panel over two iterations (de Lange et al. 2012, 2018). Our field work and the plethora of observations of this species posted on iNaturalist NZ (https://www.inaturalist.nz) confirm this assessment as still valid.

**Remarks**. *Pseudocyphellaria montagnei* differs from the other species in the *P. hookeri* clade by its distinctive morphology, with a closely attached thallus forming regular rosettes and abundant phyllidia. The only somewhat similar *Pseudocyphellaria* species in New Zealand are the unrelated *P. corbettii* D.J. Galloway and *P. multifida* (Laurer ex Nyl.) D.J. Galloway & P. James, which have loosely attached, narrow, flat lobes with marginally projecting, narrow isidia and/or phyllidia (Fig. 18A, B). However, three species in other genera can potentially be confused with *P. montagnei*. *Podostictina pickeringii* agrees in general aspect, but can easily be set apart by the bright yellow medulla and pseudocyphellae on the lower surface (Fig. 18C, D). *Lobaria asperula* (Fig. 18E) agrees in overall appearance and in the abundant, mostly marginal phyllidia, but it lacks pseudocyphellae on its lower surface and the apothecial disc is red-brown; its ascospores are mostly 3-septate and the only chemical substance is gyrophoric acid (Galloway 1985, 2007). *Sticta squamata* (Fig. 18F) is also superficially similar, but has genuine cyphellae on the underside and lacks chemical compounds (Galloway 1985, 2007). The latter three taxa often co-occur with *Pseudocyphellaria montagnei* in more exposed microhabitats.

**Specimens examined**. NEW ZEALAND. North Island: Gisborne, Lottin Point Road of Te Araroa Road, Bay, 97 km NE of Opotiki, roadside back to State Highway, near Omaio; 37.5606°S, 178.1553°E, 10 m; pohutukawa (*Metrosideros excelsa*) coastal forest with houpara (*Pseudopanax lessonii*) understorey, exposed roadside trees, on *Cordyline australis*; February 17, 2015, R. Lücking, B. Moncada & P.J. de Lange 38513 (AK, UNITEC, B, F-C0265867F; DNA voucher: MON3562). Hawke's Bay: Mahia Peninsula, Kinikini Road, Mahia Peninsula Scenic Reserve, 56 km SSW of Gisborne, trail through reserve; 39.1244°S, 177.8742°E, 150–200 m; kohekohe (*Dysoxylum spectabile*) / nikau (*Rhopalostylis sapida*) with tawa

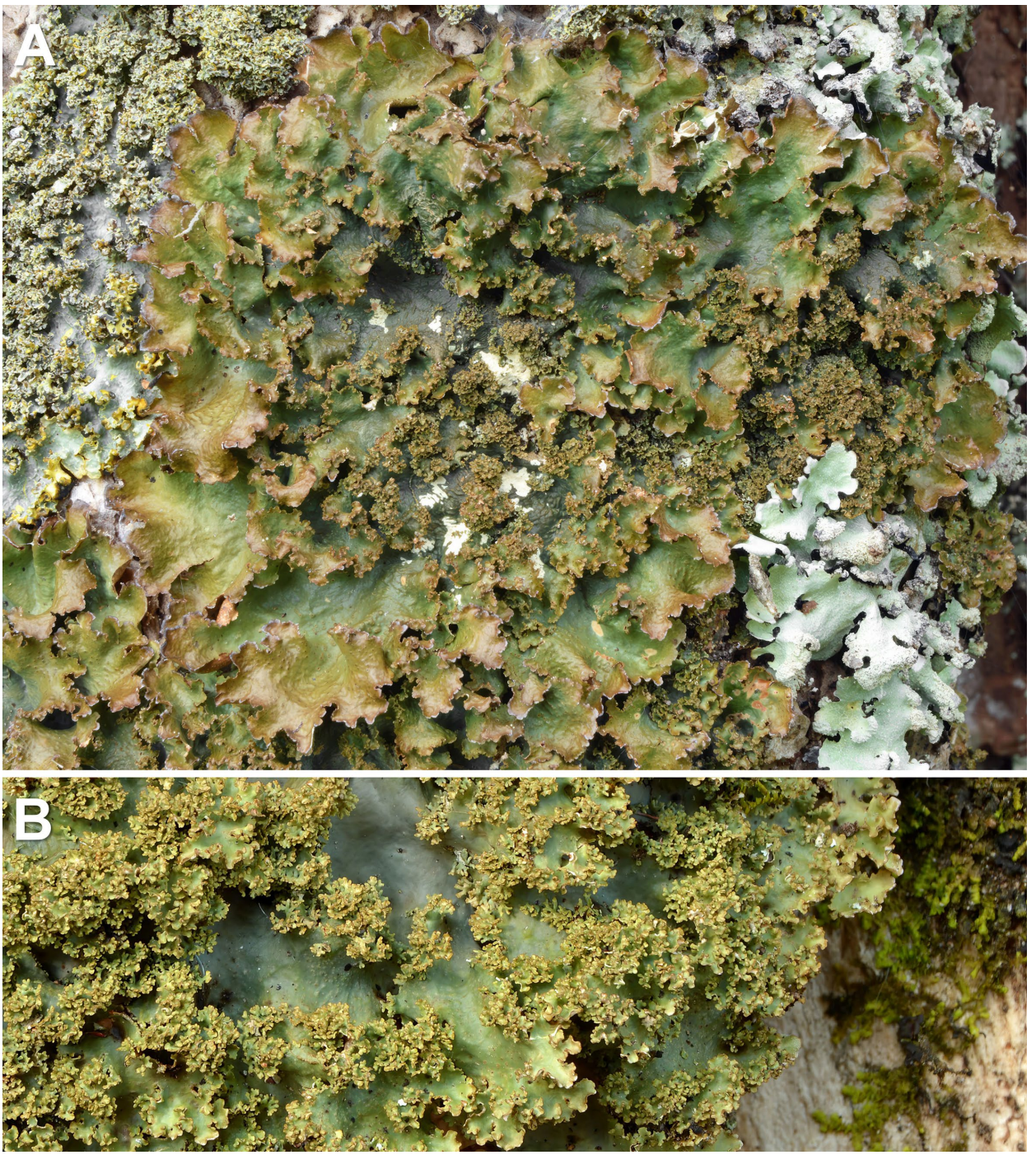


**Figure 16**. Field images of *Pseudocyphellaria montagnei*. A, B – thallus with abundant phyllidia (A: Lücking et al. 39143; B: Lücking et al. 39109). Scale = 1 mm.

(*Beilschmiedia tawa*) forest transitioning into riparian podocarp forest dominated by kahikatea (*Dacrycarpus dacrydioides*), matai (*Pruminopitys taxifolia*) and totara (*Podocarpus totara* var. *totara*) with an understorey of mahoe (*Melicytus ramiflorus* subsp. *ramiflorus*), kotukutuku (*Fuchsia excorticata*), horoeka (*Pseudopanax crassifolius*) and kaikomako (*Pennantia corymbosa*), well-preserved forest; February 19, 2015, R. Lücking, B. Moncada & P.J. de Lange 38649 (AK, B, F-C0265868F; DNA voucher: MON3703). Auckland: Mataia Bay area W of Kaipara Coast Highway, 23 km N of Helensville, Kaipara Harbour, near Glorit, Mataia Adshead Queen Elizabeth II Trust Covenant; 36.4911°S, 174.4225°E, 0–80 m; regenerating rawirinui (*Kunzea robusta*) dominated forest with pockets of kauri (*Agathis australis*) / tanekaha (*Phyllocladus trichomanoides*) forest, coastal forest dominated by puriri (*Vitex lucens*), pohutukawa (*Metrosideros excelsa*) and kohekohe (*Dysoxylum spectabile*) grading into mangrove (*Avicennia marina* subsp. *australasica*) forest and sarcocornia (*Sacrocornia quinqueflora* subsp. *quinqueflora*) saltmarsh, regenerating forest and mangrove along access trail to Mataia Bay, February 26, 2015, R. Lücking, B. Moncada & P.J. de Lange 39144 (B, F-C0265910F; DNA voucher: MON3498); ibid., on *Vitex lucens*; February 26, 2015, R. Lücking, B. Moncada & P.J. de Lange 39109 (AK, UNITEC, B, F-C0265913F; DNA voucher: MON3501), 39154 (B, F-C0265911F; DNA voucher: MON3499); ibid., on *Avicennia marina*; February 26, 2015, R. Lücking, B. Moncada & P.J. de Lange 39132 (B, F-C0265914F; DNA voucher: MON3500), 39133 (AK, UNITEC, B, F-C0265907F; DNA voucher: MON3503), 39134 (B, F-C0265908F; DNA voucher: MON3504); ibid., on *Cordyline australis*; February 26, 2015,

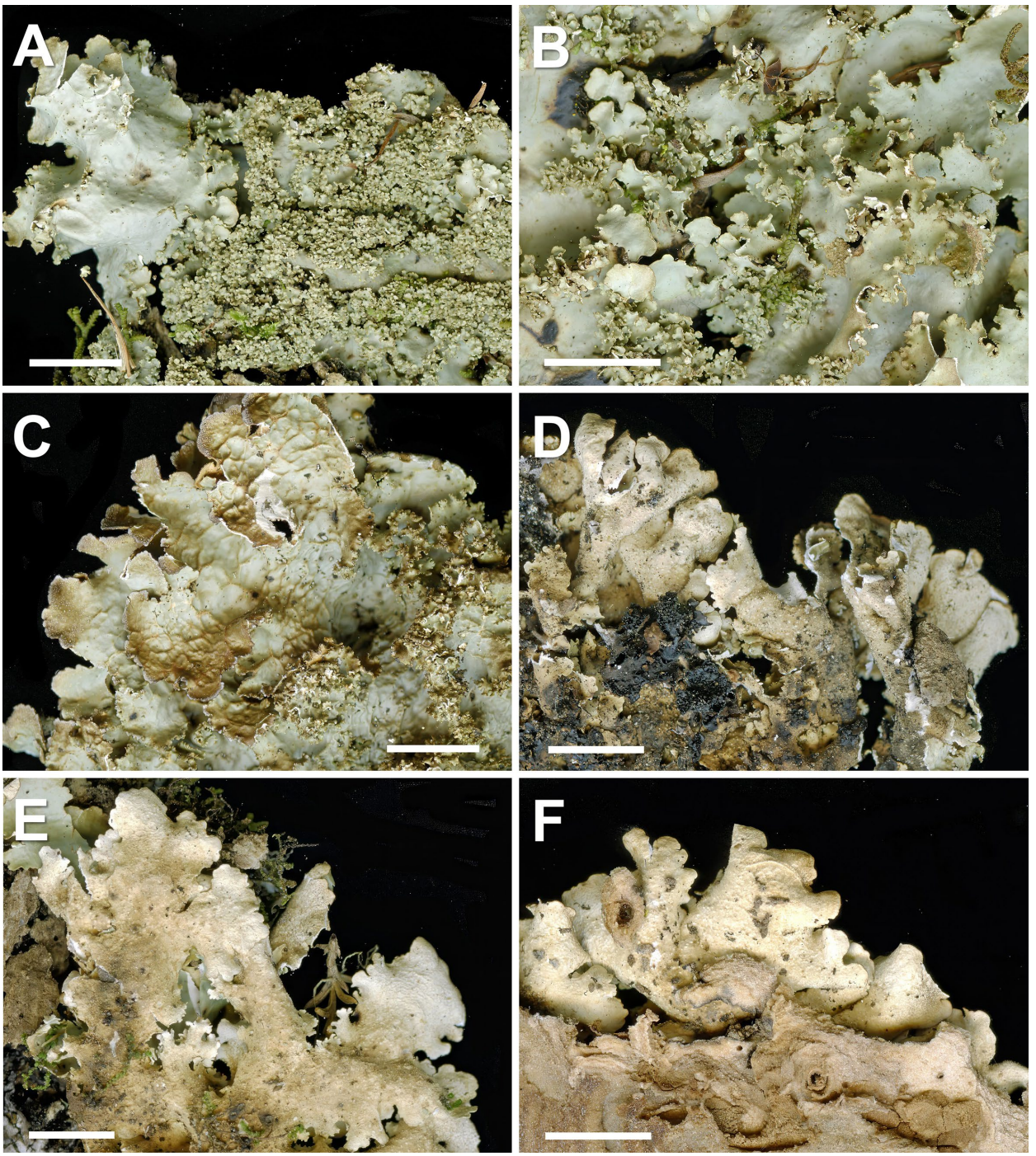


**Figure 17**. *Pseudocyphellaria montagnei*. A–C – dried specimens (upper side A, B: Lücking et al. 38649; C: Lücking et al. 39132) with phyllidia; D–F – underside showing thin tomentum and punctate pseudocyphellae (D: Lücking et al. 39132; E: Lücking et al. 39143; F: Lücking et al. 39154). Scale = 5 mm.

R. Lücking, B. Moncada & P.J. de Lange 39143 (AK, UNITEC, B, F-C0265909F; DNA voucher: MON3502). Manawatāwhi/Three Kings, Manawatāwhi Island; Dec 1982, G.C. & B.W. Hayward s.n. (AK 161562). Northland, Hokianga, Oue; 27 Feb. 2018, M. Ford s.n. (UNITEC 10368). Northland, Whangarei Heads, north Ocean Beach; 23 Aug. 1977, B.W. Hayward & G.C. Hayward (AK 161944). Northland, Hen Island, Reischek Bay; Aug 1977, B.W. & G.C. Hayward s.n. (AK 161574). North Kaipara, Wairoa River, Tokatoka Scenic Reserve; 15 Dec. 2015, P.J. de Lange 12901 (UNITEC 7629). Little Barrier Island, Hauturu Ridge; Aug 1981, B.W. Hayward & G.C. Hayward s.n. (AK 161566). Pakiri Regional Park; 3 Sept. 2020, A.J. Marshall s.n. (UNITEC 14180). Aotea | Great Barrier Island, Motukaikoura, Taraire Valley; 11 Jun. 2008, A.J. Marshall s.n. & I. Ennis (UNITEC 3505). North Auckland, Kaipara, Mataia, Mataia QE II Covenant; 20 May 2016, M. Watson s.n., & D.J. Blanchon (UNITEC 8174). North Auckland, Kaipara, Mataia, Mataia Farm, near Mataia Homestead; 19 May 2017, P.J. de Lange s.n. & D.J. Blanchon, P.J. de Lange s.n. (UNITEC 9171). Auckland, Rangitoto Island, track to lava caves at 'glade intersection' of summit track via road; 12 Feb. 2006, D.J. Blanchon s.n., C. Lockett & R. Kooperberg (UNITEC 1955). Auckland, Waitakere Ranges, Cascades Park; 19 Jul. 1994, J.E. Braggins 94100E (AK 257440). Auckland, Awhitu Peninsula, Hartner Road 'Hartner Road Bush'; 13 Feb. 2020, P.J. de Lange s.n. (UNITEC 11542). Coromandel Peninsula, Port Jackson, Pahi Stream; 22 Jan. 2016, P.J. de Lange 12958 (UNITEC 7693). Otorohanga, Te Kauri Park Scenic Reserve; 30 Oct. 1989, A.E. Wright 9170 (AK 185818). Hawke's

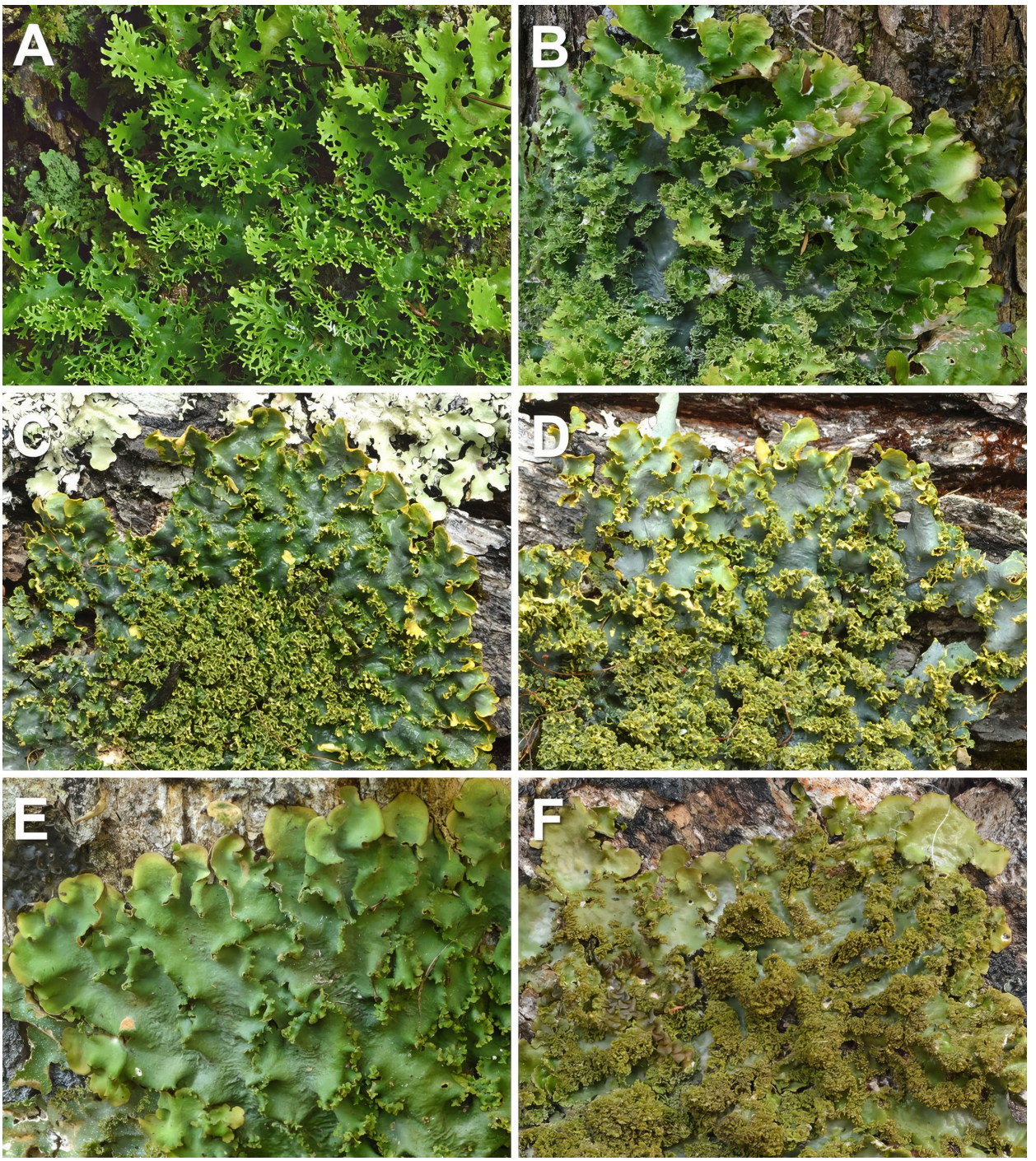


**Figure 18**. Field images of species of *Lobariaceae* present in New Zealand potentially to be confused with *Pseudocyphellaria montagnei*. A, B – *P. multifida* (A: Lücking et al. 38692; B: Lücking et al. 38664); C, D – *Podostictina pickeringii* (Lücking et al. 38503); E – *Lobaria asperula* (Lücking et al. 38665); F – *Sticta squamata* (Lücking et al. 38534).

Bay, Wairoa, Mahia Peninsula, Mahia Scenic Reserve; 21 Jan. 2013, P.J. de Lange 11525 (AK 337935). South Island: North West Nelson, Whararikiâ€“Puponga Farm Park, Cape Farewell Road; 29 Nov. 2019, P.J. de Lange 14793 & T.J.P.J. de Lange (UNITEC 12136).

## Author contributions

PJdL, DB, BM and RL performed the field work. All authors studied specimens morphologically and HR made high-resolution scans of the upper and lower side of all specimens. BM carried out the molecular work and BM and RL performed the phylogenetic analyses. PJdL and DB added further specimen data and PJdL compiled the chorological and ecological characterizations. PJdL, DB and RL revised iNaturalist records. RL drafted the initial manuscript and all authors revised the manuscript in several rounds and approved the final version.

## Data availability

All studied specimens are indicated and a list with all revised iNaturalist records is provided in the supplementary material. Voucher data are provided for the accessions used in the molecular phylogenetic analysis and the underling alignment and tree files are also included in the supplementary material (Supplementary electronic materials).

## Acknowledgements

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 H. Thorsten Lumbsch, 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 logistical support and for making possible the participation of PJdL (now with UNITEC) in the fieldwork. Unitec Institute of Technology (Auckland) provided assistance for organizing a workshop on the use of *Lobariaceae* as bioindicators of environmental health. 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. Besides overseeing the aforementioned NSF project under which the data for this paper were generated, Thorsten Lumbsch is thanked for his guidance during the project and his feedback on the topic of temporal banding and ascus structures and ascoma development in *Peltigerales*. Marley Ford, Melissa Hutchinson, Paul Bell-Butler, Jacqui Geux, Lidian Dickie, Chris Chadwick, Bevan Smith, Matt Ward, Dr. C. R. Schack and others are acknowledged for their helpful iNaturalist records of species of the *Pseudocyphellaria hookeri* clade. The authors would like to recognize the pioneering work on the Aotearoa | New Zealand *Lobariaceae* undertaken by Dr David John Galloway FRGS, FLS, FRSNZ (7 May 1942 – 6 Dec. 2014). David's critical treatments of the family, and especially *Pseudocyphellaria* and *Sticta*, laid the foundation for the revisions the authors are currently engaged in, and which, in part this paper show cases. David was a close friend and mentor to many of the authors; a man whose guidance and humor is sorely missed. Two anonymous reviewers are thanked for their constructive comments that helped to improve the manuscript.

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## Supplementary electronic materials

**File S1**. Revised iNaturalist records of the *Pseudocyphellaria hookeri* clade [Excel]. Download file

**File S2**. ITS alignment used for the phylogenetic analysis [Fasta]. Download file

**File S3**. Tree file resulting from the phylogenetic analysis [Newick]. Download file

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