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RESEARCH ARTICLE

A new red algal crust from New Zealand: *Apophlaea darchinoae* sp. nov. (Hildenbrandiales)

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ABSTRACT

New Zealand's algal flora is still far from fully explored, and new taxa continue to be discovered. The taxonomy of the red algal order Hildenbrandiales, consisting mostly of crustose members, is controversial as descriptions are largely based on limited morphological features. The order Hildenbrandiales is also in a close, apparently obligate, relationship with an endophytic fungus. *Apophlaea* is a genus in this order currently comprising two described species, both endemic to New Zealand. The morphology of this genus is more complex than that of other members of the Hildenbrandiales as it consists of extensive upright thalli. Sampling of *Apophlaea* in New Zealand, especially in the southern part of the North Island, has led to the discovery of a genetically distinct entity, that is only crustose. We propose a new species for this entity, *Apophlaea darchinoae* sp. nov., which is found on rocks in the high intertidal zone. This species has the typical tetrasporangial conceptacles of *Apophlaea* and no other reproductive structures were observed, and it consists of filaments that are laterally joined by secondary pit connections. *Apophlaea darchinoae* can be found in sympatry with *A. sinclairii* in the north of the North Island. We provide molecular evidence for the distinct nature of *A. darchinoae* and provide observations of extensive fungal filaments within this new species.

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Introduction

New Zealand is known to have many endemic taxa, making it a biodiversity hotspot (Myers et al. 2000). The relative geographic isolation and patterns of ocean currents around New Zealand have shaped the unique and diverse biota of the marine environment (Wallis and Trewick 2009). The algal diversity of New Zealand is largely understudied, with 609 species considered 'data deficient' out of the total of 938 species reviewed, and consequently the conservation status for a large proportion of New Zealand algae cannot be determined (Nelson et al. 2019). Currently, it is estimated that there are 25,000 green and red algal species in New Zealand and Australia but only 20% are described (Taxonomy Decadal Plan Working Group 2018). This high unknown diversity in New Zealand is supported by molecular studies showing high levels of cryptic diversity

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(Muangmai et al. 2015; Preuss et al. 2022) and by ongoing new species descriptions in red alga (e.g. D'Archino et al. 2020; D'Archino and Zuccarello 2020; Preuss et al. 2020; Nelson et al. 2021).

The Hildenbrandiales (subclass Hildenbrandiophycidae) is the earliest diverging lineage in the Florideophyceae, sister to all other orders (Verbruggen et al. 2010); it diverged approximately 879–681 Mya (Yang et al. 2016). This red algal order contains mostly crusts in two genera, *Hildenbrandia* and *Apophlaea*. *Hildenbrandia* has a wide distribution, including both marine (sub- and high intertidal) and freshwater species, inhabiting a variety of subpolar, temperate and tropical regions (Saunders and Bailey 1999; Sherwood and Sheath 1999; Vieira et al. 2021). Common characters of this group are a basal layer of branched filaments which laterally adhere to form a crust, often firmly attached to rocks, and secondary pit connections formed between adjacent cells without conjunctor cells (Pueschel and Cole 1982; Pueschel 1988). This anatomy is continued into the upright thalli, if formed (Hawkes 1983). Typically, these species produce zonate or irregularly divided tetrasporangia in conceptacles, with the exception of freshwater species that are only known to produce asexual gemmae (Kylin 1956; Sherwood and Sheath 2000). Sexual reproduction has not been observed in any of the Hildenbrandiales (Sherwood and Sheath 1999), and the order may have diverged before the evolution of the typical florideophycean triphasic life cycle (Yang et al. 2016). In addition, their early divergence from the other Florideophyceae is also reflected in their plastid genome architecture, which does not follow the common synteny patterns of other Florideophyceae (Yang et al. 2015; Lee et al. 2016). Another unusual feature of the Hildenbrandiales is their close association with fungi (Gardner 1917). Both known *Apophlaea* species have been found to form a myco-phyco-biosis with a fungus, described as *Mycosphaerella apophlaeae* Kohlmeyer (Kohlmeyer and Demoulin 1981; Kohlmeyer and Hawkes 1983), but later transferred to *Mycophycias apophlaeae* (Kohlmeyer) Kohlmeyer and Volkmann-Kohlmeyer (Kohlmeyer and Volkmann-Kohlmeyer 1998), a genus also found endosymbiotically in brown algae (Deckert and Garbary 2005; Toxopeus et al. 2011).

Molecular data is an important tool to distinguish species within the Hildenbrandiales since there are few distinguishing morphological features. Phylogenetic studies indicate that the diversity is greater than reflected in the present taxonomy. Furthermore, several species are paraphyletic, such as *Hildenbrandia angolensis* Welwitsch ex West and G.S. West, *Hildenbrandia rivularis* (Liebmann) J.Agardh and *Hildenbrandia rubra* (Sommerfeld) Meneghini (Sherwood and Sheath 1999, 2003), and the taxonomy is still undergoing changes (Vieira et al. 2021).

The marine genus *Apophlaea* contains two described species: *A. lyallii* J.D.Hooker and Harvey, and *A. sinclairii* J.D.Hooker and Harvey. *Apophlaea lyallii* was described from Preservation Harbour in the South Island of New Zealand, whereas *A. sinclairii* was described from the Bay of Islands on the North Island of New Zealand (Harvey 1844; Hooker and Harvey 1845; Nelson 2020). Both species have upright axes, in contrast to the crusts of *Hildenbrandia* (Sherwood and Sheath 2003). Molecular studies have shown that *Apophlaea* is nested within *Hildenbrandia*, making *Hildenbrandia* paraphyletic (Saunders and Bailey 1999; Sherwood and Sheath 1999). The aim of this study is to formally describe a new species of *Apophlaea* based on morphological and molecular data.

Materials and methods

Apophlaea specimens as crusts or uprights were collected in the high intertidal zone from a range of locations around New Zealand (Table 1; Figure S1). Collected specimens were dried in silica gel for molecular analyses, dried on rocks as voucher specimens or fixed in 5% formalin in seawater for morphological observations. Fixed samples were rinsed thoroughly with seawater and transferred to 70% ethanol.

DNA was extracted from silica dried samples using a modified cetrimonium bromide protocol (Zuccarello and Lokhorst 2005). *Rbc*L was amplified in one or two parts using a combination of forward (F57, F765) and reverse primers (R753, R-rbcS-start) (Freshwater and Rueness 1994; Wang et al. 2000), using a standard PCR protocol (2.5 mM $MgCl_2$, 45°C annealing temperature).

New plastid primers were designed covering an intergenic spacer from the plastid genome of *Apophlaea sinclairii* (NC_031172), to provide a more variable region to distinguish species. The forward primer Apo_rpl36_172019F (5`-TTATCCTTGGCGTTGTTTATGCTT) and the reverse Apo_secY_173093R (5'- TAGCAAACTTTGGAGCAACTTCAC) were created using Primer3 (Untergasser et al. 2012) in Geneious Prime (https://www.geneious.com), amplifying the intergenic region between *rpl*36 and *sec*Y. A touchdown PCR was carried out with an initial denaturation at 94°C for 3 min followed by 10 cycles of denaturing at 94°C for 30 s, annealing at 55°C for 1 min, with a reduction in annealing temperature by 1°C each cycle until 45°C, extension at 72°C for 1 min, followed by 25 cycles of 94/45/72°C for 30 s for the denaturing and annealing step and 1 min for the extension step. This was followed by a final extension of 4 min at 72°C. For fungal amplifications the internal transcribed spacer-large subunit rDNA (LSU) forward ITSf_V96 and reverse primers LR5 were used following Videira et al. (2017).

Phylogenies were produced in IQTREE. The best model was selected using Modelfinder (Kalyaanamoorthy et al. 2017) and in *rbc*L codon partitioned to select the best partitions (Lanfear et al. 2012). Three branch support methods were used: non-parametric bootstrapping (rbcL: 1000 replicates, *rpl*16-*sec*Y spacer: 500 replicates, Felsenstein 1985); Ultrafast bootstrapping (UF) (rbcL: 1000 replicates, *rpl*16-*sec*Y spacer: 2000 replicates, Hoang et al. 2018); and the approximate likelihood ratio test (SH-aLRT) (1000 replicates, Guindon et al. 2010). *Bangia atropurpurea* (Mertens ex Roth) C.Agardh and *Pyropia plicata* W.A.Nelson were used as the outgroup for the *rbc*L data set. The *rpl*36-*sec*Y alignment was unrooted.

Maximum likelihood phylogenies of the fungal LSU used the top 10 BLAST hits from GenBank for the sequenced LSU gene, plus samples, including potential genera from Toxopeus et al. (2011). Samples were aligned in MAFFT (Q-INS-i, Katoh and Standley 2013), and subject to 500 nonparametric bootstraps.

For morphological observation, sectioning was done by hand and samples were stained in acidified 1% aniline blue. Fungal hyphae were stained using chlorazol black E, following the procedures in Brundrett et al. (1984). Briefly, algal tissue was autoclaved in a 10% KOH solution for 15 min at 121°C and then rinsed repeatedly with tap water followed by deionised water. Tissue was stained in a solution of equal volumes of 80% lactic acid, glycerin and distilled water with 0.1% chlorazol black E for 1 h at 90°C, followed by a destaining overnight step in glycerin, after which it was squashed and

Table 1 . Samples collected in New Zealand for this study. Information is provided on general morphology, extraction number, collection date, location, longitude and latitude, and GenBank accession numbers.

Species	Morphology	Extraction #	Date	Location (WELT voucher number)	Coordinates	Region sequenced		
						*rbc*L	*rpl*36-*sec*Y spacer	Fungal LSU
Apophlaea darchinoae	Crust	I466	3 Dec. 2021	Moa Point, Wellington, North Island (Holotype, A034487)	41°20′32.6"S, 174° 48′33.4"E	ON146066	ON146081	ON130755
	Crust	I469	3 Dec. 2021	Moa Point, Wellington, North Island (Paratype 1, A034488)	41°20′32.6"S, 174° 48′33.4"E		ON146082	
	Crust	I470	3 Dec. 2021	Moa Point, Wellington, North Island (Paratype 2, A034489)	41°20′32.6"S, 174° 48′33.4"E	ON146068	ON146083	ON130756
	Crust	I471	3 Dec. 2021	Moa Point, Wellington, North Island (Paratype 3, A034490)	41°20′32.6"S, 174° 48′33.4"E	ON146069	ON146080	ON130757
	Crust	I270	9 Apr. 2021	Doubtless Bay, Northland, North Island	34°59′14.9"S, 173° 30′59.4"E		ON146078	
	Crust	I307	10 Apr. 2021	Tapeka, Bay of Islands, North Island	35°14′48.0"S, 174° 06′58.5"E		ON146079	
	Crust	I263	11 Apr. 2021	Tawharanui Peninsula, Auckland, North Island	36°22′44.0"S, 174° 49′06.6"E		ON146076	
	Crust	I276	9 Apr. 2021	Cable Bay, Northland, North Island	34°59′26.0"S, 173° 29′13.6"E	ON146067	ON146077	
	Crust	I271	28 Apr. 2021	Moa Point, Wellington, North Island	41°20′32.6"S, 174° 48′33.4"E	ON146070		
	Crust	I262	11 Apr. 2021	Tawharanui Peninsula, Auckland, North Island	36°22′44.0"S, 174° 49′06.6"E	ON146071		
Apophlaea lyallii	Upright	944	24 Sep. 2020	Burial Cove, Stewart Island	47°15′20.8"S, 167° 35′01.6"E	ON146075	ON146093	
	Upright	I314	18 Aug. 2021	Bluff Lighthouse, Otago, South Island	46°36′43.7"S, 168° 21′36.6"E		ON146092	
Apophlaea sinclairii	Upright	I155	8 Apr. 2021	Tapotupotu, Cape Reinga, Northland, North Island	34°26′05.4"S, 172° 42′58.4"E	ON146073	ON146084	
	Upright	I269	8 Apr. 2021	Spirits Bay, Cape Reinga, Northland, North Island	34°25′13.3"S, 172° 51′25.6"E		ON146085	
	Upright	I273	8 Apr. 2021	Henderson Bay, Northland, North Island	34°46′05.9"S, 173° 08′56.5"E		ON146086	
	Upright	I279	9 Apr. 2021	Cable Bay, Northland, North Island	34°59′26.0"S, 173° 29′13.6"E		ON146087	
	Upright	I274	9 Apr. 2021	Te Ngarere Bay, Northland, North Island	35°01′15.8"S, 173° 51′55.1"E		ON146091	

Upright	I281	9 Apr. 2021	Taupo Bay (West Bay), Northland, North Island	34°59′22.3"S, 173° 42′41.5"E		ON146089
Upright	I280	9 Apr. 2021	Cable Bay, Northland, North Island	34°59′26.0"S, 173° 29′13.6"E	ON146072	
Upright	I278	9 Apr. 2021	Cable Bay, Northland, North Island	34°59′26.0"S, 173° 29′13.6"E	ON146074	
Upright	I306	10 Apr. 2021	Tapeka, Bay of Islands, North Island	35°14′48.0"S, 174° 06′58.5"E		ON146090
Upright	I265	11 Apr. 20211	Tawharanui Peninsula, Auckland, North Island	36°22′44.0"S, 174° 49′06.6"E		ON146088

mounted on slides in glycerin. Voucher specimens of the holotype and three paratypes were deposited at the Museum of New Zealand Te Papa Tongarewa (WELT, Thiers 2022) and all unique sequences were deposited in GenBank (Table 1).

Results

*Rbc*l

The *rbc*L alignment consisted of an alignment of 1347 bp, containing both full-length and partial *rbc*L sequences with 608 variable sites when including outgroups. The ML phylogeny (Figure 1) showed that *Apophlaea* species formed a well-supported clade within a paraphyletic *Hildenbrandia*. Support for *Hildenbrandia* clades varied with this data set, but clearly some named sequences are not monophyletic (e.g. *H. rubra*). Within the *Apophlaea* clade, three supported subclades are found. One corresponded to samples from southern New Zealand matching identifications of *A. lyallii*. This clade is sister to two clades, one corresponding to samples with uprights found from the northern North Island and matching *A. sinclairii.* The other clade corresponds to wholly crustose samples from the North Island, including the Wellington region. This clade is clearly distinct from *A. sinclairii*.

rpl*36*-sec*Y spacer*

Amplification of this region, based on newly designed primers, was successful in all species of *Apophlaea*. The 1002 bp alignment, with 265 variable sites, contained 19 specimens of *Apophlaea*, and an unrooted ML tree showed three genetically distinct and well supported groupings (Figure 2). The northern upright *A. sinclairii* is 67–69 bp different from a crustose *Apophlaea* from the northern North Island (e.g. Tawharanui Peninsula) and Wellington. *Apophlaea sinclairii* has not been collected from Wellington. The southern upright *A. lyallii* is more distantly related to both northern species, indicated by 171–182 bp differences (Figure 2).

The fungal partial LSU-based ML phylogeny showed that the sequences amplified from *Apophlaea darchinoae* (from Moa point: holotype and two paratypes), were all identical, but do not group with any particular fungal group (Figure S2). The top BLAST hit was to an uncultured fungus from grasslands in Sweden (OU940498). Sequences did not group with *Mycophycias*, as *M. ascophyllii*, the genus that is supposed to contain the endophyte *M. apophlaeae* in *Apophlaea* (Figure S2).

The phylogenetic trees of the *rbc*L and the *rpl*36-*sec*Y spacer showed that the new crustose species belongs to the endemic genus *Apophlaea* and is genetically distinct from both *A. lyallii* and *A. sinclairii*, which have uprights. In addition, *A. sinclairii* and the new *Apophlaea* species can co-exist (Table 1) in several locations around the north of the Northern Island of New Zealand. We propose a new species for this crustose *Apophlaea*.

Apophlaea darchinoae *H.Webby, C.Thorn and M.Preuss, sp. nov.*

(Figure 3A–I)

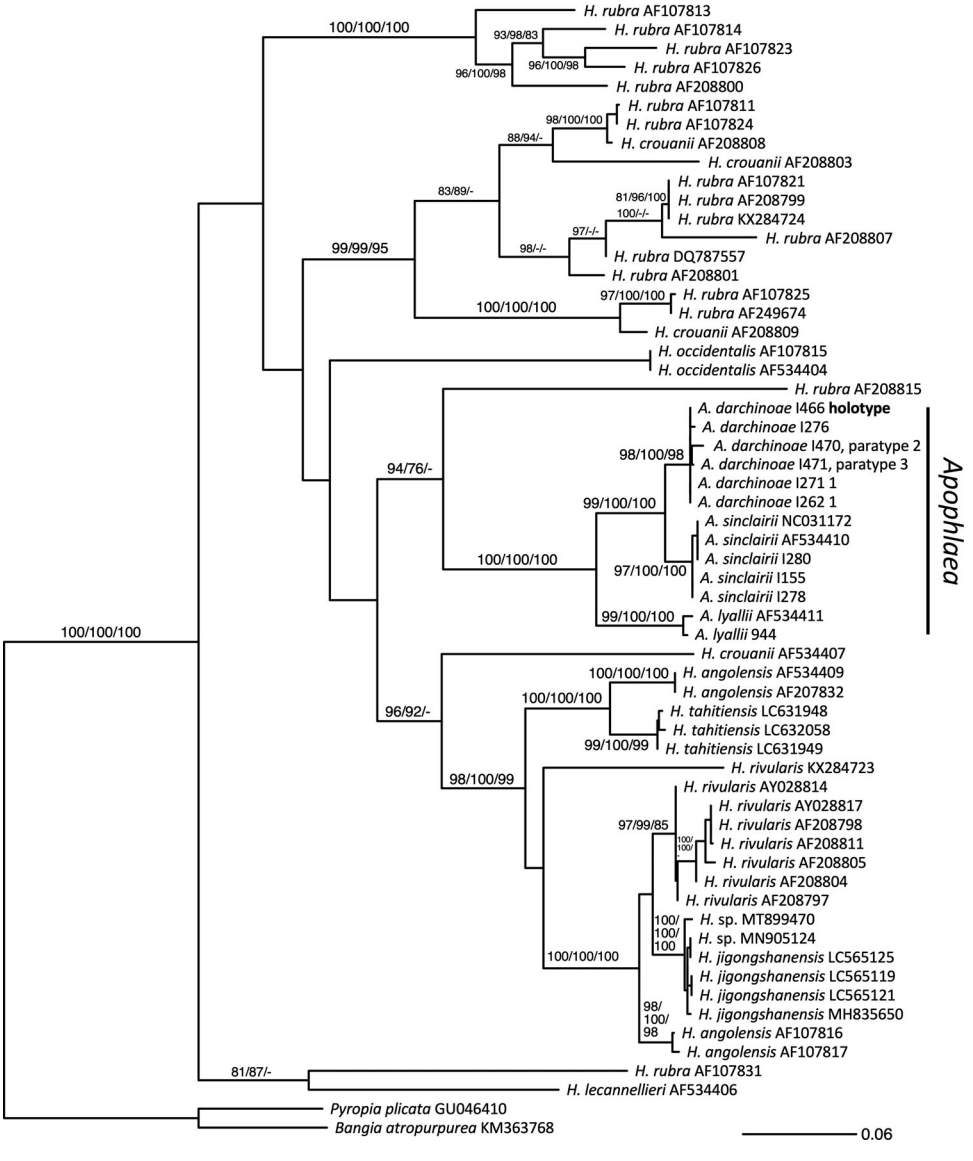

Figure 1 . ML topology of *rbc*L of *Apophlaea* and *Hildenbrandia* spp. using the best-fitting model according to BIC. Values on branches are % SH-aLRT/% nonparametric bootstrap support/% UF bootstrap support. Weakly supported branches without numbers (<80%/<70%/<95%). *Bangia atropurpurea* and *Pyropia plicata* are used as the outgroup. Collection details are given in Table 1. The holotype of *A. darchinoae* is highlighted in bold.

Diagnosis. A dark red-brown crust, 1 mm thick, in the upper intertidal zone, without uprights. Composed of irregularly branched filaments of cells (~10 μm × 2 μm), with abundant lateral fusions by secondary pit connections, especially at the base of the crusts. Conceptacles scattered over surface, oval to circular, of variable sizes (mean 200 μm × 120 μm) containing elongate tetrasporangia (mean 20 μm long × 4 μm wide), zonately, or occasionally irregularly, divided into four spores. No other

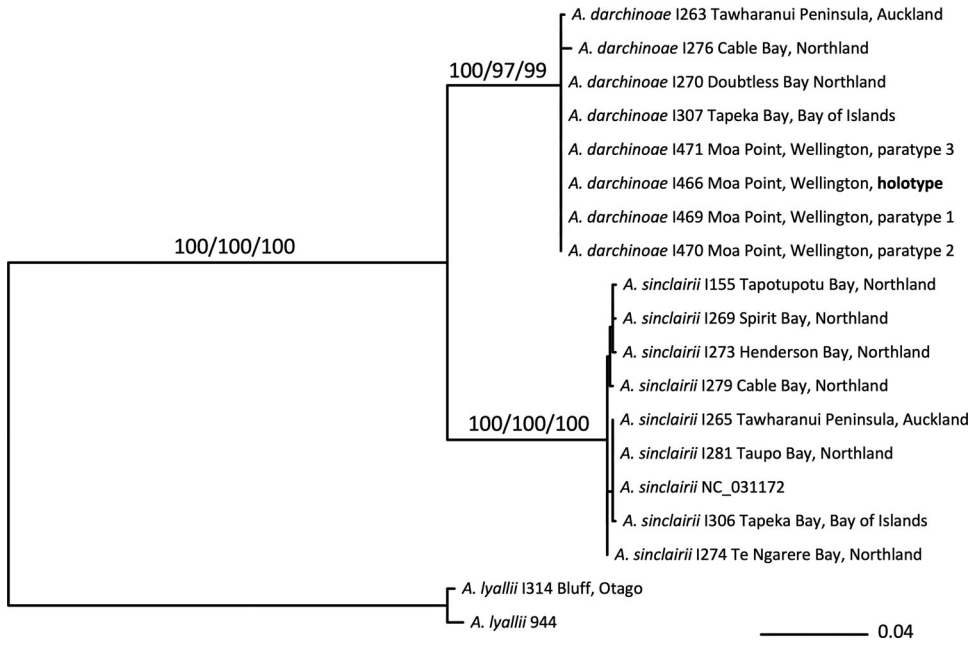

Figure 2 . Unrooted phylogenetic tree of *Apophlaea* species from New Zealand. The topology of the *rpl*36-*sec*Y spacer corresponds to the best-scoring ML tree as obtained in IQTREE. Collection details are given in Table 1. Values on branches are: % bootstrap support/% SH-aLRT/% Ultrafast bootstrap support. Weakly supported branches without numbers (<80%/<70%/<95%).

reproductive structures observed. Differs genetically from other *Apophlaea* species (*rbc*L, *rpl*36-*sec*Y spacer) and wider Hildenbrandiales (*rbc*L).

Holotype. WELT A034487.

Type locality. Moa Point, Wellington, New Zealand, 41°20'32.6.0"S, 174°48'33.4"E; collected 3 December 2021.

GenBank. *rbc*L: ON146066; rps36-SecY spacer: ON146081

Paratypes. (1) WELT A034488, Moa Point, Wellington, New Zealand, collected 3 December 2021. (2) WELT A034489, Moa Point, Wellington, New Zealand, collected 3 December 2021. (3) WELT A034490, Moa Point, Wellington, New Zealand, collected 3 December 2021.

Habitat. Grows on rocks in the high intertidal zone.

Distribution. From Northland to Wellington on the North Island, New Zealand.

Etymology. Named in honour of Dr Roberta D'Archino, in recognition of her significant contributions to the marine algal flora of New Zealand.

Description.

Thallus forms an epilithic crust, tar-like in appearance, black in colour when dry, and dark red-brown when wet (Figure 3A). Texture is tough and rubbery when wet, but smooth and rigid when dry. Crust shape is variable, but mostly circular, and approximately 1 mm thick (Figure 3B). Cells are often elongate, up to 10 µm long and 2 µm wide and in irregularly branching filaments with abundant lateral connections between filaments, especially towards the base of the crust (Figure 3C). The surface of the crust is pitted with sunken reproductive conceptacles of varying sizes, averaging

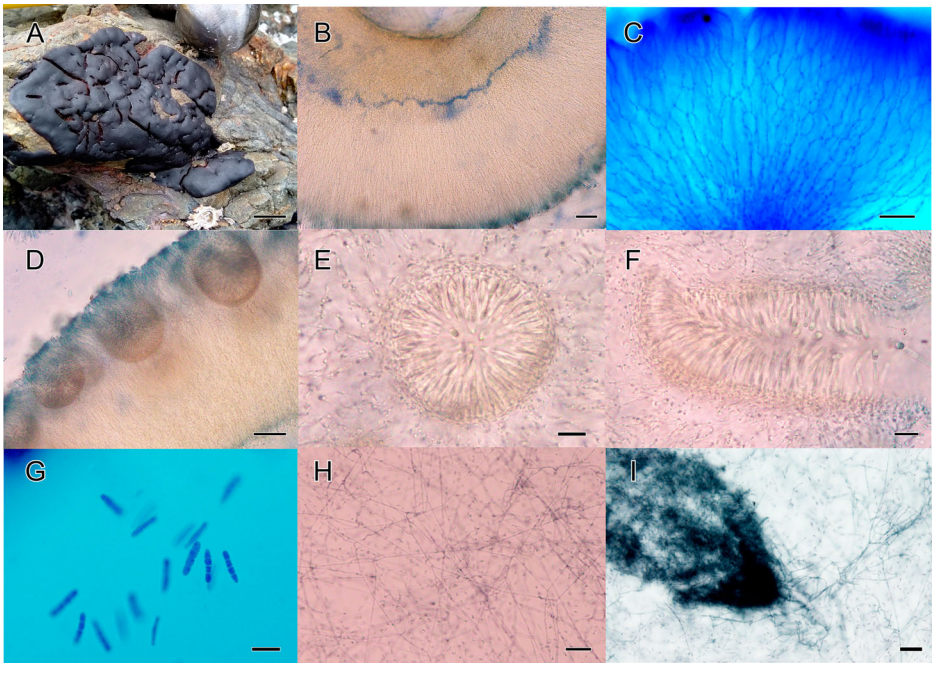

Figure 3 . Morphology of *Apophlaea darchinoae* sp. nov. **A,** Habitat of holotype from Moa Point, Wellington, attached to rock (scale bar = 1 cm). **B,** Cross section of crust (scale bar = 200 µm), base of crust is at the top. **C,** Section showing filamentous cells (scale bar = 20 µm) with lateral connections. **D,** Crust cross section showing many reproductive conceptacles open to the surface (scale bar = 100 µm). **E,** Reproductive conceptacle in transverse section (scale bar = 20 µm), visible tetrasporangia filling the cavity. **F,** Reproductive conceptacle in longitudinal section (scale bar = 20 µm). **G,** Tetrasporangia zonately divided (scale bar = 20 µm) released from conceptacle. **H,** Fungal hyphae, branched and darkly stained, using KOH/chlorazol, are found throughout the thallus (scale bar = 20 µm). **I,** Darkly staining fungal hyphae concentrated at the base of an algal conceptacle (upper left) (scale bar = 20 µm).

200 µm long × 120 µm wide (Figure 3D–F). Tetrasporangia (20 µm long × 4 µm wide) are zonately, occasionally irregularly, divided (Figure 3F) and line the interior of the conceptacles (Figure 3E, F). Gametangia unknown. Septate branched fungal hyphae are present throughout the thallus (Figure 3H), and hyphae seem to concentrate around the conceptacles (Figure 3I). Fungal reproductive structures not seen.

Discussion

Genetic evidence has shown that the crustose samples collected on the North Island warrant a new species of *Apophlaea*, for which we propose *A. darchinoae* sp. nov. This crustose species is sympatric with *A. sinclairii*, which produces uprights, in the northern North Island. *Apophlaea darchinoae* is found along the coast of the north end of the North Island of New Zealand, growing in a similar tidal range (high intertidal) as *A. sinclairii*. Although it has not been quantified, there may be local subtle ecological differentiation in the sympatric areas of these two species, as with other sympatric sister species (Muangmai et al. 2016). *Apophlaea darchinoae* lacks upright axes. Crustose

thalli found in the south of the North Island that were previously assumed to be *A. sinclairii* (but lacking distinctive uprights; Adams 1972, 1994) are likely to be *A. darchinoae*. Whether *A. sinclairii* has an extensive crustose phase before uprights are formed, or all crustose thalli in sympatric areas of northern New Zealand are *A. darchinoae*, is not known. The distribution of *A. darchinoae* around New Zealand needs further work. Whether it is found on the South Island, and even growing sympatrically with the other upright species, *A. lyalli*, needs investigation. It is known that major genetic and species disjunctions are found between the top of the South Island and the southern South Island for many seaweed species (e.g. Muangmai et al. 2015; Zuccarello and Martin 2016). It is possible that *A. darchinoae* is found on the other side of Cook Strait, i.e. northern South Island, but not on the coasts of the southern South Island.

Apophlaea darchinoae has tetrasporangia in conceptacles. It is known that in many *Hildenbrandia* species, conceptacle size is largely dependent on the age of the individual organism, and it is has been suggested that this is due to the vegetative cells lining the cell walls developing into tetrasporangia, and gradually allowing the cavity to grow through repeated rounds of reproduction and growth (Pueschel and Cole 1982). This could explain the variation seen in *A. darchinoae* conceptacle sizes. Observing only tetrasporangia in *A. darchinoae* is expected. This is a common characteristics of nearly all Hildenbrandiales. This apparent lack of a sexual cycle, if confirmed, and considering the age of this order, would indicate a potentially long-term asexual group, a controversial but not unknown phenomenon (Judson and Normark 1996; Flot et al. 2013; Hofstatter and Lahr 2019; Maciver 2019; Brandt et al. 2021).

Besides the reproductive similarity, anatomically *A. darchinoae* is also similar to other *Apophlaea* species. The thallus consists of small cells, smaller in *A. darchinoae* than *A. sinclairii* (10×2 µm versus 10×6 µm, Hawkes 1983), sparsely branched but with abundant lateral fusions (Hawkes 1983), especially in the lower parts of the thallus of *A. darchinoae*. These lateral fusions, via secondary pit connections, were thought to be produced without the aid of a conjunctor cell (Hawkes 1983) and the subsequent transfer of the conjunctor cell nucleus to the receiving cell. This process of secondary pit connection formation is thought to be found in the Hildenbrandiales (Hawkes 1983; Pueschel 1988) and common for the Corallinales (Cabioch 1971). Recent studies have shown that a conjunctor cell is involved in secondary pit connection formation in Corallinales, and could also be involved in fusions between cells in the Hildenbrandiales (Pueschel 2021). Further study is needed to determine the mode of secondary pit connection formation in *Apophlaea*.

Fungal hyphae were extensive throughout the thalli of *A. darchinoae*, and have been noted in the other two species of *Apophlaea*, *A. lyalli* and *A. sinclairii*. These fungi have been identified morphologically as *Mycophycias apophlaeae* (Kohlmeyer and Demoulin 1981; Kohlmeyer and Hawkes 1983; Kohlmeyer and Volkmann-Kohlmeyer 1998). This genus name was also applied to other mycophycobionts, for example in the mycobiont of the brown alga *Ascophyllum nodosum* (L.) LeJolis, *Mycophycias ascophylli* (Cotton) Kohlmeyer and Volkmann-Kohlmeyer. Our LSU sequences, amplified from *A. darchinoae*, did not match this genus, but we were also unable to resolve the affinity of our sequences. Whether we amplified an extraneous fungus (e.g. a surface contaminant) or the mycobiont is not in the genus *Mycophycias* needs further study. Additionally, the high concentration of fungal hyphae around algal conceptacles may

indicate that fungal reproductive structures, which were not visible in our preparations, are associated with algal conceptacles. Mycosymbiotic relationships are hypothesised to provide protection from extreme environments, such as the colonisation of algae onto land (endomycorrhizae) and algae in lichen associations, and are important in desiccation tolerance (Selosse and Tacon 1998; Barrow et al. 2008). This fungal endosymbiont may allow *Apophlaea* to maintain its high intertidal habitat.

Our newly designed primer of the plastid *rps*36-*sec*Y spacer is a promising intraspecific marker for phylogeographic studies due to its high variability. Further collections around New Zealand will give insights into the population history of these species in New Zealand.

The taxonomy of the Hildenbrandiales is still not fully resolved. While it is clear that *Apophlaea* is monophyletic, its position in the order makes *Hildenbrandia* paraphyletic, a less than ideal situation. The unique morphology of *Apophlaea*, compared to the wholly crustose nature of *Hildenbrandia*, made its distinction as a separate genus appropriate. The age and genetic diversity of *Hildenbrandia* may warrant its split into several genera, as was done for *Porphyra* (Sutherland et al. 2011), or *Hildenbrandia* could be expanded to include this New Zealand genus. Only a well-sampled multigene phylogeny, augmented by careful morphological investigation, will aid in resolving this inadequate taxonomy.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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