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Durvillaea poha sp. nov. (Fucales, Phaeophyceae): a buoyant southern bull-kelp species endemic to New Zealand

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Recent molecular and morphological research has demonstrated that the southern bull-kelp genus *Durvillaea* includes multiple as-yet-unnamed phylogenetic species. One of these, which has previously been recognised as genetically, morphologically and ecologically distinct (the 'cape' lineage of *D. antarctica*, endemic to the New Zealand region), is here described, and named *Durvillaea poha* sp. nov. Additional molecular analyses (28S sequence data) support the distinct status of this divergent lineage. No evidence of hybridisation among sympatric *D. poha* and *D. antarctica* has been observed.

Key Words: 28S, Phaeophyceae, Morphological plasticity, Environment, Taxonomy, New species

INTRODUCTION

Molecular analyses are revolutionising macroalgal systematics. Increasingly, genetic data are demonstrating that traditional morphological criteria do not always accurately diagnose phylogenetic species, sometimes showing that what had previously been considered separate species are simply morphological variants (as in the case of the now monospecific genus *Macrocystis* C. Agardh: Coyer *et al.* 2001; Demes *et al.* 2009; Macaya & Zuccarello 2010). Conversely, in some instances DNA evidence has revealed cryptic macroalgal species differences that were previously masked by morphological plasticity (e.g. *Pelagophycus* Areschoug: Miller *et al.* 2000, *Eisenia* Areschoug: Roberson & Coyer 2004). As a case in point, recent broadscale phylogeographic analyses of southern bull-kelp (*Durvillaea* Bory de Saint-Vincent; Fucales, Phaeophyceae) have revealed five genetically divergent lineages within what has been known as *Durvillaea antarctica* (Chamisso) Hariot (Fraser *et al.* 2009b, 2010). Whereas four of these phylogenetic lineages are apparently allopatric relative to one another and have yet to be correlated with morphological or life history characters, the fifth is clearly morphologically distinct and occurs in sympatry with three of the aforementioned lineages (see Fig. 1) (Fraser *et al.* 2009a, 2010). This distinct New Zealand lineage has previously been referred to as the 'cape' lineage or morphotype of *D. antarctica* (South & Hay 1979; Hay 1994; Fraser *et al.* 2009a, 2010), so called because of the wide blades' superficial resemblance to the garment (South & Hay 1979).

Although South and Hay (1979) noted morphological differences within *D. antarctica* in New Zealand, they assumed that the distinctive cape morphotype was simply an ecophenotypic variant correlated with wave-sheltered habitat. Genetic and morphological analyses of populations of *D. antarctica* from southeastern New Zealand (Fraser *et al.* 2009a) subsequently revealed that cape *D. antarctica* is genetically distinct from the more widespread and streamlined 'thonged' morphotype of *D. antarctica*. Fraser *et al.* (2009a) were not, however, in a position to describe a new species, as they had no material from the type locality and could therefore not confirm which, if any, of the New Zealand lineages should retain the species name *antarctica*. No holotype of *D. antarctica* exists, and although the original drawing of *Fucus antarcticus* by von Chamisso (1822) was designated lectotype by Hay (1979), such a type cannot, naturally, yield genetic information, so for molecular analyses it is most appropriate to consider samples from the type locality (Cape Horn) as representing *D. antarctica*. A subsequent phylogeographic analysis of the genus *Durvillaea* confirmed that the cape lineage is endemic to New Zealand's South Island, Stewart Island, the Snares Islands, and the Auckland Islands (Fraser *et al.* 2010), a range that clearly does not include the South American type locality. Genetic analysis of samples from the type locality furthermore revealed that the name *D. antarctica* must belong to – or at least include – the 'subantarctic' lineage (Fraser *et al.* 2010). We can now, therefore, consider the cape lineage as a species distinct from *D. antarctica*, and deserving of an individual name. We here provide additional nuclear genetic data supporting the reproductive isolation of the cape lineage, and a description for this newly recognised species, which we name *Durvillaea poha*. Future work should assess the taxonomic status of the remaining *D. antarctica* lineages.

MATERIAL AND METHODS

Previously published genetic data from throughout the range of *D. antarctica* (Fraser *et al.* 2009a, b, 2010), and

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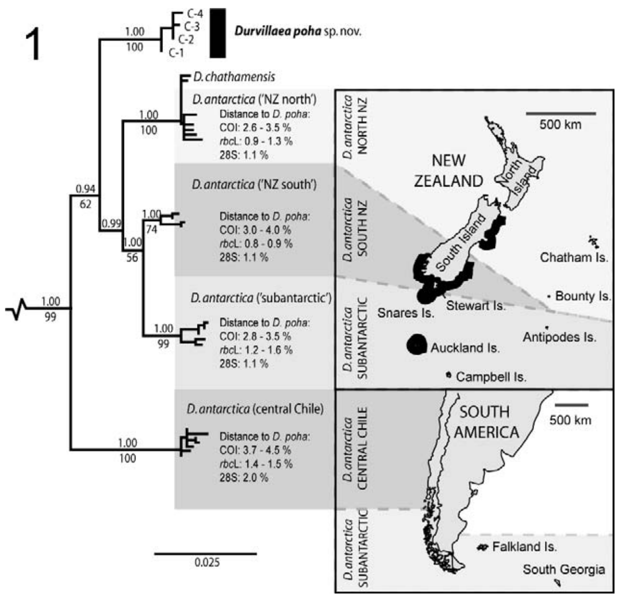

Fig. 1. Distribution of *D. poha* sp. nov. in relation to the distributions of lineages of *D. antarctica*. The maximum likelihood phylogenetic tree is based on concatenated sequence data (COI, *rbc*L, 18S and 28S) as analysed in Fraser *et al.* (2010); Bayesian posterior probabilities are shown above the branch, and bootstrap values (from 1000 bootstraps) are below the branch. COI haplotype names have been placed on the branches of the *D. poha* clade. The scale bar indicates the number of expected substitutions per site. The uncorrected p distance between *D. poha* and each *D. antarctica* lineage is indicated for each marker (excluding 18S).

morphological data from samples along the southeastern coast of New Zealand (Fraser *et al.* 2009a) provide support for the erection of a new species, as discussed in Fraser *et al.* (2010). Although detailed morphological measurements were undertaken only for samples along the southeastern coast of New Zealand (see Fraser *et al.* 2009a), samples across a broader region were also readily categorised as cape or thonged on the basis of visual morphological assessment in the field; these field-based assignments were strongly supported by subsequent genetic analyses.

In the molecular phylogeny of *Durvillaea* in Fraser *et al.* (2010), the nuclear large-subunit rRNA marker 28S (LSU) was used to test for nuclear genetic differentiation between lineages divergent at mitochondrial and chloroplast markers. Whereas the study of Fraser *et al.* (2010) included 28S sequences from only three *D. poha* individuals, we have now sequenced 22 and 20 sympatric individuals of *D. poha* and *D. antarctica*, respectively, encompassing specimens from four of the sites examined in the morphological study of Fraser *et al.* (2009a). DNA extraction, amplification and sequencing was carried out as described in Fraser *et al.* (2010). Each of the individuals sequenced for 28S had previously been sequenced for mitochondrial and chloroplast marker(s) – all but one for COI, and all but two for *rbc*L. Sequencing was carried out on individuals displaying a range of morphological and habitat characteristics (including specimens that were occasionally difficult to classify by eye, growing in proximity to the alternate lineage and exhibiting somewhat 'intermediate' morphotypes: e.g. see Fig. 2).

Fig. 2. Representatives of each of *D. antarctica* (left, with blade cross-section below) and *D. poha* (right, with blade cross-section below) from an intermediately exposed rock platform at Brighton Beach, southeastern New Zealand. In such environments, where both species occur, each can superficially resemble the other (long, thin, straplike fronds, and relatively long, slender stipes) but differences are nonetheless evident, for example in the cross-sections of blades and colour. Black scale bar represents 30 cm; white scale bars represent 3 cm. These two specimens were growing approximately 20 cm apart on the rock platform.

RESULTS

Only two unique 28S sequences, separated by five substitutions, were detected, with one restricted to *D. poha* (GenBank accession HQ386062) and the other to *D. antarctica* (GenBank accession HQ386063), completely consistent with mitochondrial and chloroplast data (Table 1). Mitochondrial (COI) diversity in *D. poha* was relatively low compared with clades within *D. antarctica*, with only four haplotypes detected, one of which (C-1) is widely distributed and dominates most populations sampled (Fig. 3). A unique COI haplotype was detected in all samples from the Snares Islands.

Durvillaea poha sp. nov.

Plantae perennes, usque ad 5–10 (12) m longae; inflatae, favosae, lamina ubi fluitans variabiliter divisa. Stipes solitarius aurantiaco-flavus, interdum divisus in ramis pluribus, saepe non contractus sectione transversa concava. Hapteron densum, discoideum, plerumque animalibus invertebratis defodientibus excavatum. Haptera plerumque coalescentia formare hapteron compositum stipites plures fulciens. Laminae interdum perforatae; laminae (et interdum *stipites) alga parasitica Herpodiscus durvillaeae (Lindauer) South frequenter infecti. Laminae semper complanatae haud teretes. Thalli dioica, dispersa in superficiebus ambabus laminae. Oogonia conceptaculi parieti affixa ad basim paraphysium ramosarum, ovis quattuor in quoque oogonio. Antheridia in fasciculis arctis in paraphysibus ramosis gesta. Habitat in zona interaestuali plerumque mediana. Invenitur in oris saxosis expositis in zona interaestuali mediana, plerumque in zona supra illam Durvillaeae antarcticae, et in oris minus expositis per totum zonae interaestualis.*

Plants perennial, up to 5–10 (12) m long. Inflated, 'honeycombed', buoyant lamina variably divided. Solitary orange-yellow stipe, sometimes divided distally into several boughs, often nontapering with a concave cross-section (Fig. 4). Holdfast dense, discoid, usually excavated by burrowing invertebrates. Holdfasts commonly coalescing to form a composite holdfast supporting several stipes. Blades occasionally perforated. Blades (and occasionally stipes) frequently infected with the parastitic alga *Herpodiscus durvillaeae* (Lindauer) South. Blades always flattened, never terete (cylindrical in cross-section). Thalli dioeceous, scattered on both surfaces of the lamina. Oogonia attached to the conceptacle wall at the base of branched paraphyses; four ova per oogonium. Antheridia in tight clusters on branched paraphyses. Habitat intertidal, commonly at mid-tide level. Found on exposed rocky coasts at mid-tide level, usually in a band above *D. antarctica*, and on semisheltered coasts throughout the intertidal zone.

ETYMOLOGY: The specific name is the Maori word for storage bags made from this species of bull-kelp for preserving titi (muttonbirds; *Puffinus griseus*) and other foodstuffs.

TYPE LOCALITY: Brighton Beach, southeastern New Zealand (45°56′53.25″S, 170°20′10.59″E).

TYPE SPECIMENS:

HOLOTYPE: Fig. 5; WELT A030888 (specimen pressed on a single large sheet at the Museum of New Zealand Te Papa Tongarewa); GenBank accession of COI sequence: JF906751. Collected: Brighton Beach, southeastern New Zealand (45°56′53.25″S, 170°20′10.59″E), 28 February 2011. Collector: Ceridwen Fraser.

ISOTYPE: WELT A030889 (over 10 sheets, as A-J, plus holdfast as K, at the Museum of New Zealand Te Papa Tongarewa); GenBank accession of COI sequence: JF906752. Collected: Brighton Beach, southeastern New Zealand (45°56′53.25″S, 170°20′10.59″E), 2 March 2011. Collector: Ceridwen Fraser.

PARATYPE: OTA 61681 (University of Otago Herbarium); GenBank accession of COI sequence: JF906753. Collected: Brighton Beach, southeastern New Zealand (45°56′53.25″S, 170°20′10.59″E), 2 March 2011. Collector: Ceridwen Fraser.

Main features distinguishing *D. poha* from other *Durvillaea* species: (1) *Durvillaea potatorum*: no stipitate lateral blades arising from either lamina margins or from the primary stipe; mature laminae inflated (honeycombed tissue); internally excavated holdfasts; grows at a higher level on the shore. (2) *Durvillaea antarctica* (all four lineages): blades broad and always flattened, never terete (cylindrical in cross-section); paler and more orange in colour; relatively wave-sheltered habitat. (3) *Durvillaea willana*: no stipitate lateral blades arising from either lamina margins or from the primary stipe; mature laminae inflated (honeycombed tissue); internally excavated holdfasts; grows intertidally. (4) *Durvillaea chathamensis*: mature laminae inflated (honeycombed tissue); grows at a higher level on the shore. (5) An undescribed *Durvillaea* species from the Antipodes Islands (Hay 1994): no stipitate lateral blades arising from lamina margins; mature laminae inflated (honeycombed tissue); internally excavated holdfasts; grows intertidally.

DISTRIBUTION: Endemic to southern New Zealand. Occurs on New Zealand's South Island [southward from 42°S on the east coast, to the entrance to Doubtful Sound (45°15′S) on the west coast; possibly farther north on the west coast]. Present in the bays of Stewart Island, Port Ross in the Auckland Islands, and the Snares Islands. Absent from the range of *D. antarctica* in New Zealand's North Island, Chile, and subantarctic islands beyond the New Zealand region.

DISCUSSION

Both *D. poha* and *D. antarctica* exhibit considerable morphological plasticity, apparently associated with environmental factors, with some morphotypes appearing almost intermediate between *D. poha* and *D. antarctica*. Although such individuals can be difficult to classify in the field, the key features of blade cross-section shape (terete or flattened) and relative colour are generally extremely reliable. For example, two adjacent plants on a relatively exposed section of rocky shore may look similar in overall morphology, but *D. poha* will always be a paler, yellow-orange colour overall, with a relatively short, stout, and sometime flattened stipe, whereas *D. antarctica* will show blades that are almost completely terete toward their tips (though generally more flattened near the palmate region), often much darker in colour, and will have a relatively long, slender stipe, bright yellow at the base but darker brown distally (Fig. 2). Extreme morphotypes of each species in New Zealand are very straightforward to identify, with *D. poha* showing broad, spread-out blade morphology, short stipes and pale yellow/orange colour, and *D. antarctica* showing straplike, dark blades (see fig. 1 in Fraser *et al.* 2009a).

No evidence of hybridisation between sympatric *D. antarctica* and *D. poha* has been detected, with all individuals studied belonging consistently to one or other lineage for all [mitochondrial DNA, chloroplast DNA and nuclear DNA] markers examined. In the study of Fraser *et al.* (2009a), the only nuclear marker examined was an approximately 1200-base-pair region of 18S, which proved only marginally informative: specifically, only one transitional change was inferred between sympatric *D. poha* and *D.antarctica* in the southern New Zealand region and the subantarctic, and three differences where they co-occur in northern South Island. The additional data provided here for the nuclear marker 28S indicate consistent and unambiguous differences between *D. poha* and *D. antarctica,* with no evidence of interspecific hybridisation.

Table 1. Lineage correspondence for sequences for each marker for *Durvillaea poha* and *D. antarctica* material included in Fraser *et al.* (2009a) and this study (28S). Codes indicate unique sequences. Asterisks show 28S sequences included in Fraser *et al.* (2010) analyses (GenBank accessions HQ386062-HQ386063).

	Site/sample code	COI	*rbc*L	18S/SSU[1]	
Species	Fraser *et al.* 2009a	Fraser *et al.* 2009a	Fraser *et al.* 2009a	Fraser *et al.* 2009a	28S/LSU
D. poha	B1	COI-C-1	*rbcL*-C-1	18S-C-1	
D. poha	B2	COI-C-1	*rbcL*-C-1	18S-C-1	
D. poha	B3	COI-C-1	*rbcL*-C-1	18S-C-1	
D. poha	B4	COI-C-1	*rbcL*-C-1	18S-C-1	
D. poha	B5	COI-C-1	*rbcL*-C-1	18S-C-1	
D. poha	B6	COI-C-1	*rbcL*-C-1		
D. poha	B7	COI-C-1	*rbcL*-C-1		
D. poha	B8	COI-C-1	*rbcL*-C-1		
D. poha	B9	COI-C-1	*rbcL*-C-1		
D. poha	B10		*rbcL*-C-1	18S-C-1	
D. poha	C1	COI-C-1	*rbcL*-C-1		
D. poha	C2	COI-C-1	*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	C3	COI-C-1	*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	C4	COI-C-1	*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	C5	COI-C-1	*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	C6	COI-C-1	*rbcL*-C-1		
D. poha	C7	COI-C-1	*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	C8	COI-C-1	*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	C9	COI-C-1	*rbcL*-C-1		28S-C-1
D. poha	C10	COI-C-1	*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	C12	COI-C-1			28S-C-1
D. poha	D1	COI-C-1	*rbcL*-C-1		28S-C-1
D. poha	D2	COI-C-1	*rbcL*-C-1		28S-C-1
D. poha	D3	COI-C-1	*rbcL*-C-1		28S-C-1
D. poha	D4	COI-C-1	*rbcL*-C-1		28S-C-1
D. poha	D5	COI-C-1	*rbcL*-C-1		28S-C-1
D. poha	E1		*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	E2	COI-C-1	*rbcL*-C-1		28S-C-1
D. poha	E3	COI-C-1			28S-C-1
D. poha	E4	COI-C-1	*rbcL*-C-1		28S-C-1
D. poha	E6	COI-C-1	*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	E7	COI-C-1	*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	E9	COI-C-1	*rbcL*-C-1	18S-C-1	28S-C-1
D. poha	F1	COI-C-1	*rbcL*-C-1		
D. poha	F2	COI-C-1	*rbcL*-C-1	18S-C-1	
D. poha	F3	COI-C-1	*rbcL*-C-1		
D. poha	F4	COI-C-1	*rbcL*-C-1		
D. poha	F5	COI-C-1	*rbcL*-C-1		
D. poha	F6	COI-C-1	*rbcL*-C-1		
D. poha	F7	COI-C-1	*rbcL*-C-1		
D. poha	F8	COI-C-1	*rbcL*-C-1		
D. poha	F9	COI-C-1	*rbcL*-C-1		28S-C-1
D. poha	F10	COI-C-1	*rbcL*-C-1		
D. poha	F11	COI-C-1	*rbcL*-C-1		
D. poha	F12	COI-C-1	*rbcL*-C-1		
D. poha	F14	COI-C-1	*rbcL*-C-1	18S-C-1	
D. poha	G3	COI-C-2	*rbcL*-C-1		
D. poha	G6	COI-C-2	*rbcL*-C-1		
D. poha	G9	COI-C-1	*rbcL*-C-1		
D. poha	G10	COI-C-2	*rbcL*-C-1		
D. poha	G11	COI-C-1			
D. poha	G12	COI-C-2	*rbcL*-C-1		
D. antarctica	A1		*rbcL*-T-4	18S-T-1	
D. antarctica	A2	COI-T-5	*rbcL*-T-4	18S-T-1	
D. antarctica	A3		*rbcL*-T-4		
D. antarctica	A4	COI-T-5	*rbcL*-T-4	18S-T-1	
D. antarctica	A5		*rbcL*-T-4	18S-T-1	
D. antarctica	A6	COI-T-5	*rbcL*-T-4	18S-T-1	
D. antarctica	A7	COI-T-5	*rbcL*-T-4	18S-T-1	
D. antarctica	A8		*rbcL*-T-4	18S-T-1	
D. antarctica	A9	COI-T-5	*rbcL*-T-4		
D. antarctica	A10		*rbcL*-T-4	18S-T-1	
D. antarctica	C11	COI-T-2	*rbcL*-T-1	18S-T-2	28S-T-1
D. antarctica	C13	COI-T-2	*rbcL*-T-1	18S-T-2	28S-T-1
D. antarctica	C14	COI-T-2	*rbcL*-T-1	18S-T-2	28S-T-1
D. antarctica	C15	COI-T-2	*rbcL*-T-1	18S-T-2	28S-T-1*

Table 1. Continued

Species	Site/sample code	COI	*rbc*L	18S/SSU[1]	
	Fraser *et al.* 2009a	Fraser *et al.* 2009a	Fraser *et al.* 2009a	Fraser *et al.* 2009a	28S/LSU
D. antarctica	D6	COI-T-2	*rbcL*-T-1		28S-T-1*
D. antarctica	D7	COI-T-2	*rbcL*-T-1		28S-T-1
D. antarctica	D8	COI-T-2	*rbcL*-T-1		28S-T-1
D. antarctica	D9	COI-T-2	*rbcL*-T-1		28S-T-1
D. antarctica	D10	COI-T-2	*rbcL*-T-1		28S-T-1
D. antarctica	D11	COI-T-2	*rbcL*-T-1		28S-T-1
D. antarctica	D12	COI-T-2	*rbcL*-T-1		28S-T-1
D. antarctica	D13	COI-T-2	*rbcL*-T-1		28S-T-1
D. antarctica	E5	COI-T-4	*rbc*L-T-2	18S-T-2	28S-T-1
D. antarctica	E8	COI-T-3	*rbc*L-T-2	18S-T-2	28S-T-1
D. antarctica	E10	COI-T-4	*rbc*L-T-2		28S-T-1
D. antarctica	E11	COI-T-4	*rbc*L-T-2	18S-T-2	28S-T-1
D. antarctica	E12	COI-T-4	*rbc*L-T-2	18S-T-2	28S-T-1
D. antarctica	E13	COI-T-3	*rbc*L-T-2	18S-T-2	28S-T-1
D. antarctica	E14	COI-T-4	*rbc*L-T-2		28S-T-1
D. antarctica	E15	COI-T-3	*rbc*L-T-2		28S-T-1
D. antarctica	F13	COI-T-3	*rbcL*-T-2	18S-T-2	
D. antarctica	F15		*rbcL*-T-1		
D. antarctica	F16	COI-T-3	*rbcL*-T-2	18S-T-2	
D. antarctica	F17	COI-T-3	*rbcL*-T-1	18S-T-2	
D. antarctica	F18	COI-T-3	*rbcL*-T-2		
D. antarctica	F19	COI-T-3	*rbcL*-T-2	18S-T-2	
D. antarctica	F20		*rbcL*-T-2		
D. antarctica	G1	COI-T-3	*rbcL*-T-2		
D. antarctica	G2	COI-T-3	*rbcL*-T-2		
D. antarctica	G4	COI-T-3	*rbcL*-T-3		
D. antarctica	G5	COI-T-3	*rbcL*-T-2		
D. antarctica	G7	COI-T-3	*rbcL*-T-2		
D. antarctica	G8	COI-T-3	*rbcL*-T-2		

[1] SSU, small subunit.

The parasitic alga *H. durvillaeae* can infect both *D. antarctica* and *D. poha*, but *D. poha* appears to be most susceptible to infection, perhaps as its wide blades offer a relatively large surface area that the parasite can colonise. The broad-bladed morphology of *D. poha* may also offer some explanation as to why this buoyant taxa has such a restricted distribution compared with *D. antarctica*; its considerably less streamlined shape (Harder *et al.* 2004) may make it less able to drift long distances at sea (Fraser *et al.* 2010). Future work on this species should address such hypotheses.

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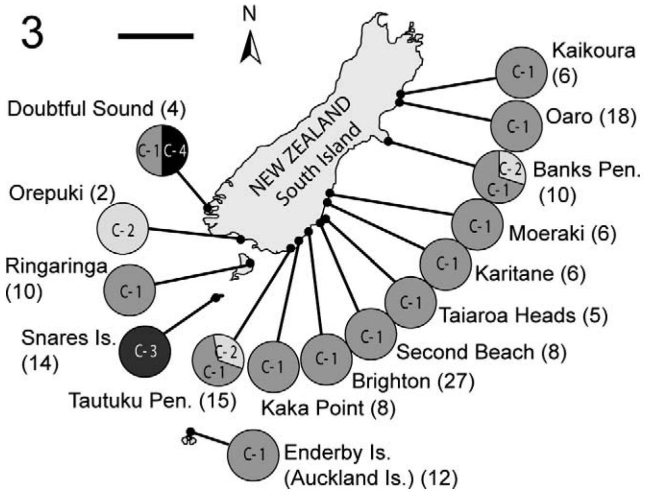

Fig. 3. Distributions and proportions of the four COI haplotypes detected for *D. poha*. The number of samples collected from each site is given in parentheses after the site name. The scale bar represents approximately 200 km. GenBank accessions: C-1: EU918566; C-2: EU918563; C-3: JN091638; C-4: JN091637.

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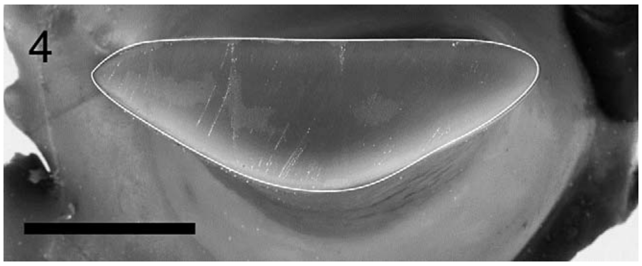

Fig. 4. Cross section of a large, stout *D. poha* stipe from Brighton Beach, 28 February 2011. The stipe circumference has been outlined in white for emphasis. The scale bar represents 3 cm. Stipes of this species are often relatively flattened and sometimes concave on one side.

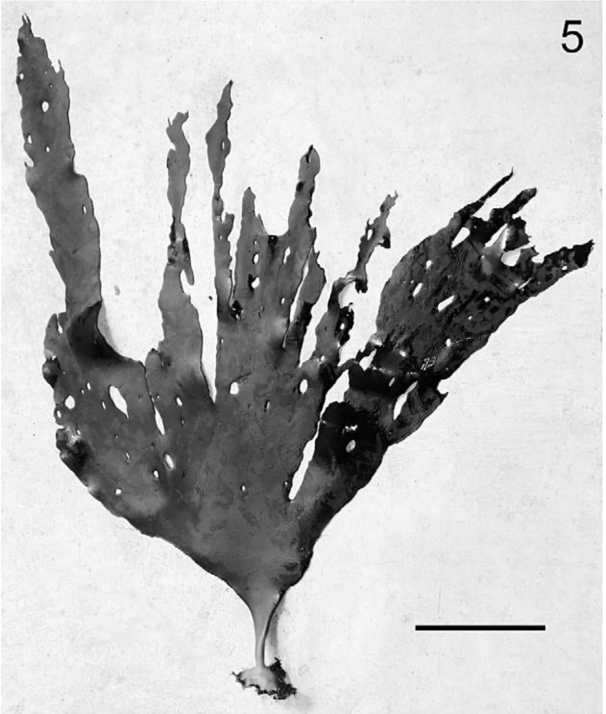

Fig. 5. Holotype of *D. poha*. Collected from Brighton Beach, southeastern New Zealand, 28 February 2011. Scale bar represents 20 cm.

material for preservation; Vickey Tomlinson (Department of Botany, University of Otago) preserved the paratype material; Ken Miller photographed the type material. This work was funded by an Allan Wilson Centre for Molecular Ecology and Evolution postdoctoral grant to CIF.

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