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Chapter 5

Cladophoropsis brachyartra from southern South America is a synonym of *Wittrockiella lyallii* (Cladophorales, Chlorophyta), previously regarded as endemic to New Zealand

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Abstract

Wittrockiella lyallii is a poorly known green macroalga that has been regarded as endemic to the south of New Zealand. A herbarium specimen from southern Chile was discovered that conforms to the description of *W. lyallii*. Subsequently, it was realised that the South American species *Cladophoropsis brachyartra* is morphologically and ecologically equivalent to *W. lyallii*. Sequences of three ribosomal genes, including the internal transcribed spacer (ITS), from material collected in Chile and New Zealand are identical, suggesting recent long-distance dispersal from New Zealand to South America. The synonymisation of *C. brachyartra* with *W. lyallii* is presented here. Furthermore, the resulting disjunct distribution of the species is discussed in the light of sea surface temperatures, habitat availability in the southern ocean and winter sea ice extent during the last glacial maximum.

Introduction

Wittrockiella lyallii (Harvey) C. Hoek, Ducker & Womersley (Cladophorales, Ulvophyceae) is a poorly known macroalga consisting of a prostrate system of filaments that form green cushions in the high intertidal, typically in marine areas subject to freshwater influx (Adams 1994, Nelson *et al.* 2002). Currently, *W. lyallii* is regarded as endemic to southern New Zealand. The knowledge of the distributions and relationships of seaweed species in the southern ocean is still relatively poor despite some recent advances (Hommersand 2007, Broom *et al.* 2010, Nelson & Broom 2010). This is especially true for members of the Cladophorales and related groups, illustrated for example by the unknown affinities of taxa such as *Lola irregularis* Zaneveld, *Rama* V.J. Chapman, *Siphonocladus voluticola* (Harvey) Børgesen and several supposedly endemic *Chaetomorpha* species, such as for example *Ch. dubyana* Kützing, *Ch. kerguelensis* Levring, or *Ch. mawsonii* Lucas, and *Cladophora* species, such as for example *C. aucklandica* Rabenhorst, *C. confusa* Hariot, *C. incompta* (Hooker f. et Harvey) Hooker f. et Harvey, *C. magellanica* Ardissone, or *C. verticillata* Hooker f. et Harvey.

In New Zealand, *W. lyallii* has been recorded from several locations in Fiordland in the southwest of the South Island (Laing 1927, Nelson *et al.* 2002), Stewart Island (Harvey 1855, Laing 1899, Chapman 1956, Adams *et al.* 1974), the Chatham Islands (Adams 1994, Nelson *et al.* 1991), and the Snares Islands (Hay *et al.* 1985), but it has not been collected from the other New Zealand subantarctic islands. In the Chatham Islands, the cold temperate-subantarctic species *W. lyallii* is part of a mixed flora consisting of both cold and warm water elements (South 1978, Nelson 1994). The species was originally described by Harvey (1855) based on material from Stewart Island as *Cladophora lyallii*, transferred to the genus *Cladophoropsis* (as *C. lyallii*) by Chapman (1956), before being placed in the genus *Wittrockiella* (van den Hoek *et al.* 1984).

Wittrockiella lyallii is distinguished morphologically from the two other species currently placed in the genus *Wittrockiella* (*W. paradoxa* Wille and *W. salina* V.J. Chapman) by the much coarser filaments and larger cell dimensions (cell diameter 200-400 µm), and its cold-temperate to subantarctic southern distribution. The range of *W. lyallii* and *W. salina* overlap on both the Chatham Islands and Stewart Island (Adams 1994). The type of the genus *Wittrockiella* is *W. paradoxa* (Wille 1909), the smallest of the three species (cell diameter < 100 µm), which is known from northwestern Europe (Polderman 1976), and from the northwestern (South 1981) and the eastern USA (Collins 1909). *Wittrockiella paradoxa* occurs in brackish habitats, as endophytes in saltmarsh plants, aerophytically on moist soil, or forming mats on soft sediments. Based on morphological similarities, it has been proposed that *W. paradoxa* might be closely related to the warm-temperate to tropical species *Cladophorella calcicola* Fritsch (van den Hoek *et al.* 1984), which is known from Australia, Bangladesh, and tropical hothouses in Europe (Fritsch 1944, Islam 1964, Cribb 1965, Ettl & Gärtner 1995, Skinner & Entwisle 2004), and typically occurs semi-terrestrially on moist limestone. The slightly bigger *W. salina* (cell diameter < 200 µm) is distributed in southern and eastern Australia, Tasmania, New Zealand, and possibly the Caribbean (Chapman 1949, van den Hoek *et al.* 1984). *Cladophorella marina* V.J.Chapman, described as an endemic species from New Zealand, is regarded as a synonym of *W. salina* (Beanland & Woelkerling 1982, Womersley 1984, Adams 1994). *Wittrockiella salina* occurs in the high intertidal, often attached on mangrove roots or forming cushions on rock in the high intertidal, but it is also known as unattached ball-shaped growth forms from one location in Australia (van den Hoek *et al*. 1984). It frequently occurs in estuarine environments with a lowered salinity (van den Hoek *et al*. 1984).

Early treatments that placed *Wittrockiella* in close proximity but outside the Cladophoraceae (Fritsch 1935), and that proposed close relationships to the genus *Aegagropila* (van den Hoek *et al*. 1984), have been confirmed by molecular studies (Hanyuda *et al*. 2002). The brackish water genus *Wittrockiella* is a member of the *Aegagropila*-lineage, an assemblage of species-poor, mainly freshwater genera such as *Aegagropila*, *Arnoldiella*, *Basicladia*, and *Pithophora* (Hanyuda *et al*. 2002, Yoshii *et al*. 2004). The placement of *W. paradoxa* and *W. lyallii* within the same genus has been shown by molecular analyses (Yoshii *et al*. 2004).

Adaptations of *Wittrockiella* to habitats with strongly fluctuating salinities include the formation of a thick mucilage cover produced by swelling of the outer cell wall layers in *W. paradoxa* (Wille 1909), an endophytic habitat in *W. paradoxa* (Polderman 1976), the presence of haematochrome/oil droplets in *W. paradoxa* and *W. salina* (Wille 1909, van den Hoek *et al*. 1984, respectively), and a cushion-like growth form to preserve moisture during exposure to air in *W. salina* and *W. lyallii*. Both *W. paradoxa* and *W. salina* can produce long septate hairs from cells in the apical parts (Wille 1909, van den Hoek *et al*. 1984), but are not always present. In addition, elongated exit tubes that ensure the release of akinetes or aplanospores to the outside of the mucilage matrix or the tissue of the host halophyte can be mistaken for hairs (C. O'Kelly - pers. comm.). In *W. lyallii*, neither hairs nor akinetes or sporangia have been observed. Very little information is available about the biology of this species, and its distribution, ecology, life history, and dispersal mechanisms are poorly known.

New Zealand has a high proportion of endemic species, *e.g.,* all native reptiles, amphibians and bats are endemic, as well as most birds and freshwater fish (Gibbs 2006), all gymnosperm trees and shrubs, and 87% of grasses (Rogers & Walker 2005). Among the benthic marine algae of New Zealand more than 40% of the species are endemic taxa, and among the Chlorophyta about 38% of the currently recognised ca. 165 species are regarded as endemic (Parsons 1985). Undoubtedly, New Zealand has a unique seaweed flora due to its long history of isolation, its position in the southern Pacific, and the range of ecological niches between the subtropical north and the subantarctic south. However, the high degree of endemism is at least partly an artifact of taxonomic inflation and reflects the lack of monographic studies across the flora. Here we present the finding of the presumed New Zealand endemic *W. lyallii* from southernmost South America, and discuss its distribution in the light of the proposed synonymy with the cold temperate-subantarctic South American species *Cladophoropsis brachyartra* (Svedelius) Wille.

Materials & Methods

A specimen from southern Chile labeled '*Cladophora Brownii*, Harv. ?' was discovered in the herbarium of the Natural History Museum London (BM) in the algal collections (voucher number BM000779086). *Cladophora brownii* Harvey is a synonym of *Aegagropila linnaei* Kützing, a temperate holarctic species, which does not occur in the southern hemisphere. In addition to the geographic location, the marine collection site and the cushion-like growth form consisting of very coarse filaments (Fig. 1) led to the suspicion that this specimen represented misidentified material of *Wittrockiella lyallii*. The specimen was collected in 1867 at Port Gallant (Brunswick Peninsula, Strait of Magellan, southern Chile) by Robert Oliver Cunningham, a naturalist onboard the HMS *Nassau* during an expedition to the Strait of Magellan 1866–69. A small part of this specimen, and herbarium material of *W. lyallii* from New Zealand (Bradshaw Sound, Fiordland, voucher WELT A023866 and Cathedral Caves, Catlins, voucher WELT A023867) for morphological comparison and imaging, were resoaked in water and brought to the boil with a drop of synthetic detergent to allow for full reconstitution of collapsed cells (van den Hoek 1963). Images were taken with a digital camera (ColorView Illu, Soft Imaging Systems) connected to a stereo-microscope (Olympus SZX10).

The suspected occurrence of *W. lyallii* in previously unknown locations in southern cold-temperate and subantarctic waters led to an extensive survey of both original publications of the main (sub)antarctic expeditions and contemporary literature in search of any possible records that could represent *W. lyallii*.

The South American species *Cladophoropsis brachyartra* (Svedelius) Wille was further investigated, and silica gel preserved material was obtained (collected 02 February 2002 by M. E. Ramírez from Isla Dring, Los Chonos archipelago, Aysén, Chile) for sequencing of nuclear ribosomal genes. The small subunit (SSU) rRNA gene, the partial large subunit (LSU) rRNA gene, and the ITS2 region were sequenced for *C. brachyartra*. For *W. lyallii*, SSU and partial LSU sequences were downloaded from GenBank, and the ITS2 region of two samples was sequenced. Collection details and GenBank accession numbers are given in Table 1. DNA extraction, PCR amplification and sequencing were performed as in Boedeker & Immers (2009), modified for the SSU and the ITS2 region as follows: the complete SSU rRNA gene was amplified using the primer pairs SR1-SS11H and SSU897-18SC2 (Leliaert *et al.* 2007a), the 540 bp containing most of the 5.8S rRNA gene and the complete ITS2 region were amplified using the primer pair ITS3-ITS4 (White *et al.* 1990) with an annealing temperature of 53°C.

Table 1. Specimens for which rDNA sequences were compared, collection data (location, collector, date of collection and voucher information) and GenBank accession numbers (newly generated sequences in bold).

Species	**Collection and voucher information**	**SSU rDNA**	**partial LSU rDNA**	**ITS2 rDNA**
Cladophoropsis brachyartra (Svedelius) Wille	high intertidal, Dring Island, Los Chonos archipelago, Aysén, Chile (M.E. Ramírez & D. M. John, 02 Feb. 2002, N61, SGO No. 158361[1])	**GU198502**	**GU198503**	**GU198504**
Wittrockiella lyallii (Harvey) C. Hoek, Ducker et Womersley	high intertidal, Rum River estuary, Bradshaw Sound, Fiordland, New Zealand (S. Heesch, 30 Sep. 2005, H67, UPN626, WELT A023866[1])	AB062717	FN257512	**GU220712**
Wittrockiella lyallii (Harvey) C. Hoek, Ducker et Womersley	high intertidal at cave entrance with mosses (freshwater runoff), Cathedral Caves, Catlins, New Zealand (S. Heesch & R. Dewdney, 25 Mar, 2006, K76, UPN1002, WELT A023867[1])	/	/	**GU936796**

[1]herbarium acronyms according to Holmgren *et al.* 1990.

Maps in Mercator-projection (Figs. 11-12) were created with the online program OMC (not available anymore). The information shown in Fig. 13 on the positions of the subantarctic front (SAF) and the subtropical convergence (STC), and the maximum winter sea ice extent during the last glacial maximum (LGM-WSI, grey area) are based on Bergstrom & Chown (1999) and Gersonde *et al.* (2005).

Results

Molecular analyses

The length of the amplified fragments was 1691 bp, 580 bp, and 516-527 bp for the SSU rRNA gene, the partial LSU rRNA gene, and the ITS2 with flanking regions, respectively. The length of the ITS2 region was 355 bp. None of the sequences contained ambiguous positions. The sequences of these three ribosomal markers of *C. brachyartra* from Chile and *W. lyallii* from New Zealand were identical in all positions (GenBank accession numbers are given in Table 1).

Morphological investigations

'*Cladophora Brownii* Harv.?' - The specimen from southern Chile (BM000779086 - Fig. 1) was identified as *W. lyallii* based on morphological agreement with the original description and all later treatments of the species. The more or less heterotrichous filaments, with cells up to 500 µm in diameter, are typically two to four times as long as broad. Branching can be sparse (Figs. 2-3) or secund (Fig. 4) or irregular, branches are typically inserted subterminally (Figs. 2 & 4). After sprouting a branch, cell wall formation is often delayed (Fig. 4). Apical cells, when not growing into a secondary rhizoid (Figs. 2 & 4), are rounded and typically slightly shorter than the rest.

Wittrockiella lyallii - Resoaked herbarium material of *W. lyallii* from New Zealand is shown in Figs. 5-6 (voucher WELT A023866). The original drawing by Harvey (1855) of the type material of *W. lyallii* (Fig. 7) does not show the most characteristic features of the species, which are clearly depicted in drawings of the type material in Hoek *et al.* (1984) (reproduced in Fig. 8). One specimen (voucher WELT A023867, Table 2) was collected in the Catlins in southeastern New Zealand, a previously unpublished location of *W. lyallii*. This specimen had the broadest cell diameter of all investigated material (up to 740 µm).

Cladophoropsis brachyartra - This species was originally described as *Siphonocladus brachyartrus* by Svedelius (1900) based on material from Puerto Angosto, Isla Desolación (Strait of Magellan, southern Chile), with the following morphological features: forming cushions, consisting of coarse, stiff, brittle filaments with a cell diameter of 200-300 µm, cells being 2-3 times as long as broad, filaments heterotrichous, without primary but with many secondary rhizoids, branch insertion subterminal with delayed cell wall formation, branching irregular or secund, filaments sterile (Fig. 9). The habitat of the type of *S. brachyartrus* is recorded as the high intertidal in a brackish bay with almost freshwater character. Fig. 10 shows *C. brachyartra* in its natural habitat, which corresponds to the habitat of *W. lyallii*.

The location of the type specimen of *S. brachyartrus* seems to be untraceable (Leliaert & Coppejans 2006), but original drawings of the type material are published in Svedelius

Table 2. Examined herbarium specimens of *Wittrockiella lyallii*, with voucher numbers[1] and collection details.

Specimens	**Vouchers**	**Country**	**Location**	**Collection information**
'*Cladophora Brownii* Harv.?'	BM000779086 (L50)	Chile	Port Gallant, Brunswick Peninsula, Strait of Magellan	R. O. Cunningham, 11 Mar. 1867
Cladophoropsis brachyartra	SGO No. 158360	Chile	Traiguén Island, Los Chonos archipelago, Aysén	unknown
Cladophoropsis brachyartra	SGO No. 158361 (N61)	Chile	high intertidal, Dring Island, Los Chonos archipelago, Aysén	M. E. Ramírez & D. M. John, 02 Feb. 2002
Cladophoropsis brachyartra	SGO No. 158362	Chile	Puerto Merino Jarpa, Katalalixar, Aysén	M. E. Ramírez, 05 Feb. 2001
Cladophora lyallii (TYPE)[2]	TCD (lectotype), BM000515828 & BM000515827 (isotypes)	New Zealand	South Island (= Stewart Island)[3]	D. Lyall, 1839-1843
Cladophoropsis lyallii	L385039, WELT A011248	New Zealand	Pryse Peak, Paterson's Inlet, Stewart Island	L. M. Jones, 28 Feb. 1935
Cladophoropsis lyallii	WELT A001053 (*Algae Novae-Zealandiae Exsiccatae* No. 253)	New Zealand	Paterson's Inlet, Stewart Island	collector unknown, February 1947
Cladophoropsis lyallii	L385043, WELT A011114)	New Zealand	Ringaringa Beach, Paterson Inlet, Stewart Island	I. B. Warnock, 01 Mar. 1935
Cladophoropsis lyallii	L385120, WELT A011107	New Zealand	Ocean Beach, Stewart Island	I. B. Warnock, 26 Feb. 1935
Cladophoropsis lyallii	L385037, WELT A011236	New Zealand	Half Moon Bay, Stewart Island	I. B. Warnock, 19 Feb. 1935
Wittrockiella lyallii	WELT A023866 (UPN626; H67)	New Zealand	high intertidal, Rum River estuary, Bradshaw Sound, Fiordland, South Island	S. Heesch, 30 Nov. 2005
Wittrockiella lyallii	WELT A013201	New Zealand	Milford Sound, Fiordland, South Island	J. Hunt & P. Anderson, 12 Jul. 1982
Wittrockiella lyallii	WELT A009968	New Zealand	Pickersgill Harbour, Dusky Sound, Fiordland, South Island	C. H. Hay, 08 Dec. 1977
Wittrockiella lyallii	WELT A023867 (UPN1002; K76)	New Zealand	high intertidal rocks (freshwater runoff), Cathedral Caves, Catlins, South Island	S. Heesch & R. Dewdney, 25 Mar. 2006
Wittrockiella lyallii	WELT A018583	New Zealand	high intertidal rocks, Point Durham, Chatham Islands	W. A. Nelson, 04 Mar. 1987
Wittrockiella lyallii	WELT A016130	New Zealand	high intertidal rocks, Boat Harbour, The Snares Islands	G. Hardy, December 1984

[1] herbarium acronyms according to Holmgren *et al.*, 1990, additional labeling of the same specimen in brackets.

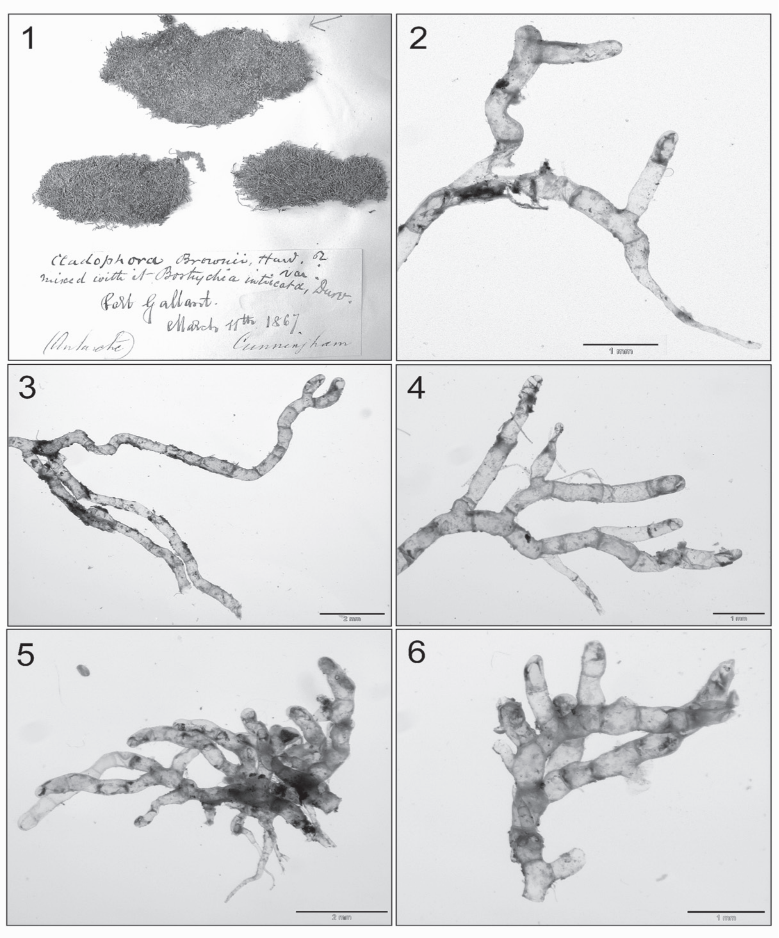
[2] The material in BM was received from TCD (in 1900) – the TCD material should be regarded as the type, the BM material as an isotype.

[3] Lyall referred to what is now known as the South Island as Middle Island.

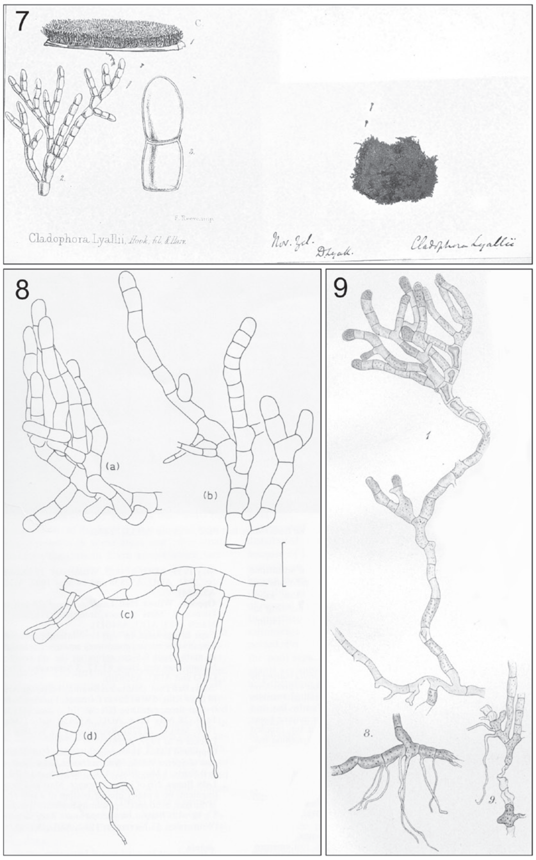
(1900) and are reproduced in Fig. 9.

Distribution of taxa

In addition to the type location, *C. brachyartra* has been reported from Reloncaví estuary, Bahía Sotomó (Puerto Montt, Chile) by Levring (1960); from Chiloé Island, western and southern Patagonia by Hylmö (1938) and Skottsberg (1941); from 'southern Chile and Patagonia' (Ramírez & Santelices 1991); from the Elefantes gulf and estuary, Laguna San Rafael National Park, Aysén (John *et al.* 2003); and from Tierra del Fuego Argentina (Borasode Zaixso 2004). In addition, specimens housed in the Museo Nacional de Historia Natural (Santiago, Chile) are from Quinchao Island (Chiloé Island), from Dring Island and from Traiguén Island (Los Chonos Archipelago, Aysén), and from Puerto Merino Jarpa (Katalalixar, Aysén) (all examined specimens are listed in Table 2). All currently known locations of *W. lyallii* (including *C. brachyartra*) are shown in Figs. 11-12.



Figs. 1-6. *Wittrockiella lyallii* from South America (Figs 1-4, voucher BM000779086) and New Zealand (Figs 5-6, voucher WELT A023866). **1** Herbarium specimen consisting of cushions of coarse filaments that were re-identified as *W. lyallii*. **2** Sparsely branched filament with a secondary rhizoid formed by the apical cell. **3** Sparsely branched filament. **4** Filament showing secund branching, subterminal insertion of branches and apical rhizoid formation. **5** Heterotrichous filament with secondary rhizoids. **6** Filament showing secund branching and rounded apical cells.



Figs. 7-9. Comparison of drawings of the type material of *Wittrockiella lyallii* (Figs 7-8) and *Cladophoropsis brachyartra* (Fig. 9). **7** Type material (isolectotype, BM 000515827) and original drawing by Harvey (1855) of *Cladophora lyallii*. **8** Drawings of the type material from Hoek *et al.* (1984), showing irregular branching, subterminal insertion of branches, rounded apical cells and secondary rhizoids. Scalebar = 1000 µm. **9** Drawings of the type material of *Siphonocladus brachyartrus* by Svedelius (1900), showing essentially the same morphological characters as in Fig. 8.

Neither *W. lyallii* nor *C. brachyartra* nor any other morphologically similar species has been mentioned in algal floras or species lists of temperate or subantarctic islands in the South Pacific (except for *W. lyallii* on the Snares Islands), such as Tasmania, the New Zealand subantarctic islands, Macquarie Island, Gough Island, Tristan da Cunha, the Juan Fernández archipelago, the Antarctic Peninsula, Kerguelen Islands, Falkland Islands, South Georgia, South Orkney Islands, South Shetland Islands, Crozet Islands, St. Paul Island, Prince Edward & Marion Islands, and Heard Island.

As a result of the molecular and morphological investigations presented here we conclude that *C. brachyartra* and *W. lyallii* are conspecific and therefore *C. brachyartra* is synonymised with *W. lyallii*.

Wittrockiella lyallii (Harvey) C. Hoek, Ducker & Womersley 1984: 45
holotype: Stewart Island, New Zealand, collector D. Lyall, TCD (isolectotypes in BM).
basionym: *Cladophora lyallii* Harvey 1855: 262
synonyms: *Siphonocladus brachyartrus* Svedelius 1900: 304, *Cladophoropsis brachyartra* (Svedelius) Wille 1910: 116, *Cladophoropsis lyallii* (Harvey) V.J. Chapman 1956: 471.

Discussion

Conspecificity of C. brachyartra *and* W. lyallii

It had already been noted earlier that the placement of *C. brachyartra* in the genus *Cladophoropsis* is not correct (Leliaert & Coppejans 2006), but no alternative affiliation had been suggested. Chapman (1956) gives a maximum filament diameter of up to 400 µm for *W. lyallii*, while filaments of *C. brachyartra* can be up to 660 µm in diameter (Hylmö 1938). However, our measurements of specimens of *W. lyallii* from New Zealand extend the range to 740 µm. Generally, morphological data of *W. lyallii* is based on few collections and the entire morphological range is unlikely to have been fully assessed. All other morphological features of specimens from New Zealand and South America are congruent, and the fact that all three sequenced ribosomal markers including the variable ITS2 are identical, lead us to conclude that these taxa are conspecific.

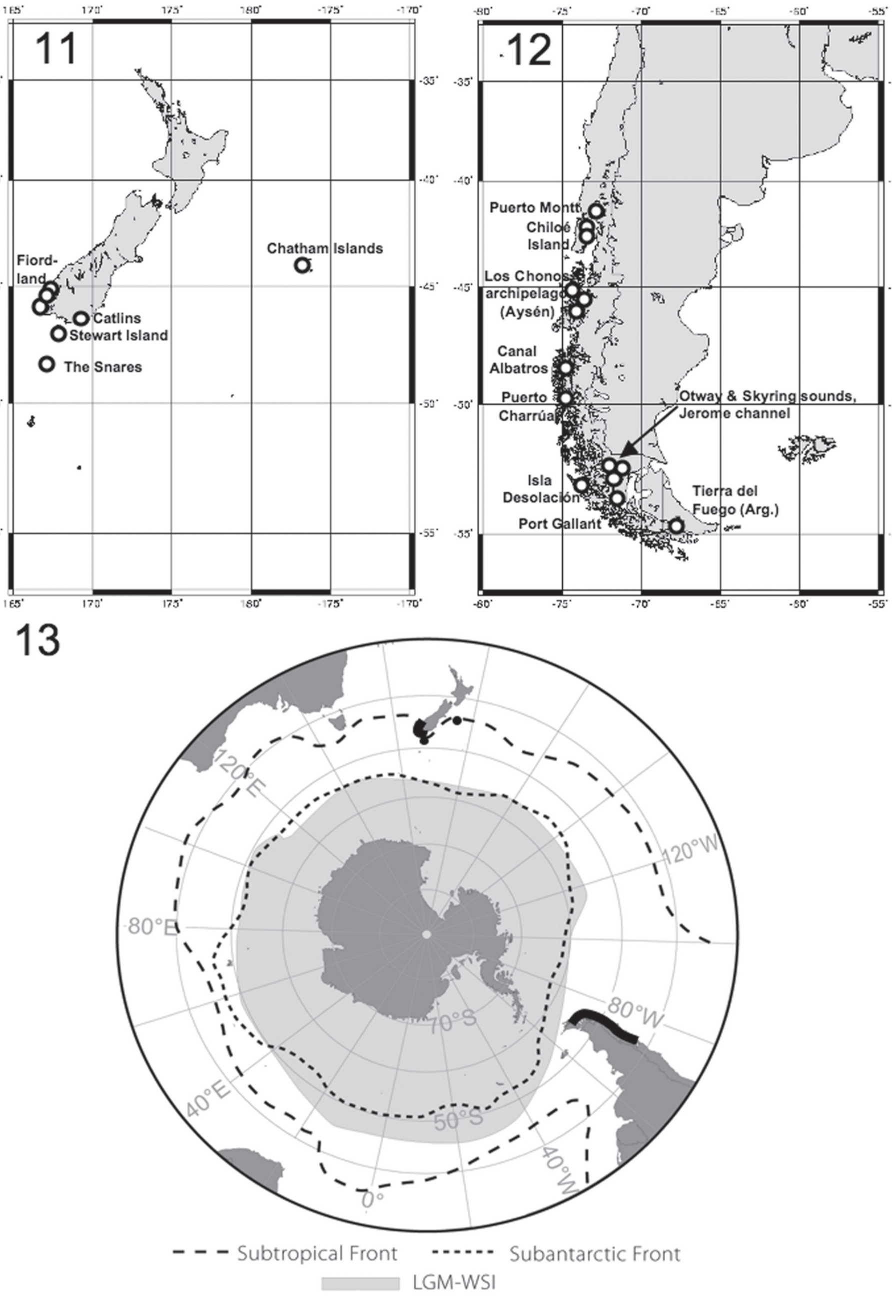
Why did Svedelius not consider the morphological similarity of these taxa when he described *S. brachyartrus* as a separate species? *Wittrockiella lyallii* was originally described as a *Cladophora* species, a possible taxonomic affinity that Svedelius (1900) only mentions briefly when discussing the generic placement of the material from Isla Desolación (Chile). Instead he saw stronger evidence in the delayed cell wall formation for inclusion in the genus *Siphonocladus* and possibly he was misled by Harvey's uninformative drawing of the type of *Cladophora lyallii* (Fig. 7).

Both *C. brachyartra* and *W. lyallii* occur in specialized habitats, typically in the intertidal in areas with freshwater seepage. Freshwater influence is explicitly mentioned for the collection sites in the Argentinian part of Tierra del Fuego (Boraso de Zaixso 2004), and most of the Chilean locations (Hylmö 1938, Skottsberg 1941, Levring 1960, John *et al.* 2003) have a reduced salinity as well (*e.g.,* Otway Sound at the river mouth, Skyring Sound, Jerome channel, Golfo and Estero Elefantes, Canal Albatross, Reloncaví estuary (Bahía Sotomó), and the Quemchi region in northeastern Chiloé Island; see Fig. 12 for locations). The situation in eastern Chiloé (Dávila *et al.* 2002) seems to be quite similar to the marine environments in the Fiordland region of New Zealand, with a low salinity surface layer more than one meter thick forming above more saline water due to intense rainfall and mountain run-off (Gibbs 2001, Nelson *et al.* 2002). In Chile, *C. brachyartra* occurs from the intertidal spray zone to rockpools in the lowermost intertidal, on beach rocks, vertical cliffs, and logs at water's edge in areas with a salinity of 25-34 psu, often in shaded locations (Skottsberg 1941, John *et al.* 2003), similar habitats to those of *W. lyallii* in New Zealand (Adams 1994).

Fig. 10. *Cladophoropsis brachyartra* (=*Wittrockiella lyallii*) in its natural habitat: a patch ca. 50 cm in diameter on vertical and shaded rocks, high intertidal, Chequián/Achao, Isla de Quinchao, Chiloé, Chile (27 January 2002).

Extended distribution of W. lyallii

The inclusion of *C. brachyartra* in *W. lyallii* extends the range of this species considerably, and results in a widely separated disjunct distribution pattern (Figs. 11-13). Populations from New Zealand and South America are separated by ca. 9000 km of Pacific Ocean. The northern distribution limits are the Chatham Islands (43°53'S, New Zealand) and Puerto Montt (41°64'S, Chile), differing only by approximately two degrees of latitude (Figs. 11-12). Records of *C. brachyartra* from northern locations (Valparaíso) of the southern Chilean coast (Etcheverry 1986) are misidentifications (M. E. Ramírez, pers. obs.). Along the coast of South America the southern distribution extends about 800 km further south than in New Zealand: *W. lyallii* does not seem to occur on the New Zealand subantarctic islands south of the Snares Islands. The locations in New Zealand are roughly situated within the sub-



Figs. 11-13. Amended distribution of *Wittrockiella lyallii* in the southern Pacific (Figs 11-12) and oceanographic features of the southern ocean (Fig. 13). **11** Map of New Zealand and its subantarctic islands with the known locations of *W. lyallii*. **12** Map of southernmost South America with the known locations of *W. lyallii* (as *Cladophoropsis brachyartra*). **13** Map of the southern ocean indicating the positions of the subantarctic front (SAF), the subtropical convergence (STC), the maximum winter sea ice extent during the last glacial maximum (LGM-WSI, grey area) (after Bergstrom & Chown 1999; Gersonde *et al.* 2005). Thick black lines and black dots show the distribution of *W. lyallii*.

tropical front (STF), whereas the South American populations are located south of the STF and north of the subantarctic front (Heath 1985, Belkin & Gordon 1996). Accordingly, southern South American populations occur at considerably lower sea surface temperatures (SSTs). Annual SSTs in New Zealand locations range from 11°C in the Snares islands to 13-14°C in Fiordland (Chown *et al*. 1998, Uddstrom & Oien 1999), while the SSTs in South America range from 13°C (Chiloé) to 7.5°C in southwestern Patagonia and Tierra del Fuego (Sepúlveda *et al*. 2009). The northern distribution limit in New Zealand and South America is similar both geographically and with regards to SSTs, and corresponds roughly to the northern edge of the west wind drift (WWD) (Strub *et al*. 1998). This major oceanic current coming from the west splits into the northward flowing Peru Chile Current and the southward flowing Cape Horn Current in the region around 41-42°S on the South American west coast, and this is a typical border in the distribution for many taxa, including seaweeds (*e.g.,* Santelices & Meneses 2000, Hernández *et al*. 2005). The high percentage of subantarctic species (ca. 35%) in the algal flora of Chile (Santelices & Marquet 1998) might be linked to the connection of subantarctic regions via the WWD. Whereas the northern distribution limit of *W. lyallii* might well be explained by SSTs, the absence from the subantarctic islands of New Zealand cannot be explained by current SSTs being too low, since the species occurs at comparable or even lower temperatures in South America.

Why does W. lyallii *not occur on subantarctic islands?*

The availability of suitable habitats is a decisive factor influencing the presence or absence of a species in a particular location or region. *W. lyallii* is restricted to shaded habitats with freshwater influence, and does not occur on very exposed rocky shores. This preference makes establishment on the exposed, rocky and largely unvegetated New Zealand subantarctic Bounty Islands and Antipodes quite unlikely (*e.g.,* Hay *et al*. 1985). Only future collection trips targeting the specific habitats will tell whether *W. lyallii* has been previously overlooked on the larger New Zealand subantarctic Auckland and Campbell Islands. These islands have a much wider range of habitats available for colonization. In particular there may be appropriate habitats in Carnley Harbour (Auckland Islands) where there is some shelter, freshwater input and overhanging vegetation.

Taking the observed annual SST range of ca. 7-13°C as a guideline (and excluding other possibly restricting factors), potentially suitable locations for *W. lyallii* in the southern ocean are the Falkland Islands, Gough Island, and the subantarctic islands of New Zealand (Chown *et al*. 1998). Amsterdam Island, St. Paul, Tristan da Cunha and the Juan Fernández Archipelago have higher annual SSTs (15-19°C) than what may be the upper limiting temperature for *W. lyallii*. South Georgia, Marion, Crozet, Kerguelen, Heard and Macquarie Islands have annual SSTs of 1.5-6°C, however, there is no indication that the lower temperature limit of *W. lyallii* was reached at 7.5°C in the very south of South America. The latter islands have been subject to extensive winter sea ice (WSI) scour though, which might prevent settlement or survival of *W. lyallii* populations in the intertidal.

The past extent of WSI plays a role in shaping the current distributions of intertidal species in the southern ocean. In a recent study on the phylogeography of the circumpolar intertidal species *Durvillaea antarctica* (Chamisso) Hariot (bullkelp), one dominant haplotype was found on all subantarctic islands that had been sampled, except on the New Zealand subantarctic islands (Fraser *et al*. 2009). The proposed explanation for a single widespread haplotype was extinction by ice scour during the last glacial maximum

(LGM) and subsequent rapid recolonisation of those islands, facilitated by the high rafting ability and the long fertility period of *D. antarctica*. The amount of floating thalli of *D. antarctica* is enormous: it has been estimated that 70 million rafts of *D. antarctica* are present in the southern ocean at any given time (Smith 2002). From the recolonisation pattern of *D. antarctica*, it was inferred that during the LGM the WSI extended further than previously estimated based on microfossil records (Gersonde *et al*. 2005). It seems probable that an intertidal species such as *W. lyallii* would have been affected by ice scour in a similar way to the hypothesized impacts on *D. antarctica*. The only offshore islands where *W. lyallii* has been found are Stewart Island, the Snares Islands and the Chatham Islands in the New Zealand region. Gough Island and the subantarctic islands of New Zealand, the Falkland Islands, and possibly Macquarie Island, were inferred to not have been affected by LGM-WSI (Fraser *et al* 2009), and thus could have functioned as refugia for *W. lyallii* (Fig. 13). However, *W. lyallii* has not been recorded from these locations (except the Snares Islands) despite considerable collection activity (Gain 1912, Cotton 1915, Taylor 1939, Skottsberg 1941, Chamberlain 1965, Hay *et al*. 1985, Ricker 1987). Stewart Island and the South Island are separated by only 30 km of water and have been repeatedly connected during glacial periods. The Snares Islands are situated only 200 km south of the South Island. The Chatham Islands are located in the STC ca. 800 km to the east of New Zealand (or rather 1400 km from the nearest extant population of *W. lyallii* on Stewart Island), but in a position favourable for migration from the mainland via the main oceanic currents (South 1978). However, these distances are much less than the ca. 9000 km between New Zealand and Chile, a voyage that would take 1-2 years traveling in the ocean current (Smith 2002, C. Law - pers. comm.). *W. lyallii* does not have any special floating ability, and would appear to be a poor disperser. Reproduction and dispersal in *W. lyallii* seem to take place only vegetatively via fragmentation of filaments. Successful establishment in a new environment after dispersal of a thallus fragment would be facilitated by subsequent spore or gamete release, but spore formation has never been observed in *W. lyallii*. A more likely long-distance dispersal mechanism for *W. lyallii* than direct transport of thallus fragments is the transport for example via floating tree logs. *W. lyallii* has been found growing on trees at the high water mark, and trees from the dense coastal forests of Fiordland or Stewart Island could have reached the ocean as a consequence of coastal erosion (see Thiel & Gutow 2004 for a review).

Long-distance dispersal vs. *vicariance*

The distribution of *W. lyallii* raises the question whether the disjunction between New Zealand and South America is explained by vicariance rather than by long-distance dispersal. In recent years, molecular data have led to a resurrection of trans-oceanic dispersal theories (*e.g.,* de Queiroz 2005, McGlone 2005), and many examples of successful long-distance dispersal have been identified (*e.g.,* Cook & Crisp 2005, Waters 2008, Fraser *et al.* 2009). Wallis & Trewick (2009) presented evidence that most of the New Zealand terrestrial flora derives from long-distance dispersal. If a Gondwanan origin and absence of long-distance dispersal are assumed for *W. lyallii*, the absence from potentially suitable subantarctic islands could be explained by the young geological age of Gough Island and the New Zealand subantarctic islands (Chown *et al.* 1998). However, the fact that ITS2 sequences of *W. lyallii* specimens from New Zealand and Chile are identical strongly implies recent dispersal from a source population. This variable marker provides good resolution at the species level in the Cladophorales (*e.g.,* Bakker *et al*. 1992, 1995, Leliaert *et al.* 2008, 2009b). Generally, ancient separations of taxa that date back to the breakup of Gondwana are reflected by high genetic divergence (*e.g.,* De Wever *et al*. 2009). Among the three species of *Wittrockiella*, the sequence divergence in the ITS2 region is ca. 20-30%, but the sequences are difficult to align (Boedeker, unpublished data). Thus, identical ITS sequences strongly indicate conspecificity of the Chilean and New Zealand populations of *W. lyallii*. Since the WWD is the dominant oceanic current in the southern ocean, the most likely dispersal direction for *W. lyallii* would have been from New Zealand to South America. The absence from subantarctic islands suggests that long-distance dispersal might be a rare event.

Future work including fieldwork targeting specific habitats in the subantarctic islands, culture experiments on the dispersal capacity and life history of *W. lyallii*, detailed phylogeographic studies of all species of *Wittrockiella*, and dated chronograms of the *Aegagropila*-lineage will shed more light on these interesting distribution patterns in the southern ocean.

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