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Fredericqia deveauniensis, gen. et sp. nov. (Phyllophoraceae, Rhodophyta), a new cryptogenic species

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Abstract – A species previously confused with *Ahnfeltiopsis devoniensis* in Ireland and with *Gymnogongrus crenulatus* in eastern Canada and north-eastern USA has remained undescribed because of its cryptogenic origin. Our published research suggested a trans-Atlantic introduction, possibly with ship ballast rock, but the relationship with *A. leptophylla* from California required further investigation and a North Pacific origin was possible. Here, we report that 34 samples of this species from Northern Ireland (UK), New Hampshire (USA) and New Brunswick (Canada) were genetically identical at the *cox*2-3 spacer locus, consistent with a recent introduction. By contrast, in *A. leptophylla*, four haplotypes were found in 9 samples from three sites in California. This species (as *G. crenulatus*) was recently discovered in the North Pacific for the first time, during surveys in British Columbia for the Canadian Barcode of Life Project. Phylogenetic analysis of plastid-encoded *rbc*L and mitochondrial *cox*1 gene sequences separate it from *A. leptophylla* in a robust clade with two North Pacific taxa, *Gymnogongrus chiton* (M.A. Howe) P.C. Silva *et* De Cew, and "*Ahnfeltiopsis gigartinoides",* both from California. It is here described as a new species in a new genus, *Fredericqia deveauniensis, gen. et sp. nov*. The two other members of the genus are *Fredericqia chiton* (M.A. Howe) *comb. nov*. and *Fredericqia decewii, sp. nov*., previously known as *Ahnfeltiopsis gigartinoides* but not conspecific with the type from Mexico. *Fredericqia* species form extensive basal holdfasts giving rise to terete or compressed erect gametophytic axes 50-300 mm high. Procarps develop either into compact cystocarps with multiple ostioles but no mucilaginous sheath, or externally protruding carpotetrasporophytes (in *F. chiton*). Life histories are potentially heteromorphic (erect gametophytes and crustose sporophytes with compact, coalescent hypobasal tissue, forming catenate sporangia, both reproduce apomictically in *F. deveauniensis*), or carpotetrasporangial. *F. deveauniensis* differs from the other members of the genus in forming internal cystocarps on flattened blades.

***Ahnfeltiopsis* / DNA barcoding / *Gymnogongrus* / introduction / molecular systematics**

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INTRODUCTION

The red algal family Phyllophoraceae Nägeli (Gigartinales), including *Mastocarpus* (formerly in the Petrocelidaceae Denizot; Fredericq & Lopez-Bautista, 2002), is characterized by multiaxial construction, compact cortex and pseudoparenchymatous or filamentous medulla, procarpy with a 1-2-celled sterile branch on the 3-celled carpogonial branch, elongate spermatangia, cruciate tetrasporangia formed singly or in catenate rows in an intercalary position in crustose thalli or in carpotetrasporophytes, and an alternation of kappa, iota or kappa-iota carrageenans in the gametophytes with lambda carrageenans in the sporophytes (Kylin, 1956; McCandless *et al*., 1982; Guiry *et al*., 1984; Maggs, 1990; Fredericq & Lopez-Bautista, 2002).

The family now includes over 110 species assigned to 14 genera (Guiry & Guiry, 2013), of which the largest are *Ahnfeltiopsis* P. C. Silva *et* DeCew and *Gymnogongrus* C. Martius with about 30 species each. *Ahnfeltiopsis* was described by Silva & DeCew (1992) for those terete or flattened species previously assigned to *Ahnfeltia* or *Gymnogongrus* that have internal cystocarps and a life history in which a crustose tetrasporophyte alternates with upright gametophytes. *Gymnogongrus* thus comprised only species with carpotetrasporophytes developing on the gametophyte, like the type species *G. griffithsiae* (Turner) C. Martius. Fredericq & Ramírez (1996) showed, however, that monophyletic genera cannot be defined by life history in the Phyllophoraceae, and several of the clades they resolved in phylogenetic analyses of the *rbc*L gene included species with internal cystocarps and those with external carpotetrasporophytes.

A species of *Ahnfeltiopsis* (as *Gymnogongrus* sp.) previously confused with *Ahnfeltiopsis devoniensis* in Ireland, and with *Gymnogongrus crenulatus* [as *G. norvegicus* (Gunnerus) J. Agardh] in eastern Canada and north-eastern USA, was studied in detail by Parsons *et al.* (1990) and Maggs *et al*. (1992). *Ahnfeltiopsis* sp. has erect, flattened female gametophytes and crustose *Erythrodermis*-like sporophytes. Nova Scotian and Irish isolates formed apomictic carpospores, tetraspores and bispores. Erect thalli developed very rarely from bispores in culture (Maggs, 1988; Maggs *et al*., 1992) but males were not found and the potential heteromorphic life history was not completed. Both sporangial crusts and female gametophytes were interpreted as diploid apomicts with c. 46 chromosomes (Maggs, 1988). In Europe, erect gametophytes of *Ahnfeltiopsis* sp. were confined to Strangford Lough, Northern Ireland, but sporophytic crusts were distributed from Roscoff, Britanny, France, to the Danish Kattegat. In the western North Atlantic, crusts and blades were observed from western Newfoundland to Massachusetts. Hybridization of labeled probes to restriction digests of partially purified plastid DNA and rubisco spacer sequences were identical for samples from both sides of the Atlantic. Maggs *et al.* (1992) therefore suggested that this species was likely to represent a transatlantic introduction, possibly with nineteenth century shipping, but the direction of movement was unknown. They also pointed out morphological and life-history similarities to the Californian species *Ahnfeltiopsis leptophylla* (J. Agardh) Silva *et* DeCew (as *Gymnogongrus leptophyllus* J. Agardh). Since then, the North Atlantic species *Ahnfeltiopsis* sp. has remained undescribed due to uncertainties about its relationship with *A. leptophylla,* and a suspicion that it might be of North Pacific origin.

Now, algal sampling along the Canadian Pacific coasts as part of the Canadian barcoding initiative has revealed the presence of *Ahnfeltiopsis* sp. (as

Gymnogongrus crenulatus) in British Columbia, suggesting either a circumboreal distribution or an introduction (Le Gall & Saunders, 2010). Comparative molecular analyses of samples from the North Atlantic and North-East Pacific using sequences of the plastid-encoded *rbc*L gene and the mitochondrial *cox*1 genes and *cox*2-3 spacer permit us to describe this new species in a clade recognized here as a new genus, which we are pleased to name in honour of Suzanne Fredericq's contributions to our knowledge of the Phyllophoraceae.

MATERIALS AND METHODS

Distributional survey and sample collection

Europe: *Ahnfeltiopsis* sp. was collected at Ballyhenry Island, Strangford Lough, Northern Ireland, at intervals from 1979 onwards by one of the authors (CAM). The site is a shallow pebble habitat with a wide range of crustose and erect algae, exposed to strong currents but sheltered from wave action. Population sampling (25 samples) of *Ahnfeltiopsis* sp. was carried out at Ballyhenry Island on 17 Sep. 2004. Samples were collected on small pebbles at 0-3 m depth by snorkeling over an area of approximately 30 × 30 m, and taking one frond from each pebble. Samples were cleaned and dried individually in silica gel. Site visits were made to other locations with suitable habitat inside Strangford Lough (Killough, Killyleagh, Jackdaw Island, Cloghy Rocks and The Dorn) and on the nearby outside coast of Co. Down (Groomsport) to establish the distribution of this species locally.

Searches for *Ahnfeltiopsis* sp. were also made by CAM in a suitable pebble habitat at Île de Callot, Roscoff, Brittany, France, near where the *Erythrodermis* phase of *Ahnfeltiopsis* sp. had previously been collected (Maggs *et al*., 1992), and where Schotter (1960) reported the presence or three or four species of *Gymnogongrus*. Various reproductive and non-reproductive *Gymnogongrus* and *Ahfeltiopsis* samples were collected and returned alive to Belfast, where they were prepared for DNA extraction.

Atlantic Canada and USA: *Ahnfeltiopsis* sp. (25 individuals) were collected from the Isle of Shoals, New Hampshire, USA on 21 Aug. 2002 by snorkelling and searching an area of approximately 50 × 50 m, collecting only one frond from each rock. At this site, the species grew on large boulders, forming extensive turfs with multiple blades. Samples were cleaned and dried individually in silica gel. Additional samples were collected by GWS in New Brunswick, Canada, and Maine, USA (20 Dec. 1999, 14 Apr. 2005, 3 Nov. 2006).

Pacific Canada and USA: As part of the Canadian Barcode of Life project, Phyllophoraceae were sampled subtidally, intertidally and from the drift along the Pacific coast of Canada in 2005 and 2007 (Le Gall & Saunders, 2010).

Samples of *Ahnfeltiopsis leptophylla* were collected at two sites in central California (Cambria and Carmel), where De Cew & West (1981) reported that this species had wide-bladed (3-4 mm) and narrow-bladed (0.5-1.5 mm) forms with different life histories. The typical narrow form (15 individuals) was collected at both sites on pebbles and bedrock in sandy gullies near low water mark, and a wide-bladed morphology was found by searching the drift at Cambria. An older sample from Jalama Beach, California, was also available.

Gymnogongrus chiton was collected from the drift at Cambria. Samples were dried in silica gel and herbarium specimens were prepared as vouchers. *G. chiton* was cultured from a collection made at Orlebar Point, Gabriola Island, British Columbia, Canada, on 5 March 1987 by P. Gabrielsen and D. Renfrew (NRCC 10660). Released tetraspores were grown in culture and chromosome counts made as previously described (Maggs, 1990; Maggs *et al.,* 1992).

DNA extraction and sequencing

Samples used for molecular analysis are listed in Table 1, along with their current names, details of collection data, vouchers and their BOLD and GenBank accession numbers for the *cox*1 marker CO1-5P, *rbc*L, LSU and *cox*2-3 spacer sequences. DNA was extracted from individual thalli using the QIAGEN DNeasy Plant Mini Kit (QIAGEN, Hilden, Germany), according to the manufacturers' instructions. In Canada samples were processed following Saunders & McDevit (2012).

***rbc*L gene**: In Belfast, the primer pair F57 5' GTAATTCCATATGCTA AAATGGG-3' and R1150 5'-GCATTTGTCCGCAGTGAATACC-3' (Hommersand *et al*., 1994) was used. PCR conditions (Perkin Elmer DNA Thermal Cycler 480; Perkin Elmer Biosystems) were 5 min at 94°C, 35 cycles of 1 min at 94°C, 1.5 min at 51°C (annealing), 2 min at 72°C, and a final extension of 5 min at 72°C. The products were purified and sequenced commercially (Macrogen, Seoul, Korea). In Canada, *rbc*L including the *rbc*L-*rbc*S spacer was amplified in three fragments covering a total of 1647 bp using the following combinations of primers: F-rbcLstart/R-753, F-577/R1381, and F-993/R-rbcS start (Freshwater & Rueness, 1994).

***cox*2-3 spacer**: The mitochondrial *cox*2-3 spacer (370 bp) was amplified in Belfast using the mitochondrial *cox*2-*cox*3 intergenic spacer primers in Zuccarello *et al.* (1999) or the following primer pair: COX2F 5'-GTACCWTCTTTDRGRRK DAAATGTGATGC-3'; COX3R 5'-GGATCTACWAGATGRAAWGGATGTC-3'. PCR was carried out on a MWG Primus thermal cycler using the following parameters: initial denaturation at 94°C for 3 min followed by 45 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s, extension at 72°C for 1 min and a final extension at 72°C for 5 min. PCR was carried out in a total volume of 20 µl containing 200 ng genomic DNA, 10 pmol of each primer, 1x PCR reaction buffer, 200 µM each dNTP, 2.5 mM $MgCl_2$ and 0.5 U GoTaq Flexi DNA polymerase (Promega). 10 µl PCR product were resolved on 1.5% agarose gels and visualised by ethidium bromide staining, and the remaining 10 µl were sequenced commercially (Macrogen).

***Cox*1**: A total of 67 *cox*1 sequences was generated for this study. For each sequence a total of 670 bp of the CO1-5P region was amplified following Saunders & Moore (2013) with the actual primer pair used for each specimens recorded with that accession on BOLD and

LSU (28S): This was amplified as three overlapping fragments using primers T01N/T20, T04/T08 and T05/T15, and the PCR primers and the internal primers T10, T16N, T19N, T22, T24, T25, T30, T33, following protocols of Harper & Saunders (2001) and Le Gall & Saunders (2010). Purification and sequencing reactions were performed by Genoscope (www.genoscope.fr, Evry, France).

Table 1. List of samples used in this study with collection details PROJ = Acronym in BOLD

Taxa	*Sample ID*	*Collectors*	*Collection Date*	*Country/Ocean*	*State/Province*	*Exact Site*	*Lat*	*Long*	*PROJ*	*CO1-5P*	*rbcL*	*cox2-3*
Outgroup												
Chondracanthus corymbiferus (Kützing) Guiry	GWS002830	G.W. Saunders	07-Jun-2005	Canada	British Columbia	Bamfield, Wizard I.	48,85800171	-125,1589966	GIPHY	1	CCU02941	
Chondracanthus exasperatus (Harvey *et* J.W.Bailey) J.R.Hughey	GWS002829	G.W. Saunders	07-Jun-2005	Canada	British Columbia	Bamfield, Wizard I.	48,85800171	-125,1589966	GIPHY	1	JN403073	
Rhodoglossum gigartinoides (Sonder) Edyvane *et* Womersley											RGU02991	
Sarcothalia crassifolia (C.Agardh) Edyvane *et* Womersley											AF146218	
Chondrus crispus Stackhouse	GWS006233	G.W. Saunders	27-Aug-2007	Canada	New Brunswick	Kouchibouguac lagoon seagrass beds	46,83480072	-64,92990112	GIPHY	1	CCU02984	
Phyllophoraceae												
Ahnfeltiopsis complicata (Kützing) P.C.Silva *et* DeCew											AF388556	
Ahnfeltiopsis concinna (J.Agardh) P.C.Silva *et* DeCew											AY135161	
Ahnfeltiopsis devoniensis (Greville) P.C.Silva *et* DeCew	LLG0510	L. Le Gall, J.M. Utge, Lucie Bittner, T. Silberfeld	27-Sep-2007	France	Brittany, Cotes d'Armor	Île de Bréhat, le moulin à marée	48,84600067	-2,997999907	FRED	1		
Ahnfeltiopsis devoniensis	LLG2909	L. Le Gall	22-Jun-2009	France	Brittany, Finistere	Roscoff	48,70510101	3,943870068	FRED	1		
Ahnfeltiopsis devoniensis	LLG2913	B. de Reviers	13-Jul-2006	France	Brittany, Finistere	Saint-Michel-de-Plouguerneau	48,73249817	-3,98939991	FRED	1		
Ahnfeltiopsis devoniensis	LLG2914	B. de Reviers	13-Jul-2006	France	Brittany, Finistere	Saint-Michel-de-Plouguerneau	48,73249817	-3,98939991	FRED	1		
Ahnfeltiopsis devoniensis	LLG2915	B. de Reviers	13-Jul-2006	France	Brittany, Finistere	Saint-Michel-de-Plouguerneau	48,73249817	-3,98939991	FRED	1		
Ahnfeltiopsis devoniensis	LLG3007	L. Le Gall, J.M. Utge, Y. Turpin	08-Dec-2009	France	Brittany, Finistere	Lampaul île Ségal	48,44110107	-4,788090229	FRED	1		
Ahnfeltiopsis devoniensis	LLG3031	Y. Gladut, A. Besnier, L. Le Gall	08-Oct-2009	France	Brittany, Finistere	Les Belvenious	48,37639999	-4,860000134	FRED	1		
Ahnfeltiopsis devoniensis		C. A. Maggs	23-mai-05	France	Brittany, Finistere	Callot, Carantec	48,691612	-3,925048			1	
Ahnfeltiopsis devoniensis	LLG1459	L. Le Gall, F. Rousseau	07-Dec-2008	France	Brittany, Ille-et-Vilaine	Les haies de la conchée, Saint-Malo	48,68830109	-2,048700094	FRED	1		
Ahnfeltiopsis devoniensis	LLG1468	L. Le Gall, F. Rousseau	07-Dec-2008	France	Brittany, Ille-et-Vilaine	Les haies de la conchée, Saint-Malo	48,68830109	-2,048700094	FRED	1		
Ahnfeltiopsis devoniensis	LLG1626	L. Le Gall, J.M. Utge, F. Rousseau	15-Jul-2008	France	Brittany, Ille-et-Vilaine	Les haies de la conchée, Saint-Malo	48,68769836	-2,049730062	FRED	1		
Ahnfeltiopsis devoniensis	LLG1694	L. Le Gall	16-Jul-2008	France	Brittany, Ille-et-Vilaine	Bizeux, Saint-Malo	48,64120102	-2,118020058	FRED	1		
Ahnfeltiopsis devoniensis	LLG1827	L. Le Gall, F. Rousseau, J.M. Utge	17-Jul-2008	France	Brittany, Ille-et-Vilaine	La Jouvente, La Rance	48,604599	-2,018160105	FRED	1		
Ahnfeltiopsis devoniensis	LLG2013	L. Le Gall, I. Rauss, B. Martin, Y. Turpin, T. Abiven, J.M. Utge	27-Aug-2008	France	Basse-Normandie, Manche	Sac à l'aviron, îles Chausey	49,12919998	-2,876110077	FRED	1		

Table 1. List of samples used in this study with collection details PROJ = Acronym in BOLD *(continued)*

Taxa	*Sample ID*	*Collectors*	*Collection Date*	*Country/Ocean*	*State/Province*	*Exact Site*	*Lat*	*Long*	*PROJ*	*CO1-5P*	*rbcL*	*cox2-3*
Ahnfeltiopsis devoniensis	LLG1913	L. Le Gall, I. Rauss, B. Martin, Y. Turpin, T. Abiven	26-Aug-2008	France	Basse-Normandie, Manche	L'Oursiere (Sound), îles Chausey	48,94829941	-2,00583005	FRED	1		
Ahnfeltiopsis flabelliformis (Harvey) Masuda											AF388571	
Ahnfeltiopsis glomerata (J.Agardh) P.C.Silva *et* DeCew											AF388552	
Ahnfeltiopsis humilis (Lindauer) J.A.Lewis *et* Womersley											AF388566	
Ahnfeltiopsis leptophylla (J.Agardh) P.C.Silva *et* DeCew	CAM1650/1-7	C.A. Maggs	23/02/06	United States	California, San Luis Obispo County	Cambria	35,535323	-121,08697			1	7
Ahnfeltiopsis leptophylla	CAM1215	M.H. Hommersand	12/05/73	United States	California	Jalama	34,5108	-120,5004				1
Ahnfeltiopsis leptophylla (wide)	CAM1652	C.A. Maggs	23/02/06	United States	California	Cambria	35,535323	-121,08697			1	1
Ahnfeltiopsis leptophylla						Pigeon Point					U21742	
Ahnfeltiopsis leptophylla	GWS004217	G.W. Saunders, B. Clarkston, D. McDevit	21-Jun-2006	Canada	British Columbia	Whiffen Spit, Sooke Harbour, Vancouver Island	48,35200119	-123,7279968	GIPHY	1	GQ338147	
Ahnfeltiopsis linearis (C.Agardh) P.C.Silva *et* DeCew	GWS003998	G.W. Saunders, B. Clarkston, D. McDevit	15-Jun-2006	Canada	British Columbia	Bamfield, Bradys Beach	48,82600021	-125,1549988	GIPHY	1	GQ338148	
Ahnfeltiopsis paradoxa (Suringar) Masuda											AF388568	
Ahnfeltiopsis polyclada (Kützing) P.C.Silva *et* DeCew											AF388558	
Ahnfeltiopsis sp.											AF388569	
Ahnfeltiopsis vermicularis (C.Agardh) P.C.Silva *et* DeCew											AF388560	
Archestenogramma profundum C.W.Schneider, Chengsupanimit *et* G.W.Saunders	BDA0368	C.W. Schneider	23-Aug-2010	Bermuda		Cathedral Rock off Castle Harbour, South Shore	32.34197	-64.65672		1	JN403075	
Besa papillaeformis Setchell	GWS009621	G.W. Saunders, B. Clarkston	20-May-2008	Canada	British Columbia	Tahsis, Island #40 on Esperenza Inlet Chart	49,8125	-126,9869995	GIPHY	1	GQ338146	
Coccotylus brodiei (Turner) Kützing	GWS003640	G.W. Saunders, L. Le Gall, D. McDevit, S. Clayden, C. Lane	25-Apr-2006	United States	Maine	End of public road, Starboard	44,60900116	-67,39700317	GIPHY	1	GQ338135	
Coccotylus hartzii (Rosenvinge) L.Le Gall *et* G.W.Saunders	GWS008787	B. Clarkston, K. Dixon, K. Roy	19-Aug-2007	Canada	Prince Edward Island	Cable Head	46,46300125	-62,60699844	GIPHY	1	GQ338136	
Coccotylus truncatus (Pallas) M.J.Wynne *et* J.N.Heine	GWS005213	G.W. Saunders, B. Clarkston, D. McDevit	19-Aug-2006	Canada	Manitoba	Out the river & right, Churchill	58,77899933	-94,15799713	GIPHY	1	GQ338134	
Erythrodermis traillii (Holmes ex Batters) Guiry *et* Garbary	GWS005655	G.W. Saunders, D. Saunders, L. Le Gall, D. McDevit	03-Dec-2006	Canada	New Brunswick	Meadow Cove exposed biodiversity site, Bay of Fundy	45,0379982	-66,89099884	GIPHY	1	GQ338133	
Fredericqia chiton (M.A. Howe) Maggs *et al.* (as *Gymnogongrus chiton*)	GWS003109	J. Mortimer	13-Sep-2005	Canada	British Columbia	Bamfield, Scotts Bay	48,83499908	-125,1460037	GIPHY	1		
Fredericqia chiton	GWS003297	R. Withall, G.W. Saunders	20-Sep-2005	Canada	British Columbia	Cape Beale, exposed front, Bamfield	48,78499985	-125,2160034	GIPHY	1		

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Taxa	*Sample ID*	*Collectors*	*Collection Date*	*Country/Ocean*	*State/Province*	*Exact Site*	*Lat*	*Long*	*PROJ*	*CO1-5P*	*rbcL*	*cox2-3*
Fredericqia chiton	GWS008624	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	15-Jun-2007	Canada	British Columbia	Point Holmes, Comox	49,68999863	-124,8700027	GIPHY	1		
Fredericqia chiton	GWS008639	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	15-Jun-2007	Canada	British Columbia	Point Holmes, Comox	49,68999863	-124,8700027	GIPHY	1		
Fredericqia chiton	GWS008640	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	15-Jun-2007	Canada	British Columbia	Point Holmes, Comox	49,68999863	-124,8700027	GIPHY	1	GQ338149	
Fredericqia chiton	GWS010904	G.W. Saunders, D. McDevit	07-Jun-2008	Canada	British Columbia	Stephenson Pt., Nanaimo	49,2132988	-123,9400024	GIPHY	1		
Fredericqia chiton	GWS014346	G.W. Saunders, K. Dixon	26-Jun-2011	Canada	British Columbia	Bamfield, Seapool Rock	48,81600189	-125,2089996	FRED	1		
Fredericqia chiton	CAM1649/2	C.A. Maggs	23-Feb-06	United States	California, San Luis Obispo County	Cambria	35,535323	-121,08697			1	1
Fredericqia chiton	GWS022093	B. Clarkston, K. Hind, S. Toews	20-May-2010	United States	California	Stillwater Cove, Pebble Beach	36,56700134	-121,9430008	FRED	1		
Fredericqia chiton	GWS022094	B. Clarkston, K. Hind, S. Toews	20-May-2010	United States	California	Stillwater Cove, Pebble Beach	36,56700134	-121,9430008	FRED	1		
Fredericqia chiton	GWS022237	B. Clarkston, K. Hind, S. Toews	21-May-2010	United States	California	McAbee Beach, Monterey	36,61500168	-121,8990021	FRED	1		
Fredericqia chiton	GWS022325	B. Clarkston, S. Toews	22-May-2010	United States	California	Lover`s Point, Pacific Grove	36,6269989	-121,9160004	FRED	1		
Fredericqia chiton	GWS022377	B. Clarkston, S. Toews	23-May-2010	United States	California	Aquarium Reef, Monterey Bay	36,61999893	-121,8990021	FRED	1		
Fredericqia chiton	GWS022383	B. Clarkston, S. Toews	23-May-2010	United States	California	Aquarium Reef, Monterey Bay	36,61999893	-121,8990021	FRED	1		
Fredericqia chiton											AY135160	
Fredericqia decewii Maggs *et al.*	GWS002712	G.W. Saunders	04-Jun-2005	Canada	British Columbia	Pachena Beach, Bamfield	48,7859993	-125,1190033	GIPHY	1		
Fredericqia decewii	GWS002891	G.W. Saunders	08-Jun-2005	Canada	British Columbia	Bamfield, Bradys Beach	48,82600021	-125,1549988	GIPHY	1		
Fredericqia decewii	GWS003222	G.W. Saunders	17-Sep-2005	Canada	British Columbia	Bamfield, Bradys Beach	48,82400131	-125,1589966	GIPHY	1		
Fredericqia decewii	GWS003415	G.W. Saunders, B. Clarkston, D. McDevit	12-Jun-2006	Canada	British Columbia	Pachena Beach, Bamfield	48,7859993	-125,1190033	FRED	1		
Fredericqia decewii	GWS003999	G.W. Saunders, B. Clarkston, D. McDevit	15-Jun-2006	Canada	British Columbia	Bamfield, Bradys Beach	48,82600021	-125,1549988	GIPHY	1		
Fredericqia decewii	GWS004003	G.W. Saunders, B. Clarkston, D. McDevit	15-Jun-2006	Canada	British Columbia	Bamfield, Bradys Beach	48,82600021	-125,1549988	FRED	1		
Fredericqia decewii	GWS008230	D. McDevit, B. Clarkston, K. Roy, H. Kucera	04-Jun-2007	Canada	British Columbia	Bamfield, Blowhole at Bradys Beach	48,82400131	-125,1620026	GIPHY	1		
Fredericqia decewii	GWS008273	D. McDevit, B. Clarkston, K. Roy, H. Kucera	05-Jun-2007	Canada	British Columbia	Pachena Beach, Bamfield	48,78620148	-125,1190033	GIPHY	1	GQ338150	
Fredericqia decewii	GWS008626	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	15-Jun-2007	Canada	British Columbia	Point Holmes, Comox	49,68999863	-124,8700027	GIPHY	1		
Fredericqia decewii	GWS020612	G.W. Saunders, K. Dixon	17-Jun-2010	Canada	British Columbia	North Beach (near Naval Station), Haida Gwaii	54,03300095	-132,0529938	FRED	1		

Table 1. List of samples used in this study with collection details PROJ = Acronym in BOLD *(continued)*

Taxa	*Sample ID*	*Collectors*	*Collection Date*	*Country/Ocean*	*State/Province*	*Exact Site*	*Lat*	*Long*	*PROJ*	*CO1-5P*	*rbcL*	*cox2-3*
Fredericqia decewii	GWS030423	G.W. Saunders, K. Dixon	06-Jun-2012	Canada	British Columbia	Raspberry Cove, Gwaii Haanas	52,16699982	-131,0839996	FRED	1		
Fredericqia decewii	GWS030460	G.W. Saunders, K. Dixon	06-Jun-2012	Canada	British Columbia	Raspberry Cove, Gwaii Haanas	52,16699982	-131,0839996	FRED	1		
Fredericqia decewii	GWS030462	G.W. Saunders, K. Dixon	06-Jun-2012	Canada	British Columbia	Raspberry Cove, Gwaii Haanas	52,16699982	-131,0839996	FRED	1		
Fredericqia decewii	GWS021202	B. Clarkston, K. Hind	14-May-2010	United States	California	Montara	37,54600143	-122,5149994	FRED	1		
Fredericqia decewii	GWS021210	B. Clarkston, K. Hind	14-May-2010	United States	California	Montara	37,54600143	-122,5149994	FRED	1		
Fredericqia decewii	GWS022323	B. Clarkston, K. Hind, S. Toews	22-May-2010	United States	California	Bird Rock, Pacific Grove	36,59199905	-121,9639969	FRED	1		
Fredericqia decewii (as *Ahnfeltiopsis gigartinoides*)											AY135159	
Fredericqia decewii (as *Ahnfeltiopsis gigartinoides*)											U21740	
Fredericqia decewii (as *Ahnfeltiopsis gigartinoides*)											U04187	
Fredericqia deveauniensis Maggs *et al.*	05-4548	S. Bard	19-Aug-2005	Canada	British Columbia	Seabreeze, Hornby Island	49,54199982	-124,6439972	GIPHY	1		
Fredericqia deveauniensis	GWS008501	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	14-Jun-2007	Canada	British Columbia	Backeddy Resort	49,75799942	-123,9380035	GIPHY	1		
Fredericqia deveauniensis	GWS008556	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	15-Jun-2007	Canada	British Columbia	Comox Marina Breakwater	49,66899872	-124,9290009	GIPHY	1		
Fredericqia deveauniensis	GWS008557	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	15-Jun-2007	Canada	British Columbia	Comox Marina Breakwater	49,66899872	-124,9290009	GIPHY	1		
Fredericqia deveauniensis	GWS008572	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	15-Jun-2007	Canada	British Columbia	Comox Marina Breakwater	49,66899872	-124,9290009	GIPHY	1		
Fredericqia deveauniensis	GWS008653	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	15-Jun-2007	Canada	British Columbia	Point Holmes, Comox	49,68999863	-124,8700027	GIPHY	1		
Fredericqia deveauniensis	GWS013693	G.W. Saunders, D. McDevit	26-Jun-2009	Canada	British Columbia	Lawn Point, Haida Gwaii	53,41600037	-131,9160004	FRED	1		
Fredericqia deveauniensis	GWS013694	G.W. Saunders, D. McDevit	26-Jun-2009	Canada	British Columbia	Lawn Point, Haida Gwaii	53,41600037	-131,9160004	FRED	1		
Fredericqia deveauniensis	GWS020804	G.W. Saunders, K. Dixon	07-Jun-2010	Canada	British Columbia	Telephone Point, Skidegate, Haida Gwaii	53,24200058	-132,0160065	FRED	1		
Fredericqia deveauniensis	GWS020899	G.W. Saunders, K. Dixon	07-Jun-2010	Canada	British Columbia	Indian Head, Skidegate, Haida Gwaii	53,2480011	-131,9839935	FRED	1		
Fredericqia deveauniensis	GWS028103	G.W. Saunders, K. Dixon	07-Jul-2011	Canada	British Columbia	Channel btw Murchison & Faraday Is., Gwaii Haanas	52,59700012	-131,4750061	FRED	1		
Fredericqia deveauniensis	GWS028104	G.W. Saunders, K. Dixon	07-Jul-2011	Canada	British Columbia	Channel btw Murchison & Faraday Is., Gwaii Haanas	52,59700012	-131,4750061	FRED	1		
Fredericqia deveauniensis	GWS000750	G.W. Saunders	20-Dec-1999	Canada	New Brunswick	Maces Bay, Lepreau, Bay of Fundy	45,10900116	-66,48200226	GIPHY	1		
Fredericqia deveauniensis	GWS003747	G.W. Saunders	27-May-2006	Canada	New Brunswick	Harrington Cove exposed biodiversity site, Grand Manan	44,625	-66,86000061	FRED	1		

Table 1. List of samples used in this study with collection details PROJ = Acronym in BOLD *(continued)*

Taxa	*Sample ID*	*Collectors*	*Collection Date*	*Country/Ocean*	*State/Province*	*Exact Site*	*Lat*	*Long*	*PROJ*	*CO1-5P*	*rbcL*	*cox2-3*
Fredericqia deveauniensis	GWS032307	G.W. Saunders	12-Sep-2012	Canada	New Brunswick	Wallace Cove Lighthouse	45,03900146	-66,80799866	FRED	1		
Fredericqia deveauniensis	GWS011714	G.W. Saunders, D. McDevit, S. Hamsher, M. Bruce	31-Jul-2008	Canada	Nova Scotia	Peggys Cove, Halifax Co.	44,49000168	-63,91699982	FRED	1		
Fredericqia deveauniensis	GWS011852	G.W. Saunders, D. McDevit	18-May-2009	Canada	Nova Scotia	Paddys Head, Halifax	44,52600098	-63,9469986	FRED	1		
Fredericqia deveauniensis	GWS011853	G.W. Saunders, D. McDevit	18-May-2009	Canada	Nova Scotia	Paddys Head, Halifax	44,52600098	-63,9469986	FRED	1		
Fredericqia deveauniensis	GWS032011	G.W. Saunders, A. Savoie	13-Aug-2012	Canada	Nova Scotia	Covey Head, Mahone Bay	44,50799942	-64,12599945	FRED	1		
Fredericqia deveauniensis	GWS032011a	G.W. Saunders, A. Savoie	13-Aug-2012	Canada	Nova Scotia	Covey Head, Mahone Bay	44,50799942	-64,12599945	FRED	1		
Fredericqia deveauniensis	GWS032018	K. Dixon, M. Bruce	13-Aug-2012	Canada	Nova Scotia	Covey Head, Mahone Bay	44,50799942	-64,12599945	FRED	1		
Fredericqia deveauniensis	GWS032021	K. Dixon, M. Bruce	13-Aug-2012	Canada	Nova Scotia	Covey Head, Mahone Bay	44,50799942	-64,12599945	FRED	1		
Fredericqia deveauniensis	GWS032022	K. Dixon, M. Bruce	13-Aug-2012	Canada	Nova Scotia	Covey Head, Mahone Bay	44,50799942	-64,12599945	FRED	1		
Fredericqia deveauniensis	GWS032022a	K. Dixon, M. Bruce	13-Aug-2012	Canada	Nova Scotia	Covey Head, Mahone Bay	44,50799942	-64,12599945	FRED	1		
Fredericqia deveauniensis	GWS032023	K. Dixon, M. Bruce	13-Aug-2012	Canada	Nova Scotia	Covey Head, Mahone Bay	44,50799942	-64,12599945	FRED	1		
Fredericqia deveauniensis	GWS032087	K. Dixon, M. Bruce	14-Aug-2012	Canada	Nova Scotia	Birchy Head, St. Margarets Bay	44,56800079	-64,03600311	FRED	1		
Fredericqia deveauniensis	GWS032088	K. Dixon, M. Bruce	14-Aug-2012	Canada	Nova Scotia	Birchy Head, St. Margarets Bay	44,56800079	-64,03600311	FRED	1		
Fredericqia deveauniensis	GWS032154	K. Dixon, M. Bruce	15-Aug-2012	Canada	Nova Scotia	Gaulman Pt.	45,35499954	-61,19400024	FRED	1		
Fredericqia deveauniensis	CAM1635/1-25	C.A. Maggs	17-sept-04	Northern Ireland	Co. Down	Ballyhenry Island, Strangford Lough	54,392536	-5,577122		1		15
Fredericqia deveauniensis	CAM186	C.A. Maggs	14/12/92	Northern Ireland	Co. Down	Ballyhenry Island, Strangford Lough	54,392536	-5,577122			AY135170	
Fredericqia deveauniensis	CAM1644	C.A. Maggs	21-80-2002	United States	New Hampshire	Isle of Shoals	42,9814	-70,6114				15
Fredericqia deveauniensis	GWS002678	G.W. Saunders	14-Apr-2005	United States	Maine	Cape Neddick, southern ME	43,16600037	-70,59200287	GIPHY	1		
Fredericqia deveauniensis	GWS005619	G.W. Saunders, D. McDevit	03-Nov-2006	United States	Maine	Cape Neddick, southern ME	43,16600037	-70,59200287	GIPHY	1		
Fredericqia deveauniensis	GWS005620	G.W. Saunders, D. McDevit	03-Nov-2006	United States	Maine	Cape Neddick, southern ME	43,16600037	-70,59200287	GIPHY	1	GQ338151	
Fredericqia deveauniensis	GWS005621	G.W. Saunders, D. McDevit	03-Nov-2006	United States	Maine	Cape Neddick, southern ME	43,16600037	-70,59200287	GIPHY	1		
Fredericqia deveauniensis	GWS018164	B. Clarkston, D. McDevit, M. Bruce, A. Savoie, C. Longtin	19-Apr-2010	United States	Maine	Two Lights, Cape Elizabeth	43,56499863	-70,1989975	FRED	1		
Fredericqia deveauniensis	GWS014764	D. McDevit, M. Bruce	13-Apr-2010	United States	Massachusetts	Folly Cove, Gloucester left side	42,68500137	-70,64099884	FRED	1		
Fredericqia deveauniensis	GWS006017	G.W. Saunders, B. Clarkston, D. McDevit	23-Apr-2007	United States	Rhode Island	Pier #5, Narragansett	41,42300034	-71,45500183	FRED	1		
Gymnogongrus crenulatus (Turner) J.Agardh	LLG1057	L. Le Gall	14-Apr-2008	France	Basse-Normandie	Huguenans, îles Chausey	48,87009811	-1,792969942	FRED	1		
Gymnogongrus crenulatus	LLG1255	L. Le Gall	26-May-2008	France	Basse-Normandie	Dielette	49,56079865	-1,864599943	FRED	1		
Gymnogongrus crenulatus	LLG1874	L. Le Gall, I. Rauss, B. Martin, Y. Turpin, T. Abiven	26-Aug-2008	France	Basse-Normandie, Manche	Le Loup (Sound), îles Chausey	48,91080093	-2	FRED	1		

Table 1. List of samples used in this study with collection details PROJ = Acronym in BOLD *(continued)*

Taxa	*Sample ID*	*Collectors*	*Collection Date*	*Country/Ocean*	*State/Province*	*Exact Site*	*Lat*	*Long*	*PROJ*	*CO1-5P*	*rbcL*	*cox2-3*
Gymnogongrus crenulatus	LLG1946	L. Le Gall, I. Rauss, B. Martin, Y. Turpin, T. Abiven, J.M. Utge	27-Aug-2008	France	Basse-Normandie, Manche	Rondes de l'Ouest, îles Chausey			FRED	1		
Gymnogongrus crenulatus	LLG2968	L. Le Gall, J.M. Utge, Y. Turpin	08-Nov-2009	France	Brittany, Finistere	Lampaul île Ségal	48,44110107	-4,788090229	FRED	1		
Gymnogongrus crenulatus	LLG2969	L. Le Gall, J.M. Utge, Y. Turpin	08-Nov-2009	France	Brittany, Finistere	Lampaul île Ségal	48,44110107	-4,788090229	FRED	1		
Gymnogongrus crenulatus	LLG2970	L. Le Gall, J.M. Utge, Y. Turpin	08-Nov-2009	France	Brittany, Finistere	Lampaul île Ségal	48,44110107	-4,788090229	FRED	1		
Gymnogongrus crenulatus	LLG3006	L. Le Gall, J.M. Utge, Y. Turpin	08-Dec-2009	France	Brittany, Finistere	Lampaul île Ségal	48,44110107	-4,788090229	FRED	1		
Gymnogongrus crenulatus	LLG3061	Y. Gladut, A. Besnier, L. Le Gall	08-Nov-2009	France	Brittany, Finistere	Beniguet	48,34500122	-4,871920109	FRED	1		
Gymnogongrus crenulatus		C.A. Maggs	23/05/05	France	Brittany, Finistere	Callot, Carantec	48,6667	-3,9167			1	
Gymnogongrus crenulatus	LLG2454	L. Le Gall, Jose Utge	19-Apr-2009	Spain	Catalonia	Platga els Castell, Palamos	41,83200073	3,088999987	FRED	1		
Gymnogongrus crenulatus	LLG2455	L. Le Gall, Jose Utge	19-Apr-2009	Spain	Catalonia	Platga els Castell, Palamos	41,83200073	3,088999987	FRED	1		
Gymnogongrus crenulatus											AY135157	
Gymnogongrus dilatatus (Turner) J.Agardh											AF388551	
Gymnogongrus griffithsiae (Turner) Martius											AY135158	
Gymnogongrus griffithsiae	LLG2005	L. Le Gall, I. Rauss, B. Martin, Y. Turpin, T. Abiven, J.M. Utge	27-Aug-2008	France	Basse-Normandie, Manche	Sac à l'aviron, îles Chausey	49,12919998	-2,876110077	FRED	1		
Gymnogongrus martinensis Setchell *et* N.L.Gardner											AY135162	
Gymnogongrus turquetii Hariot											U27019	
Gymnogongrus sp.											AF388565	
Mastocarpus alaskensis S.C.Lindstrom, J.R.Hughey *et* P.T.Martone	GWS004391	G.W. Saunders, B. Clarkston, D. McDevit	26-Jun-2006	Canada	British Columbia	Botanical Beach, Port Renfrew, Vancouver I.	48,52999878	-124,4540024	GIPHY	1	GQ338138	
Mastocarpus californianus S.C.Lindstrom, J.R.Hughey *et* P.T.Martone	GWS000073	G.W. Saunders	22-Jul-1996	United States	California	Piedras Blancas	35,66999817	-121,2910004	GIPHY	1	GQ338144	
Mastocarpus jardinii (J.Agardh) J.A.West	GWS000070	G.W. Saunders	22-Jul-1996	United States	California	Piedras Blancas	35,67039871	-121,2910004	GIPHY	1	GQ338142	
Mastocarpus pachenicus L.Le Gall *et* G.W.Saunders	GWS002844	G.W. Saunders	07-Jun-2005	Canada	British Columbia	Bamfield, Wizard I.	48,85800171	-125,1589966	GIPHY	1	GQ338145	
Mastocarpus pacificus (Kjellman) L.P.Perestenko											AY135155	
Mastocarpus papillatus (C.Agardh) Kützing											AY135154	
Mastocarpus papillatus	GWS003229	G.W. Saunders	17-Sep-2005	Canada	British Columbia	Bamfield, Bradys Beach	48,82400131	-125,1589966	GIPHY	1	GQ338139	

Table 1. List of samples used in this study with collection details PROJ = Acronym in BOLD *(continued)*

Taxa	*Sample ID*	*Collectors*	*Collection Date*	*Country/Ocean*	*State/Province*	*Exact Site*	*Lat*	*Long*	*PROJ*	*CO1-5P*	*rbcL*	*cox2-3*
Mastocarpus stellatus (Stackhouse) Guiry	GWS003669	G.W. Saunders, L. Le Gall, D. McDevit, S. Clayden, C. Lane	25-Apr-2006	United States	Maine	End of public road, Starboard	44,60900116	-67,39700317	GIPHY	1	GQ338143	
Mastocarpus vancouveriensis S.C.Lindstrom, J.R.Hughey *et* P.T.Martone	GWS004004	G.W. Saunders, B. Clarkston, D. McDevit	15-Jun-2006	Canada	British Columbia	Bamfield, Bradys Beach	48,82600021	-125,1549988	GIPHY	1	GQ338141	
Ozophora clevelandii (Farlow) I.A.Abbott											U21851	
Ozophora clevelandii	GWS022005	B. Clarkston, K. Hind, S. Toews	19-May-2010	United States	California	Santa Cruz (Four Mile)	36.966	122.123	FRED	1	1	
Ozophora lanceolata L.Le Gall *et* G.W.Saunders	GWS002905	G.W. Saunders	08-Jun-2005	Canada	British Columbia	Bamfield, Blowhole at Bradys Beach	48,82350159	-125,1610031	GIPHY	1		
Ozophora lanceolata	GWS004011	G.W. Saunders, B. Clarkston, D. McDevit	15-Jun-2006	Canada	British Columbia	Bamfield, Sparlingia Pt.`, Bradys Beach	48,82400131	-125,1589966	GIPHY		GQ338128	
Ozophora norrisii I.A.Abbott	GWS008455	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	13-Jun-2007	Canada	British Columbia	Tuwanek, near Sechelt	49,54700089	-123,7659988	GIPHY	1	GQ338129	
Petroglossum pacificum Hollenberg											AY135167	
Phyllophora ahnfeltioides Skottsberg											U22338	
Phyllophora crispa (Hudson) P.S.Dixon											U02990	
Phyllophora crispa	GWS001813	G.W. Saunders	28-Jul-2003	Northern Ireland		Co. Leitrim,Mullaghmore Head	54,45000076	-8,467000008	GIPHY	1	GQ338131	
Phyllophora heredia (Clemente) J.Agardh											AY135165	
Phyllophora pseudoceranoides (S.G.Gmelin) Newroth *et* A.R.A.Taylor	GWS003648	G.W. Saunders, L. Le Gall, D. McDevit, S. Clayden, C. Lane	25-Apr-2006	United States	Maine	End of public road, Starboard	44,60900116	-67,39700317	GIPHY	1	GQ338132	
Schottera nicaeensis (J.V.Lamouroux ex Duby) Guiry *et* Hollenberg	GWS002452	G.W. Saunders	17-Oct-2004	Australia	Victoria	Queenscliff Jetty, Port Phillip Heads	-38,26699829	144,6679993	GIPHY	1	GQ338122	
Schottera nicaeensis											U22309	
Stenogramma bamfieldiense L.Le Gall *et* G.W.Saunders	GWS008744	G.W. Saunders, B. Clarkston, D. McDevit, K. Roy	16-Jun-2007	Canada	British Columbia	Bamfield, Wizard I.	48,85800171	-125,1589966	GIPHY	1	GQ338127	
Stenogramma californicum Harvey	GWS010565	B. Clarkston, S. Toews	03-Jun-2008	Canada	British Columbia	Bamfield, Wizard I.	48,85829926	-125,1589966	GIPHY	1	GQ338125	
Stenogramma interuptum (C.Agardh) Montagne	GWS001793	G.W. Saunders	24-juil-03	Northern Ireland		Strangford Lough (stern of wreck), Portaferry	54.3833	-5.55			GQ338124	
Stenogramma phyllophoroides (J.Agardh) A.J.K.Millar	GWS001506	G.W. Saunders	28-Nov-2002	Australia	Tasmania	Arch Rock, south of Hobart	-43,29399872	147,1349945	GIPHY	1	GQ338123	
Stenogramma rhodymenioides A.B.Joly *et* Alveal	GWS003014	J. Mortimer, G.W. Saunders	13-Jun-2005	Canada	British Columbia	Bamfield, Black Fish I., near Helby I.	48,84700012	-125,1650009	GIPHY	1	GQ338126	

Alignment and phylogenetic analyses

Forward and reverse electropherograms were edited and assembled with the software Codoncode (Dedham, MA) and multiple sequence alignments were constructed for each marker using Seaview (Gouy *et al*., 2010). *cox*2-3 alignments of 370 bp were analysed using Mr Bayes version 3.1.2 (Ronquist & Huelsenbeck, 2003. For the *cox*1 datasets, genetic species groups were determined by distance analyses using the neighbor-joining algorithm in Seaview. Phylogenetic analyses were conducted on the *rbc*L alignment by Bayesian inference using MrBayes version 3.2.1 (Ronquist *et al*., 2012). ML and distance bootstrap values were calculated using Seaview. Analyses were run with four heated Monte Carlo Markov chains for 2,000,000 generations. Output trees and data were sampled every 100 generations. Appropriate burn-in for each run was determined by plotting the overall likelihood against number of generations prior to estimating the posterior probability distribution. In all analyses, likelihood values were stable after the first 200,000 generations. Final results were based on the pooled samples from the stationary phase of two independent runs.

RESULTS AND DISCUSSION

Proposal of new taxa

Analyses of *rbc*L and *cox*1 sequences showed that samples previously identified as *Gymnogongrus* sp. (later *Ahnfeltiopsis* sp.) from both sides of the Atlantic (Maggs *et al*., 1992) and *Gymnogongrus crenulatus* from the north-west Atlantic and British Columbia, north-east Pacific (Le Gall & Saunders, 2010) were conspecific. The sequences and those of two North Pacific species formed a distinct, robust clade not closely related to the type species of any recognized genera of the Phyllophoraceae. This clade corresponds to *Gymnogongrus* III in Fredericq & Ramirez (1996). *Ahnfeltiopsis* sp. is here described as a new species in a new genus, to which the two other species are transferred, as follows:

Fredericqia* Maggs, L. Le Gall, Mineur, Provan *et* G.W. Saunders, *gen. nov.

Diagnosis: Thalli multiaxial, erect gametophytic blades up to 300 mm long, terete or compressed, with compact cortex and pseudoparenchymatous medulla, monoecious or dioecious; procarpic, carpogonial branch 3-celled with one sterile cell on the basal cell; cystocarps developing as compound gonimoblasts with cells fusing to differentiated medullary cells, forming multiple carpostomes through the thickened cortex; sporophytes either crustose, *Erythrodermis*-like, with strongly cohesive cuboid cells, forming cruciate tetrasporangia in catenate rows in an intercalary position, or consisting of carpotetrasporophytes protruding externally from the gametophyte.

Type species (here designated): *Fredericqia deveauniensis,* Maggs, L. Le Gall, Mineur, Provan *et* G.W. Saunders, *sp. nov.*

Etymology: The new genus *Fredericqia* (feminine) is named in honour of Suzanne Fredericq's contributions to our understanding of the Phyllophoraceae.

Fredericqia deveauniensis, **Maggs, L. Le Gall, Mineur, Provan *et* G.W. Saunders, *sp. nov*.** **Figs 1-25**

Description: Extensive basal holdfasts up to 0.3 mm thick and 200 mm in diameter, consisting of several layers of small coalescent cells 5-11 µm in diameter, separated by horizontal discontinuities, and with an upper layer of looser vertical filaments; holdfasts giving rise to numerous erect, compressed, branched gametophytic blades 1-5 mm broad, up to 70 mm in length, with pseudoparenchymatous medulla, subcortex and 2-3-celled cortex; all gametophytes female, spermatangia unknown. Procarps consisting of large auxiliary cell and 3-celled carpogonial branch with sterile lateral cell on basal cell. Cystocarps apomictic, auxiliary cells forming secondary pit connections to neighbouring subcortical and medullary cells, developing radial protuberances that grow into gonimoblast filaments. Mature cystocarps protruding equally on either side of the blade, with multiple carpostomes through the thickened cortex. Tetrasporangial and bisporangial crusts extensive, to 300 mm, consisting of erect filaments and coalescent tissue beneath the original basal layer, forming numerous superficial sori with tetrasporangia or obliquely divided bisporangia, spore release resulting in irregular surface pits; life histories apomictic.

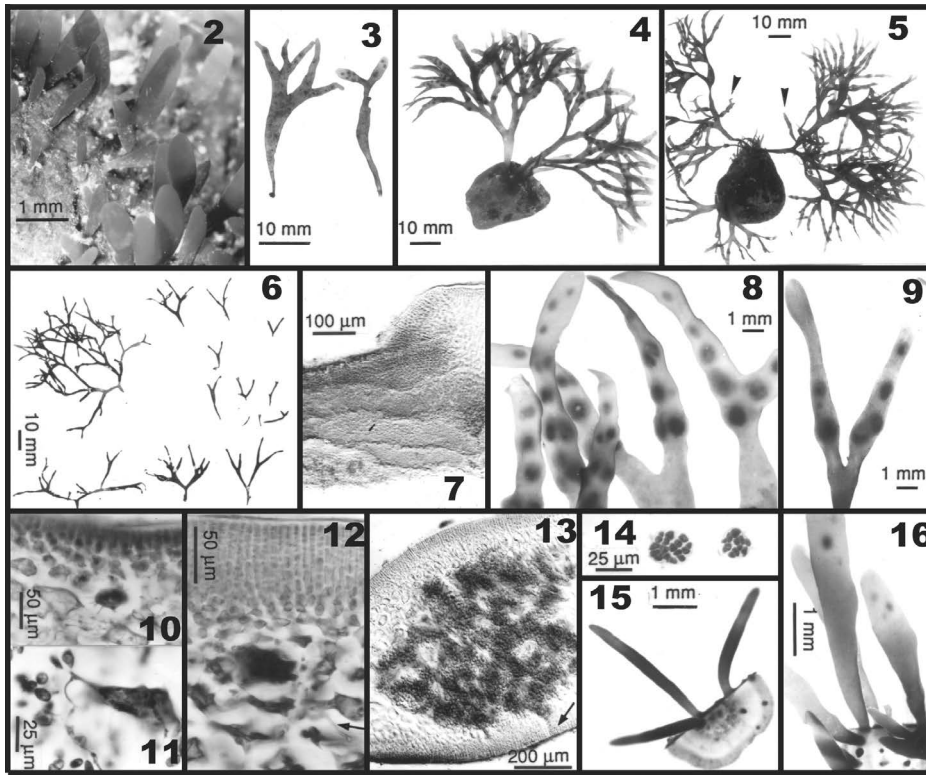
Holotype (here designated): **BM** 00103312. Ballyhenry Island, County Down, Northern Ireland (54.392536° N; 5.57712° W), 11 Nov. 1988, leg. C.A. Maggs.

Fig. 1. *Fredericqia deveauniensis* sp. nov. Holotype (**BM** 00103312) consisting of a group of erect axes taken from a single holdfast on pebble from Ballyhenry Island, Strangford Lough, County Down, Northern Ireland, 11 Nov. 1988, leg. C.A. Maggs (with its original manuscript name).

Isotypes: **PC**0144058; **UNB**.

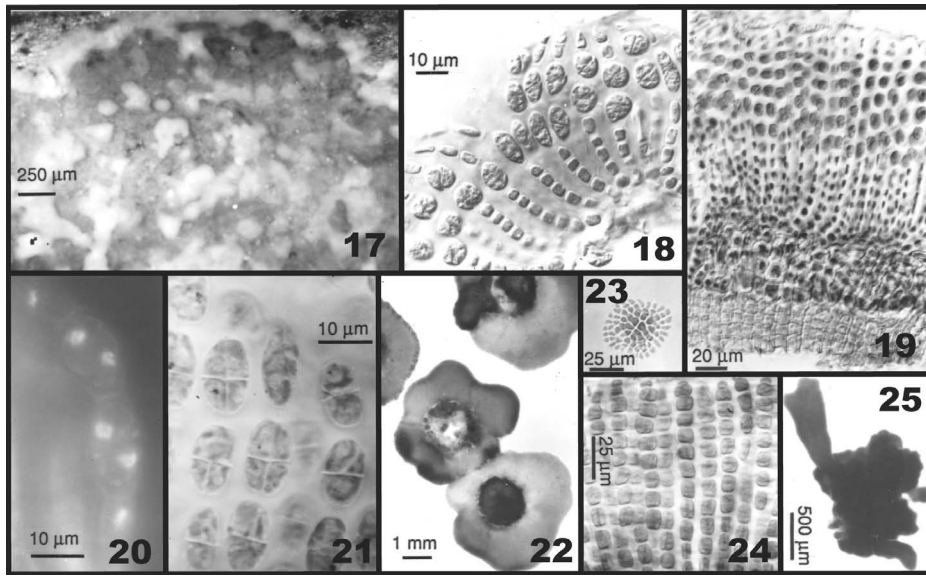
Etymology: Named after Louis Deveau, the founder of Acadian Seaplants Ltd, Nova Scotia, where this species has been in cultivation since 1988, and also referring to the original identification of specimens from Northern Ireland as *Gymnogongrus devoniensis* (Guiry *et al*., 1981).

Distribution (Fig. 26): Gametophytes are known in Europe only from Northern Ireland, on pebbles in current-exposed areas at Ballyhenry Island and Jackdaw Island in Strangford Lough and from Groomsport, Co. Down, outside Belfast



Figs 2-16. *Fredericqia deveauniensis* sp. nov. Gametophytes, field-collected from Nova Scotia (NS) and Northern Ireland (NI), and grown in culture. **2.** Numerous young blades arising from extensive holdfast, Ballyhenry Island (NI), 11 Nov. 1988. **3.** Small cystocarpic plants from Ballyhenry Island, 6 Sep. 1988. **4, 5.** Larger plants on pebbles, with dichotomous branching and proliferous branches from old axes (arrowheads), Ballyhenry Island, 11 Nov. 1988. **6.** Herbarium specimens from Pubnico Point (NS), showing range of sizes similar to Irish collections. **7.** Vertical section of holdfast showing several layers of coalescent tissue, Pubnico Point, 6 Oct. 1984. **8.** Apices with numerous irregularly oval cystocarps, Ballyhenry Island, 11 Nov. 1988. **9.** Apices with cystocarps, Northwest Cove (NS), 5 Mar. 1988. **10-12.** Cystocarp development in thallli from Ballyhenry Island, 6 Sep. 1988. **10.** Auxiliary cell with radial pit connections to medullary cells. **11.** Medullary cell contacted by gonimoblast filament bearing developing carposporangia. **12.** Auxiliary cell with developing gonimoblast filament (arrow). **13.** Transverse section of mature cystocarp, with carpostome (arrow) through thickened cortex. **14.** Carpospore germlings from Ballyhenry Island, 11 Nov. 1988, after 10 days. **15.** Carpospore culture from Northwest Cove, 27 Oct. 1986, after 4 months, with three erect axes and several peripheral initials arising from extensive holdfast. **16.** Northwest Cove culture after 6 months, with cystocarps developing on undivided fronds.

Lough (Table 1). They were not found at Roscoff, France, where *Gymnogongrus crenulatus* and *Ahnfeltiopsis devoniensis* were present, as reported by Ardré (1978). Schotter (1960) considered that there were three or four distinct species in the area, and it is possible that he found *F. deveauniensis* because fertile bisporophytes were collected near Roscoff (Guerhéon maerl bed, on pebble, 12 m depth, dredged by M.D. Guiry, 17 Sep. 1981). However, a survey of the French flora undertaken between 2007-2013 combined with a barcoding approach did not reveal the presence of this species elsewhere in Atlantic France. Our previous report of tetrasporophytes from various locations from the Kattegat, Denmark to the Isles of Scilly, Cornwall (Maggs *et al*., 1992), has not been re-investigated with molecular tools, but sporophytes are more widespread than gametophytes in Strangford Lough, in pebble habitats in Strangford Narrows. In the north-western Atlantic, gametophytes and sporophytes occur from Newfoundland to New England (Maine and New Hampshire). In the North Pacific, *F. deveauniensis* is known only from British Columbia, from a few sites in the central Strait of Georgia where it grew on breakwaters and boulders, and on the eastern coasts of Haida Gwaii (formerly the Queen Charlotte Islands).



Figs 17-25. *Fredericqia deveauniensis* sp. nov. Crustose sporophytes, field-collected from Nova Scotia (NS) and Northern Ireland (NI), and grown in culture. **17.** Habit of bisporophytic crust with irregularly raised, lumpy surface due to differential growth and shedding of sporangial filaments, Pubnico Point (NS), 7 Oct. 1987. **18.** Vertical section of bisporangial thallus with mature filaments terminating in sterile cap cells (hypobasal tissue was removed in making preparation), Northwest Cove, 2 Oct. 1986. **19.** Vertical section of bisporophyte with two layers of coalescent hypobasal tissue and long chains of bisporangia, Cloghy Rocks, Strangford Lough (NI), 15 Dec. 1983. **20.** Bisporangial filament stained with Hoescht dye to show two nuclei in each bisporangium, Cloghy Rocks, 16 Dec. 1985. **21.** Mature tetrasporangial filaments with regularly cruciate tetrasporangia, Pubnico Point, July 1987. **22.** Bisporangial crusts grown from bispores, Northwest Cove (NS), 2 Oct. 1986, after 4 months. **23.** Bispore germlings after 12 days, Pubnico Point, 6 Oct. 1987. **24.** Culture from Ballyhenry Point, 5 Oct. 1980, after 8 months, with bisporangial filaments forming oblique to transverse divisions of sporangia. **25.** Crust of Northwest Cove isolate that formed three erect axes after several bisporangial generations in culture.

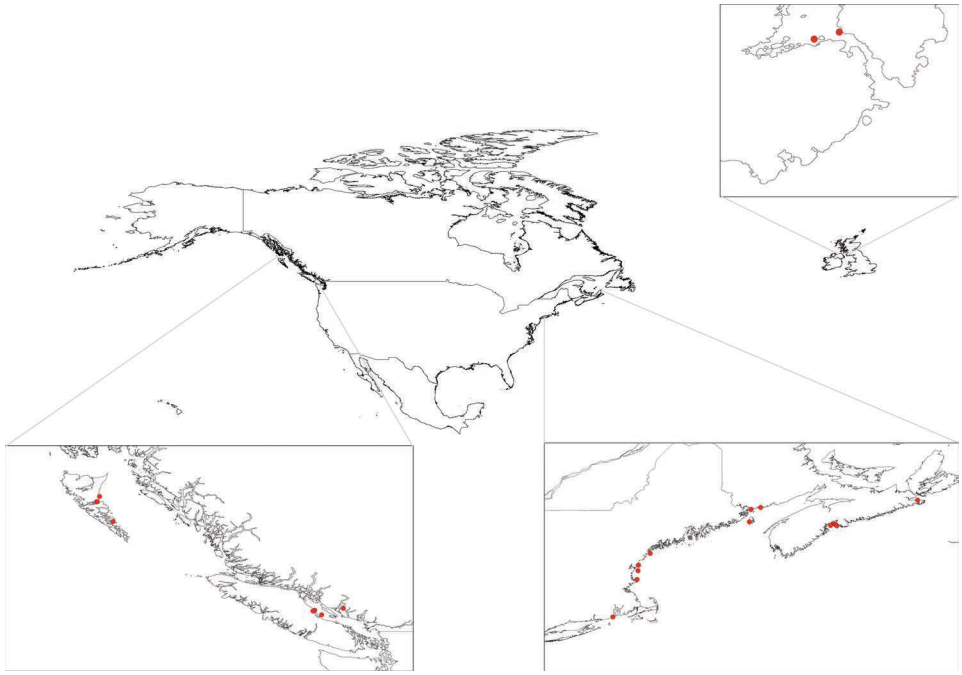


Fig. 26. Distribution of *Fredericqia deveauniensis* based on specimens for which molecular data were obtained. *F. deveauniensis* is also known from Newfoundland (Maggs *et al*., 1992) and crustose thalli attributed to this species were found at a few sites in Europe (see text).

Fredericqia decewii,* Maggs, L. Le Gall, Mineur, Provan *et* G.W. Saunders, *sp. nov. **Fig. 27**

Description: Gametophytes forming clumps of terete wiry fronds 100-300 mm tall, axes to 1.5 mm in diameter, 10-15 times dichotomously branched, red to purplish-black in colour; cystocarps borne on main axes or lateral proliferations; males apparently unknown; sporophytes crustose, cohesive, known only in culture, tetrasporangia not yet observed.

Holotype (here designated): **UNB** GWS008273. Pachena Beach, Bamfield, Vancouver Island, British Columbia, Canada (48.7862° N; 125.1191°W), mid intertidal pool on rock, 5 June 2007, leg. D. McDevit, B. Clarkston, K. Roy and H. Kucera.

Etymology: this species is named for Tom DeCew (1946-1997), who first recognized it as a distinct species.

Distribution: Alaska (Scagel *et al*., 1989, as *Ahnfeltia gigartinoides*), British Columbia to Baja California (Abbott & Hollenberg, 1976, p. 503, as *Ahnfeltia gigartinoides*). Common on rocks partially covered with sand in lower intertidal and upper subtidal zones.

DeCew (1983) showed that samples of the Californian seaweed first identified by Farlow (1875) as *Ahnfeltia gigartinoides* J. Agardh were not conspecific with *A. gigartinoides* from near the type locality in tropical Mexico.

Fig. 27. *Fredericqia decewii*, sp. nov. Holotype (**UNB** GWS008273). Pachena Beach, Bamfield, Vancouver Island, British Columbia, Canada (48.7862° N; 125.1191°N), mid intertidal pool, on rock, 5 June 2007, leg. D. McDevit, B. Clarkston, K. Roy and H. Kucera.

He noted that Californian gametophytes differed from Mexican thalli in their habitat (low intertidal sand-covered rocks vs. high intertidal pools); habit (100-200 mm high, with narrow axes vs. 30-40 mm high stout axes); texture in fresh water (cartilaginous vs. gelatinous); and position of cystocarps (on main axes or lateral proliferations vs. terminal), and concluded that the Californian entity represented an undescribed species. This was named as *Ahnfeltiopsis pacifica* DeCew *et* P.C. Silva *ex* P.C. Silva (1979, p. 322), but its publication was invalid (McNeil *et al*., 2012, ICN, Arts. 39.1, 40.1) because there was no Latin diagnosis and no type was indicated. *Ahnfeltia gigartinoides* (from Mexico) was later transferred to *Ahnfeltiopsis* by Silva & DeCew (1992) (see León-Alvarez *et al*., 1997).

Fredericqia chiton* (Howe) Maggs, L. Le Gall, Mineur, Provan *et* G.W. Saunders, *comb. nov.

Basionym: *Actinococcus chiton* M.A. Howe, 1914: Marine algae of Peru. *Mem. Torrey Bot. Club* 15: 14.
Synonym: *Gymnogongrus chiton* (M.A. Howe) P.C. Silva *et* DeCew.

Phylogenetic analyses

***rbc*L**: The lineage encompassing *Gymnogongrus crenulatus* (Fig. 28, lineage A) was resolved as the earliest diverging lineage within the Phyllophoraceae. The sequence of *Fredericqia deveauniensis* from Strangford Lough, Northern Ireland (AY135170), was identical to sequences from Maine (GQ338151: lineage B) and British Columbia. These grouped robustly with four sequences of *F. decewii* from California, Oregon and British Columbia and three sequences of *F. chiton* from California and British Columbia. Within the

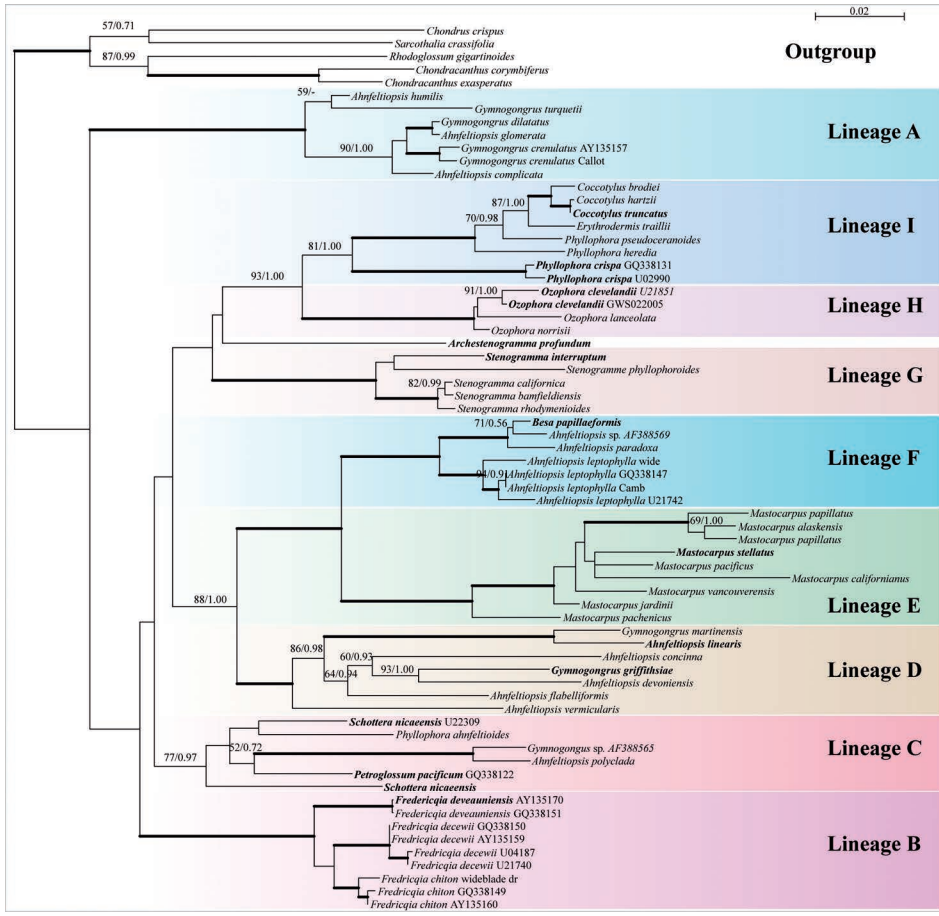


Fig. 28. Best ML *rbc*L tree with support shown at nodes (bootstrap support/Bayesian posterior probabilities). Branches leading to strongly supported nodes are indicated in bold. Generitypes are highlighted in bold. GenBank accession numbers are indicated where more than one specimen per species is included.

Fredericqia lineage, *F. deveauniensis* is sister to *F. chiton* and *F. decewii*. This lineage is not closely related to the type species of *Gymnogongrus*, *G. griffithsiae*, or the type of *Ahnfeltiopsis*, *A. linearis*. It is recognized here as the new genus *Fredericqia* and was also recovered by Fredericq & Ramirez (1996; as *Gymnogongrus chiton* and *Ahnfeltiopsis gigartinoides*) and designated as *Gymnogongrus* III from the NE Pacific.

Lineage B is sister to a large, weak, clade (lineages C-I) including species of *Ahnfeltiopsi*s, *Mastocarpus* and *Gymnogongrus* as well as several other phyllophoracean genera. Within this major lineage, *Ahnfeltiopsis leptophylla* groups robustly with *A. paradoxa, Ahnfeltiopsis* sp. and *Besa papillaeformis* in lineage F. Our sequences of *A. leptophylla* from California are closely related to the previous Californian one. The sequence from the wide-bladed specimen was more divergent than three sequences of the narrow-bladed forms, but this wide form is interpreted here as being conspecific with the typical form. Lineage F

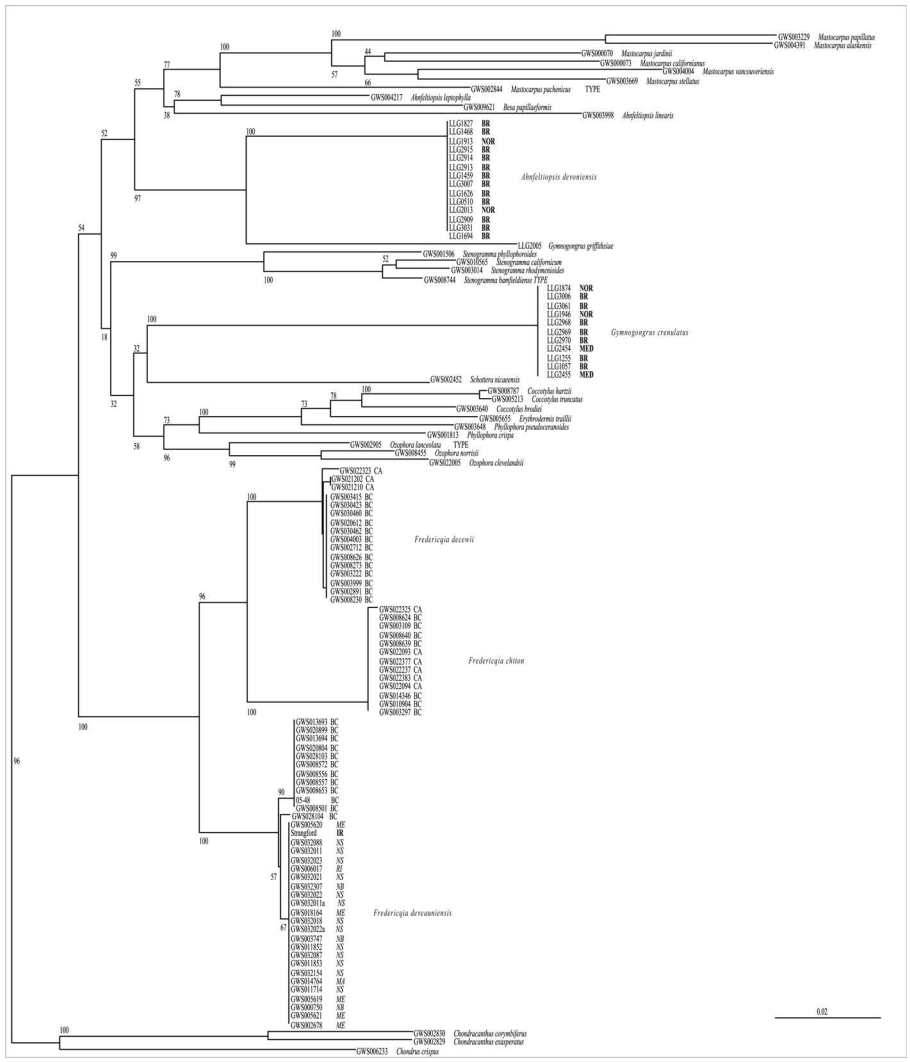


Fig. 29. Cluster analysis of *cox*1 barcode data (CO1-5P) with bootstrap values for distance analysis (NJ). Geographic origins of specimens are indicated as follows: Pacific: BC British Columbia, CA California; West Atlantic: *MA* Massachusetts, *ME* Maine, *NB* New Brunswick, *NS* Nova Scotia, *RI* Rhode Island; East Atlantic: **BR** Brittany, **IR** Northern Ireland, **NOR** Normandy; Mediterranean Sea (MED)

includes the type species of *Besa*, *B. papillaeformis,* and is sister to *Mastocarpus* (lineage E). *Ahnfeltiopsis devoniensis* is sister to *Gymnogongrus griffithsiae* in lineage D, which includes several other *Gymnogongrus* and *Ahnfeltiopsis* species.

***cox*1:** Neighbour-joining analyses of CO1-5P sequences in *Fredericqia* (Fig. 29) were congruent with the *rbc*L tree (Fig. 28). *Ahnfeltiopsis leptophylla* groups with *Besa papillaeformis*, and *Ahnfeltiopsis devoniensis* with *Gymnogongrus griffithsiae. F. deveauniensis* is sister to *F. decewii* and *F. chiton*.

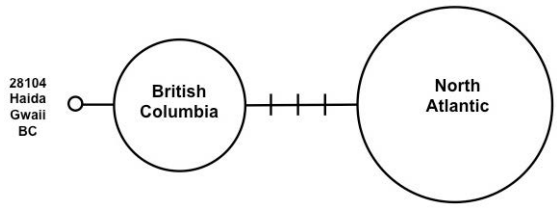


Fig. 30. *cox*1 haplotype network. Haplotypes differing by single substitutions are joined by lines; additional changes are shown as transverse bars; circle sizes are proportional to numbers of individuals with that haplotype.

All North Atlantic sequences of *F. deveauniensis* belong to one haplotype (Figs 29, 30) whilst the British Columbia samples belong to the other haplotype, with one substitution in a sequence from the offshore Haida Gwaii (formerly Queen Charlotte islands). The Atlantic and Pacific haplotypes differ by 3 bp. The high intraspecific divergence in *F. deveauniensis* for this marker suggests long isolation between the populations we sampled in the North Pacific and North Atlantic. The genetic variability in the Pacific and lack of variation in the Atlantic is consistent with a past migration from the Pacific to the Atlantic.

***cox*2-3:** All *Fredericqia deveauniensis* samples from Strangford Lough, N. Ireland, and the Isle of Shoals, New Hampshire, were found to be genetically identical at the *cox*2-3 spacer locus (Fig. 31). *F. deveauniensis* was distinct from

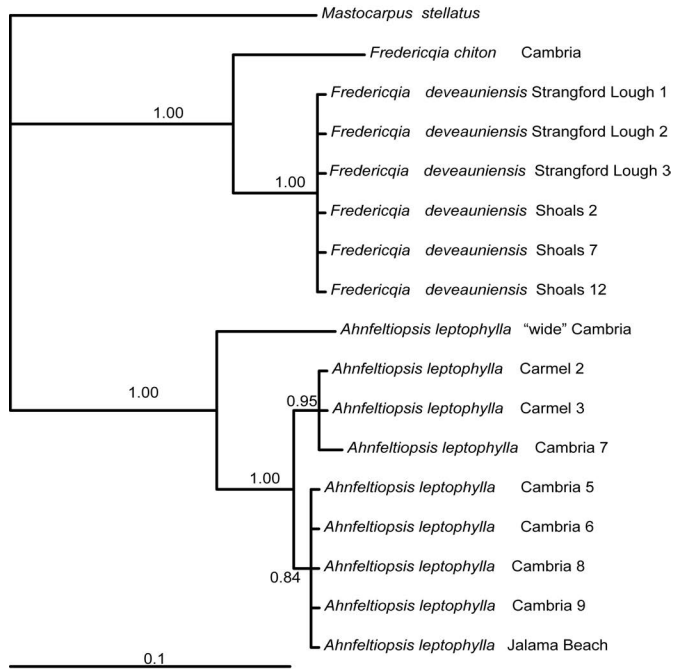


Fig. 31. Bayesian analysis of *cox*2-3 spacer sequences (showing posterior probabilities at nodes) of *Fredericqia deveauniensis*, *Ahnfeltiopsis leptophylla* and *Fredericqia chiton*, rooted with *Mastocarpus*. Scale bar indicates nucleotide divergences between sequences.

both the typical narrow-bladed and the wide-bladed forms of *Ahnfeltiopsis leptophylla* and was closely related to *Fredericqia chiton* from California. By contrast with *F. deveauniensis*, *cox*2-3 sequences of *A. leptophylla* showed several nucleotide polymorphisms, both within and between the two sampled Californian populations (Fig. 31). The single sample collected in 1993 at Jalama Beach, about 200 km south of Cambria, had the same haplotype as most of the samples from Cambria. The wide-bladed *A. leptophylla* (Fig. 32) was divergent from the narrow-bladed forms for this marker as well as *rbc*L, as predicted by DeCew & West (1981) based on contrasting heteromorphic sexual and apomictic life histories.

For all red algae that have been studied with the *cox*2-3 marker, a range of haplotypes has been detected (Zuccarello *et al*., 1999, 2006). Even in some introduced species such as *Asparagopsis armata,* large numbers of haplotypes are observed (Andreakis *et al*., 2007). In the case of *A. armata*, either multiple introductions have occurred, or a single inoculum of a large number of individuals was genetically diverse (Andreakis *et al*., 2007). We infer from the complete lack of variation in this marker for *F. deveauniensis* from Strangford Lough and the north-west Atlantic that a single introduction to the North Atlantic from outside this area was involved and that a trans-Atlantic crossing occurred, possibly with ballast rocks (see Brawley *et al.* 2009). The *cox*1 data suggest this species is of North Pacific origin. Although single introduction events can be associated with high genetic diversity (Eales *et al*., 2010), the *cox*1 marker is insufficiently variable to provide good resolution in relation to questions concerning dates or numbers of introduction events. We are therefore unable to determine whether the introduction is recent (anthropogenic) or associated with natural trans-Arctic interchanges, and *F. deveauniensis* remains cryptogenic *sensu* Carlton (1996).

Life histories in *Fredericqia*

The three known members of this genus exhibit all three of the life history types noted in the Phyllophoraceae by Silva & DeCew (1992). A heteromorphic life history was observed in *Fredericqia decewii* (as *Ahnfeltiopsis gigartinoides*) from Horseshoe Cove, Sonoma County, California (DeCew, 1983). Gametophytes were erect and presumably dioecious. Following fertilization, cystocarps developed within the female blades; released carpospores grew into *Erythrodermis*-like crusts which possibly formed sporangia when planted out in the field (surface pits and sporelings were observed). The life history of *Fredericqia deveauniensis* is derived from the heteromorphic type. All erect thalli are female, and spermatangia are unknown. Cystocarps develop by apomixis and released carpospores recycle the female gametophytes; crustose tetrasporophytes and bisporophytes recycle the sporophytes and very rarely give rise to erect gametophytes (Maggs, 1988; Maggs *et al*., 1992). The life history of British Columbian populations of *F. deveauniensis* is unknown as all specimens were non-reproductive. Further observations of field material (the presence of males would be indicative) or culture studies are required to determine whether a sexual life history takes place in the Pacific.

In *F. chiton,* gametophytes are monoecious (Doubt, 1935). Following fertilization, gonimoblast filaments arise from the auxiliary cell and grow through the gametophytic medulla, penetrating the cortex and forming outgrowths that bear tetrasporangial nemathecia (Doubt, 1935). This structure corresponds to a carpotetrasporophyte (or tetrasporoblast). Immunochemical evidence suggested that meiosis took place during tetrasporogenesis (McCandless & Vollmer, 1984). Our observations of haploid chromosome numbers (n = c. 31) in germinating

Fig. 32. Typical narrow-bladed axes of *A. leptophylla* from the sandy lower shore at Cambria, California, and (bottom right) a wide-bladed individual from the drift at the same site.

tetraspores from British Columbia confirmed that meiosis had occurred. Basal discs gave rise directly to erect axes in culture. Masuda *et al*. (1996) term this life history the *Gymnogongrus griffithsiae*-type. The cortical breaks that allow the tetrasporangial filaments to emerge may be homologous with the specialized carpostomes through which carpospores are released in *F. deveauniensis* and *F. decewii.*

Our phylogenetic analysis shows that the suggestion by Schotter (1968, p. 47) that *Gymnogongrus* species existed as pairs of closely related cystocarpic and tetrasporoblastic species (*A. linearis* and *G. chiton*; *A. devoniensis* and *G. crenulatus*) is erroneous, as predicted by Ardré (1978). However, cystocarpic and tetrasporoblastic species are closely related, and we concur with Fredericq & Ramirez (1996) that life history pattern is not a good character upon which to base genera in the Phyllophoraceae.

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