



# Taxonomic assessment of North American species of the genera *Cumathamnion*, *Delesseria*, *Membranoptera* and *Pantoneura* (Delesseriaceae, Rhodophyta) using molecular data

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Evidence from molecular data supports the close taxonomic relationship of the two North Pacific species *Delesseria decipiens* and *D. serrulata* with *Cumathamnion*, up to now a monotypic genus known only from northern California, rather than with *D. sanguinea*, the type of the genus *Delesseria* and known only from the northeastern North Atlantic. The transfers of *D. decipiens* and *D. serrulata* into *Cumathamnion* are effected. Molecular data also reveal that what has passed as *Membranoptera alata* in the northwestern North Atlantic is distinct at the species level from northeastern North Atlantic (European) material; *M. alata* has a type locality in England. Multiple collections of *Membranoptera* and *Pantoneura fabriciana* on the North American coast of the North Atlantic prove to be identical for the three markers that have been sequenced, and the name *Membranoptera fabriciana* (Lyngbye) comb. nov. is proposed for them. Many collections of *Membranoptera* from the northeastern North Pacific (predominantly British Columbia), although representing the morphologies of several species that have been previously recognized, are genetically assignable to a single group for which the oldest name applicable is *M. platyphylla*.

**Key Words:** *Cumathamnion*; *Delesseria*; Delesseriaceae; *Membranoptera*; molecular markers; *Pantoneura*; Rhodophyta; taxonomy

## INTRODUCTION

The generitype of *Delesseria* J. V. Lamour. is *D. sanguinea* (Huds.) J. V. Lamour., a species occurring in the colder waters of the northeastern Atlantic Ocean, ranging from Arctic Norway and Iceland to Spain (South and Tittley 1986), as well as a reduced form extending into the Baltic Sea (Levring 1940, Nellen 1966, Lüning 1990). Its handsome image depicted by Oeder in *Flora danica* (1766, Pl. 349, as *Fucus sanguineus*) and reproduced in Wynne (2006) was based on a specimen collected in Iceland by Johann Gerhard König, a student of Linnaeus, in 1764-

1765 and initially illustrated in the field by Helt, a young illustrator who accompanied König to Iceland. Helt's preliminary sketch was later refined in Copenhagen by Rösler (information from Peter Wagner, communicated by Ruth Nielsen, Copenhagen). Being a genus described so early (Lamouroux 1813), *Delesseria* has had numerous species assigned to it over the years. For example, J. Agardh (1872) assigned 48 species to his broadly defined *Delesseria*. Fifteen species are currently recognized in the genus (Guiry and Guiry 2012). This list of taxa now placed in *Delesseria*

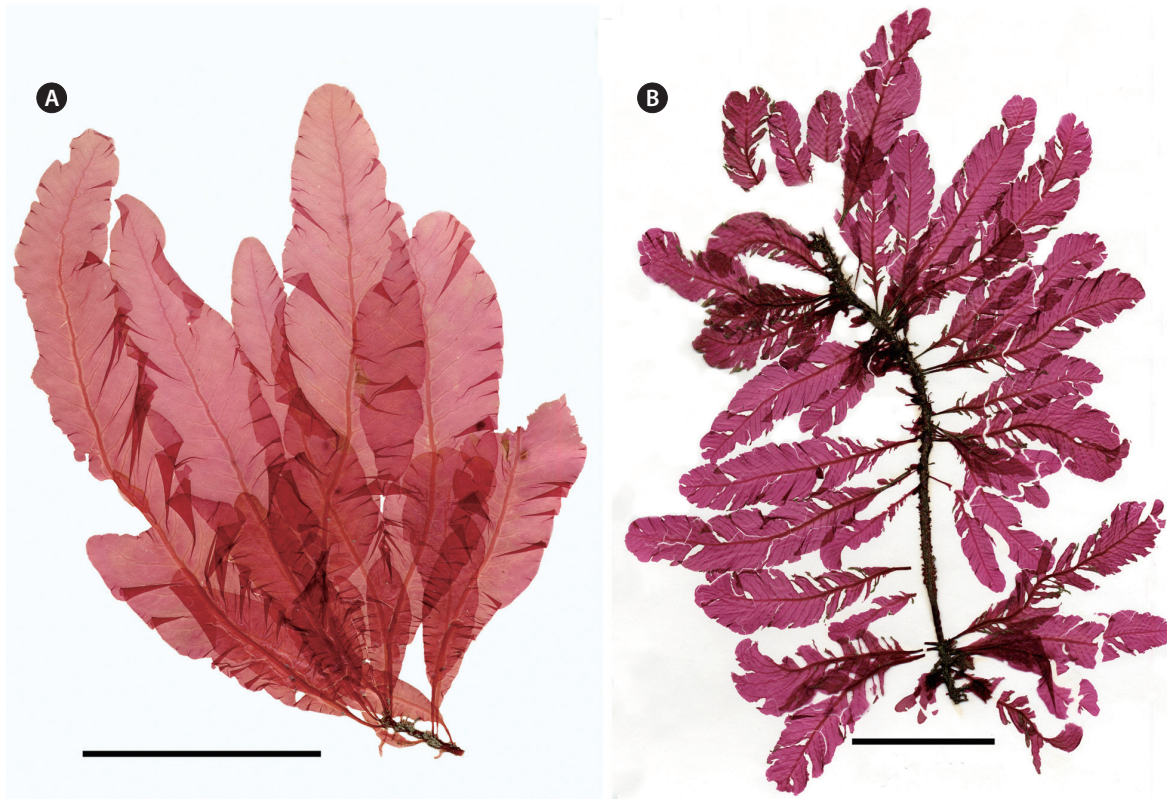
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**Fig. 1.** *Delesseria sanguinea*. (A) Vegetative blades [Kristenberg, Sweden, Jun 6, 1935, leg. T. Levring, MICH]. (B) A mature plant with small cystocarpic bladelets arising from eroded midrib and a new crop of vegetative blades [aquarium at Roscoff Biological Station, P. Potin, Mar 1990, MICH]. Scale bars represent: A & B, 5 cm.

includes two species occurring in the North Pacific, *D. decipiens* J. Agardh (1872) and *D. serrulata* Harvey (1857). Although these species share with *D. sanguinea* the same “*Delesseria*-Type” apical organization (Kylin 1923, 1924, Mikami 1972), that is, with a single transversely dividing apical cell terminating each indeterminate axis, the absence of intercalary divisions in cells of the primary row but with the presence of intercalary divisions in cells of the second-order rows, some differences have long been recognized that distinguish this pair of North Pacific species of *Delesseria* from the European generitype. The primary difference appears to be that of a life-history strategy, *D. sanguinea* being a perennial species that produces small reproductive bladelets from its perennating axes, whereas *D. decipiens* and *D. serrulata* are annual species, producing their reproductive structures on the surfaces of non-specialized blades.

We have extended our studies to include species assigned to the related genera *Membranoptera* and *Pantoneura* occurring on both sides of the North Atlantic and in the northeastern North Pacific. *Membranoptera alata*

(Hudson) Stackhouse, the generitype, has been recognized on both sides of the North Atlantic (Rosenvinge 1923-1924, Taylor 1962, Bird and McLachlan 1992, Maggs and Hommersand 1993, Sears 1998, Loiseaux-de Goër and Noailles 2008). Although some treatments (e.g., Mathieson et al. 1969, South 1984, Sears 1998) recognized only *M. alata* as present in the northwestern North Atlantic, Taylor (1962) also recognized *M. denticulata* (Montagne) Kylin as present in this region. The basionym of *M. denticulata* is *Delesseria alata* var. *denticulata* Montagne, with a type locality of Labrador, Canada (Montagne 1849). The binomial *M. denticulata* (Montagne) Kylin (Kylin 1924), however, is a later homonym, predated by *M. denticulata* Kuntze (1891), a synonym of *Heterodoxia denticulata* (Kuntze) J. Agardh, an Australian species. Thus, the name *M. denticulata* (Montagne) Kylin is not available to apply to the taxon occurring in the northwestern North Atlantic.

The species *Membranoptera spinulosa* (Ruprecht) Kuntze, with syntype localities in the Sea of Okhotsk and St. Paul Island, Bering Sea (Ruprecht 1850) has recently

been reported from the northeastern Atlantic (Mathieson et al. 2010). Earlier in an abstract, Hommersand and Lin (2009) stated that samples of *Membranoptera* from Atlantic North America were separated by only six base pairs in *rbcL* sequence from North Pacific samples of *M. spinulosa*. They also indicated that *M. alata* appeared to be restricted to Europe, a finding that our work will confirm.

On the Pacific coast of North America, a larger number of species of *Membranoptera* have been recognized, as many as six to eight (Gardner 1926, Wynne 1970, Abbott and Hollenberg 1976, Gabrielson et al. 2004, 2006, Lindeberg and Lindstrom 2010). In the North Atlantic two species of *Pantoneura* have usually been recognized, *P. fabriciana* (Lyngbye) M. J. Wynne [formerly *P. baerii* (Ruprecht) Kylin] and *P. angustissima* (Turner) Kylin (Wynne 1997). The former species is also reported to occur in Alaska (Lindstrom 1977), and *P. juergensii* (J. Agardh) Kylin is known from the Aleutian Islands and the Bering Sea (Wynne 1970, Klochkova et al. 2009).

The difficulty in separating taxa of *Membranoptera* and *Pantoneura* from the northwestern North Atlantic using morphology was discussed in detail by Lamb and Zimmermann (1964). According to them, the most common form of *M. alata* occurring in New England was a “very narrow form of the species.” In reference to Pacific North American species of *Membranoptera*, Hawkes et al. (1978) observed that it was “nearly impossible to distinguish *Membranoptera multiramosa* from *M. platyphylla*” because of inconsistencies in the descriptions of the former species. Similarly, Gabrielson et al. (2006) referred to the need to re-examine the relationship between *M. tenuis* Kylin and *M. weeksiae* Setchell & N. L. Gardner, and they also questioned the taxonomic relationships among the three species *M. multiramosa* N. L. Gardner, *M. platyphylla* (Setchell & N. L. Gardner) Kylin, and *M. spinulosa*. Thus, a background exists of workers expressing frustration with the separation of species of *Membranoptera* and *Pantoneura*.

In the present paper analyses of *rbcL*, ribosomal large subunit (LSU), and COI-5P data have demonstrated that these life-strategy differences between *D. sanguinea* (Fig. 1), the genotype and the North Pacific pair, *D. decipiens* (Fig. 2A & B) and *D. serrulata* (Fig. 2C & D), are taxonomically significant with the last two joining *Cumathamnion sympodophyllum* M. J. Wynne & K. Daniels (Fig. 3), a species with a distribution restricted to northern California (Wynne 2009) and at present placed in a monotypic genus (Wynne and Daniels 1966). Adding internal transcribed spacer (ITS) to our previous list of genetic markers, our studies on the related species *Membranoptera alata* (Fig.

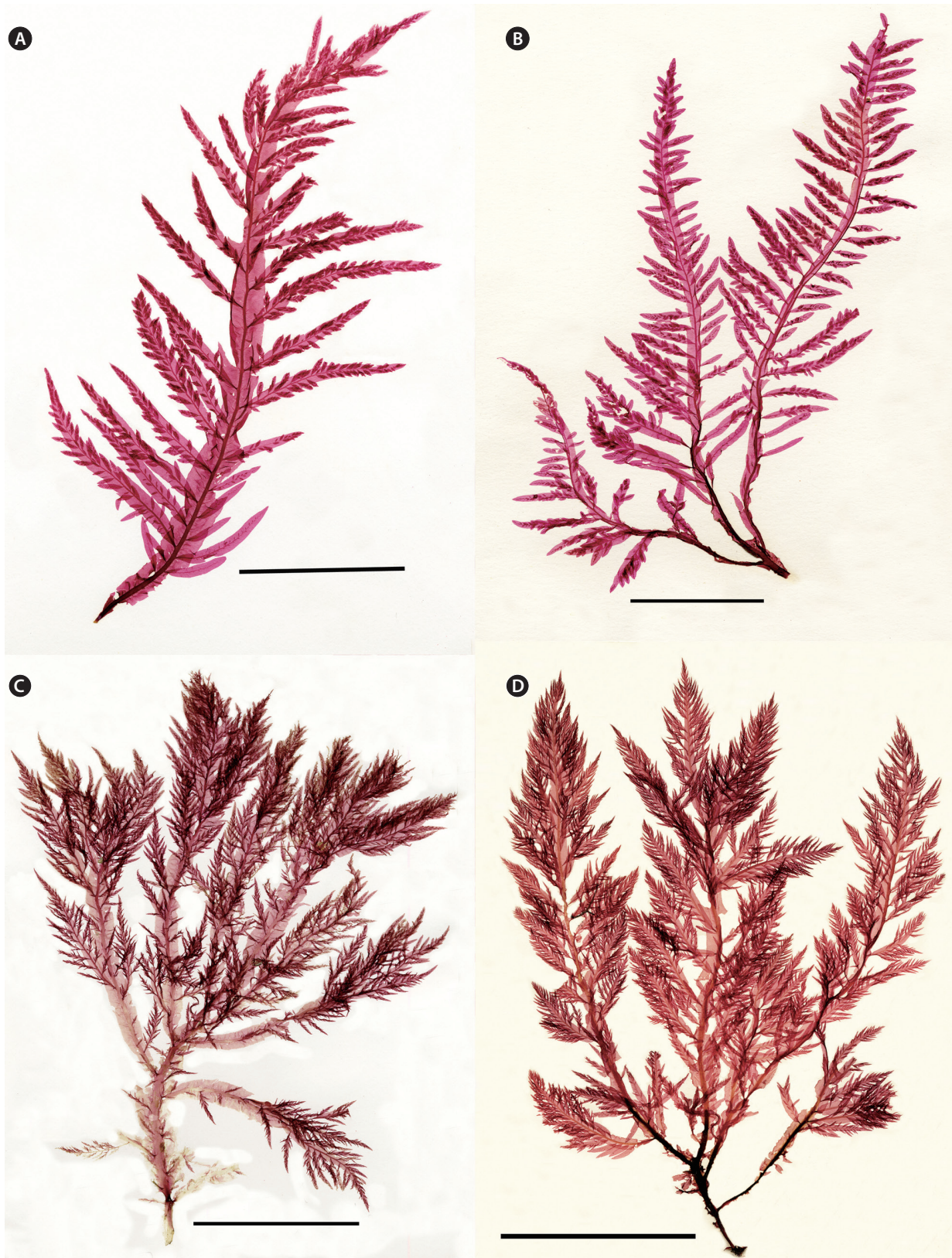
4A-C) show that specimens assigned to this species on the North American Atlantic coast are genetically distinct from this European-based species and conspecific with *Pantoneura fabriciana*. A taxonomic resolution for this result is proposed. Further, specimens from the North American Pacific coast assignable to four to six morphological species (Fig. 4D-G) (Gabrielson et al. 2012) were all resolved as a single genetic species, which again prompted taxonomic change.

## MATERIALS AND METHODS

Samples for molecular investigation (Table 1) were processed and DNA extracted following Saunders and McDevit (2012). Sequence data were generated for the mitochondrial cytochrome *c* oxidase 1 gene barcode region (COI-5P) (Saunders and McDevit 2012), the nuclear internal transcribed spacer (except the primer MEMR4 5'-AATTCAGCGCGTCACCTTATC-3' replaced the standard reverse primer G4 in collections for which diatom contaminants were a problem) (Tai et al. 2001), the LSU of the ribosomal cistron (Harper and Saunders 2001), and the plastid RUBISCO large subunit (*rbcL*) (except two new internal sequencing primers were used-forward TLF5 TC-WCARCCWTTYATGCGTTGG, and reverse TLR1 AAYTC-WGCTCTTTCRTAYAT) (Vis et al. 2007) following established protocols. In total 103 COI-5P, 30 ITS, 20 LSU, and 21 *rbcL* sequences were generated for this study (Table 1).

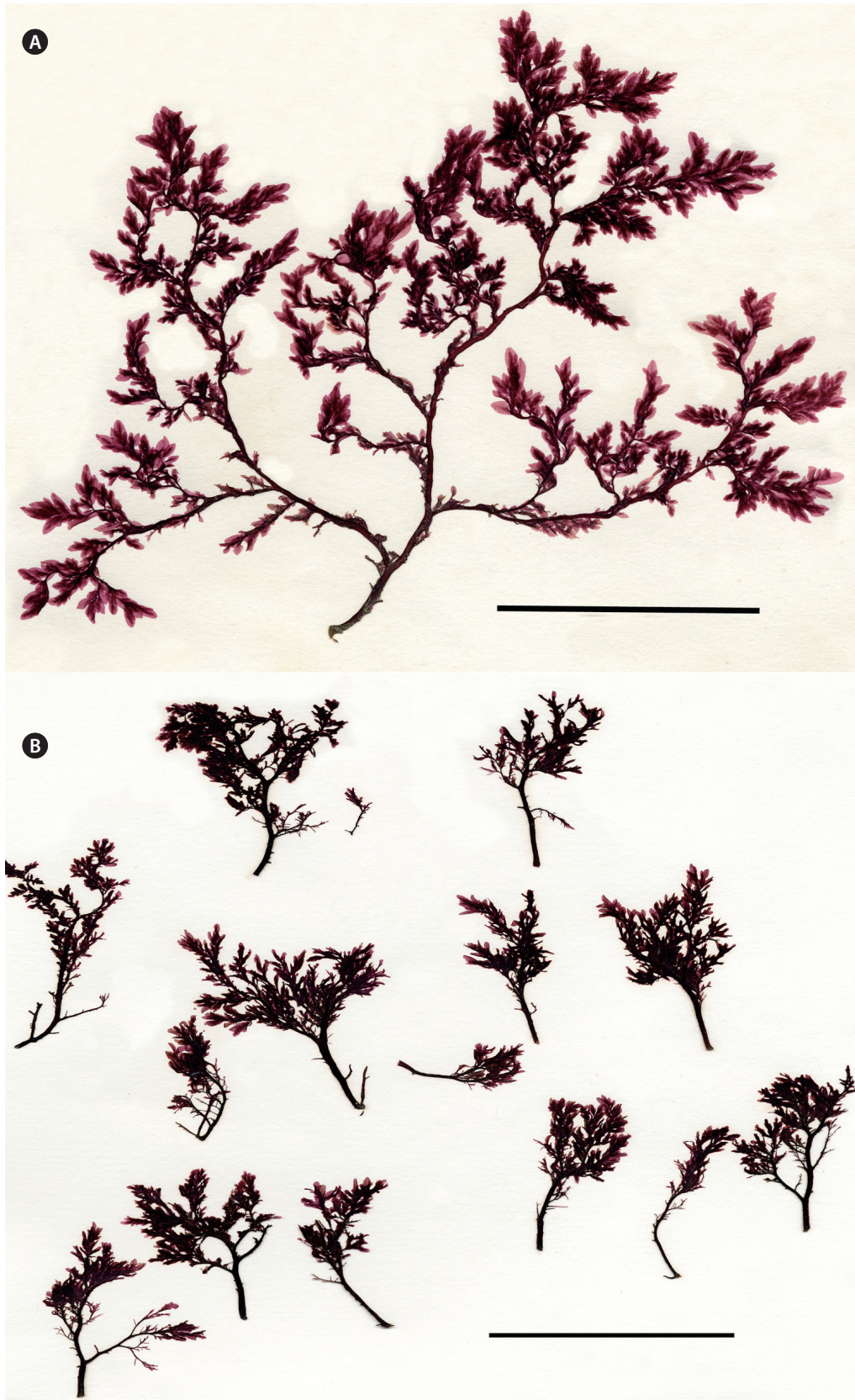
Six alignments were constructed using MacClade 4 (version 4.06) for OSX (Maddison and Maddison 2003). Firstly, a COI-5P alignment (88 individuals and 664 bp) was generated for collections of *Delesseria* and *Membranoptera* from Canada and contiguous waters (Table 1) to assign collections to genetic species groups using neighbour-joining analyses (K2P corrected distances) as implemented in PAUP\* (version 4.0b10) (Swofford 2003) in Geneious Pro version 5.6.2 (Drummond et al. 2012). To confirm the COI-5P results for a subsample of *Membranoptera* and *Pantoneura* collections (Table 1), ITS data were aligned (30 individuals and 1,041 characters) and similarly subjected to neighbour-joining analyses. Subsequent phylogenetic analyses placed these Canadian genetic species groups into an evolutionary context considering individual (COI-5P-21 taxa, 664 sites included; LSU-21 taxa, 2,957 sites, 2,631 included in analyses; and *rbcL*-23 taxa, 1,358 sites included) and a combined (COI-5P + LSU + *rbcL*-20 taxa, 4,653 sites included; *P. fabriciana* data were redundant and were removed prior to combined analyses) alignment (Table 1).





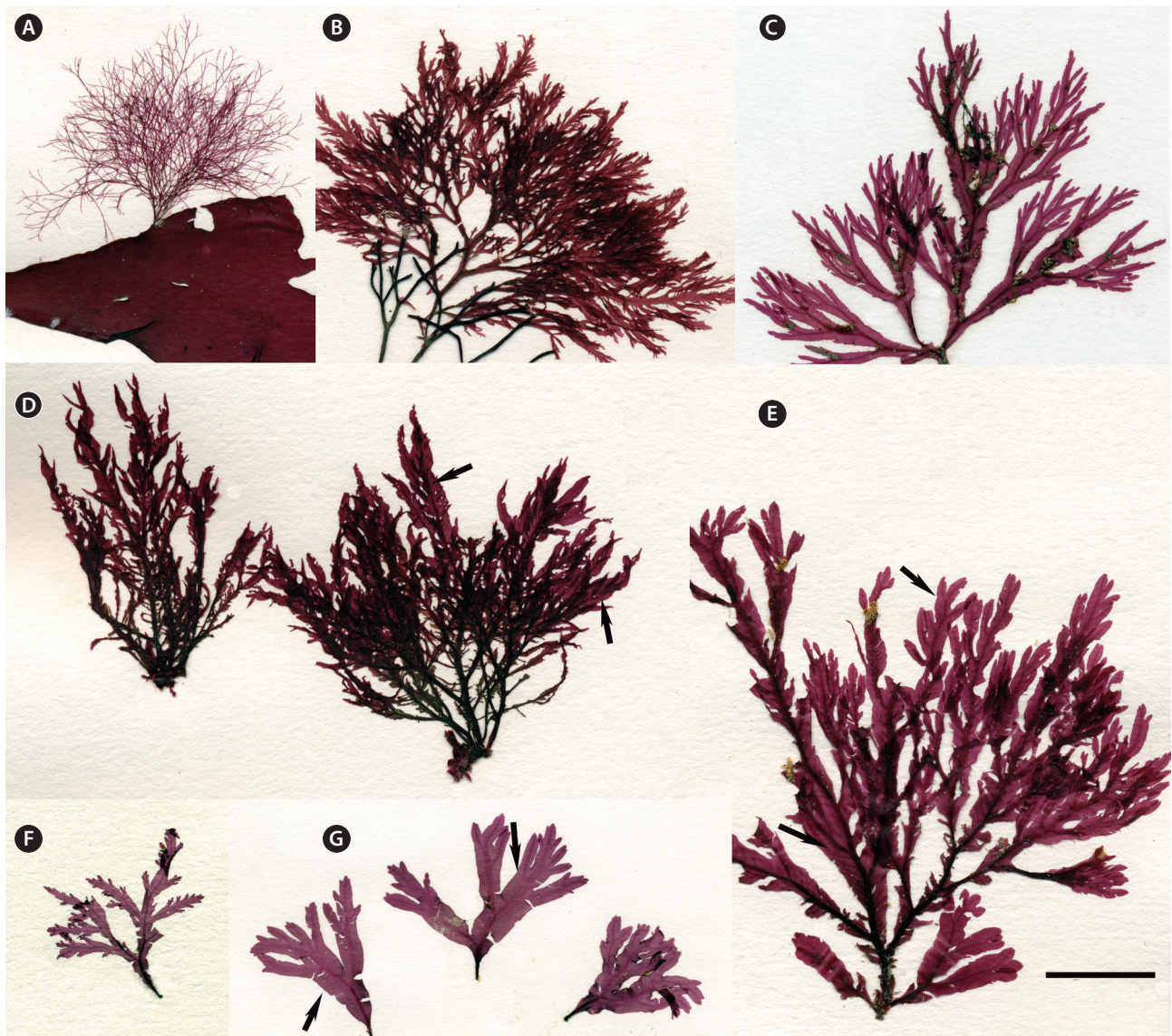
**Fig. 2.** (A & B) *Delesseria decipiens*. Thalli [A: Moss Beach, San Mateo County, California, Apr 24, 1965, leg. M. Wynne 279, MICH; B: Moss Beach, San Mateo County, California, May 26, 1967, leg. M. Wynne 1052, MICH]. (C & D) *Delesseria serrulata*. Thalli [C: Momonai, Oshoro, Hokkaido, Japan, May 4, 1970, leg. H. Mikami, MICH; D: Oshoro, Hokkaido, Japan, Feb 11, 1932, leg. T. Tanaka, MICH]. Scale bars represent: A-D, 5 cm.





**Fig. 3.** *Cumathamnion sympodophyllum*. (A) Single thallus [Mendocino City, Mendocino County, California, Jun 4, 1965, leg. M. Wynne 292, MICH]. (B) Several thalli [Elk Head, Trinidad, Humboldt County, Jun 11, 2010, leg. S. Augyte, MICH]. Scale bars represent: A & B, 5 cm.





**Fig. 4.** Examples of morphological variation for the two *Membranoptera* species in Canada. (A-C) *Membranoptera fabriciana* from the Atlantic. (A) '*Pantoneura fabriciana*' morph (GWS007303). (B) Narrow '*Membranoptera alata*' morph (GWS003664). (C) Wide '*Membranoptera alata*' morph (GWS002324). (D-G) *Membranoptera platyphylla* from the Pacific (for details on morphological identifications see Table 2). (D) '*Membranoptera dimorpha*' morph (note blades arising from midrib-arrows) (GWS006876). (E) '*Membranoptera multiramosa*' morph (note secondary veins-arrows) (GWS010469). (F) '*Membranoptera weeksiae*?' morph (GWS008413). (G) '*Membranoptera platyphylla*' morph (note secondary veins-arrows) (GWS003259). Scale bar represents: A-G, 2 cm.

Model parameters were estimated (Akaike's information criterion [AIC]) for each of the four phylogenetic alignments in Modeltest version 3.06 (Posada and Crandall 1998) as implemented in PAUP\* through Geneious Pro on a Mac Pro (OS X version 10.6.8). The selected model was used to complete maximum-likelihood analyses in PHYML version 3.0 (Guindon and Gascuel 2003) with BIONJ used to designate the starting tree and nearest neighbour interchanges (NNIs) branch-swapping in

effect. Branch support was estimated for the single gene analyses using the Shimodaira-Hasegawa-like (SH) approximate likelihood ratio test (aLRT) and for the multigene alignment with nonparametric bootstrap resampling (500 replicates). In addition to maximum likelihood for the combined alignment, Mr. Bayes (version 3.1.2) (Huelsenbeck and Ronquist 2001) was used to complete two independent trials (each with parallel runs) of Bayesian inference under a GTR + I + G model. Parallel runs



**Table 1.** Voucher numbers (UNB), BOLD accession numbers, collection details and Genbank accession numbers for samples used in the molecular analyses during this study

Name	Voucher No.	BOLD accession <sup>a</sup>	Country (province or state)	COI-5P <sup>b</sup>	ITS <sup>b</sup>	LSU <sup>b,c</sup>	<i>rbcL</i> <sup>b</sup>
<i>Branchioglossum bipinnatifidum</i> (Montagne) M. J. Wynne	GWS009533	ABMMC6720-10	Canada (BC)	HM917111	ND	JX110892	ND
	GWS009540	ABMMC6723-10	Canada (BC)	HM917113	ND	ND	JX110912
<i>Chauwiniella coriifolia</i> (Harvey) Papenfuss	GWS025405	OZSEA713-10	Australia (Western Australia)	JX111856	ND	JX110893	JX110913
<i>Claudea elegans</i> J. V. Lamouroux	GWS024991	OZSEA553-10	Australia (Western Australia)	JX111857	ND	JX110894	JX110914
<i>Cumathamnion sympodophyllum</i> M. J. Wynne & Daniels	GWS012432	OZSEA554-10	USA (CA)	JX111864	ND	JX110897	JX110917
<i>Delesseria decipiens</i> J. Agardh	GWS002755	ABMMC5815-09	Canada (BC)	HM916497	ND	ND	ND
	GWS002869	ABMMC5780-09	Canada (BC)	HM916473	ND	ND	ND
	GWS002972	ABMMC5805-09	Canada (BC)	HM916488	ND	ND	ND
	GWS002976	ABMMC5817-09	Canada (BC)	HM916498	ND	ND	ND
	GWS003348	ABMMC5808-09	Canada (BC)	HM916491	ND	ND	ND
	GWS003349	ABMMC5820-09	Canada (BC)	HM916501	ND	ND	ND
	GWS004979	ABMMC5971-09	Canada (BC)	HM916600	ND	ND	ND
	GWS005170	ABMMC5972-09	Canada (BC)	HM916601	ND	ND	ND
	GWS006358	ABMMC5987-09	Canada (BC)	HM916613	ND	ND	ND
	GWS006359	ABMMC5999-09	Canada (BC)	HM916622	ND	ND	ND
	GWS006430	ABMMC6011-09	Canada (BC)	HM916633	ND	ND	ND
	GWS006608	ABMMC5977-09	Canada (BC)	HM916606	ND	ND	ND
	GWS006612	ABMMC5989-09	Canada (BC)	HM916615	ND	ND	ND
	GWS006859	ABMMC5966-09	Canada (BC)	HM916596	ND	ND	ND
	GWS008209	ABMMC6573-10	Canada (BC)	HM916999	ND	ND	ND
	GWS008303	ABMMC6589-10	Canada (BC)	HM917010	ND	ND	ND
	GWS008356	ABMMC6599-10	Canada (BC)	HM917015	ND	ND	ND
	GWS009612	ABMMC6739-10	Canada (BC)	HM917127	ND	ND	ND
	GWS010220	ABMMC6848-10	Canada (BC)	HM917223	ND	ND	ND
	GWS010481	ABMMC6933-10	Canada (BC)	HM917293	ND	ND	ND
	GWS012738	ABMMC4037-09	Canada (BC)	HM915374	ND	ND	ND
	GWS013540	ABMMC5465-09	Canada (BC)	HM916251	ND	ND	ND
	GWS019806	ABMMC13105-10	Canada (BC)	HQ544628	ND	JX110895	JX110915
	GWS020617	ABMMC13721-10	Canada (BC)	JX111863	ND	ND	ND
	GWS021043	ABMMC14073-10	Canada (BC)	HQ919393	ND	ND	ND
	GWS021050	ABMMC14079-10	Canada (BC)	HQ545273	ND	ND	ND
	GWS021108	ABMMC14127-10	Canada (BC)	HQ919397	ND	ND	ND
	GWS021109	ABMMC14128-10	Canada (BC)	HQ919398	ND	ND	ND
	GWS021110	ABMMC14129-10	Canada (BC)	HQ919399	ND	ND	ND
	GWS021115	ABMMC14134-10	Canada (BC)	HQ919402	ND	ND	ND
	GWS021116	ABMMC14135-10	Canada (BC)	HQ919403	ND	ND	ND
	GWS021117	ABMMC14136-10	Canada (BC)	HQ919404	ND	ND	ND
	GWS021126	ABMMC14145-10	Canada (BC)	HQ919413	ND	ND	ND
GWS021448	ABMMC11480-10	USA (CA)	HQ544064	ND	ND	ND	
GWS021469	ABMMC11494-10	USA (CA)	JX111861	ND	ND	ND	
GWS021470	ABMMC11495-10	USA (CA)	JX111860	ND	ND	ND	
GWS021773	ABMMC12001-10	USA (CA)	JX111859	ND	ND	ND	
GWS021805	ABMMC12026-10	USA (CA)	HQ544166	ND	ND	ND	
GWS021826	ABMMC12043-10	USA (CA)	JX111858	ND	ND	ND	
GWS027359	ABMMC15023-11	Canada (BC)	JX111862	ND	ND	ND	

**Table 1.** Continued

Name	Voucher No.	BOLD accession <sup>a</sup>	Country (province or state)	COI-5P <sup>b</sup>	ITS <sup>b</sup>	LSU <sup>b,c</sup>	<i>rbcL</i> <sup>b</sup>
<i>Delesseria sanguinea</i> (Hudson) J. V. Lamouroux	GWS014005	ABMMC14349-10	France (Brittany)	JX111865	ND	JX110898	JX110918
<i>Delesseria serrulata</i> Harvey	GWS011932	ABMMC7058-10	Japan	HM917397	ND	JX110896	JX110916
<i>Grinnellia americana</i> (C. Agardh) Harvey	GWS001880	ABMMC5822-09	USA (MA)	HM916503	ND	EF033607	ND
	GWS005729	ABMMC6020-09	USA (RI)	HM916640	ND	ND	JX110919
<i>Hemineura frondosa</i> (Hooker f. & Harvey) Harvey	GWS016465	ABMMC8245-10	Australia (Tasmania)	HM918210	ND	JX110899	JX110920
<i>Hemineura</i> sp._1TAS	GWS015582	ABMMC7734-10	Australia (Tasmania)	HM917862	ND	JX110900	JX110921
<i>Heterodoxia denticulata</i> (Kuntze) J. Agardh sp._1	G0387	ABMMC4796-09	Australia (Western Australia)	HM915827	ND	JX110901	JX110922
<i>Heterodoxia denticulata</i> sp._2	GWS002620	ABMMC8941-10	Australia (Tasmania)	HQ919601	ND	JX110902	JX110923
<i>Membranoptera alata</i> Europe	GWS014650	ABMMC14878-11	Ireland (Kerry)	JX111877	ND	JX110906	JX110927
	LLG0942	ABMMC16463-12	France (Normandy)	JX111878	JX110885	ND	ND
	LLG1074	ABMMC16464-12	France (Normandy)	JX111876	JX110884	ND	ND
	LLG1328	ABMMC16465-12	France (Normandy)	JX111882	JX110889	ND	ND
	LLG1508	ABMMC16467-12	France (Brittany)	JX111884	JX110891	ND	ND
	LLG1651	ABMMC16468-12	France (Normandy)	JX111883	JX110890	ND	ND
	LLG1907	ABMMC16469-12	France (Normandy)	JX111881	JX110888	ND	ND
	LLG1920	ABMMC16470-12	France (Normandy)	JX111880	JX110887	ND	ND
	TJS0021	ABMMC16471-12	France (Normandy)	JX111879	JX110886	ND	ND
<i>Membranoptera alata</i> NA	GWS002324	ABMMC5802-09	Canada (NS)	HM916487	JX110877	ND	ND
	GWS003664	ABMMC5809-09	USA (ME)	HM916492	JX110876	ND	ND
	GWS003725	ABMMC5832-09	Canada (NB)	HM916510	JX110875	ND	ND
	GWS005185	ABMMC1657-07	Canada (NB)	JX111870	ND	ND	ND
	GWS005192	ABMMC1658-07	Canada (NB)	JX111866	ND	ND	ND
	GWS006141	ABMMC5998-09	Canada (QC)	HM916621	JX110873	ND	ND
	GWS006284	ABMMC5939-09	Canada (NB)	HM916574	ND	ND	ND
	GWS006285	ABMMC5951-09	Canada (NB)	HM916582	ND	ND	ND
	GWS006910	ABMMC6002-09	Canada (NB)	HM916625	ND	ND	ND
	GWS011694	ABMMC7024-10	Canada (NS)	HM917367	ND	ND	ND
	GWS011701	ABMMC7026-10	Canada (NS)	HM917369	ND	ND	ND
	GWS011702	ABMMC7027-10	Canada (NS)	HM917370	JX110866	ND	ND
	GWS013904	ABMMC5545-09	Canada (NB)	HM916318	JX110865	ND	ND
	GWS013910	ABMMC4291-09	Canada (NB)	HM915569	JX110864	JX110903	JX110924
	LLG0021	ABMMC16460-12	Canada (NS)	JX111867	JX110863	ND	ND
	LLG0198	ABMMC16461-12	Canada (NB)	JX111869	JX110874	ND	ND
LLG0202	ABMMC16462-12	Canada (NB)	ND	JX119101	ND	ND	



**Table 1.** Continued

Name	Voucher No.	BOLD accession <sup>a</sup>	Country (province or state)	COI-5P <sup>b</sup>	ITS <sup>b</sup>	LSU <sup>b,c</sup>	<i>rbcl</i> <sup>b</sup>
<i>Membranoptera platyphylla</i> (Setchell & Gardner) Kylin	GWS002862	ABMMC5756-09	Canada (BC)	HM916459	ND	ND	ND
	GWS003259	ABMMC5830-09	Canada (BC)	HM916509	ND	ND	ND
	GWS004692	ABMMC5992-09	Canada (BC)	HM916617	ND	ND	ND
	GWS004698	ABMMC6004-09	Canada (BC)	HM916626	ND	ND	ND
	GWS006538	ABMMC5953-09	Canada (BC)	HM916584	ND	ND	ND
	GWS006876	ABMMC5990-09	Canada (BC)	HQ919547	JX110879	ND	ND
	GWS008413	ABMMC6611-10	Canada (BC)	HM917025	JX110880	JX110905	JX110926
	GWS009970	ABMMC6796-10	Canada (BC)	HM917179	JX110881	ND	ND
	GWS010469	ABMMC6929-10	Canada (BC)	HM917290	ND	ND	ND
	GWS021473	ABMMC11497-10	USA (CA)	JX111872	JX110882	ND	ND
	GWS027363	ABMMC15033-11	Canada (BC)	JX111873	ND	ND	ND
	GWS027364	ABMMC15034-11	Canada (BC)	JX111874	JX110883	ND	ND
	GWS027460	ABMMC15024-11	Canada (BC)	JX111875	ND	ND	ND
	GWS027530	ABMMC15037-11	Canada (BC)	JX111871	JX110878	ND	ND
<i>Pantoneura fabriciana</i> (Lyngbye) M. J. Wynne	GWS007024	ABMMC6334-10	Canada (NL)	HM916858	JX110872	ND	ND
	GWS007085	ABMMC6346-10	Canada (NL)	HM916864	JX110871	ND	JX110925
	GWS007113	ABMMC6356-10	Canada (NL)	HM916870	JX110870	ND	ND
	GWS007125	ABMMC6361-10	Canada (NL)	HM916873	JX110869	JX110904	ND
	GWS007303	ABMMC6400-10	Canada (NL)	HM916899	JX110868	ND	ND
	GWS007306	ABMMC6402-10	Canada (NL)	JX111868	JX110867	ND	ND
<i>Paraglossum</i> sp.	GWS000518	ABMMC6098-10	Chile	JX111885	ND	JX110907	JX110928
<i>Patulophycus eclipses</i> A. J. K. Millar & M. J. Wynne	GWS022866	OZSEA561-10	Australia (New South Wales)	JX111886	ND	JX110908	JX110929
<i>Phytomophora amansioides</i> (Sonder) Womersley	GWS014861	ABMMC7132-10	Australia (Victoria)	HM917450	ND	JX110909	JX110930
<i>Phycodryx fimbriata</i> (Kuntze) Kylin	GWS013736	ABMMC5575-09	Canada (NB)	HM916343	ND	JX110910	JX110931
<i>Phycodryx rubens</i> (Linnaeus) Batters	GWS013862	ABMMC5555-09	Canada (NB)	JX111887	ND	JX110911	JX110932

ITS, internal transcribed spacer; LSU, large subunit; BC, British Columbia; CA, California; MA, Massachusetts; RI, Rhode Island; NS, Nova Scotia; ME, Maine; NB, New Brunswick; QC, Quebec; NL, Newfoundland and Labrador.

<sup>a</sup>Detailed collection information can be obtained from the BOLD database ([www.boldsystems.org](http://www.boldsystems.org)).

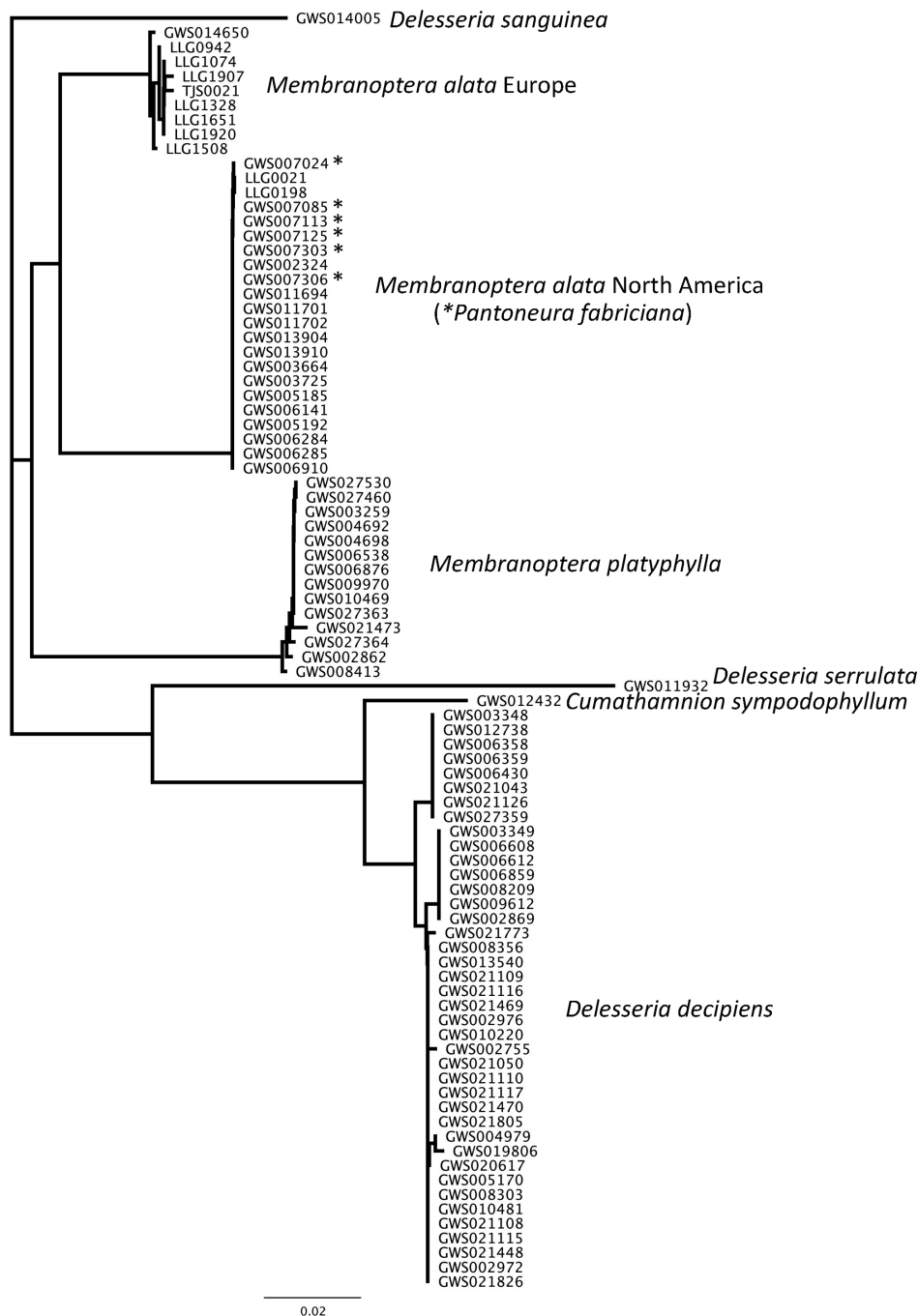
<sup>b</sup>ND indicates that a sequence was not determined for that collection and gene.

<sup>c</sup>Sequence for accession number in bold type was obtained from Genbank.

of four Markov chains were completed with two million generations and sampling each 100 generations. The data were partitioned (by gene, and then by codon for COI-5P and *rbcl*), and the parameters were unlinked across partitions with the overall rate allowed to vary across partitions. The burn-in for each run was determined by plotting overall likelihood scores against generation, which established the stationary phase of each run for estimating the posterior probability distribution; the final estimate was based on pooled samples from two independent runs.

## RESULTS

Despite a range of morphologies for our collections of *D. decipiens*, all of the collections resolved in a single genetic species group with COI-5P data (0-0.92% divergence) consistent with current taxonomic thought (Fig. 5). *M. alata* from a diversity of sites in the northeastern waters of North America (0% divergence, Table 1), however, failed to join European collections (type locality) of this species (Fig. 5). More interesting, the former had COI-5P sequences identical to collections of *P. fabriciana*



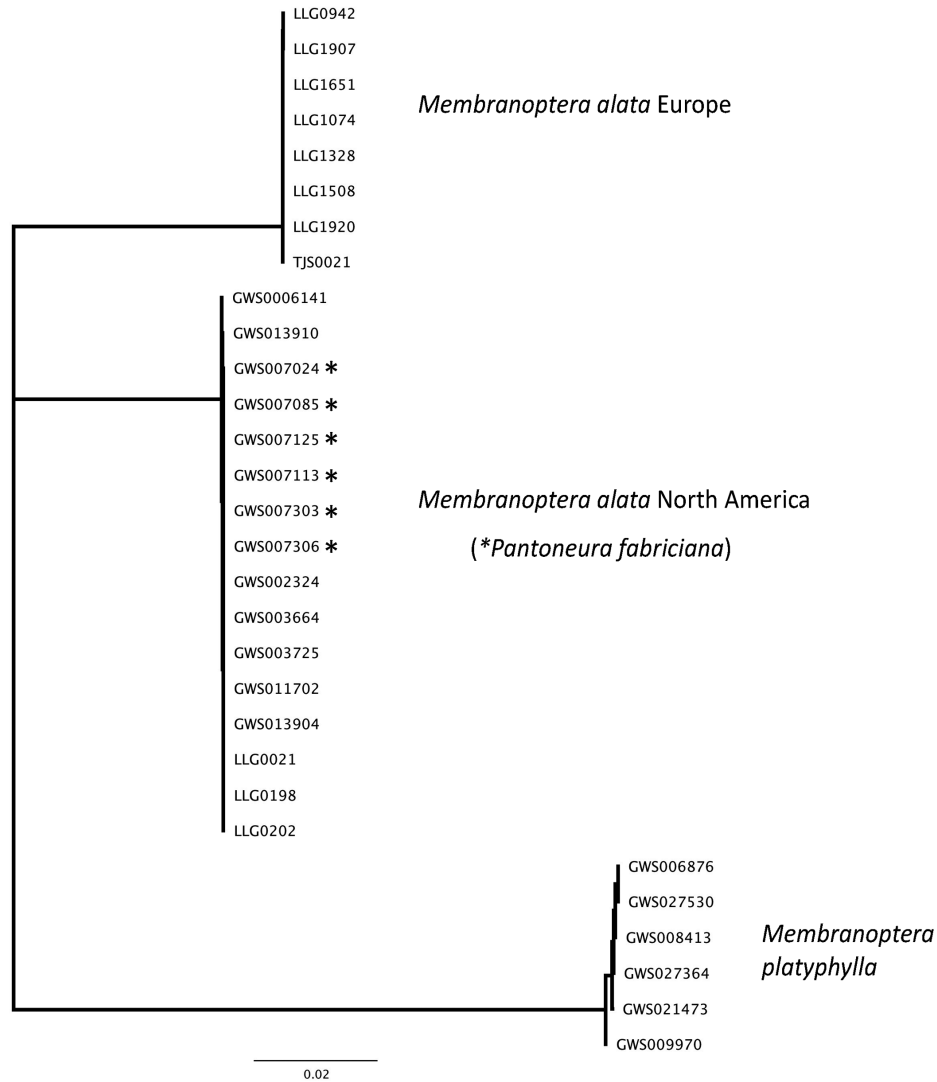
**Fig. 5.** Neighbor-joining tree generated from COI-5P (barcode) sequence for representative collections of *Delesseria* and *Membranoptera* from Canada and contiguous waters.

from Newfoundland (Table 1, Fig. 5). Equally dramatic were our results for collections from British Columbia (one from California, Table 1) that were variously field identified to all of the four-six species recognized in those waters (Table 2), but which nonetheless formed a single genetic group (0-0.46% divergence) in COI-5P analyses (Fig. 5, *M. platyphylla*). This would suggest that the sub-

stantial morphological variation that has previously been used at the species level for taxonomic discrimination is more likely phenotypic plasticity in response to the environment (Table 2).

Internal transcribed spacer data for six diverse Pacific morphs of *Membranoptera* (Tables 1 & 2) were virtually identical (four sites with ambiguities and / or substitu-



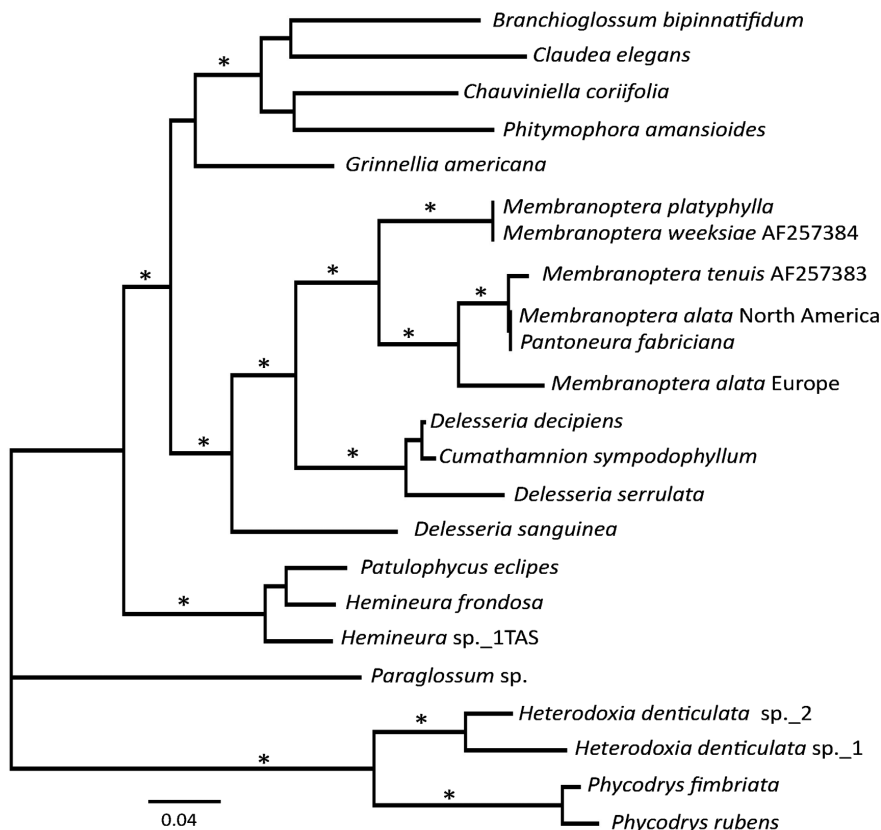


**Fig. 6.** Neighbor-joining tree generated from internal transcribed spacer (ITS) sequence for representative collections of *Membranoptera* from Canada and contiguous waters as a test of the COI-5P results.

tions indicating low level within individual and population variation) consistent with the COI-5P results (Fig. 5) that all of these collections should be assigned to a single species (Fig. 6). For the Atlantic populations ITS were generated for six individuals assignable to *P. fabriciana* and 10 individuals assignable to *M. alata* from North America (Fig. 6). All individuals were virtually identical (two specimens with an ambiguity [C and T] at the same site) indicating that the ITS data are consistent with the COI-5P data in assigning all of these collections to a single genetic species group. European collections of *M. alata* ( $n = 8$ ) similarly clustered together (Fig. 6); two collections with C and T ambiguity at the same site, one with G and T ambiguity, and one with variable number of T's (6 and 7) and were distinct from the North American collections,

again consistent with the COI-5P data (Fig. 5).

Interestingly, *rbcL* and LSU data generated for North American *M. alata* and *P. fabriciana* were also identical, as had been detected previously in our COI-5P and ITS analyses, consistent with these two distinct morphologies belonging to a single species. In phylogenetic analyses all of the single gene alignments essentially resolved the same topology as the combined alignment, but the *rbcL* phylogeny is presented because it included two sequences from Genbank, which were not ultimately included in our combined analyses (Fig. 7). First, Genbank data for *Membranoptera weeksiae* (AF257384) were identical to those generated here for *M. platyphylla* consistent with our suggestion that only a single species should be recognized for the variety of morphologies currently con-



**Fig. 7.** Maximum likelihood tree for the *rbcL* data generated here and including two entries from Genbank (number follows name in figure). \* indicates >95% Shimodaira-Hasegawa-like (SH) support.

**Table 2.** Morphological species assignments for specimens of *Membranoptera* from the west coast of North America (predominantly British Columbia), which nonetheless form a single genetic species in all of our molecular analyses

Sample	Morphological species as interpreted from Gabrielson et al. (2006) <sup>b</sup>
GWS006538	<i>M. dimorpha</i>
GWS006876 <sup>a</sup>	<i>M. dimorpha</i>
GWS021473 <sup>a</sup>	<i>M. dimorpha</i>
GWS002862	<i>M. multiramosa</i>
GWS004692	<i>M. multiramosa</i>
GWS009970 <sup>a</sup>	<i>M. multiramosa</i>
GWS010469	<i>M. multiramosa</i>
GWS027460	<i>M. multiramosa</i>
GWS027530 <sup>a</sup>	<i>M. multiramosa</i>
GWS003259	<i>M. platyphylla</i>
GWS027363	<i>M. platyphylla</i>
GWS027364 <sup>a</sup>	<i>M. platyphylla</i>
GWS004698	<i>M. weeksiae</i>
GWS008413 <sup>a</sup>	<i>M. weeksiae</i>

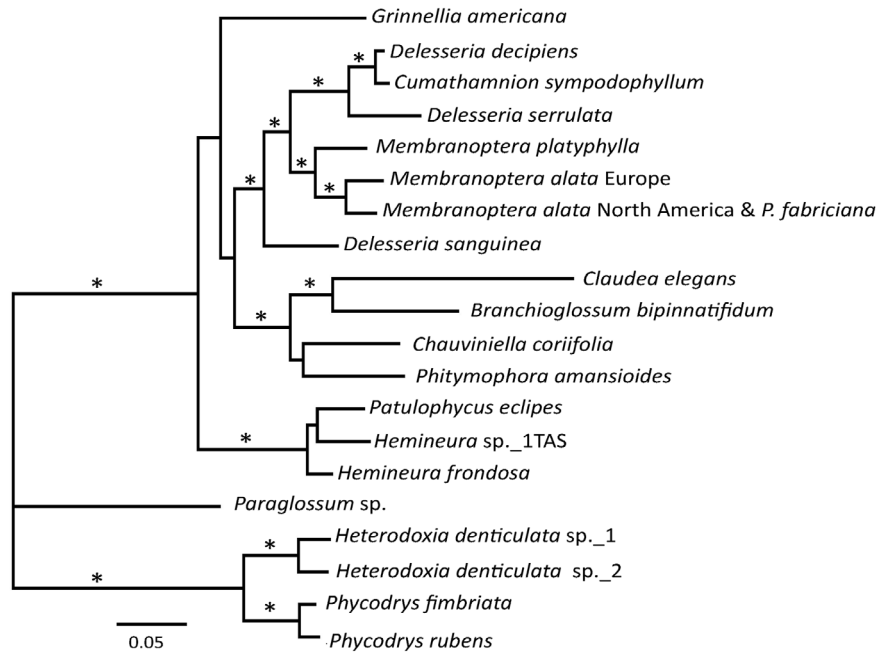
<sup>a</sup>This collection was included in ITS analyses to test further the indications of our COI-5P results.

<sup>b</sup>Many of our collections were less than 3 cm in height, an attribute consistent with another species recorded from this region, *M. tenuis*.

sidered multiple species in the Northeast Pacific (Fig. 7). Second, a sequence in Genbank attributed to *Membranoptera tenuis* (AF257383) for a collection from Alaska is very similar to our data for North American (Atlantic) *M. alata* / *P. fabriciana*-differing at only seven (likely six, one difference is at a highly conserved codon position and may represent an error in the Genbank entry) nucleotides out of the 1,354 available for comparison or 0.5%. These two taxa are thus very closely related and need further study to assess their status as distinct species.

Only maximum likelihood results for the combined analyses are presented as once again all of the trees were similar (Fig. 8). The tree for the most part was solidly resolved and showed a close affiliation between the genera *Cumathamnion*, *Delesseria* and *Membranoptera* (Fig. 8), which are currently assigned to three different tribes on the basis of morphological features (discussed below). Further, *D. decipiens* and *D. serrulata* joined the type species of *Cumathamnion* rather than *D. sanguinea*, the generitype of *Delesseria* (Fig. 8). Our molecular results thus necessitate substantive taxonomic changes at the species, genus and tribe level for species assigned to the





**Fig. 8.** Maximum likelihood (ML) phylogeny generated with the three-gene (COI-5P + LSU + *rbcl*) concatenated alignment. \* indicates >97% support in ML bootstrap and Bayesian posterior probability support of 1. LSU, large subunit.

genera *Delesseria*, *Membranoptera* and *Pantoneura* in the Canadian flora. Although beyond the scope of the current manuscript, we have also uncovered phylogenetic evidence that representatives of the diverse genera *Branchioglossum*, *Chauviniella*, *Claudea*, *Grinnellia*, *Hemineura*, *Patulophycus* and *Phitymophora*, which have been previously assigned to other tribes, resolved closely to our *Cumathamnion*, *Delesseria* and *Membranoptera* lineage and are all in need of future taxonomic revision (Figs 7 & 8).

## DISCUSSION

Much of the currently accepted classification of the Delesseriaceae is based on the investigations on the comparative vegetative organization and reproductive patterns made by Kylin (1923, 1924). Limiting the scope of our discussion to the genera included in our study, we can refer to *Delesseria* being assigned by Kylin (1924) to the “*Delesseria*-Gruppe” and *Membranoptera* and *Pantoneura* being assigned to his “*Membranoptera*-Gruppe.” When describing their new genus *Cumathamnion*, Wynne and Daniels (1966) recognized a new category, the “*Cumathamnion* Group” for that genus. Subsequently, Wynne (2001) replaced these informal “Gruppe” names with corresponding tribal names.

The critical characteristic that was used to separate *Membranoptera* and *Pantoneura* in their tribe, or Gruppe, from *Delesseria* in its tribe was that in the former genera intercalary cell divisions are absent in second-order cell rows, but they do occur in species of *Delesseria*. Such intercalary cell divisions also occur in the second-order cells rows of *Cumathamnion*, but it was separated into its own tribe because of its sympodially organized axes.

Although several entries of gene-sequence data are now listed in Genbank for *D. sanguinea*, *D. decipiens*, *D. serrulata*, and *D. lancifolia*, actual published information has been limited. On the basis of *rbcl* sequence analysis, Lin et al. (2001) showed a closer relationship between *D. decipiens* and two species of *Membranoptera* than with *D. sanguinea*, which was the deepest lineage in that clade. Small subunit rDNA data for a Korean collection of *D. serrulata* has been published by Choi et al. (2002). Sequence data on *C. sympodophyllum* has not been previously published.

Previous molecular phylogenetic research on the family Delesseriaceae has indicated in a preliminary way that *Delesseria* was a polyphyletic genus. Lin et al. (in press) demonstrated that several southern hemisphere species that had been assigned to *Delesseria* were more closely related to *Apoglossum ruscifolium* (Turner) J. Agardh and fell out in their newly described tribe Apoglosseae. According to Lin et al., the name *Paraglossum* J. Agardh

(1898), originally based on the two species *P. lancifolium* (J. Agardh) J. Agardh and *P. epiglossum* (J. Agardh) J. Agardh and later lectotypified with the former species (Lin et al. 2001), could be reinstated to accommodate those species related to *A. ruscifolium*. According to Lin et al. (in press), the tribe Apoglosseae accommodates *Apoglossum* and the reinstated *Paraglossum*. On the other hand, *D. decipiens* fell out in a clade close to two species of *Membranoptera* with *D. sanguinea* as sister to that group.

When the new genus *Cumathamnion* was established by Wynne and Daniels (1966), they stressed its sympodial development as a primary distinction from related genera of Delesseriaceae. The monotypic genus was later placed in its own tribe, the Cumathamnieae (Wynne 2001). The pattern of growth with not all tertiary initials reaching the thallus margin, the presence of intercalary divisions in cells rows of the second order, and the production of branches along the midrib are features shared by *Cumathamnion* and *Delesseria*. So the question arises: Is the sympodial development present in *C. sympodophyllum* in contrast to the monopodial development present in *D. decipiens* and *D. serrulata* too significant a difference to override their obvious affinity as expressed in the gene-sequence data?

Two types of sympodial growth in the order Ceramiales were recognized by Norris et al. (1984). In “cellulosympodial” growth, the apical cell initiates a determinate lateral branch, and the lateral cell or branch formed by the sub-apical cell carries on development of the thallus axis, and that process is continually repeated. Cellulosympodial development occurs in the family Dasyaceae (Parsons 1975). Ramisymphodial branching, on the other hand, occurs when development in a given axis ceases, and further growth of the plant is from new branches initiated in an intercalary position. Ramisymphodial organization is known in some genera of Ceramiales. Some instances are known where genera include species with monopodial growth and species with ramisymphodial growth. Examples include *Hypoglossum* in the Delesseriaceae, in which most of the species have a monopodial organization, but thalli of *H. revolutum* (Harv.) J. Agardh are ramisymphodially organized. Likewise, in *Crouania* in the Ceramiaceae some species have monopodial organization, whereas other species have a ramisymphodial organization (Norris 1986, Schneider 2004). Thus, it is not unprecedented where we now interpret *Cumathamnion* to have species with both ramisymphodial branching (in the type species, *C. sympodophyllum*) and monopodial branching, in these two species formerly assigned to *Delesseria*, *D. decipiens*

and *D. serrulata*.

*Delesseria decipiens* was first recognized by Harvey (1862) under the name “*Delesseria hypoglossum* var. *arborescens*” collected from the Strait of Juan de Fuca by Dr. Lyall, who was a surgeon with the British Boundary Commission. When J. Agardh (1872) later described *Delesseria decipiens*, he cited Harvey’s nom. ined. in taxonomic synonymy. J. Agardh indicated Vancouver Island (British Columbia, Canada) as the only location for this species. Subsequently, J. Agardh (1898) transferred this species to *Apoglossum*, *A. decipiens* (J. Agardh) J. Agardh, but its placement in *Delesseria* has been followed by most workers (Kylin 1924, Smith 1944, Abbott and Hollenberg 1976, Scigel et al. 1989, Gabrielson et al. 2000). It is now known to have a distribution in the eastern North Pacific from the Kodiak Archipelago, Alaska, to Baja California, Mexico (Abbott and Hollenberg 1976, Hawkes et al. 1978, Scigel et al. 1989, Lindeberg and Lindstrom 2010, Riosmena-Rodríguez et al. 2011). The known distribution for *D. serrulata* is from northern Japan (Okamura 1908), Korea (Lee and Kang 1986), and eastern Russia (Perestenko 1996, Kozhenkova 2009). The *Delesseria serrulata* depicted from Australia by Harvey (1858, Pl. 59) has been shown by Kurogi (1979) and Womersley (2003) to be an incorrect application of the name, and the Australian alga is now known as *Hypoglossum harveyanum* (J. Agardh) Womersley & Shepley (1982).

Foremost among the morphological differences between *D. sanguinea* and these two North Pacific species of the genus is the fact that *D. sanguinea* is a perennial plant that produces a conspicuous foliose vegetative stage in the summer growing season, but it does not bear reproductive organs on the surfaces of those large blades (Fig. 1A). In the winter, when the vegetative blade is largely eroded, the persistent midrib produces very small special fertile proliferations on which the reproductive structures (carpogonial branches and tetrasporangia) are formed. The male proliferations are also formed on the midribs, but this occurs while the blade lamina is still present (Maggs and Hommersand 1993). There is a short mid-winter fertile season, with peak production of spores (carpospores and tetraspores) from December to March (Kain 1982), although male organs appeared 3 months earlier. This production of specialized reproductive proliferations has long been recognized in *D. sanguinea* (Smith 1804-1805, Pl. 1041; Turner 1807-1808, Pl. 36; Cuvier 1816-1829; Harvey 1848, Pl. 151; Phillips 1898, Pl. 15). The persistent midribs also serve to sprout out the next generation of leafy shoots in the next growing season (Fig. 1B). In contrast to the pattern of reproduction in *D. sanguinea*, *D. decipiens*

(Fig. 2A & B), and *D. serrulata* (Fig. 2C & D) produce their reproductive organs directly on the vegetative blades at the end of the growing season, sometimes on the final order of vegetative branches [Kylin 1924, for *D. decipiens*; Okamura 1908 (as *Apoglossum violaceum*), Mikami 1972 (as *Delesseria violacea*) for *D. serrulata*]. In their annual life-history pattern and the production of reproductive organs on non-special blades, these two species of North Pacific *Delesseria* parallel the life history pattern of *C. sympodophyllum* (Wynne and Daniels 1966).

The results of a comparison of the sequence data (Figs 7 & 8) lead to the conclusion of the closer relationship of *Delesseria decipiens* and *D. serrulata* with *C. sympodophyllum* than with *D. sanguinea*, the European genotype. The following transfers are proposed:

***Cumathamnion decipiens* (J. Agardh) M. J. Wynne & G. W. Saunders comb. nov.**

**Basionym.** *Delesseria decipiens* J. Agardh 1872, Lunds Univ. Arsskr. 8(6), p. 58.

**Homotypic synonym.** *Apoglossum decipiens* (J. Agardh) J. Agardh 1898, p. 194.

**Also.** *Delesseria hypoglossum* var. *arborescens* Harvey 1862, p.170, nom. ined.

***Cumathamnion serrulata* (Harvey) M. J. Wynne & G. W. Saunders comb. nov.**

**Basionym.** *Delesseria serrulata* Harvey 1857, Narrative Perry Exped. 2, p. 331.

**Homotypic synonyms.** *Membranoptera serrulata* (Harvey) Kuntze 1891, p. 904; *Hydrolapatha serrulata* (Harvey) Kuntze 1898, p. 410.

**Heterotypic synonym.** *Delesseria violacea* J. Agardh 1872, p. 52, nom. illeg. [type locality: Japan]; this name is illegitimate because the valid and legitimate name *D. serrulata* Harvey (1857) was cited in synonymy by Agardh (1872); *Apoglossum violaceum* J. Agardh (1898) nom. illeg.; cf. Kurogi (1979).

Key to species of *Cumathamnion*:

1. Thallus monopodially organized, that is, with percurrent indeterminate axes.....2
1. Thallus ramosypodially organized, that is, with indeterminate axes continually being replaced with lateral branches assuming the focus of growth and they then being replaced.....*C. sympodophyllum*
2. Blade margins entire, smooth.....*C. decipiens*
2. Blade margins serrate, toothed.....*C. serrulata*

The next question is: What name should be applied to the taxon of so-called *Membranoptera* and *Pantoneura fabriciana* occurring in the northwestern North Atlantic? The molecular results (Figs 7 & 8) demonstrated that *Membranoptera* and so-called *Pantoneura* of the northwestern North Atlantic were assignable to a single genetic group distinct from the European-based populations of *M. alata*. Wynne (1997) reviewed the complicated history of the name *Gigartina fabriciana* Lyngbye (1819, Pl. 11D), based on a collection from Greenland. He examined type material in C and confirmed that it was a member of the Delesseriaceae and that it was an older name for *Pantoneura baerii* (Ruprecht) Kylin. Thus, the name *Pantoneura fabriciana* (Lyngbye) M. J. Wynne was proposed. The three currently recognized species of cold-water Northern Hemisphere *Pantoneura* have been placed in that genus because of their morphological similarity to type species of *Pantoneura*, *P. plocamioides* Kylin (in Kylin and Skottsberg 1919), with a type locality of South Georgia. According to Hommersand et al. (2009), however, unpublished *rbcL* sequence data by S. -M. Lin show *P. plocamioides* to be unrelated to the Arctic species *P. fabriciana*, but the latter taxon is related to *M. alata*, in agreement with our results.

Reinsch (1875) described *Hypoglossum grayanum* with three syntype localities: West Gloucester, Massachusetts, USA; Labrador, Canada; and Anticosti Island, Quebec, Canada. Farlow (1881) regarded *Hypoglossum grayanum* to be the same as *M. alata* of the New England coast. De Toni (1900) treated *H. grayanum* as a "Species mihi planae ignotae aut ulterius inquirendae," saying that it perhaps had affinities with *Caloglossa leprieurii*. But the fact that Reinsch stated that his new species was epiphytic on *Ptilota plumosa* is ample evidence that it is not in the genus *Caloglossa*, which typically occurs in estuarine habitats. Reinsch's (1875, Pl. 47) clearly depicts *Membranoptera* epiphytic on its common host *Ptilota*. But this name is predated by Lyngbye's *G. fabriciana*. Therefore, we conclude that *G. fabriciana* is the name with priority to use for the *Membranoptera* present in the northwestern North Atlantic, and we propose the binomial:

***Membranoptera fabriciana* (Lyngbye) M. J. Wynne & G. W. Saunders comb. nov.**

**Basionym.** *Gigartina fabriciana* Lyngbye, 1819, Tent. Hydrophytol., p. 48, Pl. 11D.

**Lectotype in C. Type locality.** Frederikshaab (61°59' N, 49°42' W), Greenland, collected by Bishop O. Fabricius in the period 1768-1773, *vide* Ruprecht (1851). See Wynne



(1997, Figs 1 & 3) for depictions of the apical portions of the Type.

**Homotypic synonym.** *Pantoneura fabriciana* (Lyngbye) M. J. Wynne 1997, p. 325.

**Heterotypic synonyms.** *Delesseria alata* var. *denticulata* Montagne 1849, p. 62; *Membranoptera denticulata* (Montagne) Kylin 1924, p. 16, nom. illeg.; *Hypoglossum grayanum* Reinsch 1875, p. 55, Pl. 42.

In regard to the populations of *Membranoptera* from the northeastern North Pacific, the results of the molecular analyses (Figs 5 & 6) establish that only a single species is represented in this region, despite the fact that as many as six species have been recognized (Gabrielson et al. 2006). The names of two species have equal priority, dating from Kylin (1924), namely, *M. platyphylla* (Setchell & N. L. Gardner) Kylin and *M. tenuis* Kylin. We opt to apply the name *M. platyphylla* for the representatives of *Membranoptera* occurring in the northeastern North Pacific. The type locality of *M. platyphylla* is Pleasant Beach, Kitsap County, Washington, USA (Setchell and Gardner 1903).

*Membranoptera spinulosa* (Ruprecht) Kuntze was reported from Alaska by Wynne (1970) and by Lindeberg and Lindstrom (2010) and also included in the flora of the northeastern North Pacific by Gabrielson et al. (2006). This species was based on *Delesseria alata* var. *spinulosa* Ruprecht (1850), with syntype localities of the Okhotsk Sea and St. Paul Island, Bering Sea. Because of the remote nature of these syntype localities to our collections, we have decided to apply the name *M. platyphylla* rather than *M. spinulosa*.

The earlier assignment of *Delesseria*, *Membranoptera*, and *Cumathamnion* to three different tribes within subfamily Delesserioideae (Wynne 2001) is clearly incorrect in view of their genetic relatedness seen in Figs 7 & 8. The separation of *Apoglossum* along with the reinstated *Paraglossum* J. Agardh from the Delesserieae to the new tribe Apoglosseae has been proposed by Lin et al. (in press). The newly circumscribed tribe Delesserieae includes *Delesseria*, *Cumathamnion*, and *Membranoptera*, and likely other genera such as *Phitymophora*, *Grinnellia*, and *Hemineura*, that have been previously assigned to other tribes. These latter genera, included in Figs 7 & 8, need to be re-evaluated for possible inclusion in the tribe Delesserieae.

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Note added in press: Three additional collections of *Membranoptera alata* from Norway have had COI-5P determined subsequent to completion of this study (data available at BOLD project CUMEM: ABMMC17103-12; ABMMC17104-12; ABMMC17105-12) and resolve solidly with the other European collections of this species included here. We thank J. Gitmark, J. Rueness and K. Sjøtun for providing these additional samples.

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