The diversity of the Bangiophycidae (Rhodophyta) of the Faroes in the context of the northern Atlantic

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Abstract

A study of species included in the red algal subclass Bangiophycidae indicates that they are well represented in the Faroes in comparison with other regions in the North Atlantic. However, the Porphyridiales are poorly represented which is probably a reflection of the lack of suitable habitats in the Faroe Islands, and the number of species in the Erythropeltidales is reduced but may be under-recorded. In the Bangiales, there appear to be at least as many or more species of *Porphyra* recorded than from either the northeastern or northwestern Atlantic, including at least three possibly undescribed species although analysis of the plastid encoded *rbc*L-*rbc*S intergenic spacer sequence data confirms the presence of *P. birdiae* in the Faroes flora, a species recently described from Nova Scotia. Molecular data also reveal differences between specimens of *P. umbilicalis* raising issues regarding species concepts in the genus. The arrival of *Porphyra* in the N. Atlantic is also considered. It may have occurred since the formation of the North Atlantic in the Cretaceous on numerous occasions via a number of routes including i) seaways linking the Pacific Ocean with the North Atlantic, ii) ocean currents and iii) anthropogenic influence.

The results of this paper suggest that the full extent of the Bangiophycidae, especially species of *Porphyra*, is not yet known in the Faroes, nor in the North Atlantic as a whole and that much greater sampling of these taxa from a wider geographical area in the North Atlantic and Arctic is required to elucidate diversity and biogeography of this group.

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Introduction

The BIOFAR project, the aim of which is to produce an inventory of all the marine macroalgae and benthic animal species present in the Faroe Islands, led to a paper being published on the Bangiophycideae of these islands (Brodie *et al*., 2001). This work was based primarily on collections made between 1994 and 1997, but also took into account the work of Simmons (1897), Børgesen (1902) and Irvine (1982), although species listed in these earlier works need to be treated with caution because of the taxonomic and nomenclatural problems that the Bangiophycidae present (see Brodie and Irvine, 2003). Brodie *et al.* (2001) listed 19 species of Bangiophycidae, 1 assigned to the Porphyridiales, 6 to the Erythropeltidales and 12 to the Bangiales, including 4 species of *Porphyra* that could not be identified to known taxa. A comparison with data from other parts of the North Atlantic suggests that the diversity for the Faroe Islands is as great as or

greater than other areas studied, particularly in relation to species of *Porphyra*. In the light of these data, this paper compares the diversity of the Bangiophycidae in the Faroes with areas elsewhere in the northern Atlantic. This paper also considers particular taxonomic problems associated with the group and considers the arrival of the flora within the geographical area.

Methods

Comparisons of species in the Bangiophycidae present in the Faroes with the northeastern Atlantic were based primarily on data from Brodie *et al*. (2001) and Brodie and Irvine (2003). Comparisons with the northwestern Atlantic *Porphyra* were made with data from Klein *et al.* (2003). Molecular data for the plastid encoded *rbc*L-*rbc*S intergenic spacer were obtained following the methods of Brodie *et al.* (1996; 1998). Specimens for which molecular sequences were obtained are shown in Table 1.

Results and discussion

The Bangiophycidae as a whole are well represented in the Faroes (Table 2), although the Porphyridiales are poorly represented in comparison to the northeastern Atlantic with only one species, *Stylonema alsidii*, recorded. This species is very widespread, occurring throughout the North Atlantic (Brodie and Irvine, 2003). It would be unexpected to encounter other species of the Porphyridiales in the Faroes because they occur in habitats that are not or rarely encountered in the Faroes. *Porphyridium aerugineum* is a species of saltmarsh mud in the marine environment, a habitat which does not occur in the Faroes. *Porphyridium purpureum* is typically a species found in estuarine and damp terrestrial conditions. *Rhodella maculata* is only known from the type locality in Britain and from a plankton tow in Norway. *Chroodactylon ornatum* is recorded from marine, estuarine and freshwater habitats. *Colacodictyon reticulatum* is found in *Desmarestia dresnayi* J.V. Lamouroux ex Léman, which is not recorded in

Table 1. *Species of Porphyra from the Faroes for which rbcL-rbcS sequence data were obtained. The names given to the species were based on gross morphology prior to obtaining molecular data.*

Species (molecular code)	Collection number[1]	Location	Grid ref.	Date collected	Collected by
Porphyra purpurea (PO8)	F951121 08	Arnir, Skálafjørður, Eysturoy	62º11, 60 N, 6º49, 49 W	21.06.1995	R. Nielsen
Porphyra sp. 1 (10A)	F951280 33	Oyndarfjørður, Eysturoy	62º15, 934 N, 6º51, 526 W	14.09.1995	R. Nielsen
Porphyra insolita (PO2)	F950001 02	Kaldbak, Streymoy	62º03, 655 N, 6º49, 427 W	28.01.1995	R. Nielsen
Porphyra dioica (PO9)	F971780 09	Tjörnunes, Borðoy	62º15, 47 N, 6º26, 04 W	30.07.1997	R. Nielsen

[1]Collection number recorded in the Botanical Museum Copenhagen.

Table 2. *Comparison of species of Bangiophycidae recorded for the Faroes in relation to the northeastern and northwestern Atlantic. + = present; +? = possibly present; ? unknown if present; - not present. Sources: Brodie et al. (2001), Brodie and Irvine (2003), Klein et al. (2003).*

	Faroes	northeastern Atlantic	northwestern Atlantic
PORPHYRIDIALES			
Porphyridium aerugineum Geitler	-	+	-
P. purpureum (Bory) Drew & Ross	-	+	-
Rhodella maculata L.V. Evans	-	+	-
Chroodactylon ornatum (C. Agardh) Basson	-	+	+
Colacodictyon reticulatum (Batters) Feldmann	-	+	-
Stylonema alsidii (Zanardini) Drew	+	+	+
S. cornu-cervi Reinsch	-	+	-
Neevea repens Batters	-	+	-
ERYTHROPELTIDALES			
Erythrocladia irregularis Rosenvinge	+	+	+
Erythropeltis discigera var. *flustrae* Batters	-	+	+*
Erythrotrichia bertholdii Batters	+	+	-
E. carnea (Dillwyn) J. Agardh	+	+	+
E. investiens (Zanardini) Bornet	-	+	-
E. reflexa (P. Crouan & H. Crouan) Thuret ex De Toni	-	+	-
E. welwitschii (Ruprecht) Batters	-	+	-
Porphyropsis coccinea (J. Agardh ex Areschoug) Rosenvinge	+	+	+
Porphyrostromium boryanum (Montagne) P. Silva	+	+	-
P. ciliare (Carmichael ex Harvey in Hooker) Wynne	-	+	+
P. sp.	-	+	-
Sahlingia subintegra (Rosenvinge) Kornmann	+	+	+
BANGIALES			
Bangia atropurpurea (Roth) C. Agardh	+	+	+
Porphyra amplissima (Kjellman) Setchell & Hus ex Hus	+	+	+
P. dioica Brodie & L. Irvine	+	+	-
P. drachii Feldmann	-	+	-
P. leucosticta Thuret in Le Jolis	+	+	+
P. linearis Greville	+	+	+
P. miniata (C. Agardh) C. Agardh	+	+	+
P. purpurea (Roth) C. Agardh	+	+	+
P. suborbiculata Kjellman	-	-	+
P. umbilicalis (Linnaeus) Kützing	+	+	+
P. birdiae Neefus & Mathieson	+	+	+
P. sp. 2	+?	?	?
P. sp. 3	+?	?	?
P. sp. 4	+?	?	?
P. yezoensis Ueda	-	-	+
P. yezoensis sensu Kornmann	-	+	-

*As *Erythrocladia*

the Faroes, and *D. ligulata* (Lightfoot) J.V. Lamouroux which is recorded at one station only (Nielsen and Gunnarsson, 2001). *Stylonema cornu-cervi* is a southern species, with the most northerly record being Devon (Brodie and Irvine, 2003). *Neevea repens* is endozoic in the bryozoan *Flustra foliacea* (L.). In the northeastern Atlantic this species appears to have a southerly distribution although the bryozoan host occurs in the Faroes. The northwestern Atlantic, like the Faroes, is poor in species of this order, with only *Chroodactylon ornatum* recorded in addition to *S. alsidii*.

Records suggest that the diversity of species of Erythropeltidales is reduced in the Faroes compared with other parts of the northeastern Atlantic but may be underrecorded for the area. *Erythropeltis discigera* var. *flustrae*, which appears to reach its northerly limit along the southern coasts of Britain, is epizoic on the bryozoan *Flustra foliacea*. *Erythrotrichia investiens* is not recorded further north than the British Isles although its taxonomic status is uncertain. *E. reflexa* is recorded from more northerly regions, including Norway (Brodie and Irvine, 2003). *Erythrotrichia welwitschii* is found on the brown alga *Ralfsia verrucosa* (Areschoug) Areschoug and is recorded from around the British Isles where it is not that well known and almost certainly overlooked. *Ralfsia verrucosa* is reported from four stations in the Faroes (Nielsen and Gunnarsson, 2001) but *E. welwitschii* has not been recorded from the islands. The absence of *Porphyrostromium ciliare* in the Faroes may relate to the lack of *Zostera* (eel grass) although it may have been overlooked on suitable algal hosts on which it is epiphytic. In comparison to the northwestern Atlantic, the species of Erythropeltidales are similar.

In contrast to the other orders, species in the Bangiales are at least as numerous or more so than in other areas of the northern Atlantic. *Bangia atropurpurea* sensu lato, is recorded throughout the N. Atlantic but requires further investigation in the Faroes to determine its taxonomic status (see also Müller *et al.,* 2003). Five species, *Porphyra amplissima*, *P. leucosticta*, *P. linearis*, *P. purpurea*, and *P. umbilicalis* occur in all three regions compared, although *P. amplissima* is a northerly species, confined to the northern half of the British Isles. One species, *P. miniata*, another northerly species, is present in the Faroes and northwestern Atlantic but absent from the British Isles. *Porphyra drachii* was originally described from Brittany (Feldmann, 1978/9). The most northerly record so far in the British Isles is the Orkneys.

It was noted in Brodie *et al*. (2001) that there may be at least four species which are possibly undescribed from the Faroes and this may be an underestimate. A similar situation also seems to be the case for the northwestern Atlantic where there are several undescribed species which have gone under one name (see Klein *et al.,* 2003). Comparison of the 18 base pairs at the 5' end of the *rbc*L (including the stop codon) and the *rbc*L-*rbc*S sequence data for several isolates of *Porphyra* species from the Faroes with those published by Brodie *et al.* (1998), reveal the following. An individual identified as *P. purpurea* from the

Table 3. *rbcL-rbcS sequence data for species of Porphyra from the northeastern Atlantic. TAG/TAA = stop codon for rbcL; GTG = start codon for rbcS. Species in bold have previously unpublished sequences. J = from Japan; s. K = sensu Kornmann. Sections of sequences highlighted in grey indicate regions that appear to be conserved.*

P. purpurea	CCAACAGCCAACGTCTAGTTCAATGACTACTTACAACTGC-TTAAACTAGCAAAGTATAAGTAGAATTAACTTATAAAAATAAGGAGCATAGAATAGTG
P. purpurea H	CCAACAGCTAACGTCTAGTTCAATGACTACTTACAACTGC-TTAAACTAGCAAAGTATAAGTAGAATTAACTTATAAAAATAAGGAGCATAGAATAGTG
***P.* sp.(PO8)**	CCAACAGCTAACGTCTAGTTCAATGACTACTTACAACTGC-TTAAACTAGCAAAGTATAAGTAGAATTAACTTATAAAAATAAGGAGCATAGAATAGTG
***P.* sp.(10A)**	CCAACTGCAAACGTCTAGTTTAATGACTACTTGCGACTGC-TTAAACTAGCAAAGTATAAGTAGAATTAACTTATAAAAATAAGGAGCATAGAATAGTG
P. dioica	CCAACAGCCAACGTCTAGTTTAATGACTACTTACAACTGC-TTAAACTAGCAAAGTATAAGTAGAATTAACTTATAAAAATAAGGAGCATAGAATAGTG
P. amplissima	CCAACAGCAAACGTCTAGTTTAATGACTACTTACAACTGC-TTAAACTAGCAAAGTATAAGTAGAATTAACTTATAAAAATAAGGAGCACAGAATAGTG
P. linearis	CCAACAGCAAACGTCTAGTTTAATGACTATTTATAACTGC-TTAAACTAGGAAAGTATAAGTAGAATTAACTTATAAAAATAAGGAGCATAGAATAGTG
P. umbilicalis	CCAACAGCAAACGTCTAATTTAATGACTATTTATAACTGC-TTAAACTAGGAAAGTATAAGTAGAATTAACTTATAAAAATAAGGAGCATAGAATAGTG
***P. 'umbilicalis'*(PO2)**	CCAACAGCAAACGTCTAATTTAATGACTACTTATAACTGC-TTAAACTAGCGAAGTATAAGTAGAATTAACTTATAAAAATAAGGAGCATAGAATAGTG
***P. 'umbilicalis'*(PO9)**	CCAACAGCAAACGTCTAATTTAATGACTACTTATAACTGC-TTAAACTAGCGAAGTATAAGTAGAATTAACTTATAAAAATAAGGAGCATAGAATAGTG
P. miniata	CCAACAGCAAACGTCTAGTTTAATGACTATTTACAACTGC-TTAAACTAGGAAAGTATAAGTAGAATTAACTTATAACAATAAGGAGCACAGAATAGTG
P. pseudolinearis	CCAACAGCAAACATCTAGTTTAATGACTACTTGCTAATGC-TTAAATCAGCAAATTGTAAGTAGAATTAACTTATAACAATAAGGAGCATAGAATAGTG
P. drachii	CCAACAGCAAACATCTAGTTTAATGACTACTTGCTAATGC-GTAATTTAGCAAATTGTAAGTAGAATTAACTTATAACAATAAGGAGCATAGAATAGTG
P. leucosticta	CCAACAGCAAACATCTAGTTTAATGACTACTTACTAATACTTTAAA-TAGTCAATCGTAAGTGGAATTAACTTATAACAATAAGGAGCATAGAATAGTG
P. yezoensis (J)	CCAACAGCAAACATCTAGTTTAATGACTACTTACTGATACTTTAAA-TAGTCAATTGTAAGTGGAATTAACTTATAACAATAAGGAGCATAGAATAGTG
P. yezoensis (s. K)	CCAACAGCAAACATCTAGTTTAATGACTACTTACTAATACTTTAAA-GAGTCAATTGTAAGTGGAATTAACTTATAACAATAAGGAGCATAGAATAGTG

EMBL accession numbers

P. purpurea AJ010776; *P. dioica* AJ010779; *P. amplissima* AJ010780; *P. linearis* AJ010781; *P. umbilicalis* AJ010782; *P. miniata* AJ010786; *P. pseudolinearis* AJ010787; *P. drachii* AJ010788; *P. leucosticta* AJ010789; *P. yezoensis* Japan AJ010783; *P. yezoensis* sensu Kornmann AJ010778*; *P.* sp. (PO8) AJ634465; *P.* sp. (10A) AY458657; *P.* sp. (PO2) AJ634466; *P.* sp. (PO9) AJ634467.

**P. yezoensis* sensu Kornmann was listed as *P. "insolita"* by Brodie *et al.* (1998) following the labelling of one of Kornmann's original cultures (JB pers. obs.). This is not the same as *P. insolita* Kornmann and Sahling. Individuals labelled as *P. insolita* by Kornmann had the same *rbc*L-*rbc*S sequence as for *P. umbilicalis* specimens referred to in Brodie *et al.* (2003).

Faroes (PO8) (Fig. 1A) has the same sequence as one from Hayling Island, Great Britain, and differs by one base pair towards the 5' end of the *rbc*L (Table 3). Brodie *et al.* (1998) did not feel that a single transition in the *rbc*L region warranted separation of *P. purpurea* into two separate species in the absence of any discernible morphological differences between the isolates. However, more molecular and morphological data would be useful to confirm this. All of the isolates of *P. purpurea* tested in Brodie *et al*. (1998), apart from that from Hayling Island, had identical sequences for this region. *Porphyra* sp. 1. (P10A), illustrated in fig. 4 in Brodie *et al.* (2001) and in this paper (Fig. 1B) has a sequence that matches the last 18 base pairs at the 5' end of the *rbc*L and the first 54 base pairs of *rbc*L-*rbc*S end of *P. birdiae* Neefus and Mathieson (GenBank accession number: AY180909), a species that was recently described from Nova Scotia (Neefus *et al*., 2002). Molecular data for P10A also match that of a specimen collected from Trondheim, Norway (sent to JB by Inka Bartsch). These results indicate that *P. birdiae* is present in the Faroes and provide new information on the distribution of this species which appears to be another example of a northern species in the flora.

Two species (PO2 and PO9) (Fig.1C, D), one identified as *P. insolita* and the other as *P. dioica* on the basis of their gross morphology, have the *rbc*L stop codon TAA which is characteristic for species that have been called *P. umbilicalis* from elsewhere in the northern Atlantic. However, PO2 and PO9 have one base pair difference at the 12th position in the *rbc*L-*rbc*S spacer. These results raise two issues. The first relates to whether the one base pair difference in this instance is enough to warrant species separation. The same situation is true for *P. purpurea* and *P. dioica* which only have one base pair difference between them in the rubisco spacer region. However, analysis of 18S rDNA and the whole *rbc*L gene revealed that the two species were distinct and more separated than *P. purpurea* and *P.*

Table 4. *Species described from the northern Atlantic not included in Table 2 because the taxonomic status is uncertain. (See also Brodie and Irvine 2003.)*

SPECIES	DESCRIBED FROM	MAY REPRESENT	NOTES
P. abyssicola Kjellman	Arctic	*P. miniata* or *P. amplissima*	Requires reinvestigation
P. elongata Kylin	Sweden	*P. leucosticta* or *P. amplissima*	Requires reinvestigation
P. helenae Zinova	Arctic		Requires reinvestigation
P. hiemalis Kylin	Sweden	*P. linearis**	Requires reinvestigation
P. insolita Kornmann & Sahling	Helgoland	*P. umbilicalis*	Requires reinvestigation
P. ochotensis Nagai	Helgoland	*P. dioica*	= *P. dioica* on Helgoland
P. thulaea Munda & Pedersen	Greenland & Iceland		Appears to be a good species

* See Guiry and Nic Dhonncha (2003).

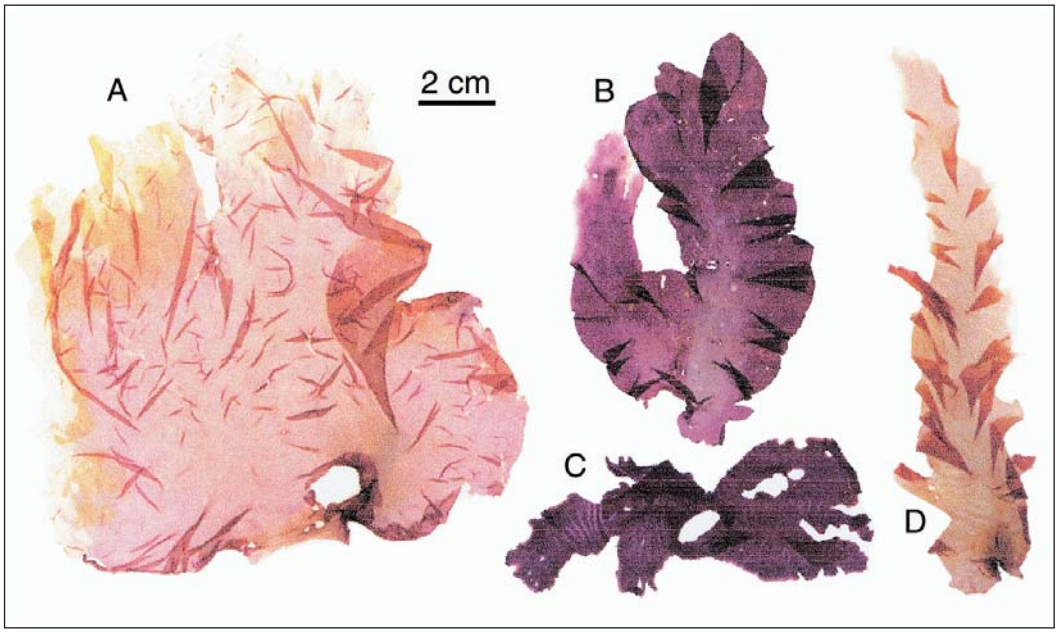

Fig. 1. *Herbarium specimens in the Botanical Museum, Copenhagen (C). A:* Porphyra purpurea *(PO8), B:* Porphyra *sp. 1 (10A)* = P. birdiae*, C:* P. insolita *(PO2), D:* Porphyra dioica *(PO9).*

umbilicalis (Klein *et al.,* 2003). Clearly more sequence data are required for specimens going under the name of *P. umbilicalis*. A similar conclusion was reached for other species of *Porphyra* by following work on sibling species in the NE. Pacific and N. Atlantic (Lindstrom and Cole, 1992; Lindstrom and Fredericq, 2003).

The second issue concerns the concept of *P. umbilicalis* and how the type relates to the species that go under this name. The typotype of *P. umbilicalis* is a Dillenius specimen in the herbarium at Oxford that was collected from Sheerness, Kent in the 18th Century (see John *et al.,* 1979). We have not been able to try to obtain DNA from this specimen and therefore do not know how it relates to material going under this name. We are of the opinion that if we are unable to obtain DNA from this specimen then we should set up an epitype, preferably from the type locality, and acquire sequence data to which all future specimens can be referred. This will also overcome the problem of using the public databases, such as GenBank, where there may be a number of different sequences that have been submitted under a particular species name.

If both the first and second of these issues can be resolved then we will be in a position to get a more true picture of the diversity of the Faroes in relation to the genus *Porphyra.*

In addition, there are a number of other species reported from the N. Atlantic (Table 4), most or all of which require rein-

vestigation to determine their exact identity. For further details see Brodie and Irvine (2003).

With regard to the presence of *Porphyra* in the N. Atlantic, it is possible that species may have arrived via a number of routes on numerous occasions during geological time, including i) via seaways linking the Pacific with the North Atlantic, ii) ocean currents and iii) anthropogenic methods. The oldest taxonomically resolved fossil taxon is a bangiacean red alga *Bangiomorpha pubescens* Butterfield from deposits in what is now arctic Canada dated 1198 ± 24 million years old (Butterfield, 2000; see also Brodie and Irvine, 2003). The origins of the N. Atlantic were in the Cretaceous. It is therefore possible that species could have travelled via the Tethys Sea (which divided Laurasia from Gondwana during the Triassic; see Cox and Moore, 1993), the Tsurgai Strait (Marincovich *et al.,* 1990), the Bering Straits via the Arctic Ocean after their opening in the mid-to-late Miocene or earliest Pliocene (Marincovich and Gladenkov, 1999) and via the Panamanian Isthmus before its closure c. 3.5 mya. See also Lindstrom (2001). The Arctic Ocean is also recognised as a 'bridge' for marine organisms between the Atlantic and Pacific Oceans (Wilce, 1990). From this route species could have spread from the Arctic to the northeastern and northwestern Atlantic.

Species might also have travelled from the S. Atlantic to the N. Atlantic, travelling in cool, deepwater currents that pass under the equator. It has been suggested that anomalous distributions of organisms, e.g. bipolar, could be accounted for in such a manner (e.g. Cooke *et al.,* 2002).

We can only speculate as to what happened to these species during the Ice Age. It might be assumed that species survived in southern regions beyond the ice sheets and then recolonised once the ice retreated. We know that spores of *Porphyra* can be kept frozen and will grow once unfrozen and that this method is used in the Nori industry (Lobban and Harrison, 1997). We do not know, however, how long species can be frozen and remain viable but this would be another potential method whereby species could reinvade once the ice melted.

Arrival could have been via anthropogenic vectors at any time over the last few thousand years. Here the life history of *Porphyra* is important. The haploid blade phase is what is seen on the shore and can often be the dominant alga. The sporophyte is an inconspicuous shell or rock-penetrating filamentous phase known as the conchocelis. Thus the potential to arrive on N. Atlantic shores is for example by shells such as oysters (e.g. Pacific oysters) or in barnacles fouling boat hulls or in ballast water and there is well documented evidence of *Porphyra yezoensis* from the N. Pacific occurring in the N. Atlantic (e.g. Klein *et al*., 2003).

In conclusion, the number of bangiophyte species found in the Faroes suggests that for this sub-class the seaweed flora is more diverse than hitherto known and than might have been anticipated from the small size of the area. This partly reflects the greater understanding of the taxonomy of the species and the use of DNA in identifi-

cation, but may also reflect the position of the Faroe Islands as a focus of colonisation. The evidence points to there being as great or greater diversity than elsewhere in the northern Atlantic and a reinvestigation of *Porphyra* diversity in particular in Greenland, Iceland, Norway, Sweden, Denmark and other related areas would give a clearer picture. However, in order to elucidate this diversity and to gain a greater understanding of the biogeography of the Bangiophycidae in the N. Atlantic there are taxonomic problems to be resolved.

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