

A NEW LOOK AT AN ANCIENT ORDER: GENERIC REVISION OF THE BANGIALES (RHODOPHYTA)¹

*Judith E. Sutherland*²

Department of Biochemistry, University of Otago, PO Box 56, Dunedin 9054, New Zealand

Sandra C. Lindstrom

Department of Botany, University of British Columbia, #3529—6270 University Blvd., Vancouver, British Columbia,
Canada V6T 1Z4

*Wendy A. Nelson*³

National Institute of Water and Atmospheric Research (NIWA), Private Bag 14-901, Wellington 6241, New Zealand

Juliet Brodie

Natural History Museum, Department of Botany, Cromwell Road, London SW7 5BD, UK

Michael D. J. Lynch

Department of Biology, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1

Mi Sook Hwang

Seaweed Research Center, NFRDI, Mokpo 530-831, Korea

Han-Gu Choi

Division of Life Sciences, Korea Polar Research Institute, KORDI, Incheon 406-840, Korea

Masahiko Miyata, Norio Kikuchi

Coastal Branch of Natural History Museum and Institute, Yoshio, Katsuura, Chiba 299-5242, Japan

Mariana C. Oliveira

Department of Botany, Biosciences Institute, University of São Paulo, São Paulo, SP 05508-900, Brazil

Tracy Farr

National Institute of Water and Atmospheric Research (NIWA), Private Bag 14-901, Wellington 6241, New Zealand

Chris Neefus, Agnes Mols-Mortensen

Department of Plant Biology, University of New Hampshire, Durham, New Hampshire 03824, USA

Daniela Milstein

Department of Botany, Biosciences Institute, University of São Paulo, São Paulo, SP 05508-900, Brazil

and Kirsten M. Müller

Department of Biology, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1

The red algal order Bangiales has been revised as a result of detailed regional studies and the development of expert local knowledge of Bangiales floras, followed by collaborative global analyses based on wide taxon sampling and molecular analyses.

Combined analyses of the nuclear SSU rRNA gene and the plastid RUBISCO LSU (*rbcL*) gene for 157 Bangiales taxa have been conducted. Fifteen genera of Bangiales, seven filamentous and eight foliose, are recognized. This classification includes five newly described and two resurrected genera. This revision constitutes a major change in understanding relationships and evolution in this order. The genus *Porphyra* is now restricted to five described species and a number of undescribed species. Other foliose

¹Received 17 September 2010. Accepted 21 January 2011.

²Present address: School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand.

³Author for correspondence: e-mail w.nelson@niwa.co.nz.

taxa previously placed in *Porphyra* are now recognized to belong to the genera *Boreophyllum* gen. nov., *Clymene* gen. nov., *Fusciifolium* gen. nov., *Lysithea* gen. nov., *Miuraea* gen. nov., *Pyropia*, and *Wildemania*. Four of the seven filamentous genera recognized in our analyses already have generic names (*Bangia*, *Dione*, *Minerva*, and *Pseudobangia*), and are all currently monotypic. The unnamed filamentous genera are clearly composed of multiple species, and few of these species have names. Further research is required: the genus to which the marine taxon *Bangia fuscopurpurea* belongs is not known, and there are also a large number of species previously described as *Porphyra* for which nuclear SSU ribosomal RNA (nrSSU) or *rbcL* sequence data should be obtained so that they can be assigned to the appropriate genus.

Key index words: *Bangia*; Bangiales; *Boreophyllum*; *Clymene*; *Dione*; *Fusciifolium*; *Lysithea*; *Minerva*; *Miuraea*; *Porphyra*; *Pseudobangia*; *Pyropia*; *Wildemania*

Abbreviations: nrSSU, nuclear SSU ribosomal RNA; *rbcL*, RUBISCO LSU

The Bangiales (Nägeli 1847) is a distinctive order of morphologically simple red algae that represents an ancient lineage (Butterfield 2000); it is the sister taxon of the morphologically complex red algal class Florideophyceae (Yoon et al. 2006). The Bangiales also includes the most highly valued seaweed aquaculture crop in the world: foliose Bangiales have been harvested and traded in Japan, China, Korea, and Southeast Asia for thousands of years (Mumford and Miura 1988), and they are also harvested in Chile, Wales, Pacific North America, and New Zealand (Colenso 1880, Williams 1979, Hoffmann and Santelices 1997, Brodie and Irvine 2003, Turner 2003).

As indicated by their widespread economic and cultural significance, members of the Bangiales are geographically ubiquitous, occurring worldwide from tropical to polar seas. Most species are intertidal, growing on rock, shell, or other algae, but some are found solely in subtidal habitats, and some are obligate epiphytes. Only one of the ~130 currently accepted species in the order occurs in freshwater habitats. Although early studies of the Bangiales (Hus 1902, Ueda 1932, Fukuhara 1968, Krishnamurthy 1972, Kurogi 1972, Conway et al. 1975) suggested that the Northern Hemisphere, particularly the North Pacific, was the center of diversity of the order, recent explorations of Southern Hemisphere Bangiales have revealed many more taxa there than previously recognized (Broom et al. 2004, 2010, Jones et al. 2004, Nelson and Broom 2005, Nelson et al. 2006). Efforts worldwide have continued to add new species to regional floras

(Lindstrom and Cole 1990, 1992b,c, Hwang and Lee 1994, 2001, Stiller and Waaland 1996, Brodie and Irvine 1997, Griffin et al. 1999, Neefus et al. 2002, Lindstrom and Fredericq 2003, Müller et al. 2005, Brodie et al. 2007, Kikuchi et al. 2010).

Molecular studies over the past decade have confirmed the monophyly of the Bangiales and of the lineage containing both the Bangiales and the Florideophyceae (Oliveira and Bhattacharya 2000, Müller et al. 2001, Saunders and Hommersand 2004). This finding has led to recognition that the Bangiophyceae should contain only the order Bangiales, and groups previously placed in that class are now identified as members of the Compsopogonophyceae, Porphyridiophyceae, Rhodellophyceae, and Stylonematophyceae. The Bangiophyceae is one of the six classes that comprise the subphylum Rhodophytina in the phylum Rhodophyta (Yoon et al. 2006).

A single family, the Bangiaceae (Engler 1892), is defined within the Bangiales. Traditionally, two genera have been recognized in the Bangiaceae on the basis of gametophyte morphology: unbranched uniseriate to multiseriate filaments have been placed in the genus *Bangia* Lyngb., and blades in the genus *Porphyra* C. Agardh. These and more recently described unbranched filamentous members of the order, *Minerva* W. A. Nelson, *Dione* W. A. Nelson, and *Pseudobangia* K. M. Müll. et Sheath (Müller et al. 2005, Nelson et al. 2005), are all characterized by bipolar spore germination, rhizoidal attachment cells internal to the cell wall, and a lack of pit connections between cells. All gametophytic thalli are parenchymatous, with intercalary cell divisions. Male gametes and products of the fertilization of female gametes occur in packets arising from the division in three planes of a cell that was originally vegetative. Some thalli reproduce asexually by archeospores, agamospores, neutral spores, or endospores (terminology after Nelson et al. 1999).

Gametophytes alternate with a microscopic, filamentous, shell-boring sporophytic phase, the conchocelis. Drew (1949, 1954) was the first to link this microscopic phase, previously known as *Conchocelis rosea* Batters, with the macroscopic gametophytic phase of a species of *Porphyra*. Subsequent research has also documented this life history for species of *Bangia* (Richardson and Dixon 1968). The conchocelis phase reproduces via conchospores, which develop into the blade phase, or via archeospores or neutral spores, which develop into the conchocelis phase. The blade phase can also develop via the differentiation of protothalli that form on the conchocelis (Cole and Conway 1980, Nelson et al. 1999). The conchocelis phase shares a number of features with the morphologically complex red algal class Florideophyceae: filamentous construction with apical growth, pit connections with a cap layer, and cellulosic microfibrils; these characters are lacking in the gametophytic phase of the Bangiales.

Until the advent of molecular tools, the recognition of species of both *Bangia* and *Porphyra* based primarily on morphological characters was challenging. Species of *Bangia* were particularly difficult to differentiate due to their uniform cylindrical morphology. Species of *Porphyra* had a few more characters for distinguishing species, such as number of cell layers (one or two), blade shape, margins, number of plastids per cell (one or two), reproductive cell division formulae, arrangement of reproductive cells, and seasonality. However, these characters alone have proved to be misleading based on the discovery, using molecular sequences, of many cryptic taxa among species with very similar morphologies (e.g., Brodie and Irvine 1997, Broom et al. 2002, 2004, Neefus et al. 2002, Lindstrom and Fredericq 2003, Lindstrom 2008).

Oliveira et al. (1995) were among the first to recognize that neither *Bangia* nor *Porphyra* was monophyletic. Although noting that *Bangia* had nomenclatural priority, they did not merge the eight species of *Porphyra* they sequenced into that genus due to the small number of taxa sampled, the wide molecular divergences among the sampled taxa, and the potential havoc created by changing the name of a commercially important taxon. Subsequent studies (e.g., Müller et al. 1998, Broom et al. 1999, 2004, Oliveira and Bhattacharya 2000, Lindstrom and Fredericq 2003, Nelson et al. 2006, Lindstrom 2008) have confirmed the monophyly of the Bangiales and provided further evidence that the generic concepts currently applied to both *Bangia* and *Porphyra* are untenable. Recent efforts have separated three monotypic filamentous genera with distinctive combinations of cytological, morphological, and molecular characters: *Pseudobangia* (Müller et al. 2005) and *Dione* and *Minerva* (Nelson et al. 2005).

Despite these additions, it has been clear for the past decade that a fundamental revision of the Bangiales is required and that the revision needs to be worldwide in scope. As noted above, significant progress has been made by various research groups in understanding local Bangiales floras. Almost all of these studies have used either nrSSU or the plastid *rbcL* gene. The use of the more conservative nrSSU locus has generally resulted in phylogenies with a well-supported “backbone,” but little differentiation of closely related taxa. The protein-coding *rbcL* gene clearly distinguishes species, but support for ancient divergences is often less than is obtained in analyses based on the nrSSU gene (Lindstrom and Fredericq 2003, Nelson et al. 2006).

Recognizing the need to deal with the nonmonophyly of *Bangia* and *Porphyra* and the necessity of resolving genus delineations before species circumscriptions can be properly prepared, we formed the Bangiales Consortium in March 2007. Our goal was to generate sequence data, using *rbcL* and nrSSU genes, for as many Bangiales taxa from as broad a geographic range as possible and to work toward a

consensus regarding the systematics of the Bangiales based on a sound phylogenetic analysis, with a focus on segregate genera and the characters supporting their recognition. The data presented in this paper reflect the consensus of the Consortium and the progress we have made to date.

MATERIALS AND METHODS

Specimen selection, vouchers, and molecular methods. Specimens were identified by Consortium members on morphological, anatomical, and ecological criteria according to modern species concepts in the Bangiales. Where possible, collections were made at or near the type locality of described species, and in some cases, type specimens were sampled. Of the 157 Bangiales entities included in these analyses, 82 are named taxa and 75 are currently undescribed. Both named and undescribed taxa are supported by voucher specimens, which have been lodged in publicly accessible herbaria. Collection information for specimens is given in Table S1 (in the supplementary material).

The identifications of named species included in our study are held with varying levels of certainty. We are confident that identifications of recently described species are correct where molecular sequence data were included in the original species delineation. This is also the case for species described many years ago that have been the subject of recent taxonomic or nomenclatural treatments. For other taxa, we have attempted to resample type localities or nearby locations to support identifications based on morphology and anatomy. However, further work is required to determine the identity of some older taxa. A number of these older species names appear several times in the analyses, pending modern treatment (Fig. 1; Table S1).

Sequences of the nrSSU and the *rbcL* genes from 157 Bangiales taxa were supplied by Consortium members or obtained from GenBank. Where possible, both the nrSSU and *rbcL* sequences were derived from a single specimen, or from two specimens for which at least partial data were available for both genes, to avoid concatenating sequences from different taxa. Where multiple similar sequences existed for a single species, sequences were selected based on level of certainty of the identification, proximity to the type locality of that species, and/or on sequence length. All taxa are represented by sequences from both genes except *Pseudobangia kaycoleia* K. M. Müll. et Sheath, for which no *rbcL* sequence was available. We chose to include this taxon in our analysis, as it is a member of a genus that is currently monotypic and is morphologically well differentiated from other members of the Bangiales. GenBank numbers, lengths of sequences, and collection locations of specimens used in our analysis are given in Table S1. Extraction, amplification, and sequencing were accomplished by members of the Consortium following published protocols (Hwang et al. 2005, Milstein and Oliveira 2005, Brodie et al. 2007, Lindstrom 2008, Lynch et al. 2008, Broom et al. 2010, Kikuchi et al. 2010).

Sequence alignment and the phylogenetic matrix. Sequences were initially aligned in Se-AL v2.0a11 (Rambaut 2007). Alignment of the *rbcL* gene was unambiguous. The nrSSU gene sequence alignment was constructed by aligning sequences to a seed structural alignment provided by the Comparative RNA Web site (Cannone et al. 2002). The alignment was subsequently evaluated manually using Jalview v.2.4 (Waterhouse et al. 2009) to ensure agreement with these structural models. Group I introns and regions of uncertain alignment were removed from the phylogenetic matrix before analysis.

Phylogenetic analysis. Three data sets were constructed—the nrSSU data set, the *rbcL* data set, and a combined data set with

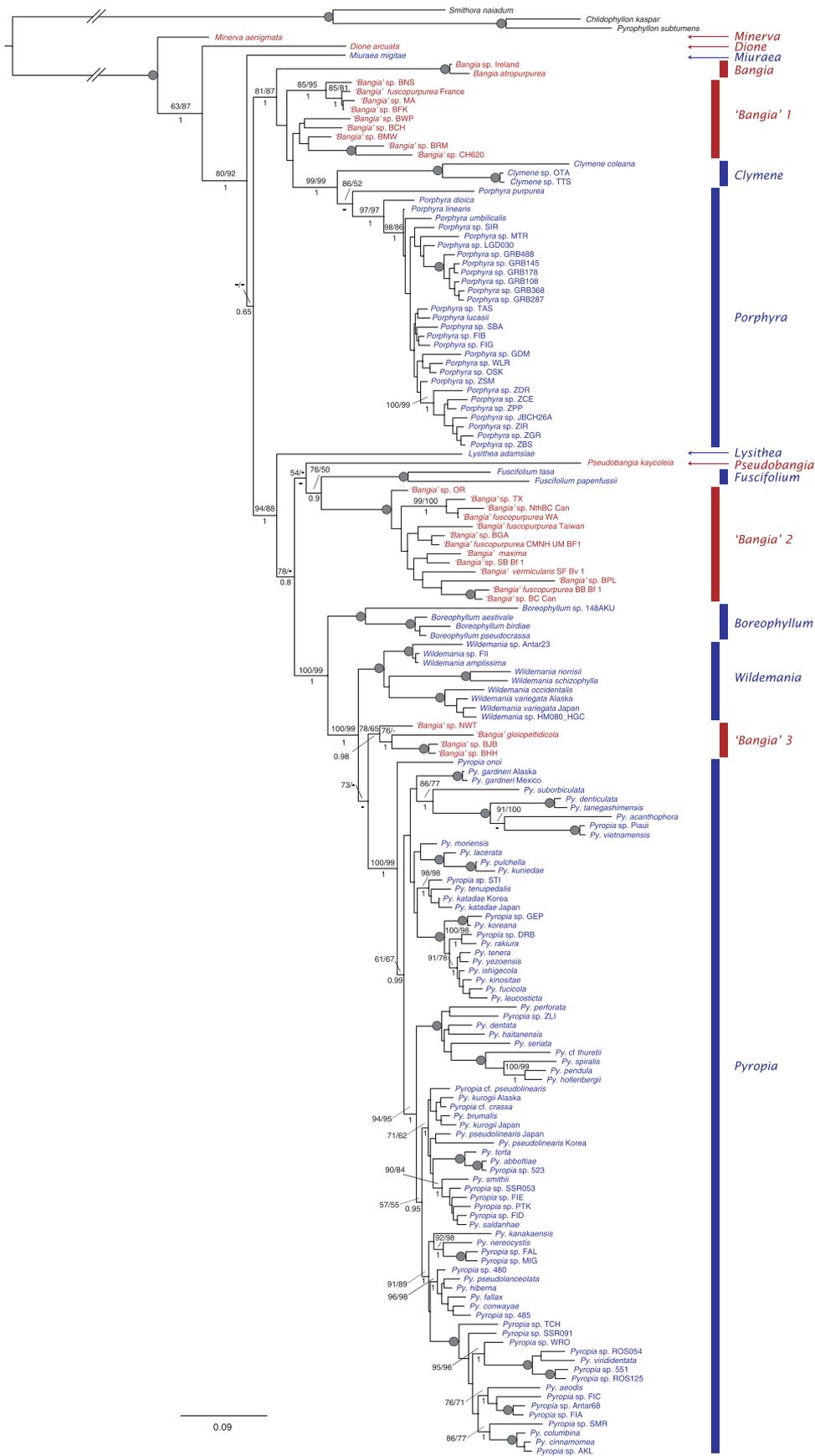


Fig. 1. Maximum-likelihood phylogram of 157 Bangiales taxa calculated from the concatenated nuclear SSU ribosomal RNA (nrSSU) and RUBISCO LSU (*rbcL*) data set under RAXML. Bootstrap values for RAXML and GARDLI are shown above, and Bayesian PP values below the nodes. Some internal support values are omitted for clarity. Gray circles indicate nodes supported at 100% RAXML/100% GARDLI/1 PP. Genera are indicated by lines, and monotypic genera by arrows. Names of filamentous taxa are shown in red, and those of foliose taxa in blue.

the genes concatenated. Three Erythropeltidales taxa [*Smithora naiadum* (C. L. Anderson) Hollenb., *Pyrophyllon subtumens* (J. Agardh ex Laing) W. A. Nelson, and *Chlidophyllon kaspar* (W. A. Nelson et N. M. Adams) W. A. Nelson] were included as outgroups. The use of Erythropeltidales taxa rather than florideophyte taxa allowed the inclusion of more nrSSU characters because there are fewer indels present between these taxa and Bangiales sequences. Preliminary analyses using florideophyte outgroups produced essentially the same topology in terms of generic level resolution (data not shown). Since there were no *rbcL* data available for *Ps. kaycoleia* the *rbcL* analysis consisted of only 159 taxa.

MrModeltest v2.3 (Nylander 2004) was used to identify appropriate models of sequence evolution for all three data sets. The GTR+I+ Γ model was selected as most appropriate for all of the data sets under both the Akaike information criterion and the hierarchical likelihood ratio test, and this model was used for initial analyses; however, the inclusion of the invariant sites parameter was found to interfere with convergence in the Bayesian analyses, and the GTR+ Γ model was used for subsequent analyses.

Partitioning strategy, from partitioning according to gene (two partitions) through to five partitions, had little impact on the resolution of major groups in the analysis, and only the results of the five-partition analysis are presented here. The five partitions were: nrSSU paired sites, nrSSU unpaired sites, *rbcL* codon 1, *rbcL* codon 2, and *rbcL* codon 3. The two single-gene data sets were concatenated for analysis, but were also analyzed individually under their respective partitioning strategies.

Bayesian analyses. Bayesian trees were constructed for both the single gene data sets and the concatenated data set using MrBayes V3.1.2 (Huelsenbeck and Ronquist 2001). Analyses were started from random trees, and consisted of two runs, each of four chains (one heated, three cold), of 5 million generations for each data set. Several temperature parameters were tested, and 0.1 was selected as the value that gave good mixing as assessed by inspection of the frequencies of successful chain swaps in preliminary analyses. The doublet model was initially employed for nrSSU paired sites under Bayesian analysis, but in these analyses, parameter estimates for the first partition failed to stabilize, and runs failed to converge to a stable stationary distribution. We therefore chose to analyze all partitions under a GTR+ Γ model, with all parameters allowed to vary independently between partitions. Tracer V1.4 (Rambaut 2007) was used to assess whether the stationary phase had been reached and to identify an appropriate burnin value.

Maximum-likelihood (ML) analyses. The data set was analyzed under the ML criterion using RAxML v.7.2.2 (Stamatakis 2006) and GARLI-PART Version 0.97 (Zwickl 2006; beta version kindly supplied by Derek Zwickl), since both of these programs allow partitioning of the data.

ML phylogenies were inferred with RAxML using the modified 16-state GTR model (16A) for structurally interacting (paired) nucleotides and the GTR+ Γ model for noninteracting nrSSU rRNA and *rbcL* sites. The secondary structure of "*B. fuscopurpurea*" NWT (GenBank Accession no. AF043355) was used as the consensus secondary structure model for analysis. The choice of structural model did not affect the resolution of major clades. One hundred independent ML iterations were performed, and the phylogeny with the best scoring likelihood was maintained. Default parameters were used, as they outperformed a collection of manually set parameters in preliminary testing. To provide support for inferred nodes, one thousand parametric ML bootstrap replicates were performed using RAxML v.7.2.2.

Using GARLI-PART V 0.97, both single gene data sets and the concatenated data set were analyzed under the GTR+ Γ model, with parameters allowed to vary independently between partitions. Five replicate analyses were run, in which 20,000

generations without topology improvement were required for termination. Five hundred bootstrap replicates were run under the same conditions.

Maximum-parsimony (MP) analyses. MP trees were estimated for the concatenated data set using the parsimony ratchet strategy implemented in PAUPRat (Nixon 1999), and PAUP* 4.0b10 (Swofford 2002), running 20 replicates of 200 iterations each, perturbing 15% of the characters in each iteration. The strict consensus tree from the parsimony ratchet searches stabilized by the 10th replicate, indicating that no further low scoring tree islands were found after this point. A strict consensus tree was constructed from all trees with the shortest tree length found in each of the 20 search replicates. Because of the size and complexity of the data set, bootstrap analysis was not attempted under MP.

RESULTS

The concatenated phylogenetic data set consisted of 160 taxa (157 ingroup and three outgroup taxa) and 2,979 characters: 1,592 from the nrSSU and 1,387 from the *rbcL* gene. The phylogenetic matrix is available from Treebase (<http://purl.org/phylo/treebase/phylo/study/TB2:S11223>). Variation in GC content across the data set was not significant ($P = 1.00000$). The ML phylogram calculated by RAxML is shown in Figure 1. A number of well-supported clades are resolved within the Bangiales. A cartoon of the phylogram, indicating the clades that we describe here as segregate genera with relevant support values, is shown in Figure 2. All generic level groups discussed in the text were also resolved in the MP analysis (not shown).

Topologies derived from the two single-gene data sets resolved the same generic level clades as the concatenated data set, albeit with reduced support, except that the nrSSU data set failed to resolve relationships among *Wildemania*, *Bangia* 3, and *Pyropia*, with none of these monophyletic. The following results pertain to the phylogeny derived from the concatenated data set (Fig. 1). Clades are treated in approximately the order in which they occur in the tree.

Two previously described filamentous genera, *Minerva* and *Dione*, are resolved on long branches and are at present defined as monotypic genera. The recently described Japanese foliose species *Miuraea migita* (Kikuchi et al. 2010) is resolved on a long branch, not closely related to any other taxa.

Bangia, containing the freshwater type species *Bangia atropurpurea* (Mert. ex Roth) C. Agardh, is resolved as a clade containing two sequences from freshwater habitats in Europe. *Bangia* is resolved within a well-supported clade that also includes two foliose clades (*Clymene* and *Porphyra*), and nine marine filamentous species ("*Bangia*" 1) from both the Atlantic and the Pacific, and from both Northern and Southern Hemispheres. These nine filamentous species are not resolved as monophyletic in our analysis, and it is likely that taxon sampling in this group is inadequate at present to resolve relationships among them. Within this larger clade, foliose

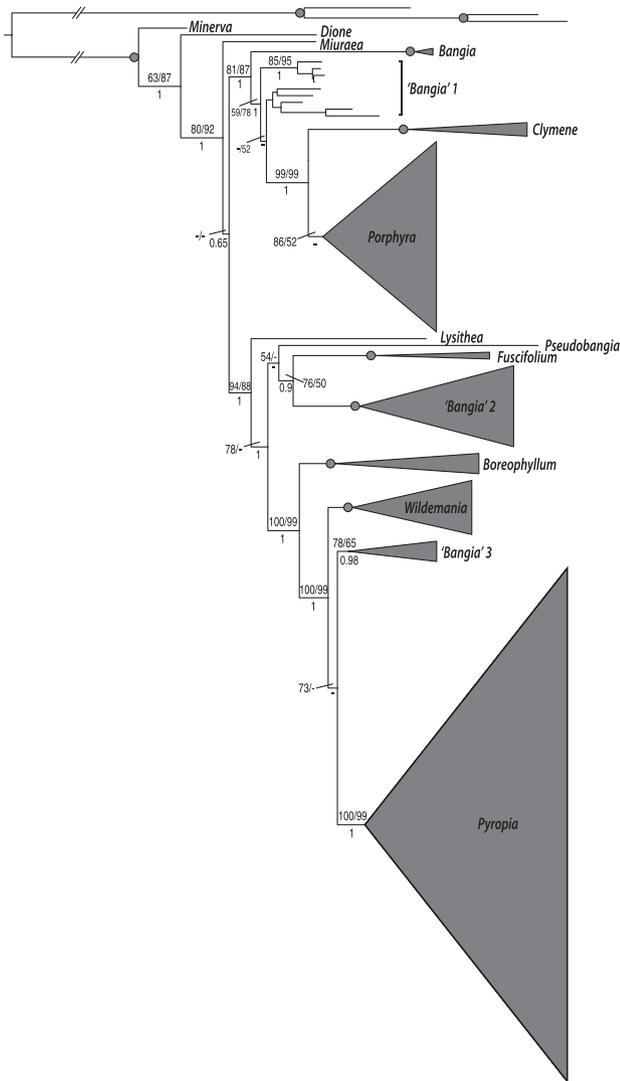


FIG. 2. Cartoon of the RAxML maximum-likelihood phylogram of 157 Bangiales taxa calculated from the concatenated nuclear SSU ribosomal RNA (nrSSU) and RUBISCO LSU (*rbcL*) data set showing existing and proposed new genera with support for nodes along the backbone of the tree. Gray circles indicate nodes supported at 100/100/1.

taxa are resolved as monophyletic with strong support.

Three New Zealand and Australian species, *Clymene coleana* gen. et comb. nov. and two undescribed species, are resolved as a monophyletic group with full support from all analyses. The nrSSU sequences of members of this group are also distinguished by a 35–37 bp insertion extending helix 42 of the nrSSU (Nelson et al. 2006) that is not present in any other Bangiales sequences. This insertion is excluded from the phylogenetic data set. We recognize *Clymene* as a new genus based on this strong phylogenetic support and distinctiveness of reproductive anatomy (Nelson et al. 2001).

A clade containing *Porphyra umbilicalis* Kütz., *Porphyra linearis* Grev., *Porphyra dioica* J. Brodie et L. M. Irvine as well as 25 species from the Southern Hemisphere is well supported. *Porphyra purpurea*, the type species of the genus *Porphyra*, is resolved as sister to these taxa in ML analyses under both RAxML and GARLI, although not under Bayesian analysis. Despite the relatively low support for this relationship, we have chosen not to recognize *P. purpurea* as a monotypic genus at this time. The addition of more taxa to this part of the tree may clarify these relationships in the future.

The remaining Bangiales species are resolved in a well-supported monophyletic group consisting of two filamentous and four foliose clades, and two singleton taxa. These singleton taxa are the foliose species *Lysithea adamsiae* comb. nov. from the New Zealand subantarctic, which is weakly supported as a sister taxon to the group, and the filamentous taxon *Ps. kaycoleia* from the Virgin Islands, which is resolved, with negligible support, as a sister taxon to the foliose genus *Fuscifolium* and the filamentous clade “*Bangia*” 2. *Ps. kaycoleia* is represented only by nrSSU sequence, which will tend to reduce support for placement of this taxon: the possibility that *Ps. kaycoleia* is sister to the large clade including *L. adamsiae* is not supported by this analysis but cannot be ruled out. There is weak-to-moderate support for *Fuscifolium* gen. nov. as sister to “*Bangia*” 2; each of these clades is strongly supported.

There is good support for each of four remaining clades: “*Bangia*” 3, which includes the obligate epiphyte “*Bangia*” *gloiopeltidicola* from Japan and three unnamed filamentous species, and the foliose clades *Boreophyllum* S. C. Lindstrom, N. Kikuchi, M. Miyata et Neefus; *Wildemania* De Toni; and *Pyropia* J. Agardh. Although the position of *Boreophyllum* is well resolved, the relationships among the other three taxa are not.

Within *Pyropia*, which is strongly supported as monophyletic, a number of clades are resolved with substantial support, such as the clade containing *Pyropia perforata* comb. nov., and that containing the commercially important species *Pyropia yezoensis* comb. nov. and *Pyropia tenera* comb. nov.

Taxonomic treatment. Fifteen genera of Bangiales, seven filamentous and eight foliose, are presented here in the order in which they appear in Figures 1 and 2. In addition to the four existing filamentous genera *Bangia*, *Dione*, *Minerva*, and *Pseudobangia*, we recognize three filamentous genera, which are not described here. Further investigations may identify reproductive, anatomical, and morphological synapomorphies for these clades. Two of these undescribed genera contain currently recognized species, and the genus to which the marine taxon *B. fuscopurpurea* (Dillwyn) Lyngb. belongs is not known. It will be necessary to determine the identity of *B. fuscopurpurea* and filamentous species described in the genus *Aspalatia* Erceg. (1927)

before we can apply genus and species names to these three unnamed genera. For foliose taxa, the genus *Porphyra* is redefined, two earlier generic names (*Pyropia*, *Wildemania*) are resurrected, and five new genera are described in this treatment (*Boreophyllum*, *Clymene*, *Fuscolium*, *Lysithea*, and *Miuraea*).

Minerva W. A. Nelson in Nelson et al. 2005: 141.

A monotypic genus endemic to the New Zealand region, *Minerva* has a widespread distribution from the northern North Island to the southern South Island. Collections of this species have been made throughout the year at different locations growing on rock in the upper intertidal zone on exposed to moderately sheltered open coasts.

Description (following Nelson et al. 2005). Gametophytic filaments simple, flaccid, 1.5–3 (10) cm long, affixed to rocky substrata in upper intertidal zone. Filaments uniseriate in lower part, multiseriate above; 13–23 μm wide in rhizoidal area, 17–40 μm wide in sterile region, widening to 30–55 (63) μm (male), (42) 45–68 (77) μm (female) in fertile upper filament. Sexual thalli monoecious, spermatangia and presumed zygotosporangia intermixed in some filaments and occurring in separate regions in other filaments. Spermatangia pale, presumed zygotosporangia darkly pigmented. Archeospores produced only in upper part of filament. Spores of filaments germinating to produce conchocelis or developing directly into filaments. Distinguished from other filamentous Bangiales by molecular sequence differences.

Type species: Minerva aenigmata W. A. Nelson in Nelson et al. 2005: 141–2.

Holotype: WELT A025775, collected by W. A. Nelson and T. J. Farr, 8 May 2001, Puheke, Great Exhibition Bay, North Island, New Zealand.

Dione W. A. Nelson in Nelson et al. 2005: 142.

A monotypic genus, endemic to the New Zealand region, this taxon has a highly restricted geographic distribution and is currently known from only two locations, ~4 km apart on the east coast of the South Island north of the Kaikoura Peninsula. *Dione arcuata* has been found only in summer (November and December).

Description (following Nelson et al. 2005). Gametophytic filaments broad, coarse, curved, unbranched to 1.5 cm long, attached to rocky substrata in shaded upper subtidal zone, basal attachment rhizoids extending from cells that have divided to form tiers of 2–4 cells as well as from undivided cells. Filaments uniseriate 47–60 μm wide immediately above rhizoidal area, widening and becoming multiseriate to 80 μm broad. Sexual thalli monoecious, either with male and female regions mixed or separate. Spermatangial regions 115–150 μm wide, presumed zygotosporangial regions 120–210 μm wide. Archeospores produced in upper part of filament. In culture spores of most filaments developing directly into new filaments; conchocelis rare. Distinguished

from other filamentous Bangiales by molecular sequence differences.

Type species: Dione arcuata W. A. Nelson in Nelson et al. 2005: 142–4.

Holotype: WELT A023126, collected by K. F. Neill and T. J. Farr, 5 Nov. 2002, Ohau Stream, Kaikoura, South Island, New Zealand.

Miuraea N. Kikuchi, S. Arai, G. Yoshida, J. A. Shin et M. Miyata **gen. nov.**

Thalli gametophytarum monostromatici, membranei, elliptici, anguste elliptici, obovati, orbiculares vel lobati, usque 25 cm longi, 13 cm lati et 47 μm crassi, basi cordati vel obtusi. Margo integer. Cellulae vegetativae plastidio solo stellato praeditae. Color igneus. Monoeciae, spermatii usque ad 128 in quoque spermatangio, divisionis regula 128 (a/4,b/4,c/8) et zygotosporis 16 in quoque zygotosporangio, divisionis regula 16 (a/2,b/2,c/4). Subaestuales, nonnisi in conchis bivalvibus mortuis et funibus relatae et cognitae nonnisi Japonia occidentali. Distinguitur a Bangialibus aliis laminatis differentiis in sequentiis molecularibus.

Description. Gametophytic thalli monostromatic, membranous, elliptic, narrow elliptic, obovate, orbicular, or lobed, to 25 cm long, 13 cm wide, and 47 μm thick, with cordate or obtuse base. Margin entire. Vegetative cells with a single stellate plastid. Color fire red. Monoecious, with up to 128 spermatia in each spermatangium, with division formula 128 (a/4,b/4,c/8), and with up to 16 zygotospores in each zygotosporangium, with division formula 16 (a/2,b/2,c/4). Subtidal, reported only on dead bivalve shells and rope, and known only from western Japan. Distinguished from other bladed Bangiales by molecular sequence differences.

Type species: Miuraea migitae (N. Kikuchi, S. Arai, G. Yoshida et J. A. Shin) N. Kikuchi, S. Arai, G. Yoshida, J. A. Shin et M. Miyata comb. nov.

Basionym: Porphyra migitae N. Kikuchi, S. Arai, G. Yoshida et J. A. Shin 2010: 347, 349, figs. 1–31.

Holotype: SAP 105477, collected by S. Arai and G. Yoshida, 26 Aug. 2003, from a depth of 6 m off Nagasaki (34°19' N, 135°09' E), Misaki, Osaka, Japan.

Etymology: *Miuraea* is dedicated to the late Professor Akio Miura, Tokyo University of Fisheries, in recognition of his many contributions to the taxonomy of the Bangiales, especially foliose species in Japan.

Bangia Lyngb. 1819: 82.

Although the name *Bangia* has at times been applied to all filamentous Bangiales, the freshwater *B. atropurpurea* is not only distinct in habitat and cytology (Gargiulo et al. 1998, Müller et al. 2003) but is also in a separate clade from all other filamentous Bangiales. Silva (1952) designated *B. fuscopurpurea* (Dillwyn) Lyngb. (*Conferva fuscopurpurea* Dillwyn 1802–1809: pl. 92) the lectotype of *Bangia*, unaware that Pfeiffer (1871–1873: 361) had chosen *B. atropurpurea* (Mert. ex Roth) C. Agardh (*Conferva atropurpurea* Mert. ex Roth 1806: 208, pl. VI) as

lectotype. Based on Silva's lectotypification, Nelson (2007) described *Bangiadulcis* for freshwater Bangiales. Silva and Nelson (2008) clarified the lectotypification and conservation of the genus *Bangia*, established that *Bangiadulcis* is a superfluous name for *Bangia* and pointed to the need for future studies to determine the name and circumscription of the genus that includes *B. fuscopurpurea*.

Description. Gametophytic filaments narrow, sometimes remaining uniseriate, unbranched, to 6 cm long and 40 μm diameter. Haploid chromosome number $n = 3$, with one chromosome shorter than the other two ($\sim 0.5 \mu\text{m}$) (Gargiulo et al. 1998, Müller et al. 2003). Sexual thalli dioecious, observed only in culture; only asexual populations known in nature, producing archeospores. Epilithic or epiphytic, occurring in freshwater, sometimes forming a band at or above the waterline. Distinguished from other filamentous Bangiales by molecular sequence differences.

Type species: *Bangia atropurpurea* (Mert. ex Roth) C. Agardh 1824: 76.

Basionym: *Conferva atropurpurea* Mert. ex Roth 1806: 208–9, pl. VI.

Lectotype: Collected by Mertens from the Weser River at Bremen; lectotypified by Pfeiffer (1871–1873: 361) (Silva and Nelson 2008).

Neotype: BM 000637980, collected by K. M. Müller and A. R. Sherwood, 24 May 1998, Ysselmeer, Enschede, the Netherlands. Müller et al. (2003) selected this neotype for *B. atropurpurea* from the closest location to the original type locality. Roth's original material is believed to have been lost during World War II.

“Bangia” 1.

In the current analysis, these taxa are not resolved as monophyletic, and it is not yet possible to say whether they represent one or more genera. This grouping includes four species that are consistently resolved together with moderate to high support. One of these has been identified as *B. fuscopurpurea* (from France), one has been collected from the Atlantic coast of North America (Massachusetts), one is from an Australian collection, and the fourth taxon has been found in Korea (east coast), New Zealand and Australia. All the New Zealand and Australian samples of this latter species come from modified habitats (such as wharves, jetties, marinas, breakwaters).

The rest of this loose grouping consists of four species that are currently known solely from New Zealand, and one species from Korea. None of these species are formally described, and we have not yet determined whether there are morphological or anatomical characters that can be used to differentiate them from members of other filamentous clades.

Clymene W. A. Nelson **gen. nov.**

Thalli gametophytarum monostromatici, lobati, fere ad basin thalli dissecti. Margo dentatus, valde corrugatus, tendentia volutus fieri. Color subroseo-

griseus, in sole claro aureo-fulvescenti. Cellulae vegetativae plastidio solo stellato praeditae. Monoeciae. Zonae fertiles marginales conspicuae. Regio spermatangialis cremeo-alba et regio phyllosporangialis marronina, laminis maculescentibus distaliter ubi sporae emissae; spermatangia et phyllosporangia non immixta. Epilithicae, superae interaestuales, cognitae nonnisi neozelandia australiae. Distinguitur a Bangialibus aliis laminatis extensione unica helices 42 in geno nucleari ribosomal SSU et differentiis in sequentiis aliis molecularibus.

Description. Gametophytic thalli monostromatic, lobed, divided nearly to base of thallus. Margin dentate; ruffled, with a tendency to become rolled. Color pink-gray, becoming golden-khaki in bright sun. Vegetative cells with a single stellate plastid. Monoecious. Marginal fertile zones conspicuous. Spermatangial region cream-white and phyllosporangial region maroon, with blades becoming speckled distally when spores released; spermatangia and phyllosporangia not intermixed. Epilithic, upper intertidal, known only from New Zealand and Australia. Distinguished from other bladed Bangiales by a unique 35–37 bp extension of helix 42 in the nrSSU gene and by other molecular sequence differences.

Type species: *Clymene coleana* (W. A. Nelson) W. A. Nelson comb. nov.

Basionym: *Porphyra coleana* W. A. Nelson in Nelson et al. 2001: 269.

Holotype: WELT A020329, collected by W. A. Nelson, 13 Jul. 1987, Kaikoura, South Island, New Zealand.

Etymology: From Greek mythology, *Clymene* is one of the Oceanids, daughter of Oceanus and Tethys.

Included species: Of the three species currently known to belong to this genus, only one has been named: *C. coleana*, a New Zealand endemic species with a widespread distribution in the North, South and Chatham Islands. One of the other two species (OTA) is only known currently from a restricted number of sites in the southern South Island of New Zealand, and the other species (TTS) is known solely from sites in Tasmania, Australia.

Porphyra C. Agardh 1824: XXXII, 190 nom. cons.

The genus *Porphyra* is redefined to include *Porphyra purpurea*, the type of the genus, and members of the clade sister to it. *P. purpurea* occurs primarily in the North Atlantic (Brodie and Irvine 2003) with a few reports from the northeastern Pacific (Stiller and Waaland 1996, Lindstrom and Fredericq 2003, both as *Porphyra rediviva*, Bray et al. 2007, Lindstrom 2008). Species that are included in the genus *Porphyra* are widely distributed in mostly temperate areas of the world's oceans, including a large group of southern hemisphere species, mostly as yet undescribed, from South America, the South Atlantic, South Africa, Australia, New Zealand, and the subantarctic islands.

Description. Gametophytic thalli monostromatic, ovate to lanceolate, occasionally falcate. Margins

entire, planar, dentate, undulate, or ruffled. Vegetative cells with a single stellate plastid. Color olive green, reddish brown, or brown. Sexual thalli monoecious or dioecious, reproductive sori marginal or scattered, sometimes confined to distinct sectors of the blade; male sori composed of packets of spermatangia, each packet formed by successive division in three planes resulting in up to 128 male gametes; female gametangial sori containing gametes often with conspicuous trichogynes; each gamete after fertilization dividing to form a packet of 8–16 zygotosporangia.

Type species: Porphyra purpurea (Roth) C. Agardh (1824), p. 191.

Basionym: Ulva purpurea Roth (1797), tab. 6, fig. 1, nom. cons. (Irvine and Brodie 1997: 769).

Neotype: BM000054930, collected by A. Wagner, 17 Oct. 1996, Nord-Ost Watt, Helgoland, Germany (Brodie and Irvine 1997: 290).

Included species:

Porphyra dioica J. Brodie et L. M. Irvine 1997: 286.

Holotype: BM000054929, collected by J. Brodie, 9 Oct. 1996, Sidmouth, Devon, Great Britain.

Porphyra linearis Grev. 1830: 170, t. 18.

Lectotype: E, collected by Greville, “Spring” [in spring], Sidmouth, Devon, Great Britain (Brodie and Irvine 2003).

Porphyra lucasii Levring 1953: 469, figs. 6H–L, 7.

Lectotype: GB (Herb. Levring), collected by T. Levring, 21 Jul. 1948, litoral [sic] basalt rocks, Bunbury, Western Australia, Australia (Womersley and Conway 1975: 63; isotype: AD A42700).

Porphyra mumfordii S. C. Lindstrom et K. M. Cole 1992b: 445, figs. 15, 16, 38–44.

Holotype: UBC A80266, collected by S. C. Lindstrom, 23 Jan. 1991, high intertidal bedrock, Orlebar Point, Gabriola Island, British Columbia, Canada [Isotypes in UBC (A80280), UC, WTU]. This species is included in this genus based on results from other studies (Lindstrom and Fredericq 2003, Lindstrom 2008).

Porphyra umbilicalis Kütz. 1843: 383.

Neotype: Scotland: Easdale, Argyll, from the back of a limpet, collected by J. Brodie and P. K. Hayes, 23 Jul. 1998 (BM000769632). (Brodie et al. 2008: 1330).

***Lysithea* W. A. Nelson gen. nov.**

Thalli gametophytorum monostromatici, ovati usque orbiculares, usque 10 cm longi et 8 cm lati, fere ad basin thalli dissecti. Margo profunde corrugatus. Cellulae vegetativae plastidio solo stellato praeditae. Color roseus. Monoecii, regione fertili ad partem tertiariam exteriorem laminae. Zonae fertiles marginales conspicuae. Regio spermatangialis cremeo-alba et regio phyllosporangialis marronina, laminis maculescentibus distaliter ubi sporae emissae; spermatangia et zygotosporangia immixta sine cellulis vegetativis. Epiphyticae, subaestuales, cognitae non nisi insulis subantarcticis ad meridiem Neozelandiae. Distinguitur a Bangialibus aliis laminatis differentiis in sequentiis molecularibus.

Description. Gametophytic thalli monostromatic, ovate to orbicular, to 10 cm long and 8 cm wide, base becoming cuneate in mature thalli. Margin deeply ruffled. Vegetative cells with a single stellate plastid. Color rosy pink. Monoecious, with the fertile region in the outer third of the blade. Spermatangia and zygotosporangia intermixed without vegetative cells. Epiphytic, subtidal, known only from the subantarctic islands south of New Zealand. Distinguished from other bladed Bangiales by molecular sequence differences.

Type species: Lysithea adamsiae (W. A. Nelson) W. A. Nelson comb. nov.

Basionym: Porphyra adamsiae W. A. Nelson 1993: 526–7, figs. 2–4.

Holotype: WELT A016435a, collected by J. Yaldwyn, 2 Mar. 1985, Anchorage Bay, Antipodes Islands, New Zealand.

Etymology: In Greek mythology *Lysithea* is one of the Oceanids, daughter of Oceanus and one of Zeus’ lovers.

***Pseudobangia* K. M. Müll. et Sheath in Müller et al. 2005.**

Pseudobangia is a monotypic genus, currently known solely from a single collection from the Virgin Islands. This taxon possesses multiple plastids per cell.

Description. Gametophytic filaments erect, unbranched, to 1 cm long, uniseriate when young, 29–49 µm diameter, becoming multiseriate, 34.3 µm (3 cells) to 83.3 µm diameter (7 cells). Vegetative cells with multiple stellate plastids, each with a pyrenoid. Sexual reproduction unknown; asexual reproduction by archeospores. Epilithic, upper intertidal; known only from the British Virgin Islands. Distinguished from other filamentous Bangiales by molecular sequence differences.

Type species: Pseudobangia kaycoleia K. M. Müll. et Sheath, in Müller et al. 2005: 154.

Holotype: UBC A84723, collected by R. G. Sheath, 29 Dec. 1995, Cane Garden Bay, Tortola, British Virgin Islands.

***Fuscifolium* S. C. Lindstrom gen. nov.**

Thalli gametophytorum distromatici usque ad ~200 µm crassitudine, coriacea et plus minusve orbiculari, usque ad ~60 cm diametro. Margines integri, irregulares, nec plicati nec corrugati. Cellulae vegetativae plastidio solo stellato praeditae. Color fuscus. Thalli sexuales monoecii, structuris masculinis et foemineis in lobis diversis thalli, vel dioecii; cellulae reproductivae portatae in regionibus distinctive coloratis rubellis flavellisve prope apices lorum. Spermatangia in 16 ordinibus disposita, spermatii usque ad 256 formati in quaque cellula matricali. Zygotosporangia in ordine solo disposita, cellulis quatuor divisionibus duabus cruciatis ad angulum rectum paginae thalli formati, pseudotrichogynis elongatis quae extendunt aliquantum ultra paginam thalli. Epilithicae, mediae

interaestuales, in regionibus temperatis frigidis Oceani Pacifici borealis occurrentes. Distinguitur a Bangialibus aliis laminatis differentiis in sequentiis molecularibus.

Description. Gametophytic thalli distromatic, to ~200 µm thick, leathery and more or less orbicular, to ~60 cm diameter. Margins entire, irregular, not folded or ruffled. Vegetative cells with a single stellate plastid. Color dark brown. Sexual thalli monoecious, with male and female structures on different lobes of the thallus, or dioecious; reproductive cells in distinctively colored reddish or yellowish regions near tips of lobes. Spermatangia in 16 tiers with up to 256 spermatia formed per mother cell. Zygotosporangia in a single tier, the four cells formed by two cruciate divisions perpendicular to the thallus surface, with elongate prototrichogynes that extend well beyond the thallus surface. Epilithic, mid intertidal, occurring in cold-temperate regions of the North Pacific Ocean. Distinguished from other bladed Bangiales by molecular sequence differences.

This genus is created for two morphologically very similar species that occur in the cold-temperate waters of the North Pacific. Both are distromatic.

Type species: *Fuscolium papenfussii* (V. Krishnam.) S. C. Lindstrom comb. nov.

Basionym: *Porphyra papenfussii* V. Krishnam. 1972: 37, fig. 8.

Holotype: WTU 255131, collected by G. J. Hollenberg, 24 Jun. 1968, south side of Deadman's Bay, San Juan Island, Washington, USA.

Etymology: *Fuscolium* refers to the dusky, brownish blades of the gametophytic phase of this genus.

Included species:

Fuscolium tasa (Yendo) S. C. Lindstrom comb. nov.

Basionym: *Wildmania tasa* Yendo 1920: 3, pl. 22, figs. 1 (cotype), 2.

Lectotype: TI, collected by Y. Yamamoto, Jul. 1903, Onkotan Island, Kurile Is., Russia, lectotypified by T. Yoshida 1991: 10, pl. 26a.

"Bangia" 2.

In this clade, 13 entities are resolved in our analysis. This clade includes *Bangia maxima* N. L. Gardner (1927: 235), the largest filamentous species reported, which reaches up to 35 cm in length, as well as *Bangia vermicularis* Harv. (1858: 55, pl. XLIX.A), both described from sites in California, USA. In the analyses presented here there are also four entities that have been previously identified as *B. fuscopurpurea* from Taiwan, Japan, British Columbia (Canada), and Washington (USA). (We note, however, that the type of *B. fuscopurpurea* is from Dunraven Castle, Glamorganshire, Wales [Silva et al. 1996: 91], so these entities are unlikely to be that species.) These four entities are resolved as separate species, as well as additional taxa from New Zealand and the Pacific and Gulf of Mexico coasts of the USA. There are also collections from Alaska, USA, and Korea that belong in this clade although they have not been included in these analyses.

Boreophyllum S. C. Lindstrom, N. Kikuchi, M. Miyata et Neefus **gen. nov.**

Thalli gametophytarum monostromatici, irregulariter orbiculares, saepe lobi, aliquanto corrugati, crassiusculi (usque ad ~75 µm), usque ad 15–30+ cm diametro. Cellulae vegetativae plastidio solo stellato praeditae (duobus in *B. pseudocrasso*). Color olivaceus, brunneus, subroseo-brunneus vel porphyreus. Thalli sexuales monoecii, in sectionibus separatis masculinis femineisque linea verticali divisi, vel dioecii. Spermatangia et zygotosporangia formantia areas continuas secus margines laminae. Epilithicae, interaestuales, in regionibus temperatis frigidis Oceanorum borealium Pacificorum et Atlanticorum occurrentes. Distinguitur a Bangialibus aliis laminatis differentiis in sequentiis molecularibus.

Description. Gametophytic thalli monostromatic, irregularly orbicular, often lobed, somewhat ruffled, moderately thick (to ~75 µm), up to 15–30+ cm diameter. Vegetative cells with a single stellate plastid (two in *B. pseudocrassum*). Color olive green, brown, pinkish brown or purple. Sexual thalli monoecious, divided into separate male and female sectors by a vertical line, or dioecious. Spermatangia and zygotosporangia forming as continuous areas along the margins of the blade. Epilithic, intertidal, occurring in cold-temperature regions of the North Pacific and North Atlantic Oceans. Distinguished from other bladed Bangiales by molecular sequence differences.

This genus contains four species, three described and one yet to be named (Lindstrom 2008, as Unknown #4).

Type species: *Boreophyllum aestivale* (S. C. Lindstrom et Fredericq) S. C. Lindstrom comb. nov.

Basionym: *Porphyra aestivalis* S. C. Lindstrom et Fredericq 2003: 219–21, figs. 3–4.

Holotype: UBC A84351, collected by S. C. Lindstrom (SCL 9971), 27 Sep. 2000, Sunshine Cove, Lynn Canal, Alaska, USA.

Etymology: *Boreophyllum* refers to the northern distribution of this bladed genus.

Included species:

Boreophyllum birdiae (Neefus et A. C. Mathieson) Neefus comb. nov.

Basionym: *Porphyra birdiae* Neefus et A. C. Mathieson in Neefus et al. 2002: 206, figs. 1, 2, 4.

Holotype: NHA 76525, collected by C. D. Neefus, 21 Sep. 2002, Herring Cove, Nova Scotia, Canada.

Boreophyllum pseudocrassum (Yamada et Mikami) N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra pseudocrassa* Yamada et Mikami in Mikami 1956: 340, figs. 1, 2.

Holotype: SAP 027640, collected by H. Mikami, 3 Aug. 1955, Erimo, Hokkaido, Japan.

Wildmania De Toni 1890: 144, 148.

Wildmania (De Toni 1890) is resurrected for a group of primarily distromatic, reddish pink, low intertidal to subtidal species. The type is *Wildmania amplissima* (Kjellm.) Foslie, based on a specimen

originally identified by Kjellman (1883) as *Diploderma*, a later homonym of *Diploderma* Link 1816. Support for the monophyly of this genus is strong in the combined analyses and the *rbcL* analysis, but is lacking in the nrSSU analysis. We have chosen to retain this group as a single genus in view of the strong support for this clade in the concatenated analysis.

Description. Gametophytic thallus monostromatic, distromatic or partially monostromatic and distromatic, elliptical, ovate or lanceolate, up to 15 cm to several meters in length. Color of most species is pinkish red (rose pink), ranging from very pale to dark crimson; other species, olive green or brown. Vegetative cells with a single plastid. Sexual thalli monoecious, with individual cells forming either spermatangia or zygotosporangia and intermixed (not in separate patches), monoecious and divided into separate male and female sectors by a vertical line, or dioecious. Reproductive cells forming as continuous areas along the margins of the blade. Epilithic, epiphytic, or epizoid, mostly low intertidal to subtidal in spring and/or summer, occurring in cold-temperate and Arctic/Antarctic regions of the North Pacific, North Atlantic and Southern Oceans. Haploid chromosome number usually three, where known. Distinguished from other bladed Bangiales by distinctive differences in DNA sequences.

Type species: *Wildemanian amplissima* (Kjellm.) Foslie 1891: 49.

Basionym: *Diploderma amplissima* Kjellm. 1883: 236, pl. 17, figs. 1–3; pl. 18, figs. 1–8 [non *Diploderma* Link 1816].

Lectotype: UPS, collected Jul.–Aug. 1876, Maasø, Norwegian Arctic (Lindstrom and Cole 1992a: 1362).

Etymology: The name commemorates Émile Auguste(e) Joseph De Wildeman (1866–1947). Although known primarily as a higher plant systematist, this Belgian botanist also studied phycology.

Included species:

Wildemanian cuneiformis (Setch. et Hus) S. C. Lindstrom comb. nov.

Basionym: *Porphyra miniata* f. *cuneiformis* Setch. et Hus in Hus 1900: 68.

Holotype: UC 95626, collected by N. L. Gardner (No. 199a), Coupeville, Whidbey I., Washington, USA.

Wildemanian miniata (C. Agardh) Foslie 1891: 49.

Basionym: *Ulva purpurea* var. *miniata* C. Agardh 1817: 42.

Lectotype: LD 12838, collected by Wormskjold, Grønland (Hollenberg 1972: 44, see also Lindstrom and Cole 1992a: 1362–3).

Wildemanian norrisii (V. Krishnam.) S. C. Lindstrom comb. nov.

Basionym: *Porphyra norrisii* V. Krishnam. 1972: 35, figs. 3a–b, 6a–g.

Holotype: WTU 255129, collected by V. Krishnamurthy (11-00041), 20 Mar. 1968, False Bay (on the

specimen) versus Deadman's Bay (in the publication), San Juan Island, Washington, USA.

Wildemanian occidentalis (Setch. et Hus) S. C. Lindstrom comb. nov.

Basionym: *Porphyra occidentalis* Setch. et Hus in Hus 1900: 69.

Holotype: UC 95678, collected by Mrs. J. M. Weeks, 23 Apr. 1897, Carmel Bay, Monterey County, California, USA.

Wildemanian schizophylla (Hollenb.) S. C. Lindstrom comb. nov.

Basionym: *Porphyra schizophylla* Hollenb. in Smith and Hollenberg 1943: 213, figs. 6–7.

Holotype: DS in UC 306400, collected by G. J. Hollenberg (GJH 1914), 31 Jul. 1939, Pescadero Point, Monterey County, California, USA.

Wildemanian variegata (Kjellm.) De Toni 1890: 148.

Basionym: *Diploderma variegata* Kjellm. 1889: 33, pl. 2, figs. 1–4.

Holotype: UPS, collected by F. R. Kjellman, 14–19 Aug. 1879, Bering I., Commander Is., Russia (E. Conway, Sept. 1974, indicated that this specimen was the holotype—Kurogi 1977).

Wildemanian schizophylla and *W. norrisii* fit uneasily in this genus based on morphology and other features, although they are resolved in the genus based on molecular studies (Lindstrom and Fredericq 2003; Fig. 1). These mid- to high intertidal distromatic species are olive-green color and have a haploid chromosome number of two (Conway et al. 1975, Mumford and Cole 1977). The conchocelis consists of thick-walled, unusually large cells, 7–10 µm diameter, compared to the more usual 3–5 µm of other species of *Porphyra* sensu lato (Cole and Conway 1980). However, there are some reproductive similarities: *W. norrisii* (as *W. schizophylla*—Cole and Conway 1980), *W. cuneiformis* (Krishnamurthy 1969, S. C. Lindstrom and M. S. Stekoll, unpubl.), and *W. variegata* (possibly *W. occidentalis* instead since *W. variegata* has not been confirmed to occur where this specimen was collected—Cole and Conway 1980) have all been shown to display direct development of the blade phase from the conchocelis without release (or possibly even formation) of conchospores.

“Bangia” 3.

This clade is represented by four entities in our analyses, including the epiphytic *B. gloiopeltidicola* Tak. Tanaka (known from Japan, Korea, and China). This clade also contains a northern species occurring from Alaska, the Northwest Territories, Greenland, and New England (Müller et al. 1998) and two epilithic species from the South Island of New Zealand. These taxa appear to favor colder climates: all have been found at higher latitudes or with winter seasonality at lower latitudes. One of the New Zealand taxa grows intertidally as thick mats in coastal conditions, whereas the other is found intertidally in fiords experiencing strongly estuarine conditions.

Pyropia J. Agardh 1899: 149–53.

We resurrect the genus *Pyropia* for a large group of more than 75 species, including some that have yet to be described. *Pyropia* was originally described by J. Agardh (1899) for *Pyropia californica*, a species now considered to be a synonym of *Porphyra nereocystis* C. L. Anderson. *Pyropia* was distinguished from *Porphyra* by cells in the distal part of the blade having small appendages as illustrated by Agardh (1899, fig. 5c). Our examination of the type material has failed to reveal these cells with appendages, and the structure of the blade appears to correspond with typical *P. nereocystis*. Since the acceptance of the name does not depend on the verity of the original description, but rather on the validity of publication, and since the type species of the genus falls within this large clade of bladed Bangiales, we place the species in this clade in the genus *Pyropia*.

A second available name for this group is *Porphyrella*, which was originally described by Smith and Hollenberg (1943, p. 215) for *Porphyrella gardneri* G. M. Sm. et Hollenb., a species that was otherwise like *Porphyra* except that “carpogonia are formed by a cell division in which there is a curving wall, quite similar to the curving walls producing the monospores of *Erythrotrichia*, and the cells thus formed are liberated singly” with [zygospores] never being liberated in packets. This distinguishing feature also appears to be due to a misinterpretation, according to Hawkes (1977), who observed the species to form typical *Porphyra*-like zygotosporangial packets and therefore subsumed the genus in *Porphyra*. Hawkes inferred that zygotosporangial packets are rarely formed in specimens from the type locality because the optimal daylength for their formation is barely achieved at that latitude, and archeosporangia (monosporangia) are more common. Hawkes reported that the type specimen (G. M. Smith 39–12, DS 406502 in UC) is exclusively archeosporangial. This genus is here considered a synonym of *Pyropia*.

We provide a revised description of *Pyropia* below.

Description. Gametophytic thalli monostromatic, linear, ovate, orbicular, or funnel shaped, up to a few cm to several meters in length. Margins entire or dentate, planar, undulate, or ruffled. Color variable (pink, red, purple, green, brown or some combination thereof). Vegetative cells with a single plastid in most species (two in some). Some basal taxa producing blade archeospores or neutral spores. Sexual thalli (i) monoecious with groups of cells forming either spermatangia or zygotosporangia, these often in streaks or rectangular to diamond-shaped patches, (ii) monoecious and divided into separate male and female sectors by a vertical or horizontal line, (iii) monoecious with spermatangia and zygotosporangia intermixed in fertile regions of the blade, or (iv) dioecious. When monoecious and sectored or dioecious, spermatangia and zygotosporangia forming as continuous areas along the margins of the blade. Epilithic,

epiphytic or epizoid, occurring in the high, mid-, or low intertidal or subtidal in winter, spring, summer, or fall. Some species very short-lived and occurring in a single season whereas others long-lived and persisting through two or more seasons. Haploid chromosome number 2–4, where known. Distinguished from other bladed Bangiales by molecular sequence differences.

This genus is not only the most speciose of the Bangiales, but it also displays the greatest morphological variation and has the widest geographic distribution. Species range from tropical to cold-temperate waters and are reported from all major land masses.

The genus *Pyropia* is subdivided into a number of clades. Bootstrap support for these groups, while mostly strong, is not uniformly so, and recognition of separate genera for these clades would require the creation of at least an additional eight genera. We leave this course of action to future work, which will likely utilize expanded data sets and other molecular markers.

Type species: *Pyropia californica* J. Agardh = *P. nereocystis* (C. L. Anderson) S. C. Lindstrom comb. nov.

[Basionym: *Porphyra nereocystis* C. L. Anderson 1892: 149]

Type: (of *P. californica*) LD 12740, Santa Cruz, California, USA.

[Type of *P. nereocystis*: NY, implied to be Farallon Is., California, although more likely Santa Cruz]

Etymology: This genus derives its name from the Greek root for “fire,” in reference to its color.

Included species:

Pyropia abbottiae (V. Krishnam.) S. C. Lindstrom comb. nov.

Basionym: *Porphyra abbottiae* V. Krishnam. 1972: 28–30, figs. 1a, 2a–j.

Holotype: WTU 255127, collected by V. Krishnamurthy, 26 May 1968, Cattle Point, San Juan Island, Washington, USA (Isotype in WTU).

Pyropia acanthophora (E. C. Oliveira et Coll) M. C. Oliveira, D. Milstein et E. C. Oliveira comb. nov.

Basionym: *Porphyra acanthophora* E. C. Oliveira et Coll 1975: 192, figs. 6, 14–16, 19, 21.

Holotype: SPF 5170, collected E. C. Oliveira and J. Coll, 25 Oct. 1973, Ubatuba, São Paulo, Brazil.

Pyropia aeddis (N. J. Griffin, J. J. Bolton et R. J. Anderson) J. E. Sutherl. comb. nov.

Basionym: *Porphyra aeddis* N. J. Griffin, J. J. Bolton et R. J. Anderson 1999: 506, figs. 1–15.

Holotype: BOL, collected by N. J. Griffin, 16 May 1995, Kommetjie, Cape Peninsula, South Africa.

Pyropia brumalis (Mumford) S. C. Lindstrom comb. nov.

Basionym: *Porphyra brumalis* Mumford 1975: 328–331, figs. 17–27.

Holotype: UBC A52021, collected by T. F. Mumford, Jr., 15 Dec. 1971, Deadman Bay, San Juan Island, Washington, USA (Isotypes in CANA, US, WTU, UC).

Pyropia cinnamomea (W. A. Nelson) W. A. Nelson comb. nov.

Basionym: *Porphyra cinnamomea* W. A. Nelson in Nelson et al. 2001: 266–9, figs. 2–8.

Holotype: WELT A022352, collected by W. A. Nelson and G. Knight, 31 Aug. 1997, Ohau, Kaikoura, South Island, New Zealand.

Pyropia columbina (Mont.) W. A. Nelson comb. nov.

Basionym: *Porphyra columbina* Mont. 1842: 14.

Holotype: PC0029833 (MA6267), collected by Dumont D'Urville, Mar 1840, Auckland Islands, New Zealand (Nelson and Broom 2010).

Pyropia conwayae (S. C. Lindstrom et K. M. Cole) S. C. Lindstrom comb. nov.

Basionym: *Porphyra fallax* subsp. *conwayae* S. C. Lindstrom et K. M. Cole 1992b: 433, figs. 14, 31–37.

Holotype: UBC A43066, collected by E. Conway, 21 Jun. 1970, Point No Point (Glacier Point), British Columbia [Isotype in UBC (A43067)].

Pyropia crassa (Ueda) N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra crassa* Ueda 1932: 27, pl. 1, f. 9, 10, pl. 6, f. 1–7, pl. 18, f. 1.

Holotype: Tokyo University of Marine Science and Technology collected at Gyeonggi-do, Korea.

Pyropia dentata (Kjellm.) N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra dentata* Kjellm. 1897: 13, pl. 1, f. 7, 8, pl. 3, f. 1–4, pl. 5, f. 8–14.

Lectotype: S, collected by J. V. Petersen, 9 Jun. 1881, Amakusa, Kumamoto Pref., Japan [lectotypified by M. Kurogi 1985 (Marianne Hamnede, pers. comm. to SCL 13 Oct. 2009)] (Syntype in UPS).

Pyropia denticulata (Levring) J. A. Phillips et J. E. Sutherland comb. nov.

Basionym: *Porphyra denticulata* Levring 1953: 467, figs. 5, 6A–G.

Holotype: GB (Algal Collection No. 16–5), collected by A. B. Cribb, (no date), Noosa, Queensland, Australia.

Pyropia endiviifolia (A. Gepp et E. Gepp) H. G. Choi et M. S. Hwang comb. nov.

Basionym: *Monostroma endiviifolium* A. Gepp et E. Gepp 1905: 105, pl. 470, figs. 1–5.

Type: Collected by R. N. R. Brown, 4 Feb. 1903, Saddle I., South Orkney Islands.

This species clearly fits within this clade based on sequence data (H.-G. Choi and M. S. Hwang, unpubl.).

Pyropia elongata (Kylin) Neefus et J. Brodie comb. nov.

Basionym: *Porphyra elongata* Kylin 1907: 110, pl. 3, figs. 1a, b, c.

Lectotype: UPS, the left hand specimen of the sheet illustrated in fig. 1, collected by H. Kylin, 21 Jul. 1905, Koster, Bohuslän, Sweden (Neefus and Brodie 2009).

This species is included in this genus based on results of other studies, including those of its taxonomic synonym, *P. rosengurttii* Coll et J. Cox 1977:

157, figs. 9–16 (Brodie et al. 2007, Neefus and Brodie 2009).

Pyropia fallax (S. C. Lindstrom et K. M. Cole) S. C. Lindstrom comb. nov.

Basionym: *Porphyra fallax* S. C. Lindstrom et K. M. Cole 1990: 371–4, figs. 1, 3, 5, 7.

Holotype: UBC A69860, collected by E. C. S. Duffield, 5 Apr. 1983, Golden Gardens, Seattle, Washington, USA (Isotype in WTU).

Pyropia fucicola (V. Krishnam.) S. C. Lindstrom comb. nov.

Basionym: *Porphyra fucicola* V. Krishnam. 1972: 32–33, figs. 1b, 4.

Holotype: WTU 255128, collected by V. Krishnamurthy, 13 May 1968, Mukkah [Makah] Bay, Clallam County, Washington, USA.

Pyropia gardneri (G. M. Sm. et Hollenb.) S. C. Lindstrom comb. nov.

Basionym: *Porphyrella gardneri* G. M. Sm. et Hollenb. 1943: 215.

Holotype: DS in UC 306401, collected by G. M. Smith (GMS 39–12), Point Joe, Monterey County, California, USA.

Pyropia haitanensis (T. J. Chang et B. F. Zheng) N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra haitanensis* T. J. Chang et B. F. Zheng 1960: 32, 35, pls. I–V.

Holotype: Herb. Inst. Oceanology, Qingdao, China, M59-2070, collected 25 Feb. 1959, Dung Au, Pingtan District, Fukien Province, China.

Pyropia hiberna (S. C. Lindstrom et K. M. Cole) S. C. Lindstrom comb. nov.

Basionym: *Porphyra hiberna* S. C. Lindstrom et K. M. Cole 1992b: 435–6, figs. 11, 17–23.

Holotype: UBC A80269, collected by S. C. Lindstrom, 29 Dec. 1990, foot of 15th Street, Pacific Grove, Monterey County, California, USA (Isotypes in GMS, MICH, UC, US, WTU).

Pyropia hollenbergii (E. Y. Dawson) J. E. Sutherland, L. E. Aguilar Rosas et R. Aguilar Rosas comb. nov.

Basionym: *Porphyra hollenbergii* E. Y. Dawson 1953: 14, pl. 13, fig. 1.

Holotype: AHFH 50462 in UC, collected by E. Y. Dawson, 12 Feb. 1940, Bahia Agua Verde, Baja California (Gulf of California), Mexico (Isotypes in UC, US).

Pyropia ishigecola (A. Miura) N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra ishigecola* A. Miura 1967: 65, pls. 1, 2, 7.

Holotype: Tokyo University of Marine Science and Technology (A. Miura 1755), collected by A. Miura, 19 Mar. 1961, Enoshima, Kanagawa Pref., Japan.

Pyropia kanakaensis (Mumford) S. C. Lindstrom comb. nov.

Basionym: *Porphyra kanakaensis* Mumford 1973: 239, figs. 1–8.

Holotype: WTU 255136, collected by T. F. Mumford, Jr., 2 Aug. 1970, Kanaka Bay, San Juan Island, Washington, USA.

Pyropia katadae (A. Miura) M. S. Hwang, H. G. Choi, N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra katadae* A. Miura 1968: 55, pls. 1–7.

Holotype: Tokyo University of Marine Science and Technology, collected by A. Miura, 6 Mar. 1957, Ominato, Ise, Mie Pref., Japan.

Pyropia kinositae (Yamada et Tak. Tanaka) N. Kikuchi, M. Miyata, M. S. Hwang et H. G. Choi comb. nov.

Basionym: *Porphyra yezoensis* f. *kinositae* Yamada et Tak. Tanaka in Tanaka 1952: 41.

Lectotype: SAP 049206, collected by Y. Yamada, 20 Mar. 1944, Utsutsu, Suttsu, Hokkaido, Japan (Yoshida 1998: 444).

Pyropia koreana (M. S. Hwang et I. K. Lee) M. S. Hwang, H. G. Choi, Y. S. Oh et I. K. Lee comb. nov.

Basionym: *Porphyra koreana* M. S. Hwang et I. K. Lee 1994: 170–5, figs. 2–4.

Holotype: HKO0011 in SNU, collected by Y. S. Oh, 23 May 1992, Pukpyongdong, Tonghaeshi, Kangwondo, Korea [Isotypes in SNU (HKO0012–HKO0015)].

Pyropia kuniedae (Kurogi) M. S. Hwang et H. G. Choi comb. nov.

Basionym: *Porphyra kuniedae* Kurogi 1957: 23, fig. 1 (lower).

Holotype: SAP 044803, collected by M. Kurogi, 22 Dec. 1952, Ishihama-Katsurajima, Matsushima Bay, Miyagi Pref., Japan.

Pyropia kurogii (S. C. Lindstrom) S. C. Lindstrom comb. nov.

Basionym: *Porphyra kurogii* S. C. Lindstrom in Lindstrom and Cole 1992c: 2071–2, figs. 1–7.

Holotype: UBC A80293, collected by S. C. Lindstrom, 15 Apr. 1979, Bridget Cove, City and Borough of Juneau, Alaska, USA [Isotypes in MICH, SAP, UBC (A66039)].

Pyropia lacerata (A. Miura) N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra lacerata* A. Miura 1967: 67–69, pl. 3 figs. 1–17, pl. 8 figs. 1–4.

Holotype: Tokyo University of Marine Science and Technology (A. Miura 1767), collected by A. Miura, 27 Feb. 1962, Enoshima, Kanagawa Pref., Japan.

Pyropia lanceolata (Setch. et Hus) S. C. Lindstrom comb. nov.

Basionym: *Porphyra perforata* f. *lanceolata* Setch. et Hus in Hus 1900: 65.

Lectotype: MO in UC 24356, collected by H. T. A. Hus, 8 Feb. 1899, Land's End, San Francisco, California, USA (Lindstrom and Cole 1992b: 433).

Pyropia leucosticta (Thur.) Neefus et J. Brodie comb. nov.

Basionym: *Porphyra leucosticta* Thur. in Le Jolis 1863: 100.

Type: PC, collected by Thuret; 28 Feb. 1857, Rochers des Flamandes, Cherbourg, France [Isotypes in CHE (Brodie and Irvine 2003: 120)].

Pyropia moriensis (Ohmi) N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra moriensis* Ohmi 1954: 231, pls. 1–4.

Holotype: Faculty of Fisheries, Hokkaido University, collected by H. Ohmi, 7 Mar. 1954, Mori, Hokkaido, Japan. (This specimen currently cannot be found in HAK.)

Pyropia olivii (Orfanidis, Neefus et T. L. Bray) J. Brodie et Neefus comb. nov.

Basionym: *Porphyra olivii* Orfanidis, Neefus et T. L. Bray in Brodie et al. 2007: 9, figs. 2–17.

Holotype: BM000806050, collected by S. Orfanidis, 16 Mar. 2004, Taverna Chara, N. Krini, Thessaloniki, Greece (Isotypes in Fisheries Research Institute, Kavala, Greece; BM, C, MGC, MS, NHA, SAP, UBC, US, WELT).

This species is included in this genus based on results from another study (Brodie et al. 2007).

Pyropia onoi (Ueda) N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra onoi* Ueda 1932: 34, pl. 1, figs. 4, 12; pl. 8, figs. 2–10; pl. 21, figs. 3, 4.

Holotype: Tokyo University of Marine Science and Technology, collected by I. Ohno, 6 Feb. 1929, Takashima, Otaru, Hokkaido, Japan.

Pyropia pendula (E. Y. Dawson) J. E. Sutherl., L. E. Aguilar Rosas et R. Aguilar Rosas comb. nov.

Basionym: *Porphyra pendula* E. Y. Dawson 1953: 16, pl. 13, fig. 2.

Holotype: AHFH 4117 in UC, collected by E. Y. Dawson, 22 Feb. 1946, Isla Partida, Gulf of California, Mexico.

Pyropia perforata (J. Agardh) S. C. Lindstrom comb. nov.

Basionym: *Porphyra perforata* J. Agardh 1882: 69, pl. 2, figs. 62–64.

Lectotype: LD, No. 13037, Agardh Herbarium, collected by S. Berggren in 1874 near the Golden Gate, San Francisco, California, USA (Conway 1974).

Pyropia pseudolanceolata (V. Krishnam.) S. C. Lindstrom comb. nov.

Basionym: *Porphyra pseudolanceolata* V. Krishnam. 1972: 40–1, figs. 7a, 10a–h.

Holotype: WTU 255133, collected by V. Krishnamurthy, 22 Jan. 1968, Deadman Bay, San Juan Island, Washington, USA.

Pyropia pseudolinearis (Ueda) N. Kikuchi, M. Miyata, M. S. Hwang et H. G. Choi comb. nov.

Basionym: *Porphyra pseudolinearis* Ueda 1932: 29, pl. 6, figs. 17, 18; pl. 7, figs. 1–5; pl. 19, figs. 1, 2.

Holotype: Tokyo University of Marine Science and Technology, collected by I. Ohno, 1 Feb. 1929, Takashima, Otaru, Hokkaido, Japan.

Pyropia pulchella (Ackland, J. A. West, J. L. Scott et Zuccarello) T. J. Farr et J. E. Sutherl. comb. nov.

Basionym: *Porphyra pulchella* Ackland, J. A. West, J. L. Scott et Zuccarello 2006: 196.

Holotype: NSW 722255, collected by J. A. West, 16 Dec. 1998, Nelson's Lagoon, Mimosa Rock National Park, New South Wales, Australia.

Pyropia rakiura (W. A. Nelson) W. A. Nelson comb. nov.

Basionym: *Porphyra rakiura* W. A. Nelson in Nelson et al. 2001: 271–2, figs. 19–24.

Holotype: WELT A022679, collected by W.A. Nelson, 4 Oct. 1994, Vaila Voe, Stewart Island, New Zealand.

Pyropia saldanhae (Stegenga, J. J. Bolton et R. J. Anderson) J. E. Sutherl. comb. nov.

Basionym: *Porphyra saldanhae* Stegenga, J. J. Bolton et R. J. Anderson 1997: 227, pl. 9.

Holotype: BOL (Stegenga Sa 2098), collected by J. J. Bolton and H. Stegenga, Yzerfontein, Cape Province, South Africa.

Pyropia seriata (Kjellm.) N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra seriata* Kjellm. 1897: 17, pl. 3, figs. 8–10; pl. 4, fig. 1; pl. 5, figs. 16–21.

Lectotype: LE, “Japonia: se. specimina (n:o 45).” [Kurogi and Yamada (1986) mentioned the type locality was unknown. Kjellman (1897) stated the specimens of this species were sent by Professor C. Gobi for examination.]

Pyropia smithii (Hollenb. et I. A. Abbott) S. C. Lindstrom comb. nov.

Basionym: *Porphyra smithii* Hollenb. et I. A. Abbott 1968: 1241, fig. 7.

Holotype: US 077804, collected by G. J. Hollenberg, Mission Point, Monterey County, California, USA.

Pyropia spiralis (E. C. Oliveira et Coll) M. C. Oliveira, D. Milstein et E. C. Oliveira comb. nov.

Basionym: *Porphyra spiralis* Oliveira and Coll 1975: 194, figs. 1, 2, 7–9, 11–13.

Holotype: SPF 4837, collected L. Behar 14 Sep. 1973, Praia da Costa, Espirito Santo, Brazil.

Pyropia drewiana Coll et E. C. Oliveira 2001: 68, figs. 1–11 is a variety of *Porphyra spiralis* (M. Oliveira, unpubl.).

Pyropia suborbiculata (Kjellm.) J. E. Sutherl., H. G. Choi, M. S. Hwang et W. A. Nelson comb. nov.

Basionym: *Porphyra suborbiculata* Kjellm. 1897: 10–13, pl. 1, figs. 1–3; pl. 2, figs. 5–9; pl. 5, figs. 4–7.

Lectotype: UPS, collected by J. V. Petersen, 25 May 1881, Goto, Nagasaki Pref., Japan (Broom et al. 2002) (Syntypes in UPS, L, S).

Pyropia tanegashimensis (Shinmura) N. Kikuchi et E. Fujiyoshi comb. nov.

Basionym: *Porphyra tanegashimensis* Shinmura 1974: 735, figs. 1, 3–5, 9.

Holotype: Kagoshima Prefectural Fisheries Experimental Station (Shinmura no. 19731), collected by I. Shinmura, 29 Sep. 1971, Iseki, Tanegashima, Kagoshima Pref., Japan.

Pyropia tenera (Kjellm.) N. Kikuchi, M. Miyata, M. S. Hwang et H. G. Choi comb. nov.

Basionym: *Porphyra tenera* Kjellm. 1897: 20, pl. 1, fig. 6; pl. 4, figs. 2–5; pl. 5, figs. 22–26.

Lectotype: S, Kurogi and Yamada (1986) mentioned the type locality was unknown. Kurogi had lectotypified the species with a specimen in S in 1985 (Syntype in UPS).

Pyropia tenuipedalis (A. Miura) N. Kikuchi et M. Miyata comb. nov.

Basionym: *Porphyra tenuipedalis* A. Miura 1961: 305, pl. 11, figs. 1–2; pl. 12, figs. 1–9; pl. 13, figs. A–G.

Holotype: Tokyo University of Marine Science and Technology (A. Miura 2375), collected by A. Miura, 6 Mar. 1958, Haneda, Tokyo, Japan.

Pyropia thulaea (Munda et P. M. Pedersen) Neefus comb. nov.

Basionym: *Porphyra thulaea* Munda et P. M. Pedersen 1978: 286, figs. 1–9.

Type: Collected by T. Christensen, 24 Aug. 1958, Godthåb, West Greenland.

This species fits within this clade based on an *rbcl* gene sequence from an isotype (Brodie et al. 2008, A. Mols-Mortensen and C. D. Neefus, unpubl.).

Pyropia thuretii (Setch. et E. Y. Dawson) J. E. Sutherl., L. E. Aguilar Rosas et R. Aguilar Rosas comb. nov.

Basionym: *Porphyra thuretii* Setch. et E. Y. Dawson in Smith. 1944: 171, pl. 40, fig. 2.

Lectotype: UC 791973, collected by W. A. Setchell, 19 May 1900, Carmel Bay, Monterey County, California, USA (Krishnamurthy 1972).

Pyropia torta (V. Krishnam.) S. C. Lindstrom comb. nov.

Basionym: *Porphyra torta* V. Krishnam. 1972: 45–6, figs. 1c, 12a–n.

Holotype: WTU 255135, collected by V. Krishnamurthy, 26 May 1968, point near False Bay, San Juan Island, Washington, USA.

Pyropia vietnamensis (Tak. Tanaka et P. H. Hô) J. E. Sutherl. et Monotilla comb. nov.

Basionym: *Porphyra vietnamensis* Tak. Tanaka et P. H. Hô 1962: 34, figs. 10–11.

Holotype: SAP 052157, collected by Pham-Hoang Hô, Jan 1960 Vung-Tau (Cap St. Jacques), Vietnam.

Pyropia virididentata (W. A. Nelson) W. A. Nelson comb. nov.

Basionym: *Porphyra virididentata* W. A. Nelson in Nelson et al. 2001: 273–6, figs. 25–30.

Holotype: WELT A022362, collected by W. A. Nelson and G. Knight, 13 Nov. 1997, Island Bay, Wellington, North Island, New Zealand.

Pyropia yezoensis (Ueda) M. S. Hwang et H. G. Choi comb. nov.

Basionym: *Porphyra yezoensis* Ueda 1932: 23, pl. 1, figs. 9, 14; pl. 4, figs. 11–17; pl. 16, figs. 3, 4.

Holotype: Tokyo University of Marine Science and Technology, collected by I. Ohno, Muroan? Hokkaido, Japan.

DISCUSSION

We recognize 15 genera in the Bangiales, a major change in understanding relationships and evolution in this order. The revision presented here is the result of detailed regional studies and the development of expert local knowledge of Bangiales floras, followed by collaborative global analyses based

on wide taxon sampling and molecular analyses. Although this revision may appear radical to those unfamiliar with recent research on the systematics of the Bangiales, the need for new segregate genera in this order has long been signaled, and in our opinion, the results presented here are a conservative interpretation of the data. We consider that the classification presented here and the establishment of new genera based largely on molecular phylogenetic data provide a much clearer framework within which to understand members of this order and will stimulate a closer examination of relationships within as well as between genera. It is highly likely that subsequent studies will conclude that more genera need to be recognized to accommodate the diversity and divergence within this order.

Our results limit the genus *Porphyra* to a subset of foliose Bangiales species, requiring that all other species of foliose Bangiales be assigned to new genera. This will have implications across a range of applied fields and areas of science, including the aquaculture industry, fisheries management of wild stock harvests, the food industry, as well as for biodiversity recognition and ecological studies. Our results provide valuable information for the aquaculture industry, which can now be guided by a clearer understanding of the relationships in the selection of species for breeding and cultivation. In the past, people working on species of *Porphyra* sensu lato have almost certainly compared members of different genera with potentially widely divergent biochemical or physiological characters despite their morphological similarity (e.g., Hemmingson and Nelson 2002).

We stress the need for caution when interpreting earlier literature on *Porphyra* and *Bangia*, as well as the identification of material deposited in GenBank as *Porphyra* or *Bangia*. Unless voucher material has been deposited in accessible herbaria, literature and database entries cannot be verified. There is considerable potential for confusion about which taxa are being referred to, at both the species and genus levels. The incorrect application of names has been one of the confounding problems in Bangiales taxonomy, and it has made studies of the ecology and comparative physiology of species exceedingly difficult. The need for molecular sequence data in Bangiales taxonomic studies is clear. Although in the future the generic and specific attributes of taxa in the Bangiales may be more fully understood, and there may be less reliance on sequence data, at present, these data are essential for the identification of specimens to species and sometimes even to genus.

This revision focused on the circumscription of genera for foliose members of the Bangiales, but an equivalent effort is required for filamentous members. Although four of the seven filamentous genera recognized in our analyses already have generic names (*Bangia*, *Dione*, *Minerva*, and *Pseudobangia*), these four genera are all currently monotypic. This

is not the case for the unnamed filamentous genera—all are clearly comprised of multiple species, and few of these species have names. However, the description of new genera for filamentous Bangiales cannot proceed until there is clarification of the identity of the genus *Aspalatia* and its species. *Aspalatia* Erceg. (1927: 82) was originally assigned to the Cyanophyceae, but was considered by Frémy (1934) to represent a developmental stage of *Bangia*. The three described species of *Aspalatia* remain poorly documented: *Aspalatia crassior* Erceg. (type of genus), *Aspalatia andalousica* P. González, and *Aspalatia tenuior* Erceg. Moreover, the description of new species cannot proceed until there is a clear understanding of the type of “*B. fuscopurpurea*,” a name that has been applied to species in at least three different genera. We do not concur with Lynch et al. (2008), who recommended recognition of multiple cryptic species within the genus *Bangia*. Their position is not supported by the molecular data presented here or by earlier authors (Broom et al. 2004, Matsuyama-Serisawa et al. 2004, Nelson and Broom 2005), as it would result in a nonmonophyletic genus. It is critical that more detailed studies are carried out on the attributes of filamentous taxa in order that unifying characters of each clade (genus) can be established.

Matsuyama-Serisawa et al. (2004) examined the 15 morphological, anatomical, and reproductive characters that have been most frequently used to distinguish members of the Bangiales (including those used to define subgenera by Kurogi 1972) in relation to an nrSSU gene phylogeny derived from 57 strains of both filamentous and foliose taxa. They found that none of the 15 characters reflected the phylogeny based on the molecular data. We anticipate that future work will identify characters that are taxonomically informative. Some potentially useful characters include cell wall polysaccharide chemistry (Hemmingson and Nelson 2002), life history and conchocelis phase features (Cole and Conway 1980, Notoya et al. 1993, Notoya 1997, Knight and Nelson 1999, Kikuchi et al. 2010), and developmental morphology of trichogynes in *Porphyra* and *Pyropia* (M. J. Holmes and J. Brodie, pers. obs.). However, at present, these characters have not been assessed for a sufficient number of taxa to make it possible to evaluate their utility across the order (not to mention the question of identity of the species on which some of the earlier studies were carried out).

The positions of *Dione* and *Minerva* as sister taxa to the remaining Bangiales suggest that the filamentous form was the ancestral condition for members of the Bangiales, and our analyses show that the foliose form has arisen multiple times. Whether the transition between blade and filament has occurred in both directions in the history of the order or has been strictly unidirectional remains to be determined.

To fully understand the occurrence and distribution of Bangiales, targeted seasonal collections from a range of habitats are required, and this type of thorough collecting has not been conducted uniformly throughout the world. This is particularly true for filamentous members of the order. In regions where there have been thorough collections, the diversity is high, for example, in New Zealand (Broom et al. 2004, this study). It is not clear whether similar diversity will be found in other regions when comprehensive field collections are conducted, but it is highly probable that regional diversity is significantly underrepresented at present.

Of the 15 genera we have distinguished, six are currently monotypic, and two others have only two (*Fuscifolium*) or three species (*Clymene*). Within the more speciose genera, particularly *Porphyra* and *Pyropia*, there are taxa that are highly restricted in distribution as well as more widely distributed taxa. There are clades within these genera that reflect both separate Southern and Northern Hemisphere radiations, as well as taxa that occur in both hemispheres. A major challenge influencing our ability to interpret the evolution and distribution of extant taxa in the Bangiales is the antiquity of the order. As noted by Hommersand (2007, p. 514), when considering the ancient floristic relationships between western North Pacific and western South Pacific Bangiales floras, “some patterns may reflect an ancient bipolar distribution, but the phylogenetic analysis is complex and will require a very large sample to be phylogeographically informative.” Hommersand (2007, p. 512) discussed the evidence for the origin of major groups of red algae and noted that “the basal genus or cluster of species commonly occurs in a cold- or cool-temperate temperature regime.” Hommersand also discussed a number of families that appear to have ancestral or relict taxa in Australasia and Antarctica and appear to have evolved in the southern hemisphere. Our revision helps to define units to which phylogeographic analyses may be applied in the future.

It is probable that the recorded distribution of at least some members of the Bangiales is a result of human-mediated transport. A wide range of marine species are distributed around the world by various vectors and transport pathways that are human mediated as well as by naturally occurring materials that raft the world's oceans (Thiel and Gutow 2004). The South African species known as *Porphyra capensis* Kütz. has been found on the feathers of jackass penguins (Randall and Randall 1984). Brodie et al. (1998) suggested that *Py. leucosticta* might be an introduced species in the North Atlantic; in our study, *Py. leucosticta* is resolved in a clade with taxa from the Pacific, lending weight to the earlier hypothesis.

In AlgaeBase, there are 130 currently accepted names in the Bangiales (Guiry and Guiry 2010). In this study, we have analyzed data for 157 taxa and have formally treated 77 named species: we were

unable to apply species names to over half of the species we sequenced. For several, we used the same species name for taxa that were clearly related but probably distinct at the species level. Creation of the molecularly circumscribed genera in this paper should aid in efforts to name these species. There are many species previously described as *Porphyra* or *Bangia* for which nrSSU or *rbcL* sequence data should be obtained so that they can be moved to the appropriate genus. This will require comparison with sequences in GenBank, using tools such as BLAST (Altschul et al. 1990; <http://blast.ncbi.nlm.nih.gov>), followed by phylogenetic analysis using one of the widely available analysis sites such as PHYML (<http://atgc.lirmm.fr/phyml/>). Care should be taken to include representatives of as many genera as possible and, in particular, not to restrict the analysis to only filamentous or only foliose species. The easily alignable *rbcL* gene may be more widely useful for this purpose than the nrSSU which frequently contains Group I introns and indels in the exon regions, complicating accurate sequence alignment between taxa.

Recognition of additional Bangiales genera will also have an impact on the quantification of regional biodiversity, with recognition of a greater diversity of taxa at a range of scales (Lindstrom 2008, Broom et al. 2010). On the basis of results of studies where thorough regional collections have been made, we predict that targeted local studies in many parts of the world are likely to result not only in the recognition of more species, but also in an increase in the number of genera recognized per region. The presence in our study of several genera that are monotypic or contain only a few species suggests that further genera await discovery.

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Supplementary Material

The following supplementary material is available for this article:

Table S1. Specimen collection information, voucher number, sequence length, and GenBank accession numbers of sequences used in the phylogenetic analysis.

This material is available as part of the online article.

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