



Note

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Splitting blades: why genera need to be more carefully defined; the case for *Pyropia* (Bangiales, Rhodophyta)

Giuseppe C. Zuccarello¹, Xingting Wen² and Gwang Hoon Kim^{2,*}

¹School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand

²Department of Biological Sciences, Kongju National University, Gongju 32588, Korea

The trend in naming genera based almost exclusively on molecular data, and not on morphological diagnostic characters, is increasing. In bifurcating phylogenetic trees generic cut-offs are arbitrary, but at the bare minimum nomenclatural changes should be supported by multiple phylogenetic methodologies using appropriate models for all the various gene partitions, strong support with all branch support methods, and should also result in adding to our knowledge of the interrelationships of taxa. We believe that a recent taxonomic treatment of the genus *Pyropia* (Yang et al. 2020) into several genera is unwarranted. We reanalysed the data presented in the recent article, using additional phylogenetic methods. Our results show that many of the newly established genera are not well supported by all methods, and the new circumscription of the genus *Pyropia* renders it unsupported. We also tested additional outgroups, which were previously suggested as sister to *Pyropia*, but this did not substantially change our conclusions. These generic nomenclatural changes of the previously strongly supported genus *Pyropia*, do not shed light on the evolution of this group and have serious consequences in these commercially important algae, that are also governed by a plethora of regulation and by-laws that now need to be amended. We suggest that the over-splitting of groups based only on poorly produced and modestly supported phylogenies should not be accepted and that the genus *Pyropia* sensu Sutherland et al. (2011) be restored.

Keywords: Bayesian analysis; branch support; delineating genera; maximum-likelihood; nomenclature; phylogenetics; red algae; taxonomy

INTRODUCTION

The Bangiales (Rhodophyta) contains some of the commercially most important red algae that have been used for millennia and support multi-million dollars industries mainly in Asia (Kim et al. 2014, Badis et al. 2020, Dai et al. 2020, Lee et al. 2021). The order contains two morphological types in the gametophytes: a group consisting mostly of monostromatic blades, and a filamentous group. The filamentous group was usually referred to as the genus *Bangia*, while the blades were referred to as *Porphyra*. This situation changed in 2011 when the

two genera were further split to several bladed genera, mostly to maintain monophyly of the bladed members in relation to the filamentous taxa (Sutherland et al. 2011). While some "*Bangia*" were renamed, most are awaiting formal change. Many species, including the commercially most important species, were placed in the genus *Pyropia* J. Agardh. A recent paper by Yang et al. (2020) proposed to further split *Pyropia* into five genera.

Molecular systematics has revolutionized our understanding of the evolution of algae (Muñoz-Gómez et al.



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*Corresponding Author

E-mail: ghkim@kongju.ac.kr

Tel: +82-41-850-8504, Fax: +82-41-850-8479

2017), the diversity of seaweed (Saunders et al. 2017) and raised many issues in algal taxonomy (Zuccarello et al. 2018). One aspect is the realization that algal diversity, and therefore speciation, is often not accompanied by morphological changes (Muangmai et al. 2022), leading to a greater reliance on molecular data to circumscribe species (Díaz-Tapia et al. 2021). This has led to cryptic species being recognized both genetically and nomenclaturally (Schneider et al. 2017). The criteria for designating species and higher taxa are varied. While species definitions have a plethora of criteria (Leliaert et al. 2014) they should directly or indirectly reflect a biological process (e.g., reproductive barriers, ecological specialization). So species are real evolutionary entities, even if they have complex histories and are difficult to circumscribe (De Queiroz 1998, Hey et al. 2003, Fišer et al. 2018). However, genera and higher taxa are another story.

RESULTS AND DISCUSSION

Genera and higher taxa are arbitrary

Genera are an example of a higher taxon whose circumscription is manmade (Clayton 1983, Entwisle and Weston 2005). Therefore, the criteria for generic distinction are arbitrary. Several criteria have been used in the past to define them. One is the 'kind', that genera are groups of organisms that are clearly distinct from other genera (Stevens 1985). Another is that genera are groups of reciprocally monophyletic species assemblages (e.g., Garnock-Jones et al. 2007). Over time there have also been trends in 'lumping' and 'splitting' species assemblages (Humphreys and Linder 2009) with often no stable consensus reached, because of the arbitrary nature of genera. With the advent of molecular phylogenies the circumscription of genera has become more complicated. It seems that a criterion that is more commonly used in algae over the past few years, is that a genus can be designated based on any 'supported' phylogenetic clade (whether reciprocal monophyly is found or not, nor whether there are clear diagnostic characters). In a bifurcating tree, the number of supported branches will increase with the number of taxa used and the number of genes sequenced (more data), practically *ad infinitum*, leading to more and more splitting of groups. This trend in red algal taxonomy to name genera based on this minimal criterion, especially with the advent of molecular-assisted systematics, is reflected in the increase in genera. For example, Schneider and Wynne's "synoptic

review of red algal genera" series (Schneider and Wynne 2007, 2013, 2019, Wynne and Schneider 2010, 2016, 2022) found a steady increase, and possibly rate, of new genera proposed since the mid-1950s (21 new genera in 2010, 27 in 2013, 40 in 2016, 58 in 2018, and 31 in 2022) (Kyllin, 1956). While this could reflect a better understanding of the diversity of higher taxa in red algae, there is also a component of splitting based on a supported lineage, often nested in an unsupported grade.

A good example of this back and forth of generic nomenclature is the red algal family Gracilariaceae (order Gracilariales), another commercially important group, that has had a complex nomenclatural history recently due to generic circumscriptions being based largely on molecular phylogenies and, correctly, attempts at finding diagnostic characters. The genus has been split into several new genera (most recently in Gurgel et al. 2018) based on diagnostic morphological differences and molecularly supported clades. It has been shown though that the diagnostic morphological characters do not correspond to the new genera, and all the recently recognized new genera have been placed back into the original genus *Gracilaria* (Lyra et al. 2021). This has led to a genus that is more easily distinguishable, has a set of exclusive characters, is genetically quite divergent, and is reciprocally monophyletic. This seems to be a fair approach.

In this study, we tried to reinvestigate the data presented in Yang et al. (2020) using additional and alternative phylogenetic methods, support measures, as well as careful selection of molecular models and partitioning of genes and codons to see if the splitting of the genus *Pyropia* into several genera is supported by more comprehensive phylogenetic analyses.

Molecular phylogenetic methodologies

A criterion for generic distinction that is used in studies that employ molecular data, is that at a minimum, phylogenies should provide strong support on a branch of either a distinct species or set of species. Sometimes this can be supported by diagnostic characters, even cryptic ones (Díaz-Tapia et al. 2017). These phylogenies and support values should be based on more than one gene, and various methods of tree reconstruction. While maximum parsimony and distance methods have lost favor in tree reconstruction, methods that incorporate realistic models of DNA (or amino acid) evolution and probabilistic estimates of tree topologies are mostly used. Maximum-likelihood (ML) methods, in programs such as RAxML (Stamatakis 2014) or IQ-TREE (Minh et al. 2020),

and Bayesian reconstruction methods are the most common. For support values, the non-parametric bootstrap (Felsenstein 1985) has a long history and for Bayesian analysis, posterior probabilities as implemented in programs like MrBayes (Ronquist et al. 2012) are common. These probabilistic methods require an estimate of molecular evolution (a model or models) to reach a maximum or high probability topology. It is an empirical fact that mutation frequencies accumulate differentially between genes (more conserved versus less so), within and between regions of genes (e.g., codon positions in protein-coding genes), and even gene location (nuclear versus organellar). These variable changes require a careful partitioning of the data to arrive at models that more accurately reflect these variations in mutations. Different models can be estimated for these different genes and partitions using various model testing programs (Santorum et al. 2014, Kalyaanamoorthy et al. 2017).

The splitting of the genus *Pyropia*

Sutherland et al. (2011) used a concatenated data set of the plastid *rbcL* (the large subunit of ribulose biphosphate carboxylase / oxygenase) and nrSSU (nuclear-encoded small subunit ribosomal RNA) genes in their comprehensive analysis of the diversity of the Bangiales. They used one molecular model for the entire data set, even though they partitioned the data by genes, and implemented both ML and Bayesian reconstruction. Results showed that a strongly supported group of bladed Bangiales was sister to filamentous Bangiales (*'Bangia'* 3), although this sister relationship was not supported using three support methods. They resurrected the genus *Pyropia* J. Agardh (1899) for this clade. *Pyropia* contains the most commercially important Bangiales (e.g., *P. haitanensis*, *P. tenera*, *P. yezoensis*). There were other supported groups, with various levels of branch support within this genus but they did not believe this warranted further splitting. This work was recently continued by Yang et al. (2020) with the same data set (*rbcL* and nrSSU), plus the addition of some new species and they made the decision to further split *Pyropia*. In their analysis, they used one molecular evolution model (GTR + I + G) for all gene partitions and implemented only one method of tree reconstruction (Bayesian analysis).

Bayesian support values (as posterior probabilities) are known to over-estimate 'confidence' of branches (Suzuki et al. 2002, Simmons et al. 2004), with potentially only high values (≥ 0.95) predicting true branches. Plus all measures of tree reconstruction and support mea-

asures are differently sensitive to model violations, priors selected, etc. (Douady et al. 2003, Simon 2022). Yang et al. (2020) did not implement any other methods. Even so, their support for the new generic clades was variable and posterior probabilities were: *Neopyropia* values were 0.92, *Neoporphyra* values were 1.00; *Pyropia* values were 0.90; *Calidia* (an illegitimate name now *Phycocalidia* – Santiañez and Wynne 2020) values were 0.99; *Porphyrella gardneri* was a singleton sister to the previous taxon but in a polytomy (unsupported sister relationship – 0.60); *Uedaea onoi* was also a singleton, sister to the reminder of the taxa but only with support of 0.93. Many of these values do not indicate high confidence in the genera (even though it was stated in the paper that they all had 'strong support'). They also argue that there are some biogeographic trends, in the distribution of genera. For example, the new genus *Neopyropia* is from cold temperate zones, whereas *Pyropia* is 'mainly' subpolar to cold temperate. The distinction is hard to fathom, especially with patterns of sampling (several well sampled areas, many poorly sampled), and the difficulty (impossibility) of species identification in new locations making distribution patterns very tentative. Thus, these new generic assignments are solely based on support values in molecular phylogenies. This practice is becoming more common in algae with simple morphologies (Verbruggen 2014), like the Bangiales that lack complex thallus structure or complex post-fertilization patterns. Making decisions of nomenclatural changes, especially in groups that are intensively studied or commercially important, needs a more rigorous analysis and clearer and unambiguous support for branches using all available methods—at least more than one.

While nomenclature should be governed by the best science available, the consequences of changes should also be considered. Most taxonomic changes have no detrimental consequences and are never further remarked on. But in an alga that is commercially exploited and for which regulations and contracts are in place, a taxonomic change, at least leads to a plethora of legal contracts and government regulatory laws needing to be amended.

Reanalysis of *Pyropia* phylogeny using several phylogenetic methods

We reinvestigated the same *rbcL* and nrSSU data presented in Yang et al. (2020) using additional phylogenetic methods, support measures, careful selection of molecular models and partitioning of genes and codons to see if the splitting of the genus *Pyropia* was supported by more

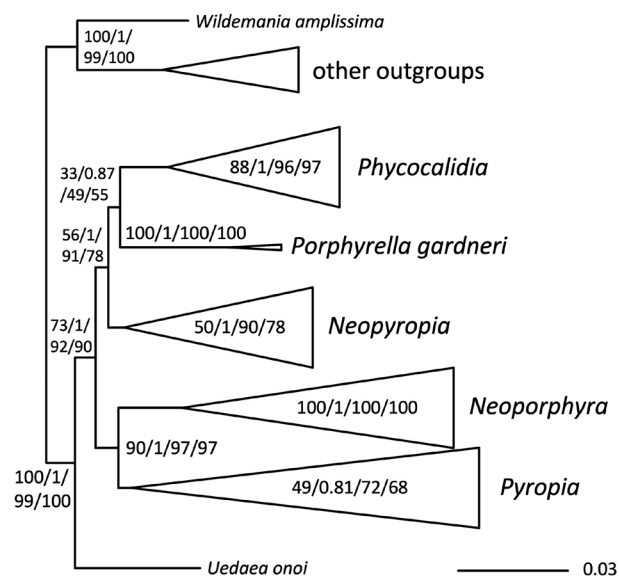


Fig. 1. Cartoon of maximum-likelihood topology of *rbcL* and nrSSU concatenated dataset of “*Pyropia*” species and outgroup taxa following Yang et al. (2020). Values on generic and inter-generic branches are displayed on branches or in triangles: non-parametric bootstrap % / Bayesian posterior probabilities / approximate likelihood-ratio test % / Ultrafast bootstrap %.

comprehensive analyses.

We used two reconstruction methods: ML analyses (not used in Yang et al. 2020) were implemented using IQ-TREE 2.2.0 (Minh et al. 2020) and Bayesian inference analysis with MrBayes v. 3.2 (Ronquist and Huelsenbeck 2003). Alignments were partitioned by gene and, for *rbcL*, by codon. Model selection (Kalyaanamoorthy et al. 2017) and partitioning to select the best partitions (Chernomor et al. 2016) were implemented in IQ-TREE, potential merging of partitions was also implemented. Three ML branch support methods were used: non-parametric bootstrapping (500 replicates) (Felsenstein 1985); Ultrafast bootstrapping (UF) (3,000 replicates) (Hoang et al. 2018) and the approximate likelihood ratio test (SH-aLRT) (3,000 replicates) (Guindon et al. 2010). These support methods provide different approaches in determining branch reliability and have different confidence thresholds in determining branch support. Bayesian inference analysis also partitioned genes and codon positions. The model partitions were unlinked, with variable rates, and six rate categories (Supplementary Fig. S1). Two parallel runs of Markov chain Monte Carlo were performed for 3,000,000 generations, sampling every 1,000 generations. Estimated samples size, split frequencies, and stationarity were checked after each run. Post-analysis, 10% of generations were removed as a burn-in and posterior

probabilities visualized in Figtree v1.1.4 (Rambaut 2009) and Canvas X Draw (Canvas GFX, Inc., Boston, MA, USA) were used to manipulate trees (e.g., collapse branches) for presentation.

Different evolutionary models were selected, for the different partitions, reflecting their different patterns of change (Supplementary Fig. S1). The bladed red algae, of the previous genus *Pyropia* comprise a strongly supported clade, but the new genera have variable support (Fig. 1, Supplementary Fig. S2). While *Phycocalidia* (88% bootstrap [BS] / 1.0 posterior probability [PP] / 96% approximate likelihood-ratio test [aLRT] / 97% UF) and *Neoporphyra* (100% BS / 1.0 PP / 100% aLRT / 100% UF), plus the singleton *Porphyrella gardneri* have strong support with all methods, the other genera showed less support. *Neopyropia* was supported only by PP analyses (as in Yang et al. 2020) and with aLRT, but not with BS or UF (50% BS / 1.0 PP / 90% aLRT / 78% UF). The newly circumscribed *Pyropia* is not supported at all (49% BS / 0.81 PP / 72% aLRT / 68% UF), again highlighting its unsupported status in Yang et al. (2020) (0.90 PP). The relationship between the genera was also often unsupported. The clade of *Phycocalidia* and *Porphyrella* is unsupported (Fig. 1), rendering reciprocal monophyly of the genera as unsupported, the sister relationship of *Neopyropia* to the two previous genera is also not well supported with all methods (56% BS / 1.0 PP / 91% aLRT / 78% UF). The clade containing *Neoporphyra* and *Pyropia* is supported (90% BS / 1.0 PP / 97% aLRT / 97% UF).

To determine if the support values changes with outgroup selection, we used the “*Bangia* 3” sequences of Sutherland et al. (2011), suggested as a sister group to their *Pyropia*. The results did not vary much (Supplementary Fig. S2), with support of genera slightly lower (e.g., *Neopyropia* (44% BS / 0.98 PP / 89% aLRT / 63% UF) and *Pyropia* (68% BS / 0.97 PP / 95% aLRT / 88% UF) and relationships between genera also not well supported. For example, the clade of *Phycocalidia* and *Porphyrella* (41% BS / 0.84 PP / 71% aLRT / 61% UF) and this clade with *Neopyropia* (59% BS / 1.0 PP / 94% aLRT / 85% UF) are not supported with all methods. In all analyses the clade of *Pyropia* as defined by Sutherland et al. (2011) is fully supported. Examining the relationship within this phylogeny in detail (Supplementary Fig. S3) also shows that there are many supported clades (only using BS and PP) within all these proposed new genera, some supported by bootstrap analysis, some by posterior probabilities, some by both. Should they be considered future genera?

CONCLUSION

In our estimation, dividing a strongly supported clade into various variably supported clades (and rendering the remainder of the former clade, in this case *Pyropia*, unsupported) does not help and is unwarranted. Phylogenies, at a minimum, should use the most up-to-date reconstruction methods, model selection methods, and various support methods (Simon 2022) before clades (which will always be found in bifurcating trees) are proposed as new genera. This is especially true when other diagnostic characters are not found. The continued splitting of bladed Bangiales, also has the disadvantage that this intensely studied marine agricultural crop and regulated industry has to contend with these arbitrary changes.

If genera are arbitrary, what is wrong with dividing and dividing? The question should be, what is gained. In seaweed taxonomy the trend appears to be to name clades that show a modicum of support as new genera (Yang et al. 2020), and this pattern appears to be increasing (see “Introduction”). If the argument for this is that nomenclature should reflect evolutionary history, then just naming clades rather than nomenclatural changes, does that (<http://phylonames.org/code/>). Another argument could be that splitting and recognizing genera aids in communication, but does changing names every few years do that? At least the change to the genus *Porphyra* to several genera (Sutherland et al. 2011), such as *Pyropia*, was done to preserve monophyly of the named bladed entities and was proposed based on supported and variously tested clades.

We suggest that generic designation should be done more cautiously in the future: (1) phylogenies need to be produced with a variety of methods, and optimally with more genes, even genomes; (2) clades should be named, if they need to at all, only if they are strongly supported with different methods of analyses, which should reflect different analytical approaches that are fallible to different model violations; (3) names should be informative to biologists about trends in evolution (e.g., different patterns of post-fertilization development, different character states possibly reflecting some selective advantages); (4) poorly supported groups should not be accepted by the scientific community and journal editors.

Taxonomic changes. Based on our findings we propose a circumscription of the genus *Pyropia sensu* Sutherland et al. (2011).

Pyropia J. Agardh 1899: 149–153; following Sutherland et al. (2011).

Generic synonyms.

*Neoporphyr*a J. Brodie & L. -E. Yang; Yang et al. 2020: 865.

Neopyropia J. Brodie & L. -E. Yang; Yang et al. 2020:865.

Phycocalidia Santiañez & M. J. Wynne 2020 [= *Calidia* E. Y. Yang & J. Brodie nom. illeg.] Yang et al. 2020:864.

Porphyrella G. M. Smith & Hollenberg emend. J. Brodie & L. -E. Yang; Yang et al. 2020:874.

Uedaea J. Brodie & L. -E. Yang; Yang et al. 2020:876.

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CONFLICTS OF INTEREST

The authors declare that they have no potential conflicts of interest.

SUPPLEMENTARY MATERIALS

Supplementary Fig. S1. Output data from the two dataset analysis, including variation in partitions, models selected per partition and -Log likelihood scores of maximum-likelihood tree, for the two different analyses (<https://www.e-algae.org>).

Supplementary Fig. S2. Cartoon of maximum-likelihood topology of *rbcL* and nrSSU (nuclear-encoded small subunit ribosomal RNA) concatenated dataset of “*Pyropia*” species with ‘Bangia 3’ used as an outgroup, following Sutherland et al. (2011) (<https://www.e-algae.org>).

Supplementary Fig. S3. Maximum-likelihood (ML) topology of *rbcL* and nrSSU (nuclear-encoded small subunit ribosomal RNA) concatenated dataset of “*Pyropia*” species and outgroup taxa following Yang et al. (2020), used for producing Fig. 1 (<https://www.e-algae.org>).

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