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Advancing the taxonomy of economically important red seaweeds (Rhodophyta)

Phaik-Eem Lim[a], Li-En Yang[b], Ji Tan[c], Christine A. Maggs[d] and Juliet Brodie[e]

[a]Institute of Ocean and Earth Sciences (IOES), University of Malaya, 50603 Kuala Lumpur, Malaysia; [b]Jiangsu Marine Fisheries Research Institute, Nantong, Jiangsu 226007, China; [c]Department of Agricultural and Food Sciences, Universiti Tunku Abdul Rahman (UTAR), 31900 Kampar, Perak, Malaysia; [d]Faculty of Science and Technology, Bournemouth University, Talbot Campus, Poole, Dorset, BH12 5BB, UK; [e]Natural History Museum, Department of Life Sciences, Cromwell Road, London SW7 5BD, UK

ABSTRACT

The cultivation of red seaweeds for food (nori), agar and carrageenans is the basis of a valuable industry. However, taxonomic knowledge of these cultivated seaweeds and their wild relatives has not kept pace with advances in molecular systematics despite the fundamental importance of being able to identify commercially important species and strains, discover cryptic and endemic taxa and recognize non-native species with potentially damaging diseases and epiphytes. This review focuses on molecular taxonomic advances in the cultivated red algae with the highest commercial value globally: *Eucheuma* and *Kappaphycus, Porphyra sensu lato* and *Gracilaria*. All three groups are similarly taxonomically challenging: speciose, morphologically plastic, with poorly resolved species boundaries. *Eucheuma* and *Kappaphycus* are frequently misidentified and the molecular markers *cox*2-3 spacer, *cox*1 and RuBisCO spacer have helped in understanding phylogenetic relationships and identifying new species and haplotypes. In *Porphyra sensu lato* (Bangiales) species identification and phylogenetic relationships were highly problematic until a taxonomic revision based on a two-gene phylogeny (18S and *rbc*L) resulted in nine genera of bladed species. *Pyropia*, with at least 89 species, three in nori cultivation, has potential for new commercial evaluation. In *Gracilaria sensu lato*, earlier efforts to resolve species-level taxonomy and generic descriptions were superseded by application of molecular tools, including DNA sequences of the RuBisCO spacer, *rbc*L gene, 18S and the ITS region. Studies of these cultivated red algal genera highlight the need for a robust taxonomy, a more standardized approach to the molecular markers used and a comprehensive dataset for each representative species. Current work on DNA-based species delimitation, the emergence of high throughput sequencing, multi-gene phylogenies, publication of whole genomes (e.g. *Porphyra umbilicalis*) and genomes in the pipeline (e.g. *Gracilaria*) are increasingly improving our understanding of phylogenomic relationships and species relationships. This knowledge, in turn, can then be applied to improving red seaweed aquaculture.

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Introduction

Red seaweeds have been collected from the wild for food and other products for thousands of years (Tseng, 1935; Brodie & Irvine, 2003; Collén *et al.*, 2014; Ramírez *et al.*, 2014 and references therein). The main uses of red algae, apart from food, have been as a source of the gelling hydrocolloids agar and carrageenan (Craigie, 1990). Until the Second World War (WWII, 1939–1945), seaweeds were mostly harvested from natural populations (Marshall *et al.*, 1949), although *Porphyra sensu lato* has been cultivated in China and Japan for hundreds of years as food (Blouin *et al.*, 2011; Yang *et al.*, 2017). After WWII, in Asia the need for a more reliable crop after a major failure of the nori harvest in Japan led to the development of the modern nori industry (Yang *et al.*, 2017). Growing demand for products over the second half of the 20th century (e.g. Marshall *et al.*, 1949; Kim, 2012) saw a fundamental shift from wild harvesting in the North Atlantic of species including *Chondrus crispus* to farmed crops, such as *Eucheuma* in warmer tropical areas, particularly in the Pacific (Doty *et al.*, 1986; Porse & Rudolph, 2017). A more recent drive towards the development and commercialization of functional foods, nutriceuticals, pharmaceuticals and bioactives from seaweeds is pushing up demand and leading to innovative methods of production (e.g. Hafting *et al.*, 2012; Gutiérrez Cuesta *et al.*, 2016). Current research indicates that macroalgal proteins contain all essential amino acids for food products and have additional bioactives (Garcia-Vaquero & Hayes, 2016).

Twelve red algal taxa are listed as currently in aquaculture production (FAO, 2015) and/or have been cultivated for consumption between 1990 and 2015 (Table 1), although the number and identity of many of these species are uncertain. The main taxa in cultivation are species of *Kappaphycus, Eucheuma, Porphyra sensu lato* and *Gracilaria*. Estimates of their wet weight harvest per continent are given in Table 2. However, the reliability of these data is questionable as the figures are based on reported

CONTACT Phaik-Eem Lim phaikeem@um.edu.my