

Red Algae

Suzanne Fredericq, *University of Louisiana at Lafayette, Lafayette, Louisiana, USA*

William E Schmidt, *University of Louisiana at Lafayette, Lafayette, Louisiana, USA*

Based in part on the previous version of this eLS article 'Red Algae' (2007) by Carlos Frederico Deluqui Gurgel and Juan Lopez-Bautista.

Advanced article

Article Contents

- Introduction: Definition and Characterisation
- Fossils and Molecular Clock Time Lines
- Genomics
- Coralline Algae, Biomineralisation and Rhodoliths
- Sexual Reproduction
- Vegetative Propagation
- Ecological Importance
- Economical Importance

Online posting date: 15th September 2016

Red algae are a phylum of about 7100 mostly marine, unicellular and multicellular photosynthetic eukaryotes that belong to the Supergroup Plantae. Multicellular taxa consist exclusively of a filamentous construction lacking true tissues despite their often superficially complex plant body. This group is unique in the Tree of Life in lacking both flagella and centrioles with a 9+2 microtubule arrangement in all stages of the life history.

They include species with elaborate life cycles, significant ecological importance and extensive economical applications. The oldest known taxonomically resolved eukaryotic fossil, ca. 1250–1100 million years ago, is a red alga.

Introduction: Definition and Characterisation

The phylum Red Algae or Rhodophyta belongs in the Supergroup Plantae or Archaeplastida, an anciently diverged group that also includes the glaucophyte (Glaucophyta), green algal (Chlorophyta) and land plant (Embryophyta) clade with which they share a single common ancestor. The red algae are composed of seven classes (i.e. Bangiophyceae, Compsopogonophyceae, Cyanidiophyceae, Florideophyceae, Porphyridiophyceae, Rhodellophyceae and Stylonematophyceae) (Yang *et al.*, 2016). The Florideophyceae is the largest class containing greater than 95% (6760 spp.) of reported species diversity in the phylum (approximately 7100 species) (Guiry and Guiry, 2016). It is

widely accepted that red algae are crucially important in the evolution of photosynthetic eukaryotes since their ancestor hosted a cyanobacterium that became the plastid through the event of primary endosymbiosis. A putative member of the Bangiophyceae played a central role in the eukaryote tree of life as a donor through a single or more likely multiple secondary plastid endosymbioses that gave rise to chlorophyll-*c* containing groups, such as diatoms, brown algae, dinoflagellates, haptophytes and cryptophytes (Bhattacharya *et al.*, 2013). See also: [Plastid Origin and Evolution](#); [Haptophyta](#); [Diatoms](#); [Gymnodinium and Related Dinoflagellates](#); [Algal Pigments](#); [Endosymbionts](#); [Phycology](#); [Green Algae](#); [Brown Algae](#)

Currently, there are approximately 41 orders of red algae (Rhodophyta) (Guiry and Guiry, 2016), but more are expected to be proposed in the future. The evolutionary relationships and taxonomic classification systems in red algae, across all levels of biological organisation, have been extensively advanced in the past 20+ years with the aid of molecular-based phylogenetic and genomics-based analyses. Red algae are a widespread group of uni- to multicellular marine and freshwater photoautotrophic plants. Multicellular taxa exhibit a broad range of morphologies ranging from simple filaments to pseudoparenchymatous thalli (**Figure 1**) and display a wide array of life cycles. About 98% of the species are marine, 2% freshwater and a few rare terrestrial/subaerial representatives. Many macroscopic species exhibit a characteristic triphasic, haplo-diplobiontic life cycle, with one haploid (gametophytic) and two diploid (carposporophytic and tetrasporophytic) stages. Characters that distinguish red algae from any other algal group are the lack of flagella and centrioles, presence of phycobilisomes on unstacked thylakoids in the chloroplast, absence of parenchyma (true tissues) and presence of pit connections between adjacent cells resulting from incomplete cytokinesis. Pit connections linking neighbouring cells are one of the diagnostic features characterising multicellular red algal orders. Diverse combinations of pit connection structures (i.e. plug core with different number of cap layers and membranes) with molecular data have been used to define the ordinal boundaries of the Florideophyceae. The characteristic red colour and its many variations are the result of the ratio between photosynthetic pigments (chlorophylls and carotenoids) plus phycobilisomes,

eLS subject area: Microbiology

How to cite:

Fredericq, Suzanne and Schmidt, William E (September 2016) Red Algae. In: eLS. John Wiley & Sons, Ltd: Chichester. DOI: 10.1002/9780470015902.a0000335.pub2

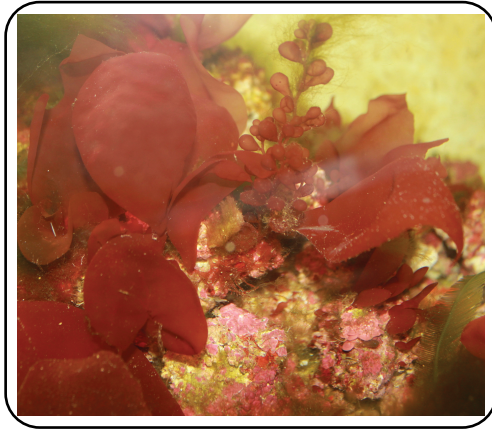


Figure 1 A sampling of red algal body plans: large and small unbranched blades (*Halymenia*); grape-like branched thalli (*Botryocladia*); crustose, non-geniculate coralline species collected in the vicinity of the Dry Tortugas, FL, at ~50 m depth.

the light-harvesting complex composed of three main classes of water-soluble protein-based pigments (phycobiliproteins): phycoerythrin (red), phycocyanin (blue) and allophycocyanin (blue–greenish). Red algal cell walls are composed of a suite of carbohydrates, for example, cellulose fibrils and a matrix of phycocolloids that are sulfated polysaccharides classified in two main groups: agar and carrageenan. **See also:** [Plant Chloroplasts and Other Plastids](#); [Cryptomonads](#); [Plant Cell Division and its Unique Features](#); [Algal Photosynthesis](#); [Evolution of Multicellularity](#)

Fossils and Molecular Clock Time Lines

The oldest known taxonomically resolved eukaryotic fossil, ca. 1250–1100 million years ago (Ma), is a red alga, *Bangiomorpha pubescens*, from the Hunting Formation, Arctic Canada. Anatomically preserved florideophyte fossils found in the 600 Ma Doushantuo Formation of China exhibit growth forms and features resembling reproductive structures of modern corallines (Xiao *et al.*, 2004). An evolutionary timeline for the divergence date of the Class Florideophyceae was estimated at approximately 943 Ma using a seven-gene concatenated dataset and several constraints based on the fossil record of both red and green algae, and plants (Yang *et al.*, 2016). The major divergences in this class involved the emergence of Hildenbrandiophycidae (ca. 781 Ma), Nemaliophycidae (ca. 661 Ma), Corallinophycidae (ca. 579 Ma), and the split of Ahnfeltiophycidae and Rhodymeniophycidae (ca. 508 Ma). Divergences within Florideophyceae were accompanied by evolutionary changes in the carposporophyte stage, leading to a successful strategy for maximising spore production from each fertilisation event. The subclass Corallinophycidae provides an excellent context to stratigraphy and molecular clock analysis because it is the only living red algal group that has an extensive fossil record

due to their calcified cell wall structure. **See also:** [Fossils in Phylogenetic Reconstruction](#); [Molecular Evolution: Rates](#)

Genomics

The field of red algal genomics, the study of total DNA (deoxyribonucleic acid) including its content and arrangement, and phylogenomics, the study of phylogenetic relationships based on comparative genomes, are still in their infancy. While currently there are only a few complete red algal genomes (nuclear, plastid, mitochondrial) released, that is, of *Chondrus crispus* with a genome size of 105 Mbp (and 9606 predicted genes, Collén *et al.*, 2013), *Pyropia yezoensis* with a genome size of 43 Mbp (and 10327 predicted genes, Nakamura *et al.*, 2013) and *Porphyridium* with a genome size of 19.7 Mbp (and 8355 predicted genes, Bhattacharya *et al.*, 2013), assembled plastid and mitochondrial genomes are becoming more available. Typically, the red algal mitochondrial genome is relative small, averaging 37 Kbp in the classes Cyanidiophyceae and Bangiophyceae and 26 Kbp in the Florideophyceae. Mitochondrial genomes among multicellular red algae of the Florideophyceae are highly conserved, supporting the notion of a rapid radiation among the morphologically divergent multicellular lineages of a major subclass, the Rhodymeniophycidae. In contrast, extensive mitochondrial gene rearrangements took place between Bangiophyceae and Florideophyceae, with multiple examples of gene loss among the different red algal lineages (Yang *et al.*, 2015). Lee *et al.* (2016) analysed plasmid-derived sequences from red algal plastid genomes to elucidate the impact of plasmids over the evolutionary history of red algae and suggested that they spread as parasitic genetic elements. **See also:** [Chloroplast Genome](#); [Genomics of Algae](#); [Mitochondrial Genome](#)

Coralline Algae, Biomineralisation and Rhodoliths

One of the most diversity-rich subclasses of red algae are the calcifying Corallinophycidae that are of two morphological types, non-geniculate crusts (**Figure 1**, lower center), and geniculate, segmented taxa (**Figure 2**). These coralline algae are of major ecological importance and grow in all marine habitats worldwide, from the poles to the tropics, and from shallow subtidal coastal habitats to offshore banks on continental shelves. The deepest growing algae on record, at 286 m depth (Littler *et al.*, 1985), corallines grow where there is sufficient light and either on hard substratum or as free-living benthic nodules of various sizes called rhodoliths (maërl) (**Figure 3**). In the tropics, they are the principal cementing agents and reef builders of nearly all tropical reefs. It is well known that coral larval settlement is chemically mediated by crustose coralline algae (Ritson-Williams *et al.*, 2014). Rhodoliths may form loose beds of aggregated live and dead material. Water motion or bioturbation is critical for rhodoliths to grow and remain unburied by sediments; it also limits fouling and enables periodic rotation to allow light exposure on all sides. The world's most expansive and contiguous

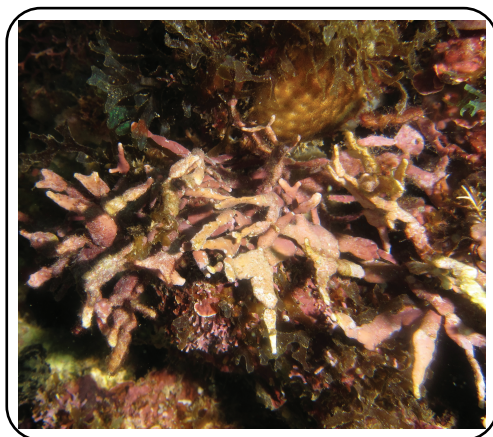


Figure 2 *Amphiroa hancockii*, a geniculate, segmented coralline, Bocas del Toro, Caribbean Panama, collected at 1 m depth.

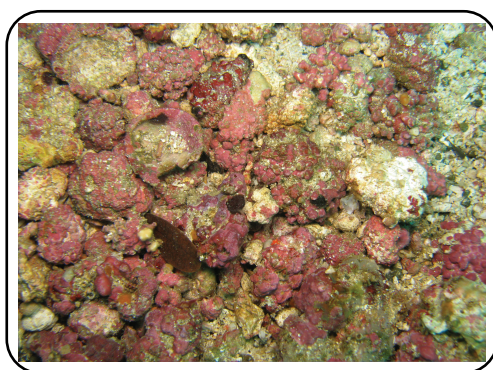


Figure 3 Rhodolith nodules in rhodolith bed, Gulf of Chiriquí, Pacific Panama, collected at ~20 m depth.

rhodolith beds cover about 20 900 km² of the Abrolhos Shelf off eastern Brazil (Amado-Filho *et al.*, 2012). Rhodolith beds cover 40–50% of the seafloor from 50 to 110 m depth in southern Queensland, Australia and 95.8% of the bottom in the Bahamas at depths of 67–91 m. They are often associated with coral reefs in tropical ecosystems. In spite of the complexity of the rhodolith habitat and supported community, their functional ecology has received little attention in contrast to other marine ecosystems such as seagrass beds, kelp forests or coral reefs.

Coralline algae are intrinsically linked with the effects of global climate change and ocean acidification. They contribute to global-scale biogeochemical cycles of carbon and other elements and are acutely sensitive to variations in ocean temperature. Their thalli are composed of high-magnesium biogenic calcite, the CaCO₃ polymorph most sensitive to decreases in ocean pH. Furthermore, they are considered to be one of the major producers of dimethylsulfoniopropionate (DMSP), which, upon being metabolised by algal-associated bacteria, produces volatile compounds such as (dimethylsulfide) DMS (Burdett *et al.*, 2015). When extrapolated to the scale of massive rhodolith beds, extensive rocky bottoms, coral reefs and algal ridges, coralline algal

communities contribute greatly to atmospheric sulfur through the breakdown of DMSP to DMS and therefore directly affect the global sulfur cycle and global climate change. Their carbonate skeleton provides protection from grazers and boring animals, strength and resistance to wave action, and space-competition advantages. These organisms are widespread, long-lived barometers of ocean health and real-time indicators of global warming and ocean acidification impacts (Adey *et al.*, 2013, 2015). Crustose coralline algae can suppress macroalgal growth and recruitment on coral reefs (Vermeij *et al.*, 2011). **See also: Biogeochemical Cycles**

The Corallinophycidae, comprised of four orders, are the only group of calcifying red algae that precipitate calcite; in contrast, all other calcified red algae deposit calcium carbonate in the form of aragonite. The presence of calcium carbonate is often in the form of high-magnesium calcite in which Ca(Mg)CO₃ is initially metabolically emplaced as 5–25% Mg within most organic cell walls. In addition, aragonite precipitates within overgrown reproductive conceptacles in *Lithothamnion* sp. (Krayesky-Self *et al.*, 2016). Dolomite and magnesite have also been discovered within living coralline algae (Nash *et al.*, 2011), leading to discussions of the geobiological implications of the various carbonate minerals in a changing world. **See also: Climate Change and Biogeochemical Impacts; Algal Calcification and Silicification**

Sexual Reproduction

It was only after culture methods were introduced in 1965 that it was finally verified that in most red algae there is a fundamental linkage of the sexual system and a life history consisting of three phases (summarised in Hommersand and Fredericq, 1990; Guiry, 1990; Hawkes, 1990; West and Hommersand, 1981, figs 4.4–4.6) summarised as follows: The basic scheme of sexual reproduction includes the development of a specialised female filament called the carpogonial branch. The female gamete (carpogonium or egg) is recognisable by the presence of the trichogyne, an elongated hair-like extension to which the male gamete (spermatium) will attach. After fertilisation, the zygotic nucleus develops, directly or indirectly, into a diploid phase, the carposporophyte, which grows parasitically on the female gametophyte. During the direct development, the fertilised carpogonium matures into a carposporophyte usually composed of diploid gonimoblast filaments bearing carposporangia. Mature carposporangia release diploid carpospores into the water column, whereupon they will settle on various substrata. However, in many groups with indirect development, the zygotic nucleus undergoes mitotic divisions and these nuclei are transferred to other specialised cells, called auxiliary cells, where they will, in turn, develop into carposporophytes remote from the original fertilisation site. The auxiliary cell can be located or originated in close proximity to the carpogonial branch, in a short distance to receive the zygotic nucleus (procarpic condition), or away from it, in another vegetative-independent filament (non-procarpic condition). In the latter case, a complex network of unsegmented connecting tubes or segmented connecting filaments can develop to deliver the diploid nuclei to several auxiliary cells.

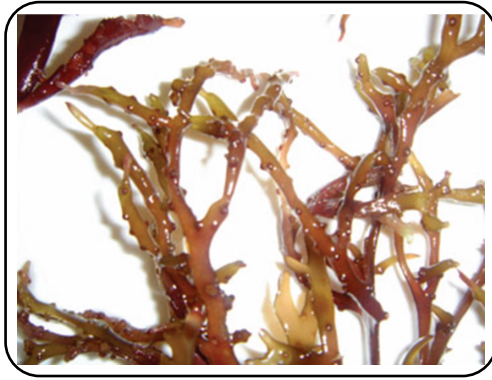


Figure 4 Post-fertilisation cystocarps (carposporophytes) growing on *Gracilaria intermedia* female gametophytes.

The arrangement, morphology and number of cells that make up the carpoogonial branch, and the origin, location and homology of auxiliary cells are prime characters for the taxonomy of multicellular red algae. In many red algae, the fully mature first diploid stage is called carposporophyte. The cystocarp (**Figure 4**) is composed of the carposporophyte plus vegetative haploid cells or filaments of the female gametophyte encircling and interacting with it (pericarp). Carpospores develop into a second free-living phase called the tetrasporophyte, which can be morphologically similar (isomorphic alternation of generations) or different (heteromorphic alternation of generations) from the gametophytes. Tetrasporophytic plants produce tetrasporangia by meiosis, which release tetraspores. This pattern of meiotic cell division in the tetrasporangium can be one of three main types: cruciate, tetrahedral and zonate. When released, tetraspores will germinate into either separate male or a female haploid (dioecious) or bisexual (monoecious) gametophytes. The carposporophyte may produce thousands of diploid carpospores from a single fertilisation event taking advantage of cell-to-cell fusions that occur between the fertilised carpoogonium and auxiliary cells. The additional carposporophyte and tetrasporophyte phases are thought to be evolutionary innovations that explain the success of the red algae. A few exceptions to a triphasic life cycle include the 'asexual tetrasporophytes' of the Hildenbrandiales, the derived diphasic life cycle in Palmariales, and abbreviated life cycles lacking a free-living tetrasporophyte in some members of the Acrochaetales, Nemaliales and Gigartinales in the Florideophycidae. In contrast to multicellular red algae, evidence for sexual reproduction in most of the unicellular red algae is not known. **See also: Gametophyte and Sporophyte; Life History Theory; Post-fertilization Reproductive Strategies**

Vegetative Propagation

Vegetative propagation is quite common in red algae. Thallus fragmentation is considered by many as the most significant kind of vegetative reproduction in red algae due to the huge drifting biomass mats observed, many times accumulating and piling high at beaches. In many places, such as the intracoastal waterways

along the Eastern coast of the United States, bottom deposits of drifting populations of seaweeds are constant components of the benthic community. Key species in this case include *Hypnea cervicornis*, *Spyridia hypnoides* and *Acanthophora spicifera*. Some species produce propagules such as spores from bisporangia (e.g. *Caloglossa apomeiotica*) monospores from monosporangia (e.g. *Monosporus* sp., Ceramiaceae), and frail branchlets designed to break apart, disperse and develop into new plants (e.g. star-shaped branchlets of *Hypnea cornuta*). Vegetative growth and fragmentation is the primary mode of reproduction in many invasive species of red seaweeds such as *Gracilaria salicornia* and *Hypnea musciformis* in Hawaii. **See also: Dispersal; Biogeography; Plant Reproduction; Algal Spores**

Ecological Importance

General importance

In many tropical and subtropical intertidal communities, red algae are the primary component of the flora in terms of biomass and species diversity. As primary producers and conspicuous members of the benthic marine community, red algae serve as a source of oxygen for the environment, food for heterotrophic species, substratum for many epiphytic species of animals and plants and as a refuge, nesting and egg depository site for many other organisms. In the marine environment, red algae can be found inhabiting the upper littoral zone to the deepest benthic region of the continental shelves. As littoral organisms, many species can endure severe abiotic stresses such as nutrient limitation, intensive light exposure, osmotic pressures and desiccation, for example, *Bostrychia* spp. growing on mangrove prop roots. The deepest known marine plant in the world is a crustose coralline red alga growing at about 265–268 m depth, offshore the Bahamas, at the limit of the photic zone, where the light available for photosynthesis is only 0.0001% of the surface irradiance (Littler *et al.*, 1985). **See also: Algal Ecology; Marine Communities; Phycology**

Invasive species

Human-mediated introductions of nonindigenous red seaweeds have been reported in several parts of the world: Australia, Brazil, Europe and the United States, among others. Compared to other seaweeds, in the United States alone, red algae account for twice the number of algal species introduced in coastal marine communities (Williams and Smith, 2007; Mineur *et al.*, 2012). In general, these introductions can be classified in two major groups: deliberate and nondeliberate introductions. Deliberate introductions have the purpose of developing local aquaculture practices of economically important exotic seaweed species; notorious among this kind of imports is the introduction of *Kappaphycus alvarezii* in many tropical coastal marine environments (Ask *et al.*, 2003; Sellers *et al.*, 2015). Nondeliberate introductions may occur as the result of marine practices such as ballast water carry over and the international animal aquaculture trade; in particular, the importation, introduction and farming of the Japanese oyster, *Crassostrea gigas*. This latter scenario includes species such as *Gracilaria*

vermiculophylla in Northern Europe and *Grateloupia* spp. in Europe and Eastern United States (Hu and Lopez-Bautista, 2014). Invasive species of red algae are a threat to coastal coral reefs and cause major ecosystem changes with conspicuous losses in biodiversity (Gulbransen *et al.*, 2012; Verlaque *et al.*, 2015). **See also: Invasion of Introduced Species; Harmful Algal Blooms; Conservation Biology and Biodiversity**

Economical Importance

Red algae have a wide array of economic applications supporting a diversified industry worth billions of dollars every year. At least 125 different species of red algae are used worldwide with different applications. The two most important uses in terms of annual economic value, aquaculture intensity and biomass production are, first, food (Loureiro *et al.*, 2015), and, second, in hydrocolloid production (agar and carrageenan – discussed in more detail below). *Porphyra* and *Pyropia* are the source of sushi wrap, kim or nori. Exploitation of natural stocks of red algae is also common and accounts for about 50% of red algae annually. Besides the food and phyllocolloid usages, other known red algal applications include the production of paper, silage for animal aquaculture (e.g. *Palmaria palmata* in abalone farming), water nutrient removal from natural (ponds) and artificial (tanks) containments in animal aquaculture, energy production (e.g. methane gas), phycobiliproteins as fluorescent tags, fertilisers and pH control for agricultural soils (i.e. calcareous species are washed, crushed and added to acid soils to correct the pH) and as a potential source of natural products with pharmaceutical relevance. Examples of biologically active substances extracted from red algae include several lectins with haemagglutinating, cell migrating and anticoagulation properties; domoic and kainic acids have anthelmintic, insecticide and medical research applications (the latter as a neuronal agonist). Certain secondary metabolites found in red algae are poisonous (e.g. manauaealide and polycavernoside found in Pacific members of Gracilariaceae), showing either antitumour or tumour-promoting activities, or display viral inhibitory activity. A plethora of other substances with pharmaceutical applications are extracted from red algae (see review in Smit, 2004; Cornish *et al.*, 2013; Mouritsen *et al.*, 2013; Blunt *et al.*, 2015; Balboa *et al.*, 2015). **See also: Phycology; Lectins; Algal Metabolism**

Phycocolloids

Red algal hydrocolloids (aka red algal phycocolloids) are polysaccharides with gel-forming capabilities. They can be classified in two classes, each bearing a basic sugar skeleton consisting of 1,3-linked β -D-galactopyranose plus either 1,4-linked 3,6-anhydro- α -L-galactopyranose (i.e. agars) or 1,4-linked 3,6-anhydro- α -D-galactopyranose units (i.e. carrageenans). However, several other sugar residues are present, making all natural phycocolloid products (whether agars or carrageenans) a complex mixture of neutral and charged polysaccharides. Phycocolloid gel quality is measured by its rheological properties such as gel strength, density, gelling and melting points. These properties are in turn influenced by the overall chemical

composition of the gels, that is, the ratio among different polysaccharides and modified sugar residues found in it. Some groups of red algae exhibit higher concentrations of one particular class and thus are known as either agarophytes (agar-producers, e.g. Gracilariales, Gelidiales and Ceramiales) or carrageenophytes (carrageenan-producers, e.g. most families currently in the Gigartinales such as Solieriaceae, Hypneaceae, Cystocloniaceae, Caulacanthaceae, Furcellariaceae, Tichocarpaceae, Sphaerococcaceae, Polyideaceae, Kallymeniaceae, Dumontiaceae, Rhizophyllidaceae, to name a few) (Bixler and Porse, 2010). **See also: Plant Gums; Algal Cell Walls**

Agar

Agar was the first phycocolloid discovered and purified, giving rise to a whitish powder product. Agar (or agar-agar) is a word derived from Malay meaning ‘seaweed jelly’. At first used as food in Eastern Asia, its applications have multiplied. Agar can be fractionated into two distinct components: agarose and agarpectin. The former is the one with the highest gelling capacity and is a neutral molecule, the latter is charged and can have several of its sugar residues replaced by methylated and sulfated sugar units, among other modifications. The ratio between agarose and agarpectin may vary according to taxonomical, ontogenetical, life-cycle phase, strain selection (genetics) and abiotic factors. In general, the higher the concentration of 3,6-anhydrogalactose, the stronger the gel and higher the quality of the agar.

The current most important economic applications of agar relate to biotechnology, molecular biology and biomedical research industries. Agar gels are the main solidifying agent in microbiological cultures (e.g. bacterial, fungi, viral culture plates), and is used in many electrophoretic applications (e.g. DNA size separation). Agar gelling point usually varies between 35 and 50.8 °C and its melting point is situated between 80 and 100 °C (Weinberger *et al.*, 2010; Croce *et al.*, 2015). **See also: Isolation of DNA from Low Gelling Temperature Agarose; Algal Ecology**

Carrageenan

Phycocolloids belonging to the carrageenan group are also heterogeneous and complex. Different carrageenan types have traditionally been designated by letters from the Greek alphabet. There are three main commercial classes of carrageenan: k-, i- and l-carrageenans. k-type may have galactose units esterified with sulfate at the 4-position, k- and i-carrageenans contain significant amounts of 3,6-anhydro-D-galactose residues (and can undergo thermally reversible gelation in the presence of potassium and certain other cations), while the l-type contain smaller amounts to none. Each type of carrageenan exhibits distinct gelling properties and are found in distinct concentrations within red algal cell walls. The amount of a particular kind of carrageenan varies taxonomically, with life-cycle phases, biotic and abiotic factors. The current most economically relevant applications of carrageenan refer to the dairy industry, where it is used as thickening and stabilising agents in items such as yogurts, heavy and whipping creams, ice creams, chocolates, and so on. (Sangha *et al.*, 2011; Li *et al.*, 2014; Collén *et al.*, 2014; Hafting *et al.*, 2015). **See also: Algal Ecology; Algal Cell Walls**

Aquaculture

China, Korea and Japan seem to lead the aquaculture of red algae in the world regarding biomass production and economic value generated. Most of their production targets the food market of direct seaweed consumption, making *Pyropia* and *Porphyra* (nori) the second most cultured seaweed in the planet in terms of biomass produced (Zemke-White and Ohno, 1999; Craigie, 2011; Food and Agriculture Organization of the United Nations, 2014). Several indoor and outdoor algal farming techniques and technologies have been developed and tested throughout the world. A significant amount of publications regarding algal aquaculture practices, techniques, management and environmental consequences are available in the literature. Tropical countries such as Indonesia, the Philippines and Tanzania are regarded as major sources of cultured carrageenan-producing species, for example, *Kappaphycus*, *Betaphycus* and *Euclidean*, while the temperate coast of Chile is the main source of agar in the world (i.e. from *Gracilaria chilensis*). Other countries recognised as red algal phycocolloid producers include Canada, the United States and France. However, seaweed aquaculture for food consumption leads the biomass production and such industries are particularly significant in China, Japan and Korea. **See also: Fisheries Management**

References

- Adey W, Halfar J and Williams B (2013) The coralline genus *Clathromorphum* Foslie emend. Adey; biological, physiological and ecological factors controlling carbonate production in an Arctic/Subarctic climate archive. *Smithsonian Contributions to the Marine Sciences* **40**: 1–83.
- Adey W, Halfar J, Humphreys A, et al. (2015) Subarctic rhodolith beds promote longevity of crustose coralline algal buildups and their climate archiving potential. *Palaos* **30**: 281–293.
- Amado-Filho GM, Moura RL, Bastos AC, et al. (2012) Rhodolith beds are major CaCO₃ bio-factories in the tropical South West Atlantic. *PLoS One* **7**: e35171. DOI: 10.1371/journal.pone.0035171.
- Ask EI, Batibasaga JA, Zertuche-Gonzalez JA and de San M (2003) Three decades of *Kappaphycus alvarezii* (Rhodophyta) introduction to non-endemic locations. *Proceedings of the International Seaweed Symposium* **17**: 49–58.
- Balboa EM, Conde E, Soto ML, Perez-Armanda L and Dominguez H (2015) Cosmetics from marine sources. In: Kim SK (ed.) *Handbook of Marine Biotechnology*, pp. 1015–1042. Berlin: Springer.
- Bhattacharya D, Price DC, Chan CX, et al. (2013) Genome of the red alga *Porphyridium purpureum*. *Nature Communications* **4**: 1941. DOI: 10.1038/ncomms2931.
- Bixler HJ and Porse H (2010) A decade of change in the seaweed hydrocolloids industry. *Journal of Applied Phycology* **23**: 321–335.
- Blunt JW, Copp BR, Keyzers RA, Munro MHG and Prinsep MR (2015) Marine natural products. *Natural Product Reports* **32**: 116–211.
- Burdett JL, Hatton AD and Kamenos NA (2015) Coralline algae as a globally significant pool of marine dimethylated sulfur. *Global Biogeochemical Cycles* **29**: 1845–1853.
- Collén J, Porcel B, Carré W, et al. (2013) Genome structure and metabolic features in the red seaweed *Chondrus crispus* shed light on evolution of the Archaeplastida. *Proceedings of the National Academy of Sciences of the United States of America* **110**: 5247–5252.
- Collén J, Cornish ML, Craigie J, et al. (2014) *Chondrus crispus* – a present and historical model organism for red seaweeds. *Advances in Botanical Research* **71**: 53–89.
- Cornish ML, O’Leary SJB and Garbary DJ (2013) Phycobilisome composition in *Chondrus crispus* (Gigartinales, Rhodophyta) from a wild type strain and its vegetatively derived green mutant. *Algae* **28**: 121–129.
- Craigie JS (2011) Seaweed extract stimuli in plant science and agricultural. *Journal of Applied Phycology* **23**: 371–393.
- Croce ME, Villar MA and Parodi ER (2015) Assessment of alternative sources of seaweed polysaccharides in Argentina: potentials of the agarophyte *Gelidium crinale* (Hare ex Turner) Gailon (Rhodophyta, Gelidiales). *Journal of Applied Phycology* **27**: 2099–2110.
- Food and Agriculture Organization of the United Nations (2014) *The State of World Fisheries and Aquaculture: Opportunities and challenges*, 243 pp. Rome: FAO Publication.
- Guiry MD (1990) Sporangia and spores. In: Cole KM and Sheath RG (eds) *Biology of the Red Algae*, pp. 347–376. Cambridge: Cambridge University Press.
- Guiry MD and Guiry GM (2016) *AlgaeBase*. Galway: Worldwide Electronic Publication, National University of Ireland. Available from <http://www.algaebase.org>.
- Gulbransen DJ, McGlathery KJ, Marklund M, Norris JN and Gurgel CFD (2012) *Gracilaria vermiculophylla* (Rhodophyta, Gracilariaceae) in Virginia coastal bays, USA: *cox1* analysis reveals high genetic richness of an introduced macroalga. *Journal of Phycology* **48**: 1278–1283.
- Hafting JT, Craigie JS, Stengel DB, et al. (2015) Prospects and challenges for industrial production of seaweed bioactives. *Journal of Phycology* **51**: 821–837.
- Hawkes MW (1990) *Reproductive strategies*. In: Cole KM and Sheath RG (eds) *Biology of the Red Algae*, pp. 455–4476. Cambridge: Cambridge University Press.
- Hommersand MH and Fredericq S (1990) *Sexual reproduction and cystocarp development*. In: Cole KM and Sheath RG (eds) *Biology of the Red Algae*, pp. 305–346. Cambridge: Cambridge University Press.
- Hu ZM and Lopez-Bautista J (2014) Adaptation mechanisms and ecological consequences of seaweed invasions: a review case of agarophyte *Gracilaria vermiculophylla*. *Biological Invasions* **16**: 967–976.
- Krayesky-Self S, Richards JL, Rahmatian M and Fredericq S (2016) Aragonite infill in overgrown conceptacles of coralline *Lithothamnion* spp. (Hapalidiaceae, Hapalidiales, Rhodophyta): new insights in biomineralization and phylomineralogy. *Journal of Phycology* **52**: 161–173.
- Lee K, Kyeong KM, Yang EC, et al. (2016) Reconstructing the complex evolutionary history of mobile plasmids in red algal genomes. *Scientific Reports* **6**: 23744. DOI: 10.1038/srep23744.

- Li L, Ni R, Shao Y and Mao SR (2014) Carrageenan and its application in drug delivery. *Carbohydrate Polymers* **103**: 1–11.
- Littler MM, Littler DS, Blair SM and Norris JN (1985) Deepest known plant life discovered on an uncharted seamount. *Science* **227**: 57–59.
- Loureiro R, Gachon CMM and Rebours C (2015) Seaweed cultivation: potential and challenges of crop domestication at an unprecedented pace. *New Phytologist* **206**: 489–492.
- Mineur F, Le Roux A, Stegenga H, Verlaque M and Maggs CA (2012) Four new exotic red seaweeds on European shores. *Biological Invasions* **14**: 1631–1641.
- Mouritsen OG, Dawczynski C, Duelund L, *et al.* (2013) On the human consumption of the red seaweed dulse (*Palmaria palmata* (L.) Weber & Mohr). *Journal of Applied Phycology* **25**: 1777–1791.
- Nakamura Y, Sasaki N, Kobayashi M, *et al.* (2013) The first symbiont-free genome sequence of marine red alga, Susabi-nori (*Pyropia yezoensis*). *PLoS One* **8**: e57122. DOI: 10.1371/journal.pone.0057122.
- Nash MC, Troitzsch U, Opdyke BN, *et al.* (2011) First discovery of dolomite and magnesite in living coralline algae and its geobiological implications. *Biogeosciences* **8**: 3331–3340.
- Ritson-Williams R, Arnold SN, Paul VJ and Steneck RS (2014) Larval settlement preferences of *Acropora palmata* and *Montastraea faveolata* in response to diverse red algae. *Coral Reefs* **33**: 59–66.
- Sangha JS, Khan W, Ji X, *et al.* (2011) Carrageenans, sulphated polysaccharides of red seaweeds, differentially affect *Arabidopsis thaliana* resistance to *Trichoplusia ni* (Cabbage Looper). *PLoS One* **6** (10): e26834. DOI: 10.1371/journal.pone.0026834.
- Sellers AJ, Saltonstall K and Davidson T (2015) The introduced alga *Kappaphycus alvarezii* (Doty ex P.C. Silva, 1996) in abandoned cultivation sites in Bocas del Toro, Panama. *BioInvasions Records* **4**: 1–7.
- Smit AJ (2004) Medicinal and pharmaceutical uses of seaweed natural products: a review. *Journal of Applied Phycology* **16**: 245–262.
- Verlaque M, Ruitton S, Mineur F and Boudouresque C-F (2015) *CIESM atlas of exotic species of the Mediterranean*. Macrophytes, pp. 1–362, many photograph and maps. Monaco: CIESM Publishers.
- Vermeij MJA, Dailer ML and Smith CM (2011) Crustose coralline algae can suppress macroalgal growth and recruitment on Hawaiian coral reefs. *Marine Ecology Progress Series* **422**: 1–7.
- Weinberger F, Guillemin M-L, Destombe C, *et al.* (2010) Defense evolution in the Gracilariaceae (Rhodophyta): substrate-regulated oxidation of agar oligosaccharides is more ancient than the oligoagar-activated oxidative burst. *Journal of Phycology* **46**: 958–968.
- West JA and Hommersand MH (1981) Rhodophyta: life histories. In: Lobban CS and Wynne MJ (eds) *The Biology of Seaweeds*, vol. **17**, chap. 4, pp. 133–193, Botanical Monographs. Berkeley: University of California Press.
- Williams SL and Smith JE (2007) A global review of the distribution, taxonomy, and impacts of introduced seaweeds. *Annual Review of Ecology, Evolution, and Systematics* **38**: 327–359.
- Xiao S, Knoll AH, Yuan X and Pueschel CM (2004) Phosphatized multicellular algae in the Neoproterozoic Doushantuo formation, China, and the early evolution of Florideophyte red algae. *American Journal of Botany* **91**: 214–227.
- Yang EC, Kim KM, Kim SY, *et al.* (2015) High conservation of mtDNA gene content and structure among multicellular red algae of the Florideophyceae. *Genome Biology and Evolution* **7**: 2394–2406.
- Yang EC, Boo SM, Bhattacharya D, *et al.* (2016) Divergence time estimates and evolution of major lineages in the florideophyte red algae. *Scientific Reports (Nature)* **6**: 21361. DOI: 10.1038/srep21361.
- Zemke-White WL and Ohno M (1999) World seaweed utilization: an end-of-century summary. *Journal of Applied Phycology* **11**: 369–376.

Further Reading

- Baghel RS, Trivedi N, Vishal G, *et al.* (2015) Biorefining of marine macroalgal biomass for production of biofuel and commodity chemicals. *Green Chemistry* **17**: 2436–2443.
- Buchholz CM, Krause G and Buck BH (2012) Seaweed and man. In: Wiencke C and Bischof K (eds) *Seaweed Biology*, pp. 471–493. chap. 22. Berlin: Springer-Verlag.
- Charrier B, Rolland E, Gupta V and Reddy CRK (2015) Production of genetically and developmentally modified seaweeds: exploiting the potential of artificial selection techniques. *Frontiers in Plant Science* **6**: 127. DOI: 10.3389/fpls.2015.00127.
- Cole KM and Sheath RG (1990) *The Biology of Red Algae*, 517 pp. Cambridge, MA: Cambridge University Press.
- Graham LE, Graham JM, Wilcox LW and Cook ME (2016) *Algae*, 3rd edn. LJLM Press. ISBN 978-0-9863935-3-2.
- Lee RE (2008) *Phycology*, 4th edn. Cambridge University Press. ISBN 9780521682770.
- Pueschel CM and Cole KM (1982) Rhodophycean pit plugs: an ultrastructural survey with taxonomic implications. *American Journal of Botany* **69**: 703–720.
- Robinson N, Winberg P and Kirkendale L (2013) Genetic improvement of macroalgae: status to date and needs for the future. *Journal of Applied Phycology* **25**: 703–716.
- Seckbach J and Chapman D (eds) (2010) *Red Algae in the Genomic Age: Volume 13 of Cellular Origin, Life in Extreme Habitats and Astrobiology*. Dordrecht: Springer, ISBN 9048137942.
- Sutherland JE, Lindstrom SC, Nelson WA, *et al.* (2011) A new look at an ancient order: generic revision of the Bangiales (Rhodophyta). *Journal of Phycology* **47**: 1131–1151.