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Quick guide

Red algae

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What are red algae? The red algae are a morphologically diverse group of eukaryotic organisms that make up the most diverse and largest group of seaweeds found in the oceans today. In evolutionary terms, the red algae form a distinct phylum within the Archaeplastida (or Plantae) kingdom called the Rhodophyta, and thus share a common evolutionary origin with the lineage that gave rise to modern-day land plants. Just like their green cousins do on land, the red algae occupy an essential niche as primary food producers in marine ecosystems across the globe, with a further 5% found in freshwater habitats. The red algae are one of just five eukaryotic phyla to have evolved complex multicellularity, with fossil evidence suggesting that they were one of the first eukaryotic lineages to do so, which is a remarkable feat considering that several genes normally essential for multicellularity in other eukaryotes were lost in the last red algal common ancestor. The red algae have also had a huge impact on the evolution of other photosynthetic life forms on the planet by being the ancient donor of plastids to other major groups of algae, like dinoflagellates, diatoms and the brown algae.

Why are red algae important and what are they useful for? The red algal lineage encompasses just under 7500 currently described species, ranging from unicellular microalgae through to multicellular macroalgae. The latter can be crustose-forming, filamentous or blade-like in form, or take the form of complex seaweeds with organised cell layers reminiscent of that seen in land plants (Figure 1). The unicellular groups of red algae represent some of the hardiest organisms on the planet, which can thrive in acidic and thermal habitats like volcanos, geysers and acid rivers. For example, *Cyanidioschyzon merolae* is adapted to live in hot spring environments with high sulfur acidic content (pH 1.5 and 45°C), and has emerged as an attractive model organism to study fundamental aspects of cell biology and photosynthesis. Nevertheless, unicellular species represent just a small fraction of the lineage, since the majority of red algal species are multicellular and manifest as complex seaweeds of great importance for marine ecology.

Although generally smaller and more inconspicuous when compared with giant brown seaweeds like the kelps, the red algae are broadly distributed in diverse marine environments, and overwhelmingly dominate the biome area of shoreline macroalgal forests across the globe, where they provide shelter and nourishment to a whole host of marine organisms. For example, the coralline red algae play a major role in building coral reefs and are characterised by tough calcified cell walls that secrete calcium carbonate. In addition to their importance for ecology, red seaweeds are also useful to humanity. Unlike traditional cultivation of land crops, seaweed cultivation

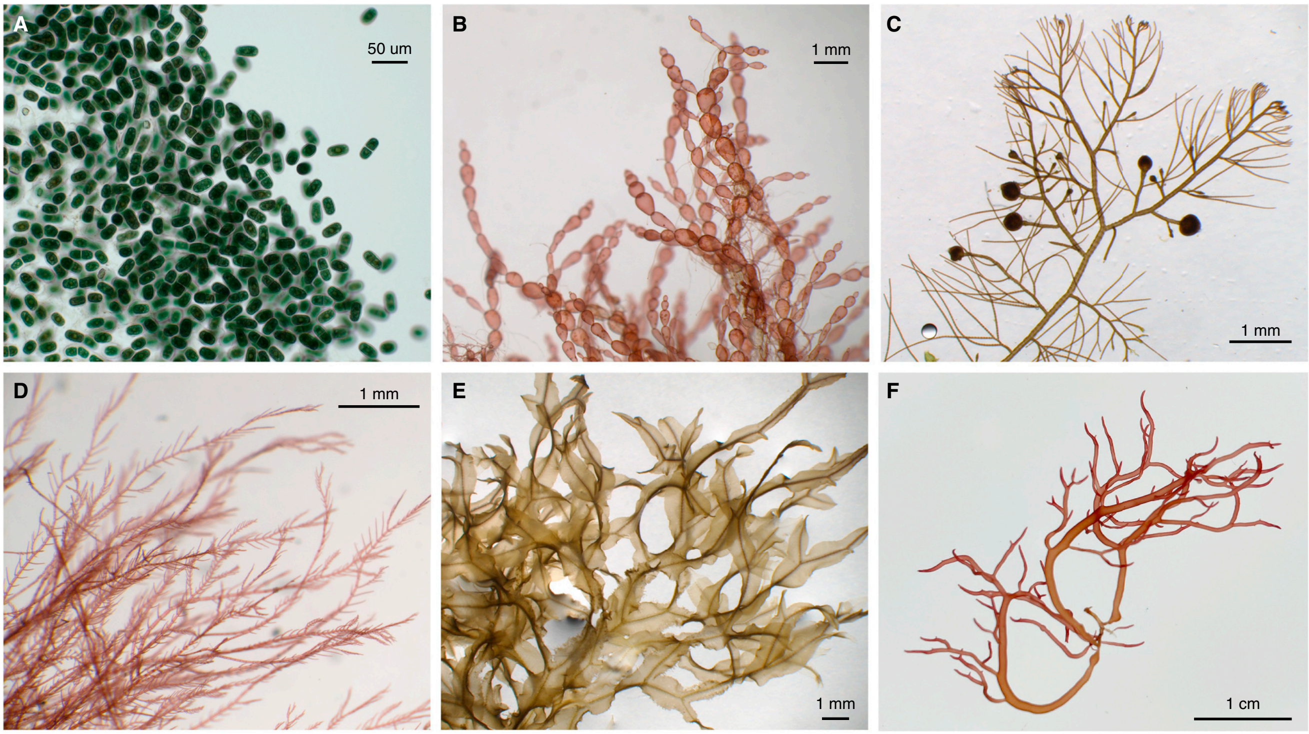

Figure 1. Morphological diversity among the red algae.
(A) *Chroodactylon* sp. (B) *Griffithsia monilis*. (C) *Bostrychia moritziana*. (D) *Pterothamnion plumula*. (E) *Caloglossa monosticha*. (F) *Gracilaria gracilis*. (Photos: Michael Borg.)

requires neither land, fresh water nor fertiliser, and offers a promising avenue for sustainable and efficient food production that has a low environmental footprint. Famous examples of red seaweed foods include nori, the dried edible sheets of *Pyropia* species typically used in Japanese cuisine, and laverbread, a preparation of boiled *Porphyra* seaweed and oatmeal commonly eaten in Wales and North Devonshire in the UK. Many red seaweeds are also a vital source of animal feed, fertilisers, cosmetics, pharmaceuticals and nutraceuticals, pigments and even biodegradable plastics, and are a major reason why the seaweed market is booming worldwide.

What distinguishes the red algae from other eukaryotic lineages? Because of their distinct evolutionary history, the red algae have acquired a host of cellular features that distinguish them from other eukaryotic lineages. For example, red algal plastids have a different structure when compared with those in plants, since their thylakoid membranes are unstacked and present as single lamellae. Red algal plastids also contain accessory water-soluble pigments called phycobilins that give red algae their striking red-to-purple colour, although some species can vary greatly in color (Figure 1). Phycobilins form part of specialised light-harvesting antennae attached to the thylakoid membranes called phycobilisomes, which allow red algae to photosynthesise in much deeper waters with lower light levels than other types of algae.

Moreover, unlike other algae and land plants, the red algae produce a distinct food reserve called floridean starch that is stored in cytosolic granules outside of the plastid. Flagella and centrioles are also not present during any stage of the red algal life cycle, which can be traced to the loss of these and other essential pathways like autophagy early on during evolution of the Rhodophyta. Another key distinguishing feature of red algae is the presence of pit plugs between cells, which can be seen preserved in a 1.6-billion-year-old fossil believed to be an ancestor of modern-day red algae. Pit plugs arise from the deposition of proteinaceous material in the pores that result either from incomplete cleavage during cell division, which is common to most red algae, or through intercellular fusions that occur during reproduction. The precise role of pit plugs still remains unclear, but they are postulated to play a role in structural reinforcement or perhaps serve as avenues for cell-to-cell communication.

Why is reproduction different in the complex red seaweeds? One of the most intriguing features of the red seaweeds is their highly elaborate reproductive mechanisms. Like other seaweeds and land plants, the red algae also evolved an elaborate life cycle, where distinct multicellular life forms — or generations — alternate with one another. This so-called ‘alternation of generations’ is particularly complex in the most dominant group of red seaweeds since it involves transition between not two, but three distinct generations — the haploid gametophytes, a diploid carposporophyte and a diploid tetrasporophyte. While the free-living gametophytes and tetrasporophyte function similarly to those in plants and other algae (i.e., by producing gametes and meiotic spores, respectively), the carposporophyte remains attached to the female gametophyte and undergoes a unique developmental process in biology. Once it arises after fertilisation, it will replicate the zygote into an abundant mass of diploid spores, often resulting in hundreds to thousands of offspring from just one single fertilisation event.

This triphasic life cycle is further supported by elaborate processes that rival the sophistication seen in land plants. For example, the lack of flagella in red algae means that the male gametes (called spermatia) are immotile, so gamete union is compensated for by the trichogyne, a thin hair-like projection produced by the egg cell (called the carpogonium). The trichogyne helps capture and mediates fertilisation with the immotile spermatia, eventually delivering the paternal nucleus to the maternal nucleus in a manner reminiscent of the pollen tube in flowering plants. Moreover, ‘pollination’-like mechanisms might be common among red algae since isopods have been shown to increase the rates of fertilisation in *Gracilaria gracilis* by transporting spermatia on their body

Why are red seaweeds still understudied at a molecular level? Despite several decades of research into the taxonomy, ecology and physiology of red seaweeds, we still know very little about their biology at the molecular level. This has been hampered by the lack of available genomes in this group as well as no *bona fide* model system with well-established genetic tools. This is expected to change in the coming years as genomic resources become increasingly available for several red seaweeds, which will further enable future exploration of their fascinating biology. This will be key to not only harness their potential as sustainable crops of the future but also to broaden our insight into the mysteries underlying the evolution of complex multicellular life.

Where can I find out more?

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DECLARATION OF INTERESTS

The author declares no competing interests.

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