Rhodophyta

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Abstract

Rhodophyta, or red algae, comprises a monophyletic lineage within Archaeplastida that includes glaucophyte algae and green algae plus land plants. Rhodophyta has a long fossil history with evidence of *Bangia*-like species in ca. 1.2 billion-year-old deposits. Red algal morphology varies from unicellular, filamentous, to multicellular thalloid forms, some of which are sources of economically important products such as agar and carrageenan.

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These species live primarily in marine environments from the intertidal zone to deep waters. Freshwater (e.g., *Batrachospermum*) and terrestrial lineages also occur. One of the major innovations in the Rhodophyta is a triphasic life cycle that includes one haploid and two diploid phases with the carposporophyte borne on female gametophytes. Red algae are also well known for their contribution to algal evolution with ecologically important chlorophyll-*c* containing lineages such as diatoms, dinoflagellates, haptophytes, and phaeophytes all containing a red algal-derived plastid of serial endosymbiotic origin. Analysis of red algal nuclear genomes shows that they have relatively small gene inventories of 6,000–10,000 genes when compared to other free-living eukaryotes. This is likely explained by a phase of massive genome reduction that occurred in the red algal ancestor living in a highly specialized environment. Key traits that have been lost in all red algae include flagella and basal body components, light-sensing phytochromes, and the glycosylphosphatidylinositol (GPI)-anchor biosynthesis and macroautophagy pathways. Research into the biology and evolution of red algae is accelerating and will provide exciting insights into the diversification of this unique group of photosynthetic eukaryotes.

Keywords

Red algae • Rhodophyta • Ultrastructure • Evolutionary timeline • Triphasic life history • Genome reduction

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Summary Classification

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●●●Florideophyceae
●●●●Hildenbrandiophycidae
●●●●Nemaliophycidae
●●●●Corallinophycidae
●●●●Ahnfeltiophycidae
●●●●Rhodymeniophycidae

Introduction

General Characteristics

The Rhodophyta (red algae) is a well-characterized and morphologically diverse lineage of photosynthetic protists. They range from unicells and uni- or multiseriate (arranged in rows) filaments, to large (up to 3 m) pseudoparenchymatous, branched or unbranched, terete (cylindrical) to foliose (blade-like) thalli, including crustose and erect forms, some of which are calcified (Figs. 1 and 2). More than 7,100 species are currently reported (www.algaebase.org). Diagnostic features of the red algae are: (1) plastids with accessory, water-soluble pigments allophycocyanin, phycocyanin, and phycoerythrin localized in structures termed phycobilisomes located on the outer faces of photosynthetic lamellae (thylakoids, Fig. 3b, c; other pigments include chlorophyll *a,* α- and β-carotene, lutein and zeazanthin); (2) thylakoids present as single lamellae (i.e., not stacked) in plastids (Fig. 3a–c); (3) lack of flagellated structures at any stage of the life history; and (4) food reserves stored as floridean starch [α-(1, 4)-linked glucan] in granules outside the plastid (Fig. 3a, b). Additional traits of some, but not all red algae include: (1) the presence of “pit connections” between cells (a misnomer because these are not connections between cells, rather plugs of proteinaceous material deposited in the pores that result from incomplete centripetal wall formation) (Fig. 3a, d); (2) mitochondria associated with the forming (cis) faces of dictyosomes (Golgi bodies) (Fig. 3e); (3) plastids surrounded by one or more encircling thylakoids (Fig. 3c); and (4) a complex life history composed of an alternation of two free-living and independent generations (gametophyte and tetrasporophyte) and a third generation, the carposporophyte, that occurs on the female gametophyte (terms are defined in the “Life Histories” section). The Rhodophyta currently consists of two subphyla and seven classes (Yoon et al. 2006).

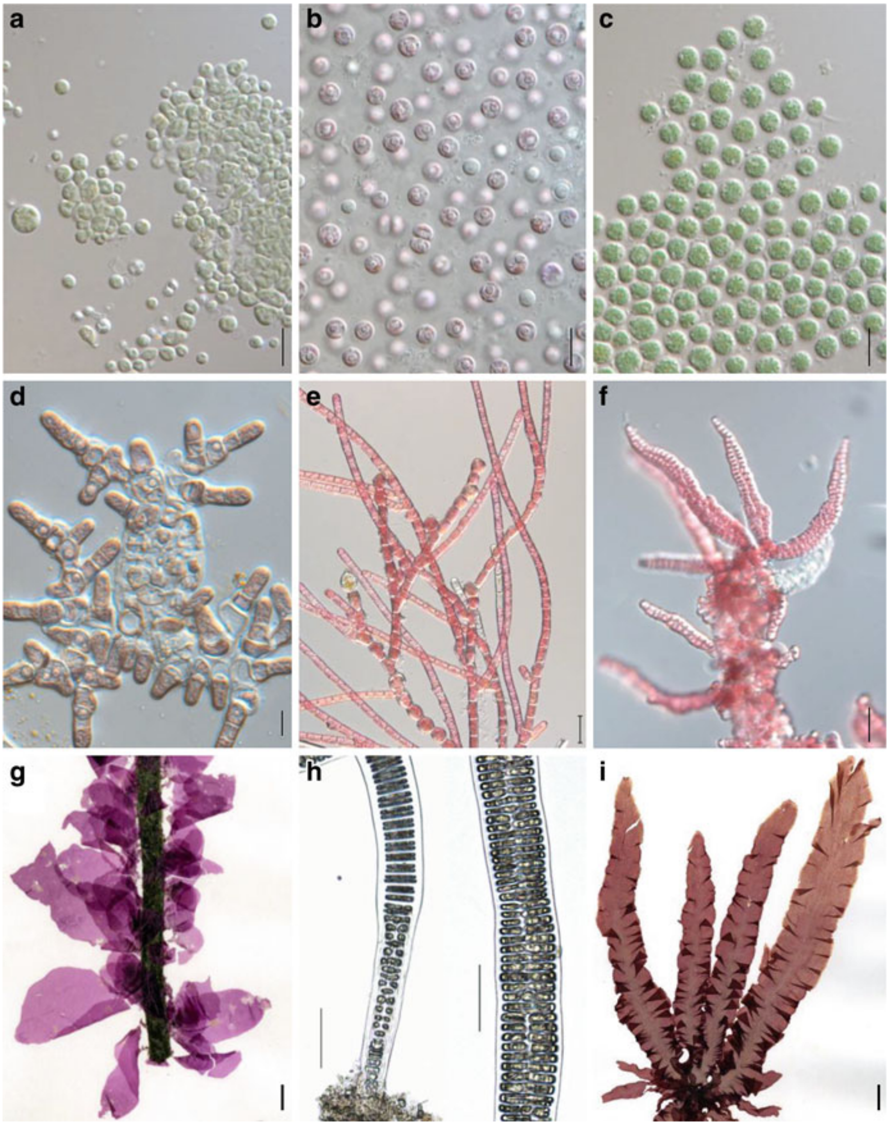

Fig. 1 (**a**–**i**) Representative species of the Rhodophyta. (**a**) *Galdieria phlegrea* (Cyanidiophyceae), (**b**) *Rhodosorus marinus* (Stylonematophyceae), (**c**) *Porphyridium aerugineum* (Porphyridiophyceae), (**d**) *Boldia erythrosiphon* (Compsopogonophyceae), (**e**) *Rhodochaete parvula* (Compsopogonophyceae), (**f**) *Stylonema cornu-cervi* (Stylonematophyceae), (**g**) *Smithora naiadum* (Compsopogonophyceae), (**h**) *Dione arcuata* (Bangiophyceae), (**i**) *Pyropia virididentata* (Bangiophyceae). (Scale = 10 μm for **a**–**c**, 20 μm for **d**–**f**, 2 cm for g, 30 μm for h, 10 cm for i)

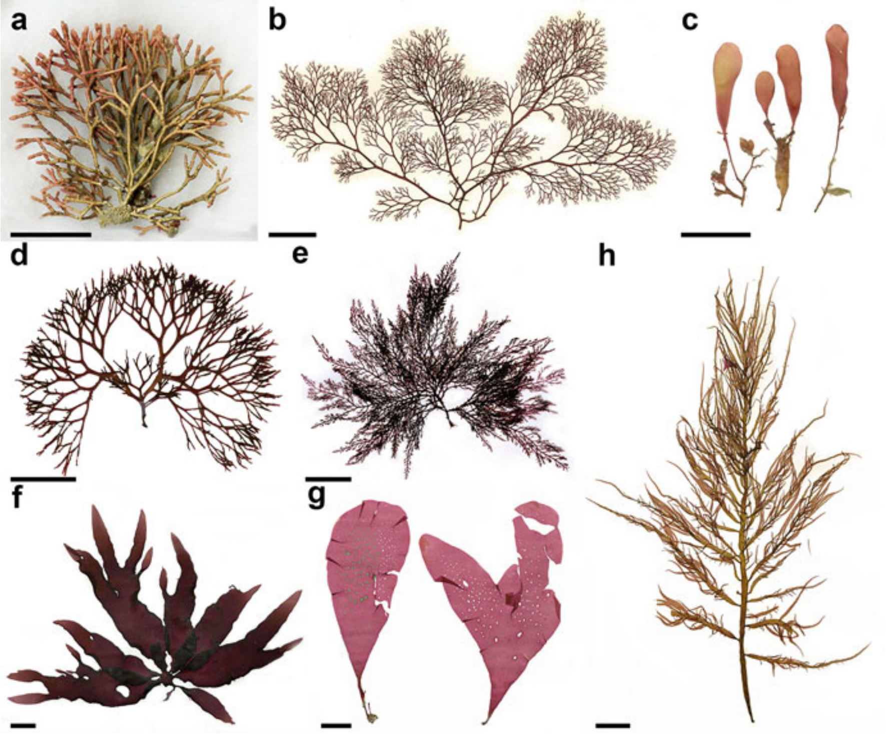

Fig. 2 (**a**–**g**) Habits of Florideophyceae. (**a**) *Actinotrichia fragilis* (Nemaliales, CNU011766) from Jeju, Korea. Scale = 1 cm. (**b**) *Ceramium kondoi* (Ceramiales, CNU013255) from Oeyondo, Korea. Scale = 1 cm. (**c**) *Schottera* sp. (Gigartinales, CNU040701), from Chujado, Korea. Scale = 1 cm. (**d**) *Ahnfeltiopsis flabelliformis* (Gigartinales, CNU033820) from Chujado, Korea. Scale = 2 cm. (**e**). *Gelidium elegans* (Gelidiales, CNU018530) from Jeju, Korea. Scale = 1 cm. (**f**) *Pachymeniopsis lanceolata* (Halymeniales, CNU049476) from Pohang, Korea. Scale = 2 cm. (**g**) *Sparlingia pertusa* (Rhodymeniales, CNU057539), from Uljin, Korea. Scale = 2 cm. (**h**) *Chrysymenia wrightii* (Rhodymeniales, CNU021964). Scale = 2 cm

Florideophyceae, the most species-rich class (6,751 spp.; 95% of all taxa), appears to be a monophyletic group characterized by the presence of tetrasporangia and a filamentous gonimoblast in most species (terms defined in the "Life Histories" section).

History of Knowledge

The process of describing and naming Rhodophyta (along with all plants and eukaryotic photosynthetic organisms) begins with Linnaeus, who placed taxa that currently belong to this phylum in three genera: *Conferva* (filamentous forms), *Ulva* (membranous forms), and *Fucus* (thalloid forms). Lamouroux was the first to use

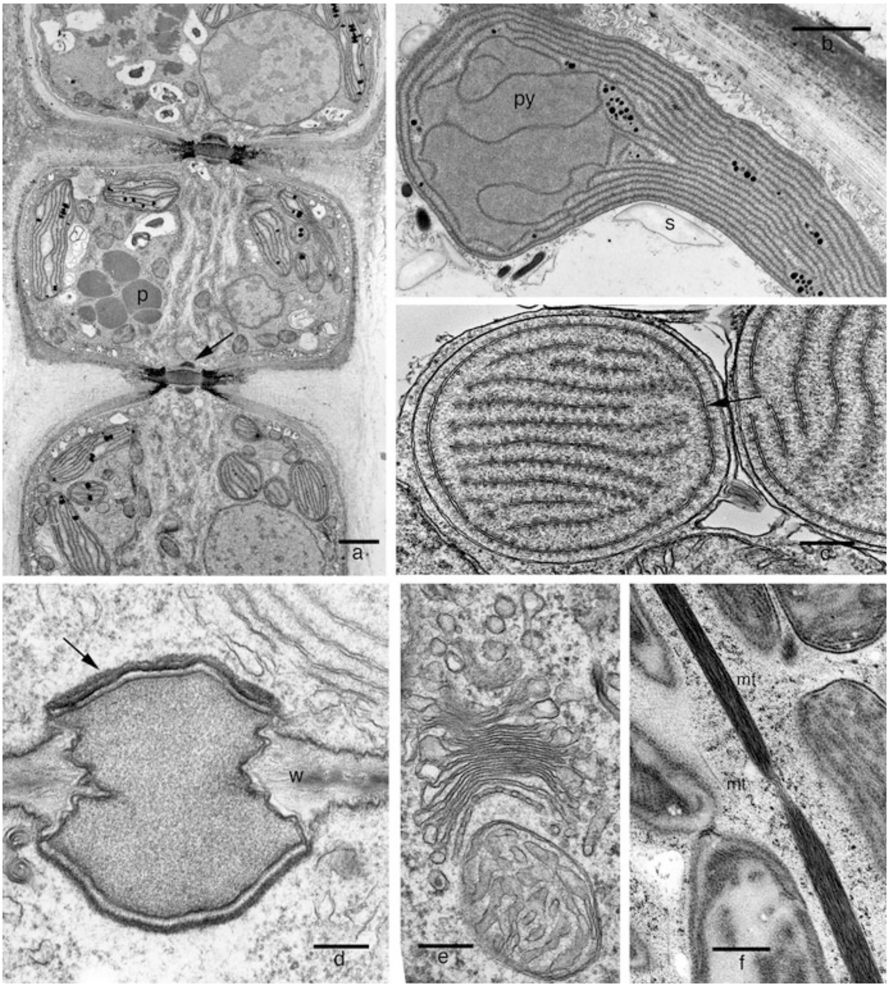

Fig. 3 (**a**–**f**) Thin-section electron microscopy of cellular features of red algae. (**a**) Multicellular epithallial filament of *Neopolyporolithon loculosum*. Cells are joined by pit plugs having dome-shaped outer caps (*arrow*). Cells contain a nucleus, numerous plastids, Golgi bodies associated with mitochondria, endoplasmic reticulum, and protein bodies (*p*). Scale = 1.0 μm. (**b**) Plastid of *Colaconema rhizoideum* containing a large pyrenoid (*py*) penetrated by thylakoids. Starch grains (*s*) are present in the cytoplasm. Scale = 1.0 μm. (**c**) Plastid of *Griffithsia pacifica*. A single peripheral thylakoid (*arrow*) just inward of plastid envelope encircles numerous plate-shaped thylakoids. Phycobilisomes are visible as granules on the surfaces of the thylakoids. Scale = 0.2 μm. (**d**) Pit plug of *Palmaria palmata*. The homogeneous plug core, flanked by cell wall (*w*), is separated from the cytoplasm by thin multilayered plug caps (*arrow*). Scale = 0.2 μm. (**e**) Golgi body-mitochondrion spatial association in *Audouinella saviana* is typical of florideophytes. Scale = 0.2 μm. (**f**) Freeze-substitution preparation of *Antithamnion kylinii* preserves cytoskeleton, including prominent cables of microfilaments (*mf*) and scattered microtubules (*mt*). Scale = 0.5 μm

color to distinguish between groups of thallophytes, and he placed some red algal genera into an order “Floridées.”

Red algae (particularly Florideophyceae) were not recognized as a monophyletic assemblage, however, until Harvey (1836) distinguished red, green, and brown algae (Rhodospermeae, Chlorospermeae, and Melanospermeae, respectively) as separate groups based on the spores being the same color as the parent thalli. Although this classification gained immediate acceptance, it was not until the elegant experiments of Haxo and Blinks (1950) that the direct link was established between the colors (presence of various accessory pigments) of algae and their photosynthetic action spectra.

During the nineteenth century, when European nations were sponsoring voyages to discover and explore new lands, plant and animal specimens were sent back to various scientific authorities. Thus, algal specimens were sent to C. A. and J. G. Agardh in Lund, F. T. Kützing in Leiden, P. C. Montagne in Paris, and W. H. Harvey in Dublin, as well as to numerous other algal systematists who published significant (and often magnificent) tomes. Their observations were restricted to morphological and anatomical features of taxa, with no clear understanding of how these features were related to the reproduction or life histories of the organisms.

Convincing documentation of sexual reproduction in red algae was provided by Bornet and Thuret, and further observations made independently by Schmitz and Oltmanns, linked morphological features with stages of sexual reproduction. With these discoveries, the criteria that formed the basis of the classification of the Florideophyceae for many years were established. By early in the twentieth century, a number of orders that are recognized today had been established, and by mid-century the voluminous works of one man, Harald Kylin (summarized in Kylin 1956), had set down an infraordinal classification scheme that was followed for about three decades. Over the past ca. 25 years, many more orders, families, and genera of red algae have been established (Schneider and Wynne 2007, 2013; Wynne and Schneider 2010).

The red algae are classified into the phylum Rhodophyta (Wettstein 1901), as one phylum of the supergroup Archaeplastida with two sister phyla, the Viridiplantae and Glaucophyta (Adl et al. 2005). The Rhodophyta has been traditionally classified into two classes, the Bangiophyceae and Florideophyceae (Gabrielson et al. 1985), or two subclasses, the Bangiophycidae and Florideophycidae (Dixon 1973). Based on cladistics and molecular phylogenetic studies, the Bangiophyceae has been identified as a paraphyletic group (e.g., Gabrielson et al. 1985; Müller et al. 2001; Oliveira and Bhattacharya 2000; Yoon et al. 2006). To reflect phylogenetic relationships, Saunders and Hommersand (2004) developed a revised classification system comprising two phyla (Rhodophyta and Cyanidiophyta), three subphyla (Rhodellophytina, Metarhodophytina, and Eurhodophytina), and five classes (Bangiophyceae, Compsopogonophyceae, Cyanidiophyceae, Florideophyceae, and Rhodellophyceae). This system was updated by Yoon et al. (2006), who inferred seven well-supported phylogenetic lineages in a multigene analysis. They proposed the Rhodophyta contain two subphyla, the Cyanidiophytina with a single class, the

Cyanidiophyceae, and the Rhodophytina with six classes (Bangiophyceae, Compsopogonophyceae, Florideophyceae, Porphyridiophyceae *classis nova,* Rhodellophyceae, and Stylonematophyceae *classis nova*). This seven-class system is now widely accepted for red algal classification. The system presented here and discussed in the "Classification" section represents a slight modification of the system proposed by Yoon et al. (2006, 2010).

Habitats and Ecology

Ecological Importance of Red Algae

Red algae can be found in many different environments – marine, freshwater, and terrestrial. The majority of red algae belong to the Florideophyceae, which are largely multicellular and nearly all inhabit marine habitats. Some species extend into estuarine environments and some are exclusively freshwater, for example, members of the Batrachospermales.

Although red algae rarely form canopies in subtidal communities, they play key roles in nearshore ecosystems. Species of red algae range from the upper reaches of intertidal shores (e.g., members of the Bangiales) to hundreds of meters in depth in clear tropical waters. As understory vegetation in kelp forests as well as turfs on intertidal shores, red algae provide habitat for a wide variety of organisms. This review supplements the earlier review of Gabrielson et al. (1990).

Calcified Red Algae

Calcified red algae are vital components of nearshore ecosystems. They can be found from intertidal shores to the deepest reaches of the euphotic zone and from polar to tropical latitudes (Foster 2001; Nelson 2009). Most calcified red algae belong to the orders Corallinales, Hapalidiales, or Sporolithales. Species in these orders are either geniculate (jointed or articulated) or nongeniculate (typically crustose). In tropical coral reef environments, crustose coralline algae reinforce the skeletal structure of corals, filling cracks and cementing together sand, dead coral, and debris, creating stable substrate, and reducing reef erosion (Adey 1998; Diaz-Pulido et al. 2007). In studying tropical coral reefs, Littler and Littler (2007) concluded that the presence of "massive corals and calcareous coralline algae relative to frondose macroalgae and algal turfs indicates a healthy spatially heterogeneous condition reflecting low nutrients and high herbivory," whereas high coverage of coralline algae suggests high herbivory levels and elevated nutrients, which can inhibit some corals.

Geniculate coralline algae are also widespread on hard substrata. They are sometimes referred to as ecosystem engineers to reflect the way their three-dimensional structure modifies the environment. Their complex, branched axes intermesh and thus resist wave action and disturbance and retain moisture when exposed at low tide, a particular advantage for intertidal species. These turfs provide habitat and shelter from several of the stresses of intertidal life (e.g., desiccation, wave action, and predation) and, in addition, they provide surfaces for settlement of microphytobenthos and trap sediments for epiphytic filter-feeding taxa. Coralline turfs have been found to harbor high diversity, density, biomass, and productivity of mobile invertebrates (e.g., Cowles et al. 2009; Kelaher et al. 2004). Another ecosystem service provided by coralline algae is the release by some species of compounds that are critical to the settlement and morphogenesis of corals and molluscs (Morse et al. 1996; Roberts 2001; Tebben et al. 2015).

Rhodoliths are free-living coralline algae found in coastal habitats extending to depths of more than 200 m (Foster 2001; Nelson 2009), and they thrive in areas with sufficient water motion to inhibit burial by sediment but not so much as to remove them from their favored habitat (Foster 2001). Rhodolith beds (maërl) are extensive communities found on a wide variety of sediments, from mud to coarse sand. Foster (2001) argued that rhodolith beds may be one of earth's "big four" seaweed-dominated communities together with kelp forests, seagrass meadows, and nongeniculate coralline algae-dominated tropical reefs. Internationally recognized as unique ecosystems, new rhodolith beds continue to be discovered (Foster 2001; Konar et al. 2006; Teichert et al. 2012; Macaya et al. 2015). The three-dimensional structure of rhodolith beds creates microhabitats for diverse invertebrates and algae, including rare and unusual species, as well as serving as nursery grounds for some commercial species of fish (e.g., Hernández-Kantún et al. 2010; Kamenos et al. 2004a, b; Neill et al. 2015; Peña and Bárbara 2008b; Steller et al. 2003; Teichert 2014). Recognition of the ecological importance of these algal-dominated communities and the need for conservation has increased over the past decade (e.g., Barbera et al. 2003; Grall and Hall-Spencer 2003; Peña and Bárbara 2008a). Maërl has a long history of use as a soil additive in Europe, and commercial mining of rhodoliths is carried out in Europe and Brazil, despite concerns about the sustainability and impacts on ecosystem services (Briand 1991; Riul et al. 2008).

Recent studies indicate that rhodoliths and other coralline algae are at risk from the impacts of a range of human activities, such as physical disruption, reduction in water quality, alterations to water movement, and global climate change (e.g., McCoy and Kamenos 2015; Nelson 2009).

Invasive Species

There is increasing recognition of the potential ecological impacts of introduced species – for example, modifying the habitats they invade, displacing native species, altering food webs and community structure, and threatening native biodiversity. Compilations of introduced seaweeds have been published as well as regional surveys (e.g., Davidson et al. 2015; Miller et al. 2011; Nelson 1999; Williams and Smith 2007).

There have been serious consequences accompanying human-assisted introductions of certain red algae, with examples of both filamentous species, such as *Heterosiphonia japonica* (e.g., Newton et al. 2013; Schneider 2010; Sjøtun et al. 2008), and large foliose species, such as *Grateloupia turuturu* (Araujo et al. 2011; D'Archino et al. 2007; Janiak and Whitlach 2012; Verlaque et al. 2005). Research has examined biological attributes that may determine the invasive nature of these species and their impacts on the receiving communities.

Both the movement of aquaculture species and ballast waters have been implicated in the spread of red algae. Molecular sequencing has been a useful tool in understanding the pathways and the timing of some introductions (Andreakis et al. 2007; Yang et al. 2008). In genera such as *Grateloupia* and *Gracilaria*, where identifying species using morphological characters can be problematic, molecular techniques as well as analyses of proteins and other compounds have proved valuable in distinguishing native from nonnative species (e.g., Kollars et al. 2015; Gavio and Fredericq 2002; Kim et al. 2010; Wilcox et al. 2007).

Biogeography

Studies continue to document the flora of some of the lesser-known areas of the globe (Harper and Garbary 1997; Hommersand et al. 2009; Klochkova and Klochkova 2001; Lindstrom 2006, 2009; Nelson and Dalen 2015; Selivanova and Zhigadlova 1997a, b, c; Wulff et al. 2009). Red algae are significant in these studies because they are generally both more numerous than either green or brown algae and more phylogenetically diverse due to their ancient history and wide environmental tolerances.

During the 1990s, biogeographic studies continued to focus on the role of physiological responses (particularly to temperature) in the distribution of red algae. Much of this work focused on Arctic, Antarctic, and tropical species (e.g., Wiencke et al. 1994 Bischoff-Bäsmann and Wiencke 1996; Bischoff-Bäsmann et al. 1997; Pakker and Breeman 1996). The role of temperature and area, particularly over geological time, was central to the thermogeographic model of Adey and Steneck (2001). This model has been used to explain the predominantly Pacific origin of the Arctic and Atlantic boreal seaweed floras (Adey et al. 2008) and was validated using subtidal seaweed assemblages in the northwestern Atlantic Ocean (Adey and Hayek 2011).

Molecular data are being used to look at the distribution and phylogeography of species (e.g., Gurgel et al. 2004; Montecinos et al. 2012) although phylogeographic patterns are not always evident in these data (e.g., Vis et al. 2012). Studies have also looked at patterns of recolonization in areas affected by Pleistocene glaciations (Hu et al. 2010; Lindstrom et al. 1997; Provan et al. 2005; Yang et al. 2009). Hommersand (2007) analyzed the Australian macroalgal flora in terms of global biogeographic patterns and in relation to vicariance events in the geological history of Australasia. He identified Australasia as "a center of origin and diversity for marine algae, especially the Rhodophyta." Molecular studies provided data to support the hypothesis that many lineages of red algae originated in the southern hemisphere, or at least extant members of lineages, are found there (e.g., Bangiales – Broom et al. 2004; Gelidiales and Gigartinaceae – Hommersand et al. 1994; Nelson et al. 2011; Gracilariales – Gurgel and Fredericq 2004). Molecular sequencing has indicated that many species actually are species complexes, and the resolution of species boundaries not evident from morphological examination is permitting a clearer understanding of their divergent ecologies (Lindstrom et al. 2011; Boo et al. 2016a, b). The evolution of a domesticated red alga, *Gracilaria chilensis*, has also been studied using a combination of phylogeographic and population genetic tools (Guillemin et al. 2014).

Ocean Acidification, Global Warming, and Red Algae

The long-term ecosystem consequences of human-mediated changes in global climate (e.g., rising temperatures, increased levels of atmospheric carbon dioxide and resulting decreases in seawater pH, changes in UV radiation, and changes in ocean circulation and upwelling patterns) are being investigated. Harley et al. (2012) reviewed how multiple stressors may affect survival, growth, and reproduction of seaweeds in a changing climate: different responses of community members to these stressors may determine persistence or extinction. For turf-forming red algae, which rely on aqueous CO_2, elevated levels should differentially favor their growth, which in turn may enhance their competitive ability (Hepburn et al. 2011). Climate change may also drive shifts in seaweed distributions at both horizontal (geographical) and vertical (elevation) scales (Brodie et al. 2014; Harley et al. 2012). These changes may be stochastic rather than gradual as shown by Harley and Paine (2009).

Roleda and Hurd (2012) summarized the responses of seaweeds to ocean acidification and examined the underlying chemistry, physiological and community-level responses, and interactions with other stressors. The contribution of calcareous algae to global carbonate production was reviewed by Basso (2012) and by McCoy and Kamenos (2015), including the response of coralline red algae to marine acidification and rising temperature. These algae showed decreased net calcification, decreased growth and reproduction, as well as reduced abundance and diversity, leading to death and an ecological shift to dominance by noncalcifying algae. In some regions, the contribution of rhodolith beds to nearshore carbonate production is very significant. Pereira-Filho et al. (2012) calculated that the summits of several seamounts are covered with extensive rhodolith beds within the tropical southwestern Atlantic. These beds are responsible for 0.3% of the world's carbonate production, and Amado-Filho et al. (2012) recorded the production from Brazilian rhodolith beds to be comparable to the world's largest $CaCO_3$ deposits, describing these beds as "major $CaCO_3$ biofactories."

Calcareous organisms can provide insight into geological processes and have the potential to be used as indicators of paleoenvironmental conditions: rhodoliths and crustose coralline algae are particularly useful in this context because of their sensitivity to ecological changes reflecting their depositional setting (e.g., Adey et al. 2015; Frantz et al. 2000, 2005; Fietzke et al. 2015; Halfar et al. 2000, 2007, 2008, 2011; Kamenos et al. 2008).

The effects of ozone depletion and UVB radiation on algae have been summarized by Bischof and Steinhoff (2012). Because there are marked species-specific responses to UVB radiation, there may be significant ecological implications in the responses at a community or ecosystem level with changes in distributional patterns (latitude and depth) as well as succession patterns, trophic interactions, and species diversity. Studies of red algae in polar regions have shown that their distribution on the shore is related to their ability of cope with UVB-mediated damage to DNA. In red algae, mycosporine-like amino acids (MAAs) have been the focus of a number of studies examining their role as UV-screening substances. In general, cellular MAA concentrations in red algae have been shown to be positively correlated with UV dose.

Commercial Importance

Red algae continue to be an important component of seaweed aquaculture, representing about 33% of the harvested weight but nearly 50% of the value, which was about US $6.4 billion in 2012 (FAO 2014). *Eucheuma* spp., including *Kappaphycus*, were responsible for more than 5 million tons of harvested seaweed, and *Gracilaria* 2.7 tons, and *Porphyra* spp., including *Pyropia*, about 1.8 million tons. Production of all species showed significant increases from the 1990s. Major production areas include Korea, Japan, China, Indonesia, and the Philippines, with minor production occurring in Malaysia and Zanzibar. Buchholz et al. (2012) summarize the methods employed in cultivation of farmed red algae including both monoculture methods and integrated multitrophic aquaculture (IMTA–Chopin et al. 2008).

The majority of red seaweeds, either collected from the wild or farmed, are used in the production of human food (Buchholz et al. 2012; Pereira et al. 2012). Direct consumption as sea vegetables is important in the Asia Pacific region, and red algal hydrocolloids are used widely in the food and other industries. New applications are being developed for marine algal products, for example, in functional foods, medicine (as anti-inflammatory, antiviral, anticancer uses), as well as in cosmetics and cosmeceuticals, and as biomaterials in skeletal replacement or regeneration, including dental applications.

Seo et al. (2010) revealed a potential use of rhizoidal filaments in *Gelidium* as raw material for papermaking. The handsheets of *Gelidium* pulp had very high Bekk smoothness and opacity, which are essential properties for high-valued printing paper, when compared to those of wood pulp.

Novel Chemistry

Galloway et al. (2012) showed that different groups (phyla, orders, families) of marine macrophytes, including red algae, have distinct essential fatty acid signatures, and the signatures of red algae were more variable than those of brown, particularly those in the orders Corallinales, Gigartinales, and Gracilariales. Because animals cannot synthesize these molecules and rely on plant sources, essential fatty acids are useful trophic markers for tracking sources of primary production through food webs.

Some red algae are known to produce secondary metabolites, which appear to play a key defensive role against both herbivory and fouling (e.g., Blunt et al. 2011; Dworjanyn et al. 2006; Oliveira et al. 2013). Amsler et al. (2009) found that chemical defenses against herbivory are very important in structuring Antarctic macroalgal communities but not the single Arctic community examined to date, and they suggested that this may be a consequence of the different evolutionary histories of these regions. Nylund et al. (2013) examined the costs and benefits of chemical defense in *Bonnemaisonia hamifera* and found that although costly in energetic terms, there were significant fitness benefits by protecting against harmful bacterial colonization. Lignin and secondary walls were reported in red algae by Martone et al. (2009), raising questions about the biosynthetic pathways and the convergent or deeply conserved evolutionary history of these traits.

Population Biology

Many of the ecological studies of red algae have focused on aspects of their biology in relation to their life histories and reproductive modes. Although little studied, vegetative reproduction via multicellular propagules is widespread in red algae, increasing local populations, and it may be that this is the way in which some human-mediated introductions are effected (reviewed by Cecere et al. 2011).

Differential responses to environmental factors by isomorphic life history stages have intrigued researchers who have grappled with the implications of the predominance of one phase of an alternating life cycle. A number of studies have modeled the impacts of changes in fertilization success and reproductive output on the abundance of isomorphic generations (e.g., Fierst et al. 2005; Scrosati and DeWreede 1999; Thornber and Gaines 2004). Guillemin et al. (2008) explored genetic diversity in the agarophyte *Gracilaria chilensis*, a species farmed extensively in Chile. Their results suggested that the farming practices favored asexual reproduction and reduced genetic diversity in the farmed stocks. A subsequent study showed that adult tetrasporophytes grew more rapidly than gametophytes under the same conditions. Guillemin et al. (2012) hypothesized that during domestication this difference led to selection of the tetrasporophyte now dominating commercial farms.

Molecular tools are providing new insights into aspects of the ecology and population dynamics of red algae enabling examination of connectivity between populations, as well as the genetic structure of populations at small spatial scales (Andreakis et al. 2009; Donaldson et al. 2000; Engel et al. 1999, 2004; Krueger-Hadfield et al. 2011).

Characterization and Recognition

Ultrastructure

Study of the fine structure of red algae began in earnest in the mid 1960s, and progress was recounted in a series of reviews in the early 1990s. The general features of red algal ultrastructure were reviewed in detail by Pueschel (1990), and knowledge of the fine structure of cell division was summarized by Scott and Broadwater (1990) in the same volume. Broadwater et al. (1992) reviewed the cytoskeleton and spindle. The fine structure of the unicellular red algae was surveyed by Broadwater and Scott (1994).

Although red algae have a typical eukaryotic cell structure (Fig. 3a), they possess a unique combination of cellular features. Their distinctive coloration stems from their water-soluble phycobilin accessory pigments, which are visible ultrastructurally as granules, called phycobilisomes, on the surface of the unstacked photosynthetic membranes of the plastids (Fig. 3b, c). Light energy captured by phycobilisomes is transferred to chlorophyll *a*, which is a constituent of the photosynthetic membranes. The presence of phycobilisomes on single photosynthetic membranes is a feature inherited from the endosymbiotic cyanobacteria that were the progenitors of red algal plastids. Also related to the primary endosymbiotic origin of red algal plastids is the absence of periplastid endoplasmic reticulum (PER) (Fig. 3c). Bounding membranes external to the two membranes of the plastid envelope are typical of many algal lineages and are considered remnants of secondary endosymbiotic acquisition of plastids from another photosynthetic eukaryote. The red algae, like the green algae and glaucophytes, which also became photosynthetic by cyanobacterial primary endosymbiosis, lack PER.

Red algae deposit starch as an insoluble carbohydrate reserve. Floridean starch differs from green-plant starch in being free in the cytoplasm (Fig. 3b), rather than in the plastids, and in consisting solely of amylopectin, without an amylose component. Amylopectin is an α 1–4 linked glucan with abundant α 1–6 linkages, similar to animal glycogen, but in light and electron microscopy the grains of floridean starch appear similar to those of green plants and unlike the fine granules of animal glycogen.

The crucial CO_2-fixing enzyme, ribulose-1,5-biphosphate carboxylase/oxygenase (RuBisCO), occurs throughout the stroma of plastids, appearing as small granules similar in size to plastid ribosomes. In many lineages of algae, dense aggregations of RuBisCO form visible structures termed pyrenoids (Fig. 3b). Only a small proportion of red algal species possess pyrenoids, but those that do are taxonomically widespread, occurring in some representatives of most of the presently recognized classes. Pyrenoids provide a variety of distinguishing features: number per plastid, location within the plastid, whether thylakoids penetrate the pyrenoid matrix (Fig. 3b), proximity to starch grains, and, in the Rhodellales, the peculiar feature of the pyrenoid is that it is deeply penetrated by an RNA-enriched projection of the nucleus (Waller and McFadden 1995).

One of the most distinctive features of the red algae is the absence of any form of flagellated motility. Centrioles, which have a microtubular substructure similar to flagellar basal bodies and in some organisms give rise to flagella, are also absent from the red algae. The near universality of flagella or centrioles among eukaryotes and their absence in red algae was reasonably interpreted as evidence that the red algae diverged from the main line of eukaryotic evolution before the advent of eukaryotic flagellation. Molecular evidence provides a different explanation: these structures were lost by an ancestor of all living red algae. Although centrioles are absent, small, ring-shaped, or discoid structures with no structural similarity to centrioles are present at the poles of mitotic and meiotic spindles (Scott and Broadwater 1990).

Another intriguing ultrastructural feature of red algae is the variety of spatial associations that Golgi bodies form with other organelles (Broadwater and Scott 1994). The close association of the cis-face of Golgi bodies with mitochondria is decidedly the most common configuration in red algae (Fig. 3e). This arrangement contrasts strongly with the cis-Golgi being associated with the nuclear envelope, which is found only in some unicellular species. The association of Golgi with endoplasmic reticulum, the typical arrangement in eukaryotes, is also found, and cisternae of ER are often present near the mitochondrion-Golgi pairings, as well.

All but a few genera of multicellular red algae possess persistent intercellular connections, termed pit connections (Fig. 3a, d), which are the product of incomplete cytokinesis (Pueschel 1990). A structure called the pit plug is deposited within the connection, separating the cytoplasm of the two cells, but the cell membranes of the connected cells remain continuous along the sides of the pit plug. Pit connections are present in all members of the Florideophyceae and Bangiophyceae (although in the case of the latter, not in all life history stages) and some members of the Compsopogonophyceae. The proteinaceous plug core is the only universal element of pit plugs. The plug core may be separated from the adjacent cytoplasm by one or two cap layers of differing chemical composition (Pueschel and Cole 1982). In a multilayered plug cap, the cytoplasm-adjacent outer layer may be either a dome (Fig. 3a) or a thin plate (Fig. 3d), but both of these morphological types have similar cytochemical properties. A membrane, termed the cap membrane, may or may not be present, whether cap layers are present or not. The cap membrane and outer cap layer must have originated within the Florideophyceae because neither feature is found in other classes. Evidence for intercellular transport across pit plugs is largely circumstantial (Pueschel 1990), and compelling experimental proof of the function of pit plugs is not yet in hand.

The cytoskeleton is the most poorly known of typical red algal cellular constituents because it is composed mainly of microtubules and microfilaments, both of which are labile in conventional chemical fixation for electron microscopy. Freeze substitution provides a different preparative approach, and using this technique, Babuka and Pueschel (1998) demonstrated thick bundles of microfilaments and numerous cortical microtubules in axial cells of *Antithamnion* (Fig. 3f). Freeze substitution has been used extensively by Kuroiwa and associates (e.g., Miyagishima et al. 2003; Suzuki et al. 1995) to explore the role of ring-shaped structures, some actin – some not, in the division of plastids, mitochondria, and cells of *Cyanidium* and related genera. Light microscopic studies of fluorescently labeled microfilaments and microtubules, often used in conjunction with specific cytoskeletal inhibitors, have demonstrated a role of one or both of these cytoskeletal elements in cytokinesis (Garbary and McDonald 1996), plastid movement (Russell et al. 1996), fertilization (Kim and Kim 1999; Wilson et al. 2002a, 2003), vesicle transport (Wilson et al. 2006), and the formation of pseudopodia in spores (Ackland et al. 2007). The rotation of plastids in the unicellular alga *Rhodosorus* is another striking example of subcellular movement, but the motive force is unknown (Wilson et al. 2002b). Using time-lapse microscopy, Pickett-Heaps et al. (2001) demonstrated that directional gliding motility is common and widespread in spores and among unicellular species of red algae. Mucilage secretion accompanies this movement, but the mechanism that generates directional motility remains to be elucidated.

Despite the ultrastructural characterization of the many diverse cellular inclusions found in red algal cells, we still have insufficient understanding of their functions. For example, protein bodies (Fig. 3a) are a prominent component of many vegetative cells. It has been proposed that these inclusions might serve as a seasonal nitrogen store (Pueschel 1992), but this idea has not been tested in red algae. Calcium oxalate crystals are common in higher plants and are present in some algal groups, including red algae (Pueschel 1995), but the physiological functions usually assigned to such inclusions in higher plants are unlikely to apply to the algae (Pueschel and West 2007). Progress has been made in the characterization of refractile inclusions that are associated with some kinds of specialized vegetative cells (Paul et al. 2006) and can form distinctive structures, such as the *corps en cerise* in cortical cells of *Laurencia* (Reis et al. 2013). These inclusions consist of halogenated sesquiterpenes, which can be transported to the thallus surface (Salgado et al. 2008) where they have a role in discouraging herbivory and fouling. In cortical cells of *Plocamium,* specialized vacuoles, dubbed mevalonosomes, have been demonstrated by ultrastructural enzyme localization techniques to contain enzymes of the mevalonate pathway (Paradas et al. 2015), whose products also have an antifouling function.

The greatest complexity of cell structure in red algae is found in reproductive cells and specialized vegetative cells. A large portion of the ultrastructural literature addresses the many subcellular changes associated with sporogenesis (Pueschel 1990). Although there is likely a phylogenetic signature in the fine structural details of sporogenesis, the taxonomically diverse survey work needed to explore this potential has not been pursued. The fine structure of the many kinds of specialized vegetative cells, such as rhizoids, gland cells, and hair cells, was studied early in the ultrastructural explorations of red algae (Pueschel 1990). Hair cells have continued to receive attention (Judson and Pueschel 2002; Oates and Cole 1994), as have some kinds of gland cells (Paul et al. 2006). Increased interest in the Corallinales has led to detailed examination of one of the most distinctive types of specialized cells in the red algae, the corallinalean epithallial cell. Although they are apical cells, the epithallial cells undergo terminal differentiation, senescence, and sloughing in a programmatic fashion (e.g., Pueschel et al. 1996). Intercalary meristematic cells divide to produce replacement epithallial cells. This highly unusual process is hypothesized to have an antifouling function or, alternatively, to be an adaptation to frequent grazing. The fact that the walls of coralline algae are heavily calcified makes these epithallial dynamics all the more complex and interesting.

The discovery, description, and elucidation of phylogenetic affinities of new species of red algae are ongoing and for unicellular red algae, ultrastructural study continues to play a critical role in this endeavor. Given the simplicity of unicellular red algae and the paucity of structural features, one might expect to find molecularly distinct but structurally indistinguishable lineages. Instead, the several rhodophyte orders containing unicellular species possess a variety of distinctive ultrastructural characters. That these simple taxa should differ in their basic cellular features presumably reflects the antiquity of their evolutionary divergences. Scott et al. (2011) summarized the systematics of several of the orders containing unicellular red algae and their ultrastructural features. Compared to the diversity of cellular features of unicellular red algae, the basic features of typical vegetative florideophycean cells are relatively uniform.

Life Histories

The red algal life history is unique in having an additional third phase (i.e., a triphasic life history) in most Florideophyceae (except the Hildenbrandiales, Batrachospermales, and Palmariales). The “basic” biphasic life history is found in the early-diverged red algal lineages as well as in some florideophycean taxa. There are, however, numerous variations in the life histories of red algae.

The triphasic life history is an alternation of generations of three phases, the gametophyte, carposporophyte, and tetrasporophyte. It is generally called a “*Polysiphonia*-type” life history because it was first observed in the genus *Polysiphonia*. The triphasic life history is composed of haploid gametophytes (thalli that produce gametes), diploid carposporophytes, and diploid tetrasporophytes (thalli that typically produce four spores by meiotic division) (Fig. 4a). Gametophytes and tetrasporophytes are generally independent photosynthetic thalli, whereas the carposporophyte is diploid tissue that occurs on or within the haploid female gametophyte as a result of fertilization of the egg cell and subsequent development of the zygote.

Male gametophytic plants produce spermatia (= nonmotile sperm) from spermatangial initial cells. Female gametophytic plants produce carpogonial branches that are composed of a terminal carpogonium (= egg cell) with a trichogyne (a hair-like extension) and differing numbers of subtending cells depending on taxonomic group. Fertilization starts with attachment of spermatia to the trichogyne. Fusion of the gametic nuclei occurs in the carpogonium. The resulting diploid nucleus is either transferred, via an outgrowth from the carpogonium, to another cell (called the auxiliary cell), or remains in the carpogonium. In both cases, mitotic divisions of the diploid nucleus within a filamentous outgrowth (the gonimoblast) eventually result in the production of diploid carposporangia. Carpospores are released from the carposporangia and germinate to give rise to free-living diploid tetrasporophytes. Meiosis then occurs in specialized cells (tetrasporangial initial

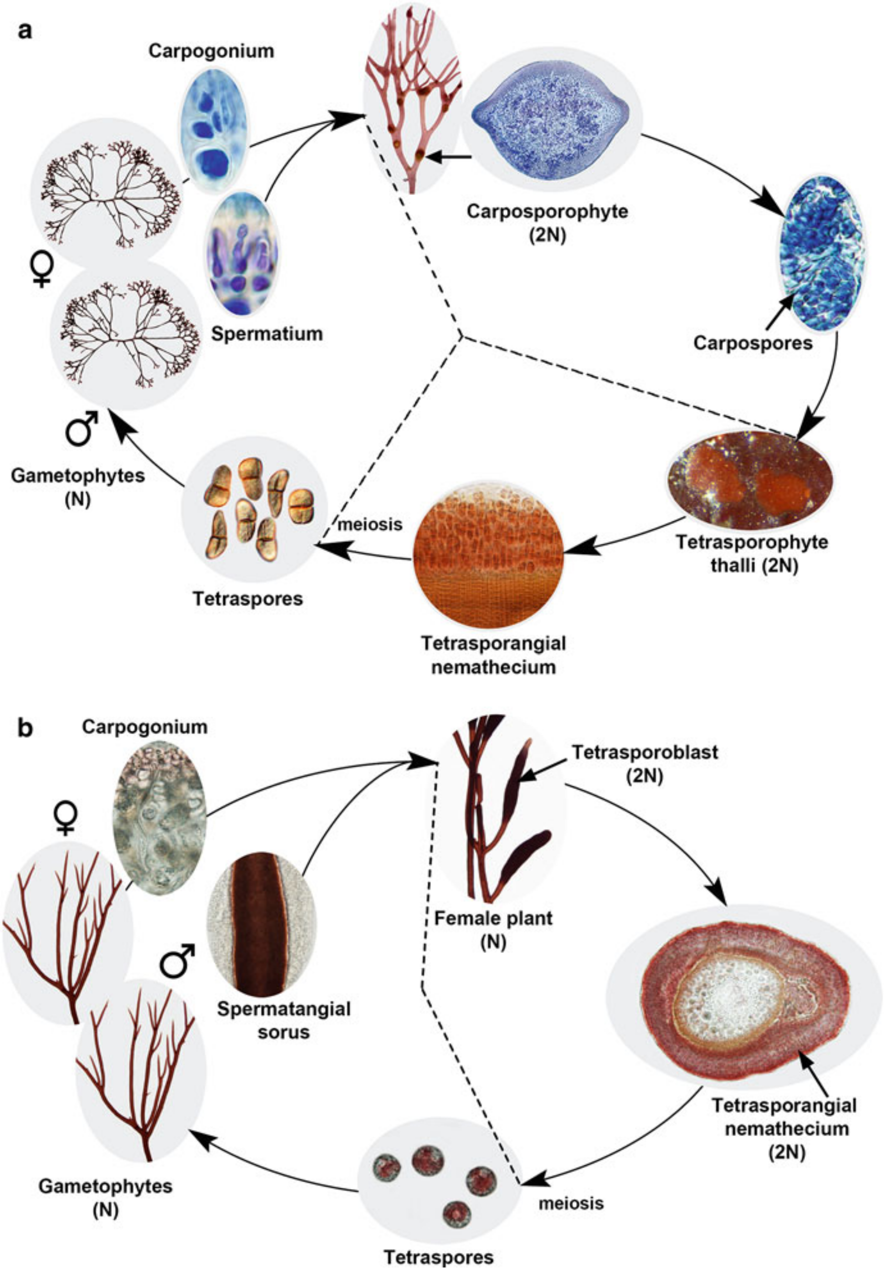

Fig. 4 (**a**, **b**) (**a**) Triphasic life history of *Ahnfeltiopsis catenata.* It shows branched gametophytes and a free-living crust attached to rock. (**b**) Tetrasporoblastic life history of *Pikea yoshizakii*. Tetrasporoblastic life history exhibits a truncated life history in which fertilized females produce tetraspores in nemathecia rather than carpospores in cystocarps

cells) in the tetrasporophyte, and the resulting tetrads of haploid spores are shed from the thallus. Individual spores germinate to give rise to gametophytes, completing the cycle.

The typical *Polysiphonia*-type life history includes isomorphic gametophytes and tetrasporophytes; however, in other red algae heteromorphic generations, in which the tetrasporophyte is morphologically distinct from the gametophyte, also occur. For instance, some species of Gigartinales have a heteromorphic life history in which sporophytes are crustose (see Fig. 4a). Heteromorphic generations also occur in the Nemaliales and Bonnemaisoniales, in which the tetrasporophyte is a minute branched filament. In some species of the Acrochaetiales, the tetrasporophyte is the more conspicuous phase, while the gametophyte is diminutive. The Palmariales are characterized by a life history in which male gametophytes and tetrasporophytes are the conspicuous macrophytes, and female gametophytes are microscopic and after fertilization are overgrown by the tetrasporophytes without benefit of a carposporophyte generation.

Several species of Gigartinales produce tetrasporoblasts and exhibit a truncated life history (Fig. 4b) in which fertilized females produce tetrasporangia in nemathecia rather than carposporangia in cystocarps, bypassing the free-living tetrasporophytic phase, for example, *Pikea yoshizakii* (Boo et al. 2016a). The tetrasporoblastic filaments are homologous to gonimoblast filaments, originating from auxiliary cells following diploid nucleus transfer, and, like the carposporophyte, are also borne on the female gametophyte. Tetrasporangia undergo meiosis, releasing tetraspores that germinate to produce gametophytes.

The biphasic life history is an alternation of generations of two phases: the gametophyte and sporophyte. Among reported sexual species in the Bangiales (Bangiophyceae) (Hawkes 1978), small colorless spermatia (previously referred to as β-spores) are produced (from 16 to 256 per parental cell) which, when released, may fuse with larger pigmented cells. Although formerly referred to as carpogonia, Nelson et al. (1999) concluded that the use of the terms “carpogonium” and “carpospore” is not appropriate for members of the Bangiophyceae, given the significant differences in the ontogeny of the female reproductive structures. The products resulting from this union are termed zygotospores (formerly known as α-spores) and most frequently germinate into the alternate conchocelis phase of the life cycle. The conchocelis phase in the Bangiales regenerates the gametophytic blades or filaments through conchospores (spores produced by the conchocelis phase). Although some species expressing this alternation of generations are reported to be sexual, others apparently are not. In *Pyropia yezoensis*, meiosis has been reported to occur upon germination of the conchospores, resulting in gametophytic thalli that are genetic chimeras (Ma and Miura 1984).

Asexual reproduction occurs in many red algal classes. It can occur through vegetative means (including simple cell division, fragmentation, and production of propagules) and through the production of spores. The term “archeospore” is applied when there is a single-cell product, and “monospore” where single spores are produced by an unequal cell division (Magne 1991). In the Bangiales, archeospores are produced from conversion of vegetative cells in both the gametophytic and sporophytic phases and are an important means of reproduction. Endosporangia are produced in some members of the Bangiales. Some florideophycean red algae have apomictic (lacking meiosis) and apogamic (no fusion of gametes) life histories.

Evolutionary History

The fossil record of the red algae is meager (except for the Corallinales), due to the delicate or gelatinous nature of the vast majority of taxa. Even when thalli are preserved, it is rare that the minute reproductive structures on which the infraordinal classification is based also remain intact. Despite a growing range of Proterozoic fossils, few can be unambiguously assigned to an extant taxon.

There are, however, two exceptional cases of taxonomically resolved Proterozoic red algae. The first is *Bangiomorpha pubescens* from the Hunting Formation, Somerset Island, Arctic Canada (Butterfield 2000). This well-preserved modern *Bangia*-like fossil is generally considered as the oldest taxonomically known eukaryotic fossil (Fig. 5a–e). Large populations, with material ranging from a single cell to reproductively mature filaments, were embedded in a shallow-water chert/carbonate dated at 1174–1222 million years ago (Ma) (see Knoll 2011 for a review of the age constraints). Within this population, up to 2 mm long, unbranched multicellular filaments of uniseriate, multiseriate, and both uni/multiseriate habits (Fig. 5b, c) were found in clusters of up to 15 individuals (Fig. 5a) (see detail, Butterfield 2000). Two cells were usually paired in a uniseriate filament, suggesting transverse intercalary cell division. In multiseriate filaments, four to eight radially arranged wedge-shaped cells were usually identified in transverse cross-section (Fig. 5d). These transverse and radial intercalary cell division patterns are commonly found in species of modern filamentous Bangiales (e.g., Fig. 1h) and are conspicuously distinct from the apical cell division in other algae and filamentous cyanobacteria. Furthermore, *Bangiomorpha* contains spore-like, spheroidal cells within multiseriate filaments (Fig. 5e), indicating development of sexual reproduction in the ancestral red alga.

The second taxonomically resolved fossil red alga consists of anatomically preserved florideophyte fossils from the phosphorites of the late Neoproterozoic [570 (633–551) Ma] Doushantuo Formation at Weng'an, southern China (Condon et al. 2005; Xiao et al. 1998, 2004). Fossils in Doushantuo phosphorites preserved diverse three-dimensional cellular structures comprising cyanobacteria, acritarchs, animal embryos, and multicellular algae. These fossils provide key paleontological evidence about the early radiation of multicellular eukaryotes (Xiao et al. 2014). In the algal fossils, pseudoparenchymatous thalli exhibit specialized tissues including cell growth patterns (e.g., cortex-medulla differentiation, secondary pit connection between cells) and distinct reproductive structures (e.g., spermatangia, tetraspores and octaspores, and carposporangia, see Fig. 5f–i) that closely resemble key characters of Paleozoic relatives (Brooke and Riding 1998) and modern corallines (Xiao et al. 1998, 2004, 2014). Based on anatomical characters mapped on a molecular

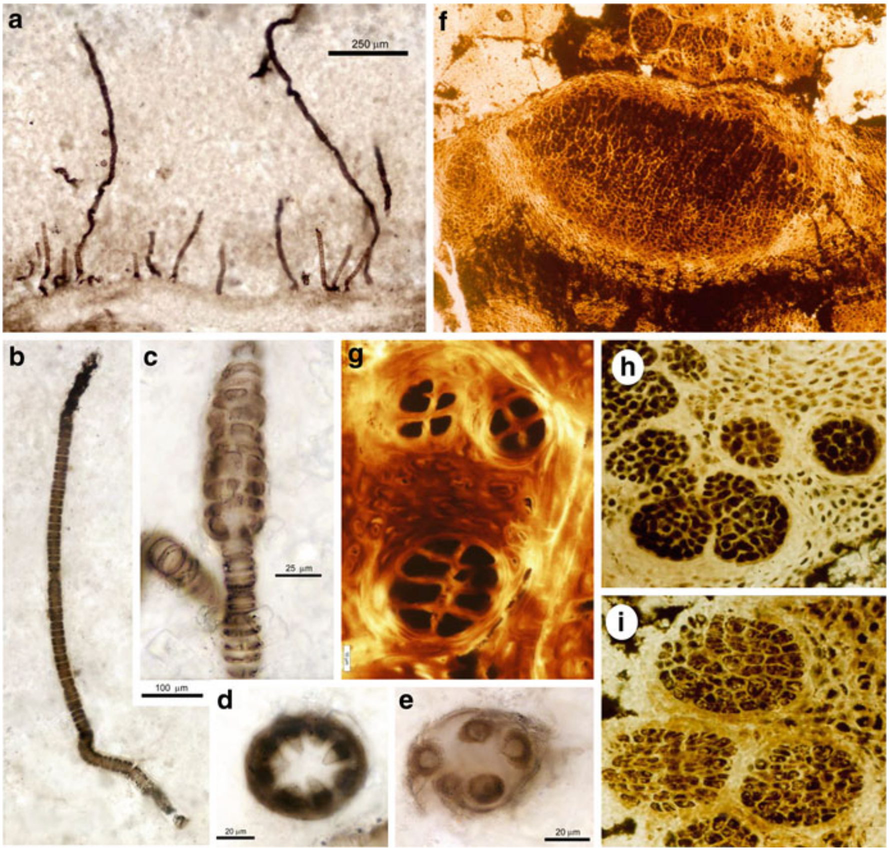

Fig. 5 Proterozoic red algal fossils. (**a**–**e**) *Bangiomorpha pubescens* fossils from the ca. 1200 million-year-old Hunting Formation, Somerset Island, arctic Canada (Courtesy of N. J. Butterfield). (**a**) Population of *Bangiomorpha* that clustered with up to 15 individuals. (**b**) Two paired cells reflecting transverse intercalary cell division. (**c**) Mature thallus showing both uniseriate and multiseriate portions of a filament. (**d**) Transverse cross-section of a multiseriate filament showing eight radially arranged wedge-shaped cells. (**e**) Spore-like spheroidal cells within multiseriate filaments from transverse cross-section. (**f**–**i**) Coralline fossils from the late Neoproterozoic 570 Ma Doushantuo Formation at Weng'an, southern China (Courtesy of S. Xiao). (**f**) A spermatangia-like reproductive structure with filaments. (**g**) Tetraspores and octaspores embedded in algal thallus showing possible tetrasporangium with subtending stalk cells. (**h**, **i**) Carposporangia

phylogeny, Xiao et al. (2004) concluded that these fossils are stem groups that may have diversified into the crown group of Corallinophycidae in the Mesozoic Era. In addition, some Doushantuo algal fossils are related to the zygotosporangia of modern thallose Bangiales (Xiao et al. 1998, 2014), indicating diversification of the Bangiophyceae as well as the Florideophyceae during the Neoproterozoic Era or earlier.

More recently, crown groups of coralline fossils were reported from Mesozoic and Cenozoic sedimentary rocks (Aguirre et al. 2000, 2010). These species have been placed within the Sporolithales (136–130 Ma), Hapalidiales (115–112 Ma), and Lithophylloideae (65.5–61.7 Ma), providing additional time constraints on coralline and florideophyte evolution.

Divergence time estimation using relaxed molecular clocks usually provides an overview of the evolutionary timeline, despite the large degree of uncertainty associated with fossil constraints. To estimate a more reliable timeline, three fundamental requirements are critical: (i) a well-supported accurate phylogeny representing diverse lineages, (ii) reliable fossil calibrations, and (iii) robust molecular clock methods (Soltis et al. 2002). Several divergence time estimations indicated a Mesoproterozoic origin of red algae. For example, based on a phylogeny using six genes from 46 taxa, Yoon et al. (2004) estimated 1,474 Ma for the origin of red algae, after the primary endosymbiosis between a heterotrophic protist and a cyanobacterium sometime before 1,558 Ma. Parfrey et al. (2011) suggested approximately 1,500 Ma for the origin of red algae based on a 15-gene dataset from 88 eukaryotic taxa. Although they used multigene data from diverse eukaryotic phyla, both studies included only limited florideophycean taxa; therefore, they were not able to suggest a detailed timeline for the Florideophyceae, which includes ca. 95% of red algal species.

A comprehensive molecular clock analysis was recently published with special focus on the Florideophyceae (Yang et al. 2016) (see Fig. 6). This analysis was based on a robust seven-gene phylogeny including 91 red algal taxa representing all seven classes and 34 orders (i.e., 27 of 29 florideophycean and seven nonflorideophycean orders). Seven reliable fossils were used as constraint points: *Bangiomorpha,* Doushantuo and Mesozoic coralline fossils, and four land plants (i.e., 471–480 Ma for the liverwort and vascular plant split; 410–422 Ma for the fern and seed plant split; 313–351 Ma for the gymnosperm and angiosperm split, and 138–162 Ma for the monocot-eudicot split, see Magallón et al. 2013). This study suggests that the Florideophyceae diverged approximately 943 Ma, followed by the emergence of the five subclasses: Hildenbrandiophycidae (781 Ma), Nemaliophycidae (661 Ma), Corallinophycidae (579 Ma), and the split of Ahnfeltiophycidae and Rhodymeniophycidae (508 Ma).

This red algal evolutionary timeline was used to interpret the emergence of key morphological innovations (Fig. 6). The triphasic life cycle is the most distinctive feature of red algae, ancestrally present in nonhildenbrandiophycidean Florideophyceae (except the Palmariales and Batrachospermales). Because it is not possible to rule out secondary loss of the carposporophyte phase in the Hildenbrandiophycidae, Yang et al. (2016) suggested that the triphasic life cycle was enabled by the evolution of the carposporophyte sometime between the divergence of ancestral Florideophyceae (943 Ma) and the divergence of Nemaliophycidae (661 Ma). After the development of the carposporophyte (i.e., gonimoblast development on the female gametophyte), two distinct innovations evolved in the postfertilization development in diploid gonimoblast filaments. The first is found in the Corallinophycidae (except Rhodogorgonales), Ahnfeltiophycidae,

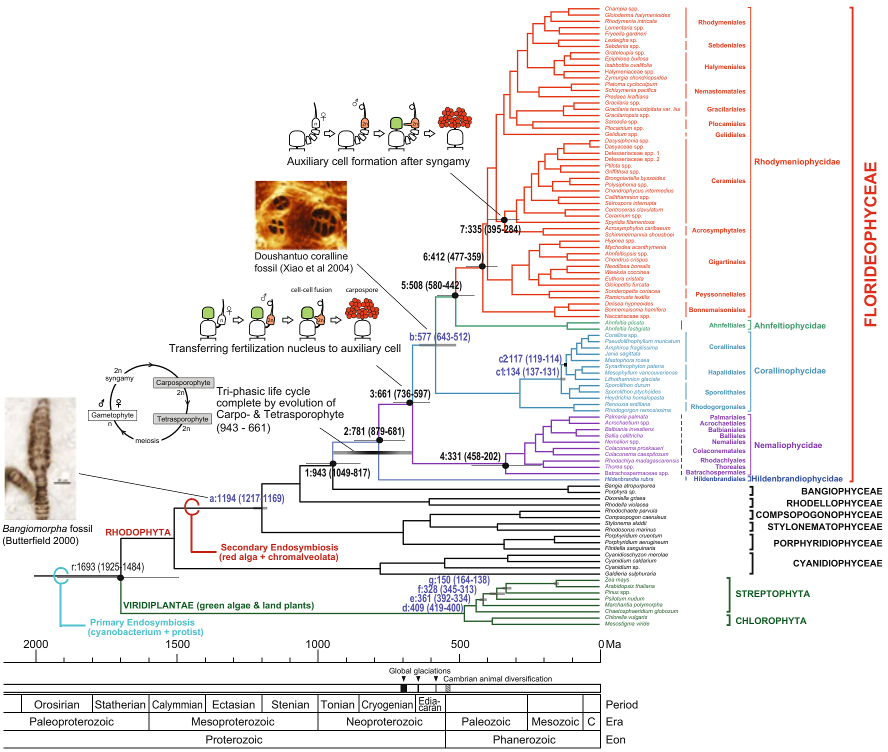

Fig. 6 Divergence time and evolution of the red algae. Primary and secondary endosymbiosis events are indicated with *cyan* and *red lines*, respectively. The three key evolutionary events are indicated with diagrams at the estimated evolutionary timeline. Triphasic life cycle, postfertilization "cell-to-cell fusion" mechanisms between carpogonium (fertilized egg) and an auxiliary cell, and the formation of an auxiliary cell after fertilization (syngamy) are indicated (Modified from Yang et al. 2016)

and Rhodymeniophycidae (661 Ma), where the zygotic nucleus and derivatives in the carpogonium move to an auxiliary cell by "cell-to-cell fusion" mechanisms followed by carposporophyte development, release of carpospores, and eventual sporic meiosis on the tetrasporophyte. The second innovation is only found in the Ceramiales (335 Ma) of the Rhodymeniophycidae, where an auxiliary cell is formed after fertilization (syngamy) followed by movement of the zygotic nucleus to the auxiliary cell. In addition within the Florideophyceae, especially in the Rhodymeniophycidae, there are numerous types of pre- and postfertilization cell-to-cell fusion mechanisms that have been used for ordinal diagnostic characters in florideophyte classification schemes (i.e., Hommersand and Fredericq 1990; Krayesky et al. 2009; Withall and Saunders 2006). The great diversity in pre- and postfertilization strategies in the Rhodymeniophycidae has resulted in the most successful subclass that comprises more than 70% of species richness in the entire Rhodophyta.

Evolutionary Relationships

The monophyly of Rhodophyta, Viridiplantae (green algae and land plants), and Glaucophyta, collectively referred to as the Archaeplastida (Adl et al. 2005), is supported by diverse molecular data (Chan et al. 2011; Hackett et al. 2007; Jackson and Reyes-Prieto 2014; Moreira et al. 2000; Rodriguez-Ezpeleta et al. 2005; Price et al. 2012; Reyes-Prieto and Bhattacharya 2007; Yoon et al. 2002b; Yoon et al. 2004), although a paraphyletic origin of these lineages cannot yet be ruled out (Parfrey et al. 2010; Yabuki et al. 2014; Yoon et al. 2008). However, because of the consistency between plastid and nuclear gene phylogenies, the single primary endosymbiosis hypothesis is widely accepted. This theory posits the origin of the plastid by acquisition of a cyanobacterium in the common ancestor of Archaeplastida >1,500 million years ago (see Fig. 6), followed by divergence of the greens, glaucophytes, and red algal lineages. These three major photosynthetic lineages share two-membrane-bounded plastids. Internal relationships (i.e., red-green monophyly vs. green-glaucophyte monophyly), however, are not fully resolved.

One of the most important evolutionary contributions of the red algae has been as a plastid donor through secondary endosymbiosis to the chlorophyll-*c* containing eukaryotic groups including the SAR group (Stramenopiles; Alveolates – dinoflagellates, apicomplexa, and ciliates; Rhizaria), cryptophytes, and haptophytes (Bhattacharya et al. 2004; Hackett et al. 2007; Yoon et al. 2002a, b) (see, e.g., ► Ciliophora ► Dinoflagellata ► Cryptophyta (Cryptomonads) and ► Haptophyta). Although the monophyly of these groups is still debated (Burki et al. 2016; Parfrey et al. 2011), plastid monophyly of the noncyanidiophycean red algal and chlorophyll-*c* containing lineages is strongly supported (Yoon et al. 2002a, b, 2004). Photosynthetic groups from these lineages have plastids bounded by three (i.e., peridinin-containing dinoflagellaes) or four (stramenopiles, cryptophytes, and haptophytes) membranes. Based on molecular clock analysis, Yoon et al. (2004) suggested 1,274 Ma as the date for the red algal secondary endosymbiosis (see Fig. 6).

Phylogenetic relationships between all major groups of Rhodophyta have been studied by Yoon et al. (2006), Le Gall and Saunders (2007), Verbruggen et al. (2010), and Yang et al. (2015). Based on a broadly sampled multigene phylogeny, with a focus on nonflorideophycean red algae, Yoon et al. (2006) identified several well-supported lineages, with the earliest diverged being the Cyanidiophyceae, and a strong monophyly of the Bangiophyceae and Florideophyceae. They proposed the seven-class system, although internal relationships among the four classes Compsopogonophyceae, Porphyridiophyceae, Rhodellophyceae, and Stylonematophyceae remain unresolved. In contrast, Le Gall and Saunders (2007) focused on the internal relationships of the Florideophyceae using combined EF2, SSU, and LSU rDNA sequences. They resolved five subclasses and established the subclass Corallinophycidae. Recently, Yang et al. (2015) largely resolved the internal relationships of the 12 orders of the Rhodymeniophycidae with a strong to moderately supported phylogeny based on

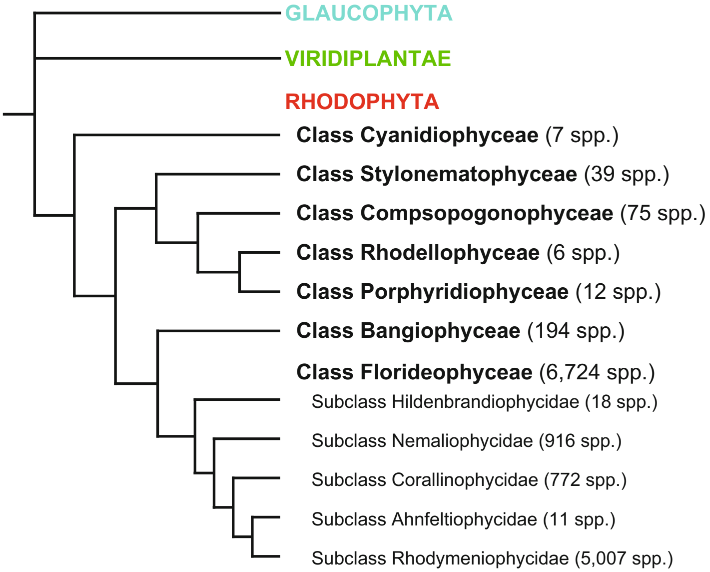

Fig. 7 Schematic phylogenetic relationships of the red algal classes and subclass based on Le Gall and Saunders (2007), Yoon et al. (2006), and Lee et al. (unpublished)

mitochondrial genome data. A more recent analysis using red algal plastid genome data from 45 species in all seven classes, 5 Florideophyceae subclasses, and 12 Rhodymeniophycidae orders resolved the four classes (i.e., Compsopogonophyceae, Porphyridiophyceae, Rhodellophyceae, and Stylonematophyceae) that diverged early (Lee et al., unpublished). After the divergence of the Cyanidiophyceae, the Stylonematophyceae diverged next, followed by the Compsopogonophyceae, and the Rhodellophyceae + Porphyridiophyceae clade (Fig. 7). Results from mitochondrial (e.g., Yang et al. 2016) and plastid genome analyses (Lee et al., unpublished) strongly suggest that organellar genome data can provide sufficient phylogenetic information to resolve most phylogenetic relationships in the Rhodophyta.

Genome Reduction in Rhodophyta

Although the red and green algal lineages putatively share a sister group relationship in the Archaeplastida (as described above), each has followed a vastly different path since their split. Genomes in the green lineage show dramatic expansion of gene families associated with the birth of land plants. In contrast, red algae likely have survived an ancient phase of extremophily (i.e., life in extreme environments such as volcanic hot springs) that resulted in extreme genome reduction (GR). This so-called hot start was followed by diversification into normal habitats and the origin of multicellularity, without massive gene gains (Bhattacharya et al. 2013; Collén et al. 2013; Collén 2015; Nakamura et al. 2013).

GR is a hallmark of symbionts, intracellular pathogens, and parasites (Keeling and Slamovits 2005; McCutcheon and Moran 2012). The highly simplified gene inventory and reduced functions in these taxa precipitates an obligate association with a host (Keeling and Slamovits 2005; Moran 2002). In free-living organisms, GR is associated with reduced metabolic flexibility and life in specialized niches such as in oligotrophic [e.g., *Prochlorococcus* (Dufresne et al. 2003) and *Ostreococcus* (Derelle et al. 2006)] and extremophilic [e.g., Cyanidiophytina red algae (Qiu et al. 2013), *Galdieria sulphuraria* (Schönknecht et al. 2013) and *Cyanidioschyzon merolae* (Matsuzaki et al. 2004)] environments that are relatively invariant over time. Given the narrowing of genetic potential, GR presumably precludes subsequent taxonomic and ecological diversification. Intriguingly, red algae appear to provide a counter-example to this perspective. The ability of this lineage to diversify and adapt to novel mesophilic habitats, despite a highly reduced gene inventory, ultimately led to the rise of a remarkably successful branch of life that shows immense morphological diversity and complex life cycles (Saunders and Hommersand 2004). The available data suggest that GR in red algae provides a model for deciphering the lower limits of gene diversity in free-living taxa and potentially offers insights into how novel solutions evolved for promoting the diversity of Rhodophyta.

Evidence for Genome Reduction in the Red Algal Common Ancestor

Available complete genome data suggest that red algae encode only a modest gene inventory when compared to Viridiplantae, with extant species typically containing fewer than 10,000 genes, e.g., in the mesophilic unicellular red alga *Porphyridium purpureum* (Bhattacharya et al. 2013) and in the extremophilic unicellular red algae *C. merolae* (Matsuzaki et al. 2004) and *G. sulphuraria* (Schönknecht et al. 2013). Even red seaweeds such as *Chondrus crispus* (Collén et al. 2013) and *Pyropia yezoensis* (Nakamura et al. 2013), which are complex multicellular lineages and have sophisticated life cycles, contain a gene inventory comparable to their unicellular relatives (i.e., 9,606 and 10,327 putative genes, respectively). An analysis of gene family evolution under a phylogenetic framework that incorporated all available genomic data (e.g., novel transcriptomes from the Marine Microbial Eukaryote Transcriptome Sequencing Project; Keeling et al. 2014) is summarized in Fig. 8a. These results correlate the estimated number of core gene families and thallus morphology in each lineage and provide evidence for limited gene expansion in the derived, mesophilic lineages (Qiu et al. 2015). Fig. 8b shows the results of the analysis of orthologous gene families [using OrthoMCL (Li 2003)], based on Dollo parsimony (Farris 1977), and the estimation of gene family gains and losses under the same parameters as described in Qiu et al. (2015).

The results shown in Fig. 8 suggest that the net loss of genes was most severe in the stem lineage of red algae and in the common ancestor of the Cyanidiophytina.

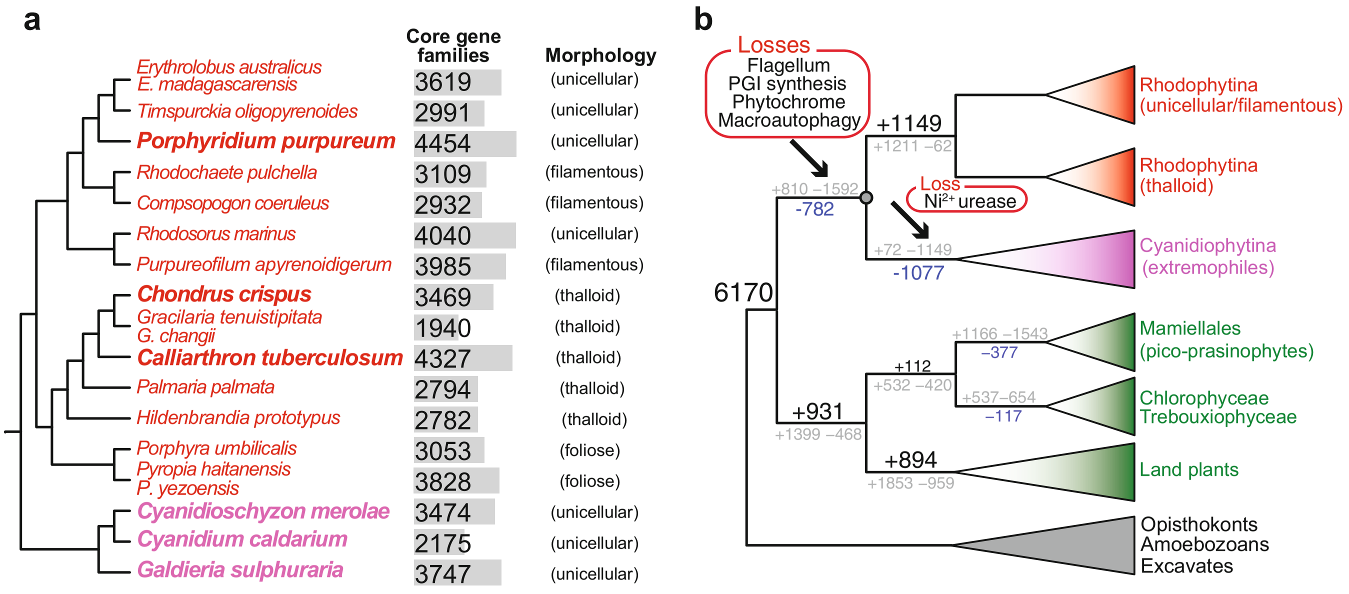

Fig. 8 (**a**, **b**) Genome-wide analysis of red algae. (**a**) The number of core gene families in red algal taxa for which genome or transcriptome data are available. A core gene family is defined as those present in the Cyanidiophytina or Rhodophytina ancestor, or earlier (for details, see Qiu et al. 2015). Using the number of core gene families as a measure, *Rhodosorus marinus* shows a coverage (e.g., 91%) that is comparable to that of *Porphyridium purpureum*, which has a completely sequenced genome. The approximate sequence coverage in other species is expressed likewise. Sequences from *Gracilaria tenuistipitata* and *Gracilaria changii* were pooled. The same was the case for *Pyropia yezoensis* and *Pyropia haitanensis* sequences. Taxa in boldface have complete genome sequences available. The tree topology of the mesophilic lineages is tentative and has no impact on the estimation of core gene families that have more ancestral origins. (**b**) Estimate of the number of gene family gains and losses (*gray* number at each branch) in *red* algae and Viridiplantae. Net gene family gains or losses are shown in *black* and *blue* text, respectively. Net gene family changes, when >600, are shown as proportionately sized numbers. The *arrows* indicate the two major phases of net gene loss in *red* algae. The major functional losses associated with each phase of genome reduction are also shown (for details, see Qiu et al. 2015)

Remarkably, about one-quarter (1,592/6,170, or 26%) of conserved algal "core" genes were lost in the red algal common ancestor. This is in contrast to the pronounced net gene gains in the Viridiplantae stem lineage (+931) and in the lineage leading to land plants (+894; Fig. 8b). Although we expect these numbers to change as more genomes are added to the analysis, the most compelling comparison is between the stem lineages of red and green algae. The Rhodophyta ancestor would have to gain ca. 1,700 genes on this branch to achieve the expansion found in Viridiplantae. The large gene gains at the root of mesophilic red algae (+1,149) needs to be interpreted with caution because some of these genome assemblies are highly fragmented (i.e., leading to over-estimation of gene numbers) and there are contamination issues associated with the EST data included in the analysis (Qiu et al. 2015).

Functions Lost in the Red Algal Ancestor

The impact of GR on red algae is most obviously manifested in the absence of flagella and basal bodies. Other notable losses in the red algal stem lineage include light-sensing phytochromes, glycosylphosphatidylinositol (GPI)-anchor biosynthesis, macroautophagy pathways (Qiu et al. 2015), and then subsequent loss of the nickel-dependent urease pathway in the Cyanidiophytina common ancestor (Qiu et al. 2013) (Fig. 8b). Interestingly, flagella and the GPI-anchoring function are preserved in parasites such as *Trypanosoma* species and *Giardia lamblia* (Das et al. 1994) that also underwent drastic GR. This observation suggests a differential impact of GR in cells adapted to different lifestyles, i.e., intracellular pathogens versus free-living cells. Whereas flagella loss is relatively common in eukaryotes, GPI anchoring is a highly conserved function and plays critical, perhaps indispensible roles in a wide variety of organisms (Kawagoe et al. 1996; Lillico et al. 2003; Takeda and Kinoshita 1995), as is the case for macroautophagy (Mizushima and Levine 2010). It is currently unknown how red algae cope with the loss of these conserved functions.

Classification

Here we follow the seven-class system (Yoon et al. 2006) of the Rhodophyta (see Table 1 and Fig. 7) and describe the basic diagnostic characters and classification status for each class based on the previous review (Yoon et al. 2010).

Cyanidiophyceae is a group of asexual, unicellular red algae that thrive in acidic (pH 0–4) and high-temperature (25–55 °C) conditions around hot springs and/or acidic sulfur fumes (Pinto et al. 2003). This is the first group to diverge, and members contain the ultrastructural character of a Golgi-ER association. The class Cyanidiophyceae contains one order Cyanidiales, two families Cyanidiaceae and Galdieriaceae, and three genera *Cyanidium*, *Cyanidioschyzon*, and *Galdieria*, based on morphological characters. Molecular phylogenetic studies, however, have revealed great hidden diversity in this lineage (Gross et al. 2001; Pinto et al. 2003;

Table 1 Current taxonomic system of the red algae according to Yoon et al. (2006, 2010) and Le Gall and Saunders (2007)

Kingdom Plantae Haeckel
Phylum Rhodophyta Wettstein
Subphylum Cyanidiophytina Yoon, Müller, Sheath, Ott, et Bhattacharya
Class Cyanidiophyceae Merola, Castaldo, De Luca, Gambardella, Musacchio, et Taddei
Order Cyanidiales Christensen
Subphylum Rhodophytina Yoon, Müller, Sheath, Ott, et Bhattacharya
Class Bangiophyceae Wettstein
Order Bangiales Nägeli
Class Compsopogonophyceae Saunders et Hommersand
Order Compsopogonales Schmitz in Engler et Prantl
Order Erythropeltidales Garbary, Hansen, et Scagel
Order Rhodochaetales Bessey
Class Florideophyceae Cronquist
Subclass Hildenbrandiophycidae Saunders et Hommersand
Order Hildenbrandiales Pueschel et Cole
Subclass Nemaliophycidae Christensen
Order Acrochaetiales Feldmann
Order Balbianiales Sheath et Müller
Order Balliales Choi, Kraft, et Saunders
Order Batrachospermales Pueschel et Cole
Order Colaconematales Harper et Saunders
Order Entwisleiales Scott, Saunders, et Kraft
Order Nemaliales Schmitz
Order Palmariales Guiry et Irvine
Order Rhodachlyales Saunders, Clayden, Scott, West, Karsten, et West
Order Thoreales Müller, Sherwood, Pueschel, Gutell, et Sheath
Subclass Corallinophycidae Le Gall et Saunders
Order Corallinales Silva et Johansen
Order Hapalidiales Nelson, Sutherland, Farr, et Yoon
Order Rhodogorgonales Fredericq, Norris, et Pueschel
Order Sporolithales Le Gall, Payri, Bittner, et Saunders
Subclass Ahnfeltiophycidae Saunders et Hommersand
Order Ahnfeltiales Maggs et Pueschel
Order Pihiellales Huisman, Sherwood, et Abbott
Subclass Rhodymeniophycidae Saunders et Hommersand
Order Acrosymphytales Withall et Saunders
Order Bonnemaisoniales Feldmann et Feldm.-Maz.
Order Ceramiales Oltmanns
Order Gelidiales Kylin
Order Gigartinales Schmitz
Order Gracilariales Fredericq et Hommersand
Order Halymeniales Saunders et Kraft

(*continued*)

Table 1 (continued)

Order Nemastomatales Kylin
Order Peyssonneliales Krayesky, Fredericq, et Norris
Order Plocamiales Saunders et Kraft
Order Rhodymeniales Schmitz
Order Sebdeniales Withall et Saunders
Class Porphyridiophyceae Yoon, Müller, Sheath, Ott, et Bhattacharya
Order Porphyridiales Kylin ex Skuja
Class Rhodellophyceae Cavalier-Smith
Order Dixoniellales Yokoyama, Scott, Zuccarello, Kajikawa, Hara, et West
Order Glaucosphaerales Yang, Scott, Yoon, et West
Order Rhodellales Yoon, Müller, Sheath, Ott, et Bhattacharya
Class Stylonematophyceae Yoon, Müller, Sheath, Ott, et Bhattacharya
Order Rufusiales Zuccarello et West
Order Stylonematales Drew

Yoon et al. 2002a, b) from comprehensive sampling in Italy (Ciniglia et al. 2004), Yellowstone National Park, Japan, and New Zealand (Skorupa et al. 2013; Toplin et al. 2008), Iceland (Ciniglia et al. 2014), and Taiwan (Hsieh et al. 2015). As Yoon et al. (2010) suggested, taxonomic revision in the Cyanidiophyceae is required at the order, family, and genus levels.

Compsopogonophyceae is a group of multicellular but simple filamentous, blade, and tubular red algae. It is characterized by having a Golgi-ER association and floridoside as the low molecular weight carbohydrate (LMWC) (Broadwater and Scott 1994; Karsten et al. 2003). *Rhodochaete* and *Compsopogon* contain pit plugs with a simple plug core without a cap or membrane (Scott et al. 1988). The class Compsopogonophyceae is classified into three orders: one freshwater order, Compsopogonales, with two families Boldiaceae and Compsopogonaceae, and two marine orders, Erythropeltidales and Rhodochaetales, with 14 genera. The presence of sex was reported from two sister taxa *Erythrotrichia* and *Rhodochaete* (Hawkes 1988; Magne 1960, 1990), and packets of spores may be indicative of sexual reproduction in *Pyrophyllon* and *Chlidophyllon* (Nelson et al. 2003).

Porphyridiophyceae is a group of unicellular red algae that contain a single branched or stellate plastid without a peripheral thylakoid, a Golgi association with ER/mitochondria (Scott et al. 1992), and floridoside as a LMWC (Karsten et al. 2003). This class has a single order Porphyridiales, one family Porphyridiaceae, and four unicellular genera *Erythrolobus*, *Flintiella*, *Porphyridium*, and *Timspurckia*.

Rhodellophyceae is a class that includes the unicellular red algae *Corynoplastis*, *Dixoniella, Glaucosphaera*, *Neorhodella*, and *Rhodella* and contains three orders Dixoniellales, Glaucosphaerales, and Rhodellales (Scott et al. 2011; Yokoyama et al. 2009; Yoon et al. 2006). Dixoniellales and Rhodellales contain mannitol as the LMWC. The LMWC for the Glaucosphaerales is unknown (Karsten et al. 2003). *Dixoniella*, *Glaucosphaera*, and *Neorhodella* have a Golgi-nuclear association, differing from *Corynoplastis* and *Rhodella*, which have a Golgi-ER association (Scott et al. 1992, 2011).

Stylonematophyceae comprises diverse morphological forms of unicellular, pseudofilamentous, and filamentous taxa with thick mucilaginous walls and cells lacking pit plugs. A Golgi-ER association and digeneaside and sorbitol as LMWCs are diagnostic characters for this group (Broadwater and Scott 1994; Karsten et al. 2003) although digeneaside is missing in *Chroodactylon*, and dulcitol is present in *Rhodospora*. A single stellate plastid with a pyrenoid is found in most taxa. This class has two orders, Stylonematales and Rufusiales, two families, Stylonemataceae and Rufusiaceae, and 14 genera (*Bangiopsis, Chroodactylon, Chroothece, Colacodictyon, Empselium, Goniotrichopsis, Kylinella, Neevea, Purpureofilum, Rhodaphanes, Rhodosorus, Rhodospora*, *Rufusia,* and *Stylonema*) that are all reported from marine habitats.

Bangiophyceae has either simple unbranched filaments or leaf-shaped foliose thalli, and most species live in the marine environment. The Bangiales includes the most highly valued seaweed aquaculture crops in the world (i.e., *Pyropia*, previously known as *Porphyra*). A biphasic life cycle is common in this group, with a macroscopic gametophyte alternating with a microscopic conchocelis phase. The conchocelis phase in the Bangiales has pit plugs with a single cap layer but no cap membrane (Pueschel and Cole 1982). The class Bangiophyceae includes one order Bangiales, one family Bangiaceae, and 12 currently recognized genera with ca. 130 species. The real diversity, however, is likely underestimated, and further genera need to be formally described (Sutherland et al. 2011).

A sister group relationship of the Bangiophyceae and Florideophyceae has been suggested based on numerous morphological and molecular data including features of the reproductive cells, Golgi association with ER/mitochondria, the presence of pit connections, and the presence of group I introns (Gabrielson et al. 1985; Gabrielson et al. 1990; Freshwater et al. 1994; Ragan et al. 1994; Oliveira and Bhattacharya 2000; Müller et al. 2001; Yoon et al. 2002b; Yoon et al. 2004; Yoon et al. 2006).

Florideophyceae includes around 6,700 species that are mostly macroscopic; they are the most morphologically and genetically diverse of all red algal classes. The triphasic life cycle comprising a carposporophyte, tetrasporophyte, and a gametophyte phase is common in this group. Five subclasses are recognized (Hildenbrandiophycidae, Nemaliophycidae, Corallinophycidae, Ahnfeltiophycidae, and Rhodymeniophycidae) with 29 orders that are distinguished by molecular data, ultrastructural features (i.e., pit plug connection between neighboring cells including number of cap layers and membranes), and reproductive development (i.e., pre- and postfertilization processes) (see review by Saunders and Hommersand 2004).

The subclass **Hildenbrandiophycidae** contains a single order the Hildenbrandiales, with two genera *Hildenbrandia* and *Apophlaea*, characterized by pit plugs with a single cap layer covered by a membrane (Pueschel and Cole 1982). Although zonately and irregularly divided tetrasporangia have been reported, there are no reports of recognizable gametophytic reproductive structures (carpogonia or spermatangia) or a sexual life history. The **Nemaliophycidae** is characterized by the presence of pit plugs with two cap layers. Ten orders are recognized: Acrochaetiales, Balbianiales, Balliales, Batrachospermales, Colaconematales, Entwisleiales, Nemaliales, Palmariales, Rhodachlyales, and Thoreales. The **Corallinophycidae** is characterized by pit plugs with a domed outer cap layer and calcified thalli. It contains four orders: the Corallinales, Hapalidiales, Rhodogorgonales, and Sporolithales. The **Ahnfeltiophycidae** includes two orders the Ahnfeltiales and Pihiellales that are characterized by having naked pit plugs lacking caps and membranes (Maggs and Pueschel 1989). The **Rhodymeniophycidae** is the most taxon-rich (ca. 5,000 spp.) red algal subclass and is divided into 12 orders: Acrosymphytales, Bonnemaisoniales, Ceramiales, Gelidiales, Gigartinales, Gracilariales, Halymeniales, Nemastomatales, Peyssonneliales, Plocamiales, Rhodymeniales, and Sebdeniales. All have pit plugs covered by a membrane only (Pueschel and Cole 1982).

Summary

Red algae occupy a wide variety of habitats and play important economic and ecological roles on our planet. They remain poorly studied at the genetic level but have a rich history of morphological, biochemical, and life history analyses. Ultimately all of these diverse areas of science will need to unite to provide comprehensive understanding of the features that make red algae unique members of the tree of life. As an example of recent advances, the explosion of genomic data has significantly changed our views of red algal evolution. Rather than being typical photosynthetic members of the Archaeplastida, we now recognize Rhodophyta as a distinct group that does not share the expected large gene inventory with Viridiplantae and Glaucophyta. In fact, they appear to have shed about one-quarter of the ancestral gene set, leading to nuclear genome reduction. This finding may be explained by an ancient adaptation to an extremophilic environment such as in the vicinity of hot springs: this is the so-called hot start hypothesis for Rhodophyta. Despite this surprising revelation about their early evolution, which is expected to result in severely reduced taxonomic diversity [i.e., extant Cyanidiophytina are species depauperate; 6–10 species/lineages (Reeb and Bhattacharya 2010)] and further habitat restriction, the Rhodophytina ancestor managed to re-emerge, diversify into a variety of mesophilic environments, and develop multicellularity and a complex triphasic life cycle. If this hypothesis is correct, then understanding how this feat was achieved remains a major unanswered question to be addressed by future researchers.

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