Phaeophyta

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Abstract

Brown algae (Phaeophyceae) are benthic macroalgae constituting a primary element of coastal ecosystems in temperate and cold water seas and are also economically important. Currently ca. 2,000 species in ca. 300 genera are recognized. They are mostly marine and only a few genera are known in freshwater habitats. They are photosynthetic organisms, sharing chloroplasts originated from secondary endosymbiotic events with photosynthetic heterokonts (chromists, stramenopiles) and surrounded by four layers of membranes. Major photosynthetic pigments are chlorophylls *a* and *c* and fucoxanthin and produce laminaran as the storage polysaccharide. All known species are multicellular, with cell walls composed of alginates, fucoidan (fucan), and cellulose, and traversed by plasmodesmata. Basal taxa generally show isomorphic life history and apical growth. Derived taxa have evolved heteromorphic life histories and modified life history patterns, some with only a diploid generation (thallus), as well as diverse growth patterns such as diffuse and intercalary growth. They commonly reproduce by asexual heterokont zoospores, or zygotes formed by fusion of motile or nonmotile female gametes with heterokont male gametes.

Keywords

Algal bed • Alginate • Brown algae • *Ectocarpus* • Fucoidan • Fucoxanthin • Heterokont • Heterokonta • Kelp • Life history • Multicellular alga • Ochrophyta • Phaeophyceae • Secondary endosymbiosis • Stramenopile • Tripartite tubular mastigoneme

Summary Classification

• **Phaeophyceae**
•• **Discosporangiales** (*Choristocarpus, Discosporangium*)
•• **Ishigeales** (*Ishige*)
•• **Dictyotales** (*Dictyopteris, Dictyota, Lobophora, Padina*)
•• **Sphacelariales** (*Cladostephus, Halopteris, Phaeostrophion, Sphacelaria*)
•• **Onslowiales** (*Onslowia, Verosphacela*)
•• **Syringodermatales** (*Microzonia, Syringoderma*)
•• **Desmarestiales** (*Arthrocladia, Desmarestia, Himanthothallus*)
•• **Ascoseirales** (*Acroseira*)
•• **Sporochnales** (*Carpomitra, Nereia, Sporochnus*)
•• **Scytothamnales** (*Asteronema, Bachelotia, Scytothamnus, Splachnidium*)
•• **Ectocarpales s.l.** (*Acinetospora, Chordaria, Dictyosiphon, Ectocarpus, Scytosiphon*)
•• **Laminariales** (*Aureophycus, Agarum, Alaria, Chorda, Laminaria*)
•• **Asterocladales** (*Asterocladon*)
•• **Fucales** (*Durvillaea, Fucus, Himanthalia, Sargassum, Xiphophora*)
•• **Nemodermatales** (*Nemoderma, Zeacarpa*)
•• **Tilopteridales** (*Cutleria, Phyllariopsis, Haplospora, Tilopteris*)

  - **Stschapoviales** (*Halosiphon, Platysiphon, Stschapovia*)
  - **Ralfsiales** (*Analipus, Mesospora, Neoralfsia, Ralfsia*)

Introduction

General Characteristics

Brown algae (Phaeophyceae, Heterokonta/Ochrophyta) are multicellular organisms that vary in size from microscopic branched filaments less than a millimeter in diameter to large macroscopic fleshy thalli that may attain lengths in excess of 50 m (Bold and Wynne 1985; van Den Hoek et al. 1995; Graham and Wilcox 2000). They are essential elements of coastal ecosystems, often forming dense algal beds comparable to the forests in terrestrial ecosystems (Dayton 1985). They commonly reproduce by asexual heterokont zoospores, or zygotes formed by fusion of motile or nonmotile female gametes with heterokont male gametes. They are photosynthetic organisms, with chloroplasts originated from a secondary endosymbiotic event in a common ancestor shared with photosynthetic heterokonts and surrounded by four membranes (Fig. 1). All known species are multicellular, with cell walls composed of alginates, fucoidan (fucan) and cellulose, and traversed by plasmodesmata (cytoplasmic continuity retained through cell division) (Figs. 2 and 3) (Terauchi et al. 2012, 2015).

Brown algae comprise approximately 2,000 species in around 300 genera (AlgaeBASE: http://www.algaebase.org/). Genera such as *Cystoseira, Dictyota, Ectocarpus, Sargassum*, and *Sphacelaria* include large numbers of species, which present considerable taxonomic difficulty and are in need of critical review (Stache-Crain et al. 1997; Peters et al. 2010; Ni-Ni-Win et al. 2010; 2011a; b; Tronholm et al. 2010; Silberfeld et al. 2014a). Furthermore, a number of cryptic species have been discovered in the course of taxonomic re-examinations employing molecular phylogenetic analyses. The life histories of brown algae are varied. Most involve meiosis and fertilization, with an alternation of haploid and diploid phases. The haploid gametophyte generation often exhibits varying degrees of morphological reduction. In some taxa, the reduced generation has become cryptic so that they superficially lack alternation of generations.

Morphology varies greatly among brown algae. Some of the smaller species form inconspicuous filamentous tufts and cushions or grow as crusts in close contact with the substrate. Larger forms include a variety of simple and branched thalli with differentiation into foliose blade, stem-like stipe, and basal holdfast. Some thalli are exceedingly mucilaginous. The larger fleshy species include the intertidal and upper subtidal seaweeds known as wracks and kelps.

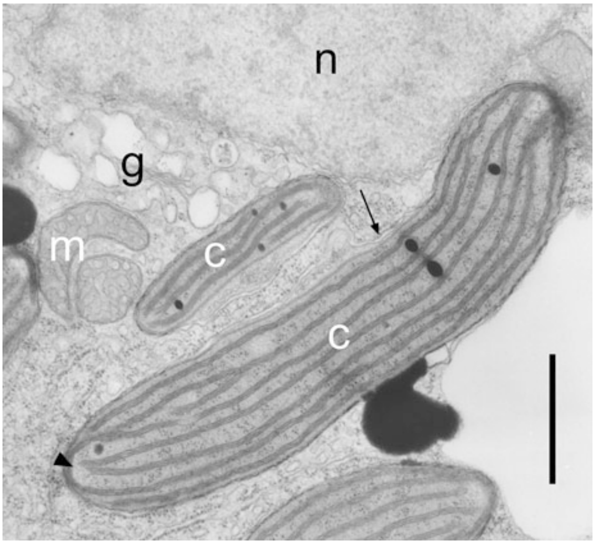


Fig. 1 Brown algal chloroplasts (*c*) of *Saccharina* sp. with four surrounding membranes. The outermost chloroplast membrane with attached ribosomes is shown by an *arrow*. The chloroplast has girdle lamella, and ring-shaped DNA within the girdle lamella (*arrowhead*). *g* Golgi body, *m* mitochondrion, *n* nucleus. Scale bar, 1 μm (TEM micrograph courtesy of Taizo Motomura)

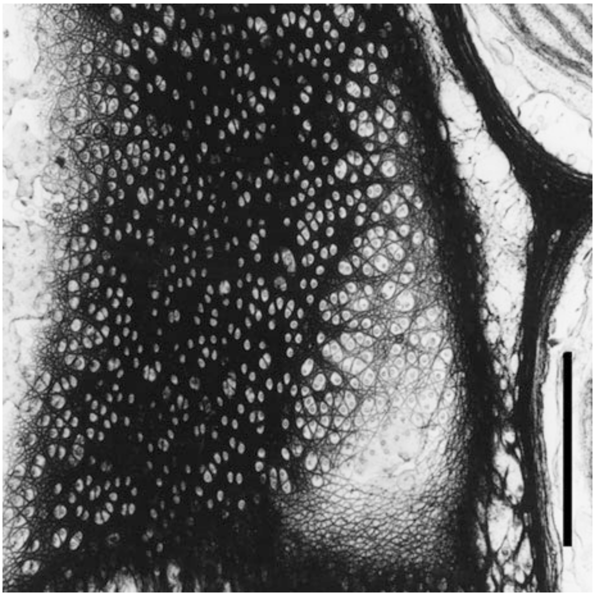


Fig. 2 Tangential section of a cell wall showing plasmodesmata (cytoplasmic continuity between cells) in *Chorda asiatica*. TEM micrograph. Scale bar, 1 μm

Occurrence

Brown algae are almost exclusively marine organisms that inhabit the intertidal and subtidal zones of coastal regions throughout the world. They grow to varying depths depending on the availability of light and substrates. Only a few species grow in estuarine and freshwater habitats. Most of the freshwater taxa are considered to be

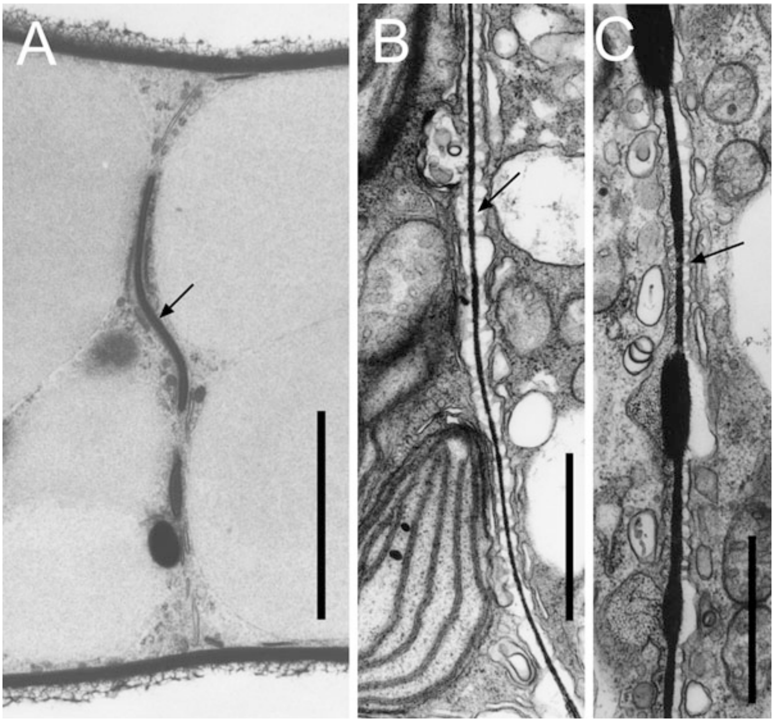


Fig. 3 Formation processes of cell walls and plasmodesmata. (**a**) Cross section of *Scytosiphon* gamete germling showing the initial stage of the deposition of wall substances (arrow). Freeze substitution TEM micrograph (Courtesy of Chikako Nagasato). (**b**, **c**) TEM micrograph by chemical fixation showing the early stages of cell wall formation and plasmodesmata (arrows) in *Chorda* meristematic cells

relatively recent descendants of marine taxa and are scattered among diverse phylogenetic groups, although the taxonomic positions of some taxa need reexamination (McCauley and Wehr 2007).

Most brown algae grow attached to a great variety of surfaces including rock, concrete, metal, and wood structures, as well as the surfaces of other organisms such as other macroalgae or shells. A few species that grow on macroalgae and sea-grasses penetrate the tissues of their living hosts (Kawai and Tokuyama 1995; Burkhardt and Peters 1998; Garbary et al. 1999), sometimes exhibiting a semiparasitic habit (Peters 1989). Some brown algae grow free-floating in sheltered habitats such as bays and estuaries. In the Sargasso Sea in the middle North Atlantic Ocean, a large biomass of floating *Sargassum* species propagates only vegetatively.

Many brown algae are easily collected from their natural habitats and can be grown and maintained in culture. Some taxa (e.g., *Cladosiphon, Laminaria, Saccharina, Sargassum, Undaria*) are grown on a large scale in the field (mariculture) and used for food and industrial materials. Numerous culture strains available for research purposes are deposited in several culture collections: KU-MACC (Kobe

University Research Center for Inland Seas, Japan), NCMA (National Center for Marine Algae and Microbiota, USA), SAG (Sammlung von Algenkulturen der Universiät Göttingen, Germany), and UTEX (The Culture Collection of Algae, University of Texas at Austin, USA). Most of the available strains are unialgal, and some are axenic. Some strains are cryopreserved in the culture collections (Heesch et al. 2012).

Literature and History of Knowledge

Papers concerning brown algae appear in a range of botanical and marine biological journals, including the specialist algal journals *Phycologia, Journal of Phycology*, *European Journal of Phycology*, *Phycological Research*, *Algae, Cryptogamie Algologie*, *Journal of Applied Phycology*, and *Botanica Marina.* Pioneering studies on the morphology and development of a wide range of brown algae were described in the publications of Kylin (1933), Kuckuck (1929, 1964), and Sauvageau (1929, 1931, 1933); Fritsch (1945) comprehensively reviewed the literature before 1945. Brown algae are also discussed in comprehensive phycology textbooks in English (Wynne 1981; Bold and Wynne 1985; South and Whittick 1987; van den Hoek et al. 1995; Graham and Wilcox 2000; Lee 2008; Reviers et al. 2015). Life histories of the brown algae have been reviewed by Wynne and Loiseaux (1976), Pedersen (1981), Peters (1987), and Hori (1993). Ecological and physiological studies of brown algae were reviewed by Lobban and Harrison (1994). Entire genome sequences of brown algae were first reported in the model species *Ectocarpus siliculosus* (Cock et al. 2010), followed by the kelp species *Saccharina japonica* (Ye et al. 2015), and diverse information on their genomes has become available.

Traditionally the classification schemes devised by Kylin (1933), Papenfuss (1955), and Wynne and Loiseaux (1976) have been widely accepted, but the basic concept of the fundamental importance of life history patterns and thallus constructions has been challenged by recent biological studies (e.g., life histories, sexual pheromones), and have been considerably revised based on molecular analyses, mostly using ribosomal DNA and RuBisCO gene sequences (Tan and Druehl 1996; Siemer et al. 1998; Reviers and Rousseau 1999; Draisma et al. 2001; Sasaki et al. 2001; Cho et al. 2004; Kawai et al. 2007; Lim et al. 2007; Draisma et al. 2010). More recently, molecular phylogenetic studies using multiple gene data sets have elucidated the general phylogenetic relationships among orders (Phillips et al. 2008; Silberfeld et al. 2010, 2011, 2014b; Kawai et al. 2015a). Information on taxonomic names is available at AlgaeBASE (http://www.algaebase.org/) and Index Nominum Algarum (http://ucjeps.berkeley.edu/INA.html).

Brown marine algae were recognized by European phycologists as a distinct group of organisms in the early nineteenth century. Detailed studies of their structure and reproduction, along with the first attempt at cultivation, began to appear in the latter half of the century. Some of the more notable works include that of Thuret, who made the first microscopical observations of fertilization in algae using the eggs and flagellated sperm of *Fucus* (Thuret 1854). Improved microscopical and histochemical techniques have made possible critical investigations of brown algal anatomy (Gantt 1980). Alternation between macroscopic sporophyte and microscopic gametophytes in the life histories of kelps was first reported by Sauvageau (1915), who also made the first culture studies of many other brown algae. The culturing of brown algae was greatly advanced by development of growth media by Shreiber (1927) and Provasoli (Tatewaki 1966; Provasoli 1968; Starr 1978). Culturing techniques of brown algae are reviewed in Kawai et al. (2005b; for details see below).

Practical Importance

Species of Laminariales with foliose thalli (3–4 families) and Fucales (*Ascophyllum* and *Durvillaea*) are utilized commercially as sources of alginates, the salts of alginic acid, a major component of brown algal cell walls. Alginates, polysaccharide compounds composed of mannuronic and guluronic acid subunits, can form highly viscous solutions and readily form gels (Percival and McDowell 1967). Alginates are used widely in the manufacture of products including foods, cattle and poultry feeds, adhesives, dyes, and explosives (Chapman and Chapman 1980). Species harvested for alginate extraction include *Ascophyllum nodosum, Durvillaea potatorum, Eisenia bicyclis, Ecklonia cava, Macrocystis pyrifera, Laminaria* spp., and *Saccharina* spp.

Brown algae are a particularly valuable natural source of vitamins and minerals, notably iodine (Critchley and Ohno 1998). The larger species of brown algae are utilized as fertilizers and growth promoters by coastal agricultural communities. Extracts of some, for example, *Ascophyllum nodosum,* are manufactured and sold widely for use in agriculture and horticulture (Chapman and Chapman 1980). Fucoidan (one of the sulfated polysaccharides in brown algae) extracted from some taxa (*Cladosiphon, Laminaria*, *Undaria*) are used as a functional food. A number of species, primarily belonging to Laminariales (*Ecklonia*, *Laminaria, Saccarhina, Undaria,* etc.), are widely cultivated and used as food in Japan, Korea, and China.

Habitats and Ecology

Geographical Distribution

Studies of the biogeography of benthic marine algae (e.g., van den Hoek 1975; Lawson 1978; South 1975; Santelices 1980; Womersley 1981; Lüning 1990) include information on the distribution of brown algal species. Brown algae dominate many benthic marine biotas. The characteristics of the marine biotas of four types of region – polar, cold temperate, warm temperate, and subtropical/tropical – have been outlined by Womersley (1981). The polar regions, which possess more limited algal biotas, include some distinctive taxa, for example, the Antarctic

Himantothallus in the Demarestiales, *Ascoseira,* and the Arctic species of *Laminaria*, *Saccharina*, *Saccorhiza* and *Chorda*. A high species diversity is found among the marine algal biotas of cold temperate regions. Fucales (e.g., *Ascophyllum*, *Fucus* spp., *Hormosira banksii*) dominate the intertidal zone of rocky shores and the kelps form dense communities in the subtidal and lower intertidal zones. The coastal regions of the world with the greatest numbers of species and genera of brown algae include Japan, Pacific North America, Southern Australia, and Britain, all regions of temperate climate with a significant cold temperate component. Large kelps are absent on tropical coasts and are not conspicuous in warm temperate regions. The Dictyotales and *Sargassum* spp. (Fucales) are the common brown algae of tropical and subtropical regions (Womersley 1981; Silva et al. 1996; Silberfeld et al. 2014a).

Temperature and salinity strongly affect horizontal distributions of species of benthic marine algae (Druehl 1981). Experimentally determined lethal or growth- and reproduction-limiting temperatures correlate with phytogeographic boundaries of several species of marine benthic algae, including some phaeophycean taxa (van den Hoek 1982).

Measuring Seaweed Vegetation

Methods have been developed for describing and analyzing the composition, distribution, and structure of local communities of benthic marine algae (Russell and Fielding 1981). Protocols for long-term monitoring of seaweed communities are described by Kautsky and Maarel (1990), Kautsky (1993), Shirayama et al. (2002), and Kawai and Henry (2007).

Environmental gradients and the physiological tolerance limits of species have been studied with the goal of understanding zonation, the vertical banding of seaweed communities. Biotic interactions between different algal species and intertidal animals are significant in determining the vertical limits of seaweed distribution (Chapman 1974; Russell and Fielding 1981).

Kelp Ecosystems

Large brown algae called kelps are either Ascoseirales (*Ascoseira*), Desmarestiales (*Himantothallus*), Fucales (*Durvillaea*), Laminariales (*Alaria*, *Chorda*, *Ecklonia, Eualaria*, *Macrocystis, Laminaria, Nereocystis, Saccharina*), or Tilopteridales (*Sacchorhiza, Phyllariopsis*) and dominate the kelp communities of the world. *Chorda* is dominant on sheltered coasts in Arctic regions. Kelp communities dominated by *Alaria*, *Laminaria,* and *Saccharina* occur in the northern Atlantic and on the coasts of China and Japan, whereas *Macrocystis*-dominated communities are found along the Pacific coast of North America and the temperate Atlantic and Pacific coasts of South America and New Zealand (Lüning and tom Dieck 1990; Santelices et al. 1980). *Ecklonia*-dominated kelp communities are found in

Australasia and South Africa (Mann 1982). *Durvillaea* and *Lessonia* kelp beds occur in the circumpolar cold temperate regions of Australasia, South America, and around the subantarctic islands (Hay 1979). *Ascoseira* and *Himantothallus* are primary elements of Antarctic regions.

Kelp species have very high levels of productivity, on the order of 1,000 g of carbon per square meter annually (Mann 1982). Growth in many species is seasonal (*Macrocystis pyrifera* is an exception) with the highest rates in winter and early spring (Chapman 1974; Kain 1979). Several methods have been used to describe and measure the growth and productivity of kelp species (Kain 1979, 1982), including measurements of standing crop, morphological parameters (including the use of punched holes), chemical components such as alginic acid (cell walls), fucoidan, laminaran, and mannitol (food reserves) (Hellebust and Craigie 1978), and in situ measurements of the rate of photosynthesis (Kremer 1978). In *Laminaria* spp., reserves are built up during the summer when levels of radiant energy are high and are used up during the winter growth phase (Chapman 1974). Many so-called kelps growing seasonally from holdfasts are perennials. Some, like *Laminaria saccharina,* have life spans of less than 3 years (Kain 1979), whereas others (*Durvillaea*) may live for 7 or more years. Thalli of *Laminaria hyperborea* up to 15 years old have been recorded (Kain 1979). Sea urchins are often the most important herbivores in kelp communities. In many localities, they feed on detritus, drifting kelp, and ephemeral algae and cause little disturbance to the attached kelps. Along the northern Pacific coasts, the increase in sea urchin (*Strongylocentrotus* spp.) populations related to the decrease in populations of their major predator, the sea otter (Mann 1982), has led to considerable damage to the kelp beds.

Fucoid Communities

Fucales species are dominant in the rocky intertidal zone in many temperate regions of the world, whereas in the tropics they more commonly form subtidal communities. *Fucus* spp. and *Ascophyllum* abound on temperate shores in the northern hemisphere. In the southern hemisphere, subtidal fucoid communities are often better developed than the intertidal ones, e.g., in Australasia extensive dense stands of *Sargassum* and species in the Cystoseiraceae and Seirococcaceae. *Durvillaea* belongs to Fucales, but is treated as kelp in this chapter (see above).

Fucoids are highly productive, but stresses in the intertidal environment may cause them to exude a considerable amount of soluble organic matter that is rapidly taken up by bacteria (Mann 1982) so that in contrast to kelps, a significant proportion of fucoid productivity is not realized as algal biomass. Intertidal northern hemisphere fucoids grow predominantly during the summer and to a limited extent accumulate storage carbohydrates that permit survival during the winter, when levels of radiant energy and the rate of photosynthesis are very low (Chapman 1974). Sea urchins, starfish, limpets, chitons, littorinid snails, and fish influence the structure of intertidal fucoid communities by grazing, affecting the species composition and biomass (Mann 1982).

Effects of Environmental Factors on Growth and Reproduction

Brown algae are notorious for their morphological plasticity in response to the environment. Thallus form changes in response to variation in such factors as irradiance, water movement, temperature, and salinity. The more dramatic effects occur in the larger species. Kelp species growing on high wave-energy coasts tend to have highly digitate fronds, whereas in calmer water the laminae are more likely to be entire. Unattached fucoids (e.g., *Ascophyllum, Fucus,* and *Hormosira*) in extremely sheltered localities tend to develop a number of distinctive characteristics. Holdfasts are lacking, branching is more profuse, reproduction is often by means of fragmentation, and sexual reproduction is inhibited (Norton et al. 1981).

Changes from the asexual to sexual modes of reproduction are environmentally elicited. Seasonal changes in light quality, irradiance, and temperature have been shown to regulate the fertility of kelp gametophytes. In many species, low temperatures (e.g., 5 °C) and a certain quantum dose of blue light are required to induce gametogenesis, which in nature occurs in winter and spring (Lüning 1981). In *Scytosiphon,* a member of the Scytosiphonaceae, a photoperiodic response controls the transition between the two phases (blades and crusts) of the heteromorphic life history. Blades in laboratory culture develop in response to short days; in nature, blades develop in winter and spring, crusts in summer. Temperature affects reproduction in many species of brown algae. In *Ectocarpus siliculosus*, the development of unilocular (meiotic) sporangia on the sporophyte occurs only below 13 °C so that the gametophyte generation is initiated at lower temperatures. At higher temperatures, only asexual plurilocular sporangia are formed (Müller 1964). Species of brown algae from different orders (Ectocarpales, Sphacelariales, and Fucales) produce their gametes in winter or spring in temperate regions when seawater temperatures are low. Relatively little is known of the factors initiating the developmental sequence leading to gametogenesis in the gametophytes of most brown algae.

Trans-ocean Introductions: Some brown algal species have been introduced across the oceans by human activities intentionally (e.g., fisheries) or accidentally (e.g., associated with ship transportation) and have spread widely and become a considerable threat to local ecosystems. *Sargassum muticum* and *Undaria pinnatifida* were introduced from Asia to North America and Europe attached to young oysters, or as ship hull communities (Critchley and Dijkema 1984; Uwai et al. 2006; Russell et al. 2008). Another Asian-origin *Sargassum* species, *S. filicinum,* has recently spread on the North American Pacific coast (Miller et al. 2007).

Collection of Brown Algae: Brown algae are best collected in buckets and bags from the intertidal zone of the seashore when the tide is low, preferably during spring tides. They may be collected from subtidal habitats by snorkeling and SCUBA diving. Specimens from deep water may occasionally be found in storm drift, caught in fishing nets, or by dredging. Brown algae in the temperate and cold water regions should be kept moist and cool and processed as soon as possible after collection. Only the more tolerant intertidal species survive more than 2 or 3 days of temporary storage in a cold room or refrigerator (see below*). Tropical and subtropical species are generally better kept at room temperature.

Specimens for herbaria must be prepared from healthy and, if possible, entire thalli. Most species can be preserved as dried herbarium specimens. Individual specimens are spread in a shallow dish of seawater, cleaned of sand, any epibionts, and, if very bushy, carefully pruned of some fronds so that the form can be seen clearly. The specimen is then floated and arranged over a sheet of mounting paper in a tray of clean water, and the paper is slowly tilted and removed from the tray, allowing the water to drain off and the seaweed to remain spread over the paper. Covered with a piece of cheesecloth or plastic nonwoven fabric and pressed between several sheets of newspaper, specimens are stacked and placed in a press. Newspaper must be changed frequently during the first day or two and then daily until the specimens are quite dry. Instead of changing newspapers for removing moisture of the specimens, the pressed specimens on mounting paper and covered with cheese cloth may be put between corrugated cardboard sheets, and the stack placed in a continuous air flow from a fan, so that the moisture is removed through the channels of the corrugated cardboard. Steady firm pressure is essential to obtain flat, unwarped sheets. Delicate soft algae adhere very firmly to the mounting paper and less firmly to the cheesecloth, which can be peeled off when drying is complete. Coarse, thick, or wiry algae do not adhere satisfactorily but can be attached to paper with glue or strips of gummed paper after they are dry. The collector's name, date, and site of collection, code number, and other data are recorded in pencil on each herbarium specimen before mounting. A permanent label is affixed later. Dried specimens, stored flat and away from light, will keep indefinitely and not lose their color.

To preserve specimens, the larger brown algae may be soaked in 50 % glycerol, to which some phenol has been added to discourage the growth of microorganisms. The thalli will remain soft and flexible. Brown algae are commonly preserved in seawater-formalin at a concentration of 2–5 %. For critical light and electron microscope studies, great care should be taken to select a suitable schedule for the fixation and preparation of the tissue. For this purpose, recent studies on related species should be consulted (see also references in Gantt 1980). For DNA extraction for molecular analyses, fresh specimens should be quickly dried in silica gel and kept desiccated, or frozen.

Some species (e.g., *Desmarestia* spp., *Dictyopteris* spp., *Spatoglossum* spp.) are remarkably delicate and apt to die and turn green when exposed to air or fresh water, revealing the strong acidity within their cell vacuoles when so damaged (Sasaki et al. 1999, 2004).

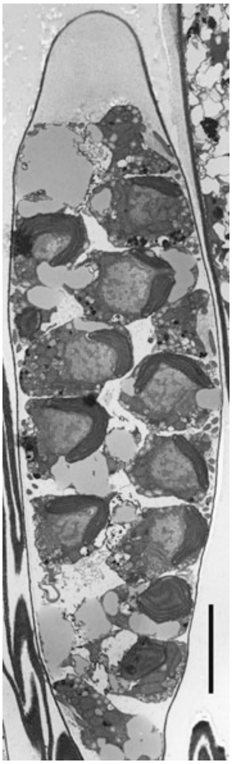


Fig. 4 Unilocular sporangia of *Saccharina japonica* in longitudinal section (TEM micrograph courtesy of Taizo Motomura). Scale bar, 5 μm

Characterization and Recognition

Definition of the Class

Brown algae are heterokont, multicellular algae with varying life cycles involving an alternation of haploid and diploid nuclear phases. In a large portion of the taxon, there is a corresponding alternation of independent haploid gametophyte and diploid sporophyte generations. Some orders tend toward an increase in size and morphological complexity of the sporophyte generation and reduction of the gametophyte generation. Meiosis occurs in cells known as unilocular zoidangia (meiosporangia, Fig. 4) borne on sporophytic thalli, resulting in the formation of haploid spores (meiospores). These are, in most taxa, motile cells (zoospores) having two unequal flagella; they settle, germinate, and give rise to the gametophyte generation. The gametes are generally produced in plurilocular gametangia (Fig. 5) borne on gametophyte thalli. Fertilization varies from isogamous (gametes of different sex are the same size) to oogamous (gametes are nonmotile eggs and motile spermatozoids).

Sexual attractants (pheromones) are known to be involved in the sexual reproduction in brown algae. Attractants, mostly volatile hydrocarbons of low molecular

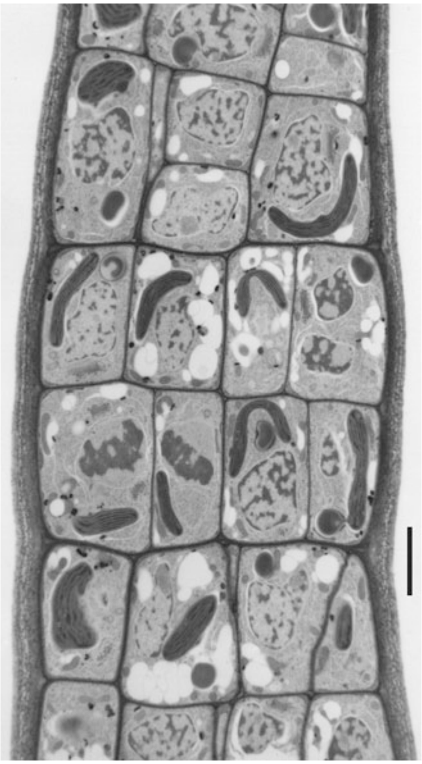


Fig. 5 Immature plurilocular sporangia of *Ectocarpus* sp. Freeze substitution (TEM micrograph courtesy of Taizo Motomora). Scale bar, 2 µm

weight (Müller 1981a; Maier and Müller 1986), which are secreted by female gametes to attract male gametes, have been isolated from several species and characterized chemically. In Laminariales, the sexual attractant also induces the release of sperm from the spermatangia (antheridia) (Maier 1995). The diploid zygote develops into the sporophyte generation. In many species, asexual reproduction involving the production of zoospores (motile cells) in multichambered plurilocular sporangia borne on either the gametophyte or sporophyte generation is very common. Brown algae produce heterokont reproductive zoids and sperm with characteristic ultrastructure: two unequal flagella inserted laterally, the anterior bearing mastigonemes and the posterior one lacking them (Figs. 6 and 7). The genes of the proteins constituting mastigonemes have been identified in a unicellular heterokont (*Ochromonas*, Yamagishi et al. 2007) and shown to be comparable to the corresponding genes of the proteins in brown algae.

Most brown algal zoids show photo-orientation responses (phototaxis). In the posterior flagellum, a green autofluorescent substance and a basal swelling, appressed to an eyespot of carotenoid globules in the adjacent chloroplast (Fig. 8), is involved in the photoreception of blue light (Kawai et al. 1990; Kawai 1992a; Kawai and Kreimer 2000). In contrast, zoids of Laminariales and sperm that lack phototaxis in some other orders lack these structures.

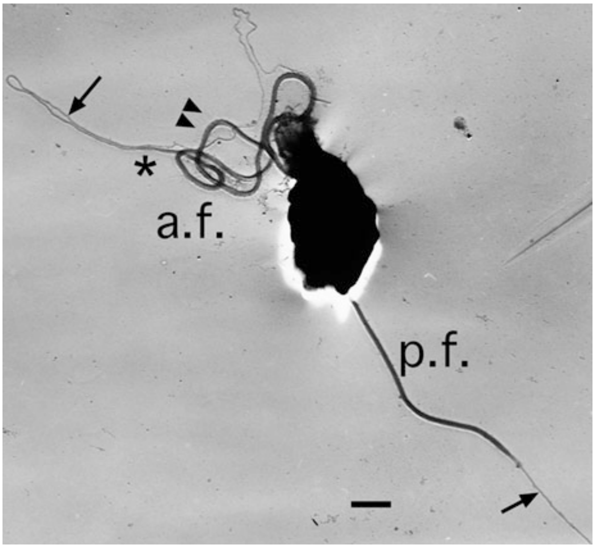


Fig. 6 Sperm of *Stschapovia flagellaris* with hairy anterior flagellum having very long acronema at the tip, and posterior flagellum with shorter acronema. Whole mount TEM micrograph. Scale bar, 2 μm

Structural characteristics of brown algal chloroplasts (plastids) include the arrangement of thylakoids in groups of three, the presence of a lamella lying just inside the plastid membrane (called the girdle lamella), and the plastid endoplasmic reticulum, which is continuous with the nuclear envelope. The chloroplast DNA is arranged in a peripheral ring (Coleman 1985). The characteristic brown accessory pigment fucoxanthin is active in photosystem II of photosynthesis (Braun and Braun 1974); carotenes, violaxanthin, and chlorophylls a, c and c_1 are also present. Pyrenoids, appendages of chloroplasts, are observed in species of the orders Ectocarpales *s.l.* and Scytothamnales (Kawai 1992b) (Fig. 8). Pyrenoids are lacking or not obvious in other orders including basal taxa, and those in Ectocarpales (Nagasato et al. 2003) and Scytothamnales (Tanaka et al. 2007) have distinctive morphological features; therefore, pyrenoids are considered to have evolved (or became elaborated) multiple times in brown algae (Silberfeld et al. 2011). The carbon storage material commonly found in the phaeophytes is laminaran, a β-(1, 3) glucan containing mannitol.

Brown algal cell walls are composed chiefly of three kinds of polymer: cellulose, alginic acid, and the heterogeneous fucose-containing sulfated polysaccharides (fucan, fucoidan). The microfibrillar organization of cellulose contributes to the skeletal role of the walls (Kloareg et al. 1986). The cellulose-synthesizing terminal complexes (TCs) associated with the tips of microfibril impressions in the plasmatic fracture face of the plasma membrane (observed by freeze-fracture techniques) consist of subunits arranged in a single linear row (Peng and Jaffe 1976; Tamura et al. 1996). Alginic acid, a polymer of mannuronic and guluronic acids, and other sulfated polysaccharides such as fucoidan (McCandless and Craigie 1979), even though they are chemically more complex than cellulose, do not form structural wall components. Alginic acid was long considered to be a defining characteristic in the

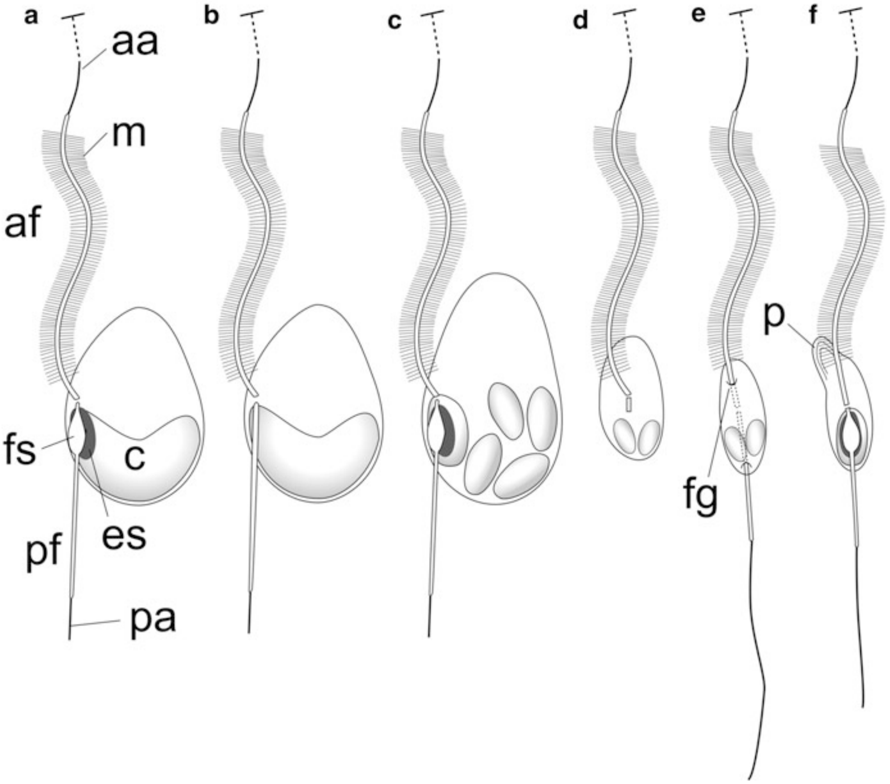
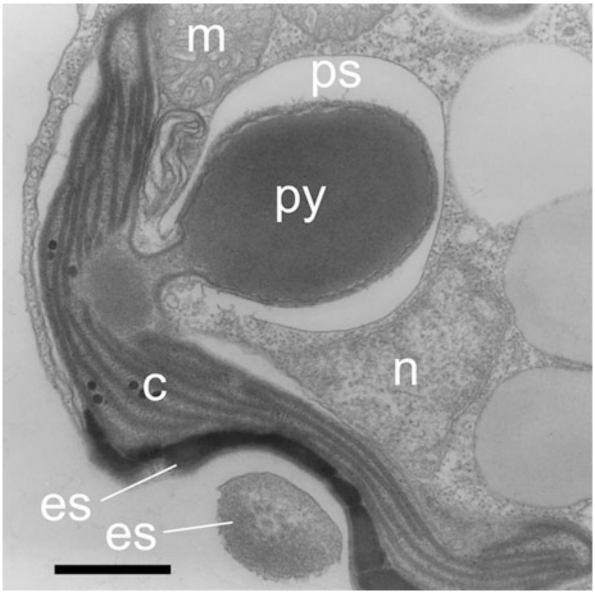


Fig. 7 Schematic representation of brown algal flagellated cells. (**a**) Typical (perhaps plesiomorphic) type with long anterior flagellum (*af*) and short posterior flagellum (*pf*). Chloroplast (*c*) has eyespot (*es*) spatially associated with flagellar swelling (*fs*) on the basal part of the posterior flagellum. Anterior flagellum has long acronema (*aa*), which is easily detached by fixation. Posterior flagellum has relatively short, but more persistent acronema (*pa*). (**b**) Laminarialean type without eyespot and flagellar swelling and lacking phototaxis. (**c**) Female anisogamous gamete with multiple chloroplasts. (**d**) Dictyotalean sperm with remnant posterior flagellum and reduced chloroplast. (**e**) Laminarialean sperm with long posterior flagellum, reduced chloroplasts, and deep flagellar gullet (*fg*). (**f**) Fucalean sperm with proboscis (anterior protuberance) and eyespot

Phaeophyta (Phaeophyceae) among the Chromista, but has now also been shown to be present in members of Schizocladiophyceae, Xanthophyceae, and Chrysomeridales (Chi et al. 1999; Kawai et al. 2003). Whatever skeletal functions alginates possess are thought to derive from their property of forming gels and viscous solutions. Fucans apparently have a role in the desiccation resistance of intertidal brown algae by virtue of their strong affinity for highly hydrated magnesium ions (Percival 1979).

Physodes, vacuole-like refractive bodies containing osmiophilic material of phenolic nature, are common in brown algae cells. Chemical analysis (Ragan 1976) has shown physodes to contain primarily phloroglucinol derivatives along with tannins

Fig. 8 Chloroplast with protruded type of pyrenoid with pyrenoid sac in *Ectocarpus* gamete. TEM micrograph. Scale bar, 0.5 μm



and terpenes. The phenolic compounds in brown algal cells are thought to act as herbivore deterrents in a similar way as the tannins in higher plants (Targett and Arnold 1998), but they are also suggested to play a role in polyspermy block and protection against UV radiation (Schoenwaelder 2002).

Classification of the Phaeophyceae

In the ordinal classification of the Phaeophyceae since Kylin (1933), basic construction of the thallus, growth mode, and life history pattern have been regarded as characters reflecting higher-rank phylogeny. Based on the general concept using phenotypic characters, 13–17 orders have been recognized in the Phaeophyceae: Ascoseirales, Chordariales, Cutleriales, Desmarestiales, Dictyosiphonales, Dictyotales, Discosporanigiales, Durvillaeales, Ectocarpales, Fucales, Laminariales, Ralfsiales, Scytosiphonales, Sphacelariales, Sporochnales, Syringodermatales, and Tilopteridales. However, molecular phylogenetic data showed some incongruence with some of the conventional ordinal assignments. Major updates are as follows: de Reviers and Rousseau (1999) proposed to reduce Durvillaeales to family status within the Fucales, as well as the unification of the Chordariales, Dictyosiphonales, Ectocarpales, and Scytosiphonales into Ectocarpales sensu *lato* (de Reviers and Rousseau 1999). Cutleriales was shown to be sister group of Tilopteridales, and so was merged with Tilopteridales (Silberfeld et al. 2010). Silberfeld et al. (2014b) proposed new subclasses Discosporangiophycidae, Ishigeophycidae, and Dictyophycidae in addition to the subclass Fucophycidae proposed by Cavalier Smith (1986), as well as a new order Phaeosiphoniellales. Kawai et al. (2015a)

Table 1 Orders, families, and genera of Phaeophyceae

I. Order Discosporangiales
1. Choristocarpaceae: *Choristocarpus*
2. Discosporangiaceae: *Discosporangium*
II. Order Ishigeales
1. Ishigeaceae: *Ishige*
III. Order Dictyotales
1. Dictyotaceae: *Canistrocarpus*, *Chlanidophora, Dictyopteris, Dictyota, Dictyotopsis, Distromium, Exallosorus, Herringtonia, Homoeostrichus, Lobophora, Lobospira, Newhousia, Padina, Rugulopteryx, Scoresbyella, Spatoglossum, Stoechospermum, Stypopodium, Taonia, Zonaria*
IV. Order Sphacelariales
1. Cladostephaceae: *Cladostephus*
2. Phaeostrophiaceae: *Phaeostrophion*
3. Sphacelariaceae: *Battersia, Herpodiscus, Sphacelaria, Sphacella, Sphacelorbus*
4. Sphacelodermaceae: *Sphaceloderma*
5. Stypocaulaceae: *Halopteris, Phloiocaulon, Protohalopteris, Ptilopogon*
V. Order Onslowiales
1. Onslowiaceae: *Onslowia, Verosphacela*
VI. Order Syringodermatales
1. Syringodermataceae: *Microzonia, Syringoderma*
VII. Order Desmarestiales
1. Arthrocladiaceae: *Arthrocladia*
2. Desmarestiaceae: *Desmarestia, Himanthothallus, Phaeurus*
VIII. Order Ascoseirales
1. Acroseiraceae: *Acroseira*
IX. Order Sporochnales
1. Sporochnaceae: *Austronereia, Bellotia, Carpomitra, Encyothalia, Lucasia, Nereia, Perisporochnus, Perithalia, Sporochnema, Sporochnus, Tomaculopsis*
X. Order Scytothamnales
1. Asteronemataceae: *Asteronema*
2. Bachelotiaceae: *Bachelotia*
3. Splachnidiaceae: *Scytothamnus, Splachnidium, Stereocladon*
XI. Order Ectocarpales sensu *lato*
1. Adenocystaceae: *Adenocystis, Caepidium, Chordariopsis, Utriculidium*
2. Ectocarpaceae (Ectocarpales *sensu stricto* + Chordariales + Dictyosiphonales)
Acinetospora, Acrothrix, Acrotrichium, Actinema, Adenocystis, Ascoseirophila, Asperococcus, Australofilum, Botrytella, Buffhamia, Chilionema, Chordaria, Chuckchia, Cladochroa, Cladosiphon, Cladothele, Clathrodiscus, Climacosorus, Coelocladia, Coilodesme, Corycus, Corynophlaea, Cylindrocarpus, Delamarea, Dermatocelis, Dictyosiphon, Ectocarpidium, Ectocarpus, Elachista, Elachistiella, Entonema, Epinema, Eudesme, Feldmannia, Flabellonema, Fosliea, Geminocarpus, Giraudia, Gononema, Halonema, Halorhipis, Halorhiza, Halothrix, Hamelella, Haplogloia, Hecatonema, Herponema, Heterosaundersella, Hincksia, Hummia, Internoretia, Isthmoplea, Kuckuckia, Kuetzingiella, Kurogiella, Laminariocolax, Laminarionema, Leathesia, Leblondiella, Leptonematella, Levringia, Leblondiella, Liebmannia, Litosiphon, Melastictis, Mesogloia, Mesogloiopsis, Microcoryne, Microspongium, Mikrosyphar, Myriactula, Myriocladia, Myriogloea, Myrionema, Myriotrichia, Nemacystus, Neoleptonema,

(*continued*)

Table 1 (continued)

Omphalophyllum, Papenfussiella, Petrospongium, Phaeophysema, Phaeostroma, Phaeostromatella, Pilinia, Pilocladus, Pleurocladia, Pogotrichum, Polycerea, Polytretus, Proselachista, Protectocarpus, Punctaria, Pylaiella, Rhadinocladia, Saundersella, Sauvageaugloia, Soranthera, Spermatochnus, Sphaerotrichia, Spongonema, Stegastrum, Stictyosiphon, Stilophora, Stilopsis, Streblonema, Streblonemopsis, Strepsithalia, Striaria, Suringariella, Tinocladia, Trachynema, Ulonema, Vimineoleathesia, Xanthosiphonia, Zeacarpa, Zosterocarpus
3. Scytosiphonaceae (Scytosiphonales)
Chnoospora, Colpomenia, Compsonema, Diplura, Endarachne, Endopleura, Hapterophycus, Hydroclathrus, Iyengaria, Jolyna, Myelophycus, Melanosiphon, Petalonia, Rosenvingea, Scytosiphon, Sorapion, Stragularia, Symphyocarpus
XII. Order Laminariales
1. Akkesiphycaceae: *Akkesiphycus*
2. Pseudochordaceae: *Pseudochorda*
3. Chordaceae: *Chorda*
4. Aureophycaceae: *Aureophycus*
5. Agaraceae: *Agarum, Costaria, Dictyoneurum, Thalassiophyllum*
6. Laminariaceae: *Arthrothamnus, Costulariella, Cymathere, Feditia, Laminaria, Macrocystis, Nereocystis, Pelagophycus, Phyllariella, Postelsia, Pseudolessonia, Saccharina, Tauya*
7. Alariaceae: *Alaria, Ecklonia, Eckloniopsis, Egregia, Eisenia, Eualaria, Pleurophycus, Pterygophora, Undaria, Undariella*
8. Lessoniaceae: *Lessonia, Lessoniopsis*
9. *Phaeosiphoniellaceae: *Phaeosiphoniella*
XIII. Asterocladales
1. Asterocladaceae: *Asterocladon*
XIV. Order Fucales
1. Bifurcariopsidaceae: *Bifurcariopsis*
2. Durvillaeaceae: *Durvillaea*
3. Fucaceae: *Ascophyllum, Fucus, Hesperophycus, Pelvetia, Pelvetiopsis, Silvetia*
4. Himanthaliaceae: *Himanthalia*
5. Hormosiraceae: *Hormosira.*
6. Notheiacaea: *Notheia*
7. Sargassaceae*: Acrocarpia, Anthophycus, Axillariella, Bifurcaria, Brassicophycus, Carpoglossum, Carpophyllum, Caulocystis, Cladophyllum, Coccophora, Cystophora, Cystoseira, Halidrys, Hormophysa, Landsburgia, Myagropsis, Myriodesma, Nizamuddinia, Oerstedtia, Phyllotricha, Platythalia, Polycladia, Sargassopsis, Sargassum, Scaberia, Sirophysalis, Stephanocystis, Stolonophora, Turbinaria*
8. Seirococcaceae: *Axillariella, Cystosphaera, Marginariella, Phyllospora, Scytothalia, Seirococcus*
9. Xiphophoraceae: *Xiphophora*
XV. Order Nemodermatales
1. Nemodermataceae: *Nemoderma*
2. Zeacarpaceae: *Zeacarpa*
XVI. Order Tilopteridales
1. Culteriaceae: *Cutleria, Mutimo, Zanardinia*
2. Phyllariaceae: *Phyllariopsis, Saccorhiza*

(*continued*)

Table 1 (continued)

3. Tilopteridaceae: *Haplospora, Tilopteris*
XVII. Order Stschapoviales
1. Halosiphonaceae*: Halosiphon*
2. Platysiphonaceae: *Platysiphon*
3. Stschapoviaceae: *Stschapovia*
XVIII. Order Ralfsiales
1. Heterochordariaceae: *Analipus*
2. Mesosporaceae: *Acrospongium, Hapalospongidion, Mesospora*
3. Neoralfsiaceae: *Neoralfsia*
4. Ralfsiaceae: *Heteroralfsia, Jonssonia, Lithoderma, Myrionemopsis, Petroderma, Porterinema, Pseudolithoderma, Ralfsia*

*Classified in a separate order Phaeosiphoniellales in Silberfeld et al. (2014b)

proposed Stschapoviales and moved Halosiphonaceae and Stschapoviaceae from Tilopteridales to this order together with newly proposed Platysiphonaceae.

The orders and families are listed, as is customary, in sequences of increasing structural complexity. The list of genera, not exhaustive because it is based on only the more accessible recent taxonomic literature, is in alphabetical order. However, the ordinal and familial assignment of ectocarpalean taxa are currently considerably confused in Ectocarpales excluding Scytosiphonaceae, because of the insufficient resolution and the coverage of taxa in relevant molecular phylogenetic studies, although several new families have been described based on molecular data. Therefore, familial assignment is suspended in those taxa in the present chapter.

Representative families and genera in the orders are listed in Table 1. Diagnostic characters of the above-mentioned 17 orders currently recognized within the Phaeophyceae are presented in Table 2.

Order Discosporangiales

The genera *Choristocarpus* and *Discosporangium*, with uniseriate filamentous thalli with apical growth cells, have been classified in Sphacelariales (Prud'homme van Reine 1982). However, recent molecular studies (Draisma et al. 2001; Burrowes et al. 2003; Kawai et al. 2007) revealed that they form a monophyletic clade that first branches off from all other brown algae, sharing the following characters which are considered to be plesiomorphic characters in the brown algae: (1) apical (and diffuse) growth; (2) uniseriate, subdichotomously branched filaments; (3) multiple chloroplasts per cell without pyrenoids; and (4) lack of heterotrichy and phaeophycean hairs. Regarding their higher-rank systematic positions, reinstatement of Discosporangiaceae and Discosporangiales (Schmidt 1937) was proposed, and the inclusion of Choristocarpaceae in the order was also suggested (Kawai et al. 2007). *D. mesarthrocarpum* has unique disk-shaped plurilocular reproductive organs.

Table 2 Characteristic features of brown algal orders

Order	Thallus structure or prominent generation	Chloroplast	Life history pattern	Reproduction (sexual/asexual)	Remarks
Discosporangiales	Uniseriate, filamentous	Multiple, discoid, without pyrenoids	Isomorphic	Isogamy?/uni-zoids	Most basal taxon in Phaeophyta, only a few species recognized
Ishigeales	Parenchymatous, foliose or terete	Multiple, discoid, without pyrenoids	Isomorphic	Isogamy/uni-zoids	Only a few species recognized
Dictyotales	Parenchymatous, foliose or membranous	Multiple, discoid, without pyrenoids	Isomorphic	Oogamy/tetraspores in most taxa	Large order including many tropical/subtropical taxa
Sphacelariales	Parenchymatous, filamentous, terete or foliose	Multiple, discoid, without pyrenoids	Isomorphic	Isogamy, anisogamy, oogamy/uni-zoids, propagules	
Onslowiales	Uniseriate, filamentous, partly with longitudinal walls	Multiple, discoid, without pyrenoids	Isomorphic	anisogamy/uni-zoids, propagules	
Syringodermatales	Foliose thalli formed by adhesion of filaments; some with longitudinal walls	Multiple, discoid, without pyrenoids	Isomorphic or heteromorphic[a]	Isogamy/uni-zoids	Only known from relatively deep habitats, life histories remarkably diverse
Desmarestiales	Pseudoparenchymatous, terete or foliose	Multiple, discoid, without pyrenoids	Heteromorphic	Oogamy/uni-zoids	Some spp. forming large thalli exceeding 5 m, important ecological element in Antarctic region

Ascoseirales	Parenchymatous, terete	Multiple, discoid, without pyrenoids	Only diploid generation is evident	Isogamy	Distributed only in cold water regions of the southern hemisphere
Sporochnales	Pseudoparenchymatous, terete	Multiple, discoid, without pyrenoids	Heteromorphic	Oogamy/unizoids	
Scytothamnales	Parenchymatous, terete	Single or multiple, embedded pyrenoid with tubular invaginations	Heteromorphic	Isogamy/unizoids	Characterized by distinctive pyrenoids
Ectocarpales *s.l.*	Uniseriate, pseudoparenchymatous or parenchymatous; filamentous, terete, foliose or saccate	Single to multiple, discoid or ribbon-shaped, with projected pyrenoid	Isomorphic[b] or heteromorphic	Isogamy, anisogamy/unizoids	Including taxa formerly classified in Chordariales, Dictyosiphonales and Scytosiphonales
Laminariales	Parenchymatous, foliose or terete	Multiple, discoid, without pyrenoids	Heteromorphic	Oogamy/unizoids	Largest thalli attaining to 50 m and major component of kelp forests
Asterocladales	Uniseriate, filamentous, partly with longitudinal walls	Multiple, separate pyrenoids grouped in center of cell	Isomorphic	Anisogamy/unizoids	
Fucales	Parenchymatous, foliose or terete	Multiple, discoid, without pyrenoids	Only diploid generation is evident	Oogamy	Some spp. forming large thalli exceeding 10 m and major component of algal beds
Nemodermatales	Pseudoparenchymatous, crustose	Multiple, discoid, without pyrenoids	Isomorphic	Anisogamy	Characterized by intercalary or tufted lateral unilocular zoidangia in upright filaments

(*continued*)

Table 2 (continued)

Order	Thallus structure or prominent generation	Chloroplast	Life history pattern	Reproduction (sexual/asexual)	Remarks
Tilopteridales	Parenchymatous, terete or filamentous	Multiple, discoid, without pyrenoids	Heteromorphic, nearly isomorphic or only haploid generation is evident	Oogamy or asexual/uni-zoids	Distributed only in cold or cool water regions of the northern hemisphere
Stschapoviales	Parenchymatous, terete	Multiple, discoid, without pyrenoids	Heteromorphic or regenerating a single type of thallus	Oogamy or asexual/uni-zoids	Distributed only in cold water regions of the northern hemisphere
Ralfsiales	Parenchymatous, crustose, or terete	Single or multiple without pyrenoid	Isomorphic or heteromorphic	Isogamy/uni-zoids	Predominantly crustose

[a] Gametophyte may be considerably reduced and not free-living

[b] In some taxa, sporophyte and gametophyte thallus sizes are not remarkably different but are distinguishable by their gross morphology

Order Ishigeales

The Ishigeales have branched, terete or flattened parenchymatous thalli of up to 10–20 cm high. The genus *Ishige*, including two species distributed in the warm temperate Pacific Ocean, has been classified in Chordariales. However, the lack of prominent pyrenoids in the chloroplast (Hori 1971) and the indication of isomorphic life history (Tanaka in Hori 1993), as well as preliminary molecular phylogenetic data (Tan and Druehl 1994; Peters and Ramírez 2001), made this systematic position doubtful. Later Cho et al. (2004) proposed a new order Ishigeales to accommodate the genus.

Order Dictyotales

The isomorphic sporophyte and gametophyte thalli are foliose and parenchymatous. Dictyotales are unique in brown algae including taxa with calcified thalli (i.e., *Padina* and *Newhousia*). *Dictyota* has a single apical cell, whereas other genera have several to many localized apical cells forming dichotomously branching thalli or arranged along the entire margin and hence forming fan-shaped thalli. Cells that are cut off from the apical cell undergo further longitudinal and transverse divisions (Katsaros and Galatis 1988; Gaillard and L'Hardy-Halos 1990). Sexual reproduction is anisogamous or oogamous. The sperm have only an anterior flagellum, but have a second flagellar basal body (Manton 1959), except for *Zonaria angustata*, which is reported to have two flagella (Phillips and Clayton 1991).

Order Sphacelariales

The Sphacelariales is a well-defined order (Prud'homme van Reine 1982, 1993) in which branched filaments grow from a conspicuous apical cell. During growth, segments cut off from the apical cell by transverse division subsequently enlarge and undergo further transverse and longitudinal segmentation. Sphacelariales show isomorphic life histories. Isogamy occurs in *Cladostephus,* isogamy or anisogamy in *Sphacelaria,* and anisogamy or oogamy in the Stypocaulaceae. Kawai et al. (2005a; 2015a) suggested classifying *Phaeostrophion* in Phaeostrophiaceae in Sphacelariales, and thereby to emend the order to also include foliose taxa.

Order Onslowiales

Onslowiales comprises two genera *Onslowia* and *Verosphacela*. The isomorphic sporophyte and gametophyte thalli of apical growth are filamentous and irregularly branched, and slightly polystichous with transverse walls (Searles and Leister 1980; Henry 1987; Draisma et al. 2010).

Order Syringodermatales

Syringodermatales include the genera *Syringoderma* and *Microzonia*, formerly included in Dictyotales (Henry 1984; Burrowes et al. 2003). The fan-shaped macrothalli develop by the cohesion of filaments arising from a marginal meristem. The gametophyte morphologies are remarkably divergent among *Syringoderma* species, being either filamentous or reduced to only 4 or 2 cells (Henry and Müller 1983; Henry 1984; Kawai and Yamada 1990).

Order Desmarestiales

In most species, the pseudoparenchymatous thallus is derived from apical meristems situated at the base of a hair (trichothallic). A cortex and a meristoderm (a meristematic surface layer of tissue) are formed from the lateral outgrowths of axial filaments. A parenchyma-like anatomy is formed from this filamentous growth in the Antarctic *Himantothallus* (Moe and Silva 1981). The taxonomy of the species of *Desmarestia* is confused, and a worldwide revision of the 40 or so species is needed (Moe and Silva 1977). Some members show strong acidity by accumulating SO_4^{2-} ion within cells, and the evolution of this character is considered to have occurred once in the order (Peters et al. 1997).

Order Ascoseirales

The Ascoseirales comprise the single Antarctic genus *Ascoseira*, which has a large parenchymatous thallus consisting of a dissected lamina, holdfast, and stipe. Growth is intercalary with reproductive structures borne in conceptacles that produce large cells containing eight large eggs capable of developing directly into the sporophytic thallus (Moe and Henry 1982) and eight vegetative vestigial cells (Clayton 1987).

Order Sporochnales

The sporophytic thalli are filamentous and growth occurs in meristems located at the base of dense apical tufts of hairs. The pseudoparenchymatous (= formed of filamentous aggregates) fronds are formed from the downgrowth of corticating filaments below the apex. The minute, filamentous gametophytes (microthalli) produce eggs and sperm (Caram 1965).

Order Scytothamnales

The Scytothamnales have branched, terete, parenchymatous thalli, up to 30 cm high, growing from a small holdfast or crustose base. The cells include one or more stellate chloroplasts with a central pyrenoid with tubular invaginations and lacking a pyrenoid sac (Peters and Clayton 1998; Tanaka et al. 2007).

Order Ectocarpales sensu ***lato (including Chordariales, Dictyosiphonales, Ectocarpales sensu stricto,*** and ***Scytosiphonales)***

The taxa formerly classified in Chordariales are mucilaginous, simple, or branched thalli of closely compacted filaments (pseudoparenchymatous). A few genera (in the Elachistaceae, and *Papenfussiella*) also have free filaments. Growth is intercalary in the Elachistaceae, Leathesiaceae, and Chordariaceae and apical in the Acrotrichaceae, Spermatocthnaceae, Splachnidiaceae, and Notheiaceae. Macrothalli are sporophytes with unilocular and, in some species, plurilocular sporangia. Sexual life histories have been described for a number of species (Müller 1981b; Peters 1987).

The taxa formerly classified in Dictyosiphonales were defined by their polystichous character. That is, their cells divide longitudinally as well as transversely to form parenchyma. Longitudinal cell divisions produce a parenchymatous thallus. This is least developed in the Myriotrichiaceae, which possess finely divided, almost filamentous thalli. The macrothallus sporophytes possess both unilocular and plurilocular sporangia in most species. Gametophytes, where known, are filamentous and produce anisogametes (Fiore 1977). Adenocystaceae (Rousseau *et al*. 2000) is considered to have its closest phylogenetic relationship with this order.

Ectocarpales *sensu stricto* have simple thalli consisting of branched filaments in which growth occurs by intercalary cell division. Reproduction is by zoids produced in plurilocular and unilocular structures. Sexual reproduction is either isogamous or anisogamous, but the life histories of only a few species have been studied in detail (Wynne and Loiseaux 1976). *Ectocarpus siliculosus* and species in the Myrionemataceae (Loiseaux 1967), for example, have more or less isomorphic sporophyte and gametophyte generations (Müller 1967). The Sorocarpaceae, classified previously in the Ectocarpaceae, was erected (Pedersen 1977) for three genera with terminal hairs, sympodial branching, and distinctive aggregates of plurilocular sporangia (sori). Some authors have placed them in the Chordariales. Some authors have merged Ectocarpales with Chordariales, Scytosiphonales, Tilopteridales, and Dictyosiphonales because the boundaries separating these taxa are indistinct (Russell and Fletcher 1975).

In the taxa formerly classified in Scytosiphonales, the thalli are parenchymatous with variously shaped, simple, or branched forms. Growth is intercalary. The cells contain one plastid. The macrothalli are gametophytes, bearing only plurilocular reproductive structures, some of which are gametangia. Mating is isogamous or anisogamous (Nakamura and Tatewaki 1975; Clayton 1979; 1980). The sporophytes are filamentous or crustose microthalli that produce unilocular sporangia. Taxonomy of the order was revised by Kogame et al. (1999).

Order Laminariales

The Laminariales (see Bold and Wynne 1985) have large parenchymatous thalli differentiated into lamina, stipe, and holdfast. The thallus consists of an outer meristoderm, a cortex, and a central medulla. The trumpet-shaped filaments (hyphae) constituting the medulla are distinctive to the order, comparable to sieve tubes in higher plants. Growth occurs at intercalary meristematic regions. The macrothallus sporophytes reproduce by means of spores formed in unilocular sporangia. Microscopic gametophytes produce sperm or eggs. Egg formation (Lüning 1981) and fertilization (Lüning and Müller 1978) are similar to that in the Desmarestiales, but the laminarialean egg has vestigial flagella (Motomura and Sakai 1988).

Members of Laminariales are major components of lower intertidal to subtidal vegetations in cold water regions, except the Antarctic. Higher rank taxonomy of the order has been considerably revised based on life history and molecular studies (Kawai 1986; Kawai and Kurogi 1985; Kawai and Sasaki 2000; Kawai et al. 2008, 2013; Kawai 2014). Kawai et al. (2008, 2013) reported a novel laminarialean species with distinctively simple sporophyte structure and forming sori on the discoid holdfast. Phylogeography of Laminariales was recently reviewed by Bolton (2010) and Kawai (2014).

Order Asterocladales

Asterocladales comprise two filamentous genera with characteristic chloroplast configurations. Vegetative cells include several elongate plastids per cell, which are linked in a stellate configuration via their stalked and protruding pyrenoids without invaginations, as seen in Scytothamnales (Müller and Parodi 1994; Müller et al. 1998; Uwai et al. 2005; Tanaka et al. 2007).

Order Fucales

The Fucales have fairly large parenchymatous thalli. Branching is either dichotomous, monopodial and radial, or bilateral. The thallus is differentiated into a meristoderm, cortex, and medulla; growth results from the division of apical cells and cell division in associated meristematic regions. Ooogonia and spermatangia are borne on specialized branches known as receptacles. Meiosis occurs in the first division of the sexual parental cells. The haploid gametophyte generation is so greatly reduced that it is not recognizable as such.

Members of Fucales are major components of coastal vegetations of cold water regions of the northern hemisphere (*Fucus, Ascophyllum, Pelvetia*, etc.) and southern hemisphere (*Durvillaea*), and warm temperate to tropical coastal ecosystems (*Sargassum, Cystoseira*, etc.).

Order Nemodermatales

Nemodermatales comprise Nemodermataceae and newly described Zeacarpaceae (Kawai et al. 2016). Both families are monotypic including *Nemoderma tingitanum* and *Zeacarpa leiomorpha,* respectively. It has crustose thalli characterized by the formation of reproductive sori with intercalary or tufted lateral unilocular zoidangia in upright filaments. Each cell includes multiple chloroplasts without pyrenoids. By molecular phylogeny, *N. tingitanum* was shown to be distinctive from other crustose algae, and treatment in a separate order was suggested (Phillips et al. 2008). Later, *Zeacarpa* was shown to phylogenetically most related to *Nemoderma* and also transferred from Ralfsiales to Nemodermatales.

Order Tilopteridales

Tilopteridales comprise Tilopteridaceae, Phyllariaceae, and Cutleriaceae. The family Tilopteridaceae includes three polystichous, filamentous genera (South 1975; Hooper et al. 1988). *Haplospora* sporophytes resemble the gametophytes, and sexual reproduction involves eggs and sperm. The sporophyte of *Haplospora* bears meiotic sporangia that produce a multinucleate nonmotile spore. In *Haplospora* a life history alternating between nearly isomorphic filamentous sporophytes forming monospores and asexual gametophytes forming two types of monospore-like reproductive cells (i.e., eggs and neutral spores) and sperm are reported, whereas the sporophyte is considered to be reduced in *Tilopteris* (Kuhlenkamp and Müller 1985). In either case, sexual reproduction is considered to be reduced. In contrast, some members of Cutleriaceae (e.g., *Cutleria*, *Mutimo*), which used to be classified in its own order Cutleriales, have a life history alternating between heteromorphic terete or membranous gametophytes and crustose sporophytes, whereas *Zanardinia* is isomorphic (Fritsch 1945). Phyllariaceae comprise kelp-like genera such as *Sacchorhiza* and *Phyllariopsis* and have characteristic anatomy with multinucleate conducting filaments (i.e., solenocysts) comparable in function to the trumpet-shaped hyphae in laminarialean kelp.

Order Stshapoviales

Kawai et al. (2015a) proposed to classify Halosiphonaceae, Stschapoviaceae, and Platysiphonaceae in Stschapoviales, mainly based on molecular phylogeny. These are cold water taxa having polystichous, terete thalli with assimilatory filaments in whorls or on the distal end. *Halosiphon* shows a typical heteromorphic life history with large sporophyte and monoecious gametophytes, but *Stschapovia* and *Platysiphon* are suggested to have a modified life history without alternation between two apparent generations, as in Fucales (Kawai and Sasaki 2004; Kawai et al. 2015a, b).

Order Ralfsiales

The validity of Ralfsiales has been challenged, but it was shown to be a monophyletic group after emendation (Lim et al. 2007). The Ralfsiales primarily have crustose thalli, but some have terete erect thalli (e.g., *Analipus, Heteroralfsia*) (Kawai 1989), characterized by discoidal early development of the thallus, intercalary plurilocular gametangia with terminal cells, terminal unilocular zoidangia, and a crustose phase in the life history (Nakamura 1972; Lim et al. 2007). Many members have a single parietal chloroplast without pyrenoids. The new families Mesosporaceae (Tanaka and Chihara 1982) and Neoralfsiaceae (Lim et al. 2007) have been added to the order.

Maintenance and Cultivation

Isolation from Nature

Collecting and Establishing Unialgal and Axenic Cultures: Collected specimens are transported in plastic bags, bottles, or containers suitable to their size, avoiding excess solar irradiation and temperature shocks relative to the prevailing habitat conditions. An insulated cool box or refrigerator is convenient for the temporary storage and transport of brown algae under most climatic conditions, although tropical species may be adversely affected by such low temperatures. Most intertidal taxa are more tolerant of stresses such as desiccation and rapid temperature changes, compared to subtidal taxa. Fertile specimens collected under desiccating conditions tend to release zoids and eggs as soon as they are reimmersed in seawater, such as in the containers used for transportation. Therefore, they may preferably be transported moist in plastic bags or plastic containers, instead of immersed in seawater.

A number of techniques are available for initiating cultures, some of which are more suited to particular orders of the Phaeophyceae (Kawai et al. 2005b). Either vegetative tissue or reproductive cells may be used for establishing unialgal cultures.

In both cases, clean specimens without epiphytes and epizoa are preferred, and fertile specimens should be selected in the field. When fertile portions of the specimens are recognizable, only those portions need to be excised and transported to the laboratory, to avoid damage and contamination from the other specimens. Acid-containing taxa (e.g., some *Desmarestia* spp., *Dictyopteris* spp. and *Spatoglossum* spp.) and some other delicate subtidal taxa (e.g., *Dictyota*, *Sporochnus*, etc.) should be transported in containers with a relatively large volume of sea water and separated from other algae, or the thalli will deteriorate very rapidly, which damages the other algae.

For unialgal cultures, sterilized grass vessels or plastic Petri dishes are commonly used. Suitable sizes depend on the targeted algal sizes, but 55–90 mm (diameter) dishes and 200–300 mL vessels are commonly used. Aeration is usually not required for the culture of this size, but is often used for larger cultures.

Unialgal cultures of marine brown algae grow readily in culture media of sea water enriched with basic autotroph nutrients. The most widely used formula is Provasoli's ES (PES) medium and modified Provasoli's ES medium (PESI), omitting vitamins but adding iodine (Tatewaki 1966). Related literature and recipes of the culture media are listed in Harrison and Berges (2005).

Isolation from vegetative thalli: Most brown algal species have high potential for regeneration and totipotency, so that unialgal cultures can be established for many species from vegetative tissues. However, in practice epiphytic algae and cyanobacteria tend to grow faster than the desired species and overwhelm it. Therefore, isolation by this technique is effective only for minute taxa and some larger ones with apical meristematic growth (e.g., Dictyotales, Sphacelariales, Discosporangiales). For those species, a razor blade may be used to first cut out a small fragment including the apical cell(s) into a Petri dish filled with sterilized seawater. Then, under a dissecting microscope, smaller pieces of tissue including intact apical cell(s) are cut out and transferred into individual wells of a multiwell plate or individual Petri dishes (or test tubes) filled with culture medium, using a clean fine forceps (sterilized by wiping with 70 % ethanol) or sterilized capillary pipettes. GeO_2 and antibiotics can be used to eliminate diatom and cyanobacteria contamination, respectively. After 1–2 weeks of culture in an illuminated chamber of suitable temperature, unialgal isolates can be selected using an inverted microscope to carefully inspect each isolate for contaminants.

Isolation from swimming zoids: Many species release zoids (zoospores and gametes) vigorously and synchronously 1 or 2 days after collection, rather than immediately after, if specimens are properly stored in cool and dark conditions. They tend to release zoids soon after reimmersion in seawater, stimulated by temperature rise and illumination. For zoid isolation, place a small fragment of fertile tissue in a small Petri dish, depression slide, or watch glass filled with sterilized seawater and examine the zoid-release under dissecting microscope. When release starts, observe any phototactic behavior of the zoids under a dissecting microscope to determine the orientation of the taxis and isolate clean zoids using a fine pipette into new Petri dish filled with sterile seawater culture medium. Wynne's hanging drop method (Chapman 1973) is useful when mass release of zoids fails and the isolation of individual reproductive structures is precluded. Alternatively, mature reproductive organs (unilocular zoidangia, plurilocular gametangia, etc.) may be cut out from the squashed or fragmented tissues including them and individually isolated and precultured until new offspring (germlings) from them become available. Then the germlings may be reisolated into individual Petri dishes to establish unialgal cultures.

Axenic culture: For axenic cultures, thalli should be cleaned thoroughly using sterile seawater. Guillard's antibiotic mixture, which consists of penicillin G 124.5 mg per liter, streptomycin sulfate 50 mg per liter, and chloramphenicol 20 mg per liter made up in sterile sea water, has been used to purify isolates of laminarialean (Druehl and Hsiao 1969) and *Dictyosiphon* (Saga and Sakai 1982) gametophytes.

Routine sterility tests should be carried out. For this purpose, Fries (1977) recommended transferring pieces of algae into test tubes containing culture medium to which is added 2 g glucose, 2 g galactose, 1 g mannose, 1 g asparagine, 0.5 g yeast extract (Oxoid), and 0.5 g bacteriologic peptone per liter.

Evolutionary History

Fossil Record

The fossil evidence of the evolution of the Phaeophyta is very scanty. This is perhaps because of their generally soft-bodied habit, very limited occurrence of calcified taxa (e.g., *Padina* spp.), and relatively recent evolution compared with red and green algae. The oldest undoubted brown algal fossils are kelps from the Tertiary. Parker and Dawson (1965) described from the upper Miocene fossil kelp, *Julescranea grandicornis,* which is intermediate in appearance between *Pelagophycus* and *Nereocystis. Paleohalidrys, Cystoseirites, Cystoseira,* and *Paleocystophora* have been assigned to the Cystoseiraceae in the Fucales, described from Miocene deposits in California.

Sister Taxa and Divergence Time of Phaeophyceae

It is rather difficult to infer the origin of the brown algae or to clarify the sister relationships with other Phyla, because of the sparse fossil record and lack of known unicellular taxa. The available evidence consists of molecular phylogenetic analyses, and the compositions of accessory photosynthetic pigments (i.e., carotenoids) and cell walls (e.g., presence/absence of cellulose and alginates), fine structure of flagellar apparatus (e.g., presence/absence of transitional helix and rhizoplast), and presence and absence of periplasmic opaque substances. Based on this information, Schizocladiophyceae is considered to be the closest sister group of Phaeophyceae, and both group with Phaeothamniophyceae and Xanthophyceae (Bailey and Andersen 1998; Bailey et al. 1998; Kawai et al. 2003).

The divergence time of Phaeophyceae from Schizocladiphyceae is estimated to be ca. 260 Ma in the Permian Period, based on molecular phylogeny calibrated based on the fossil records of diatoms and brown algae (i.e., *Padina* and *Julescranea*).

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