

# Rhodophyta

## RHODOPHYCEAE

The Rhodophyceae, or **red algae**, comprise the only class in the division Rhodophyta. The Rhodophyceae are probably one of the oldest groups of eukaryotic algae. The red algae are most likely directly descended from a cyanome in the Glaucophyta (see Chapter 3). It is likely that the first red alga evolved into an ecological niche that was unoccupied by cyanobacteria, the only extant photosynthetic alga that evolved oxygen. This ecological niche would have been in waters with a pH less than 5, which, for some unknown reason, cyanobacteria are not able to inhabit (Brock, 1973). Indeed, modern phylogenetic studies utilizing nucleic-acid sequencing have shown that *Cyanidium*, an alga that lives in acidic waters, is probably the oldest extant red alga (Oliveira and Bhattacharya, 2000).

The Rhodophyceae lack flagellated cells, have chlorophyll *a*, phycobiliproteins, floridean starch as a storage product, and thylakoids occurring singly in the chloroplast.

A majority of the seaweeds are red algae, and there are more Rhodophyceae (about 4000 species) than all of the other major seaweed groups combined. Although marine red algae occur at all latitudes, there is a marked shift in their abundance from the equator to colder seas. There are few species in polar and subpolar regions where brown and green algae predominate, but in temperate and tropical regions they far outnumber these groups. The average size of the plants also

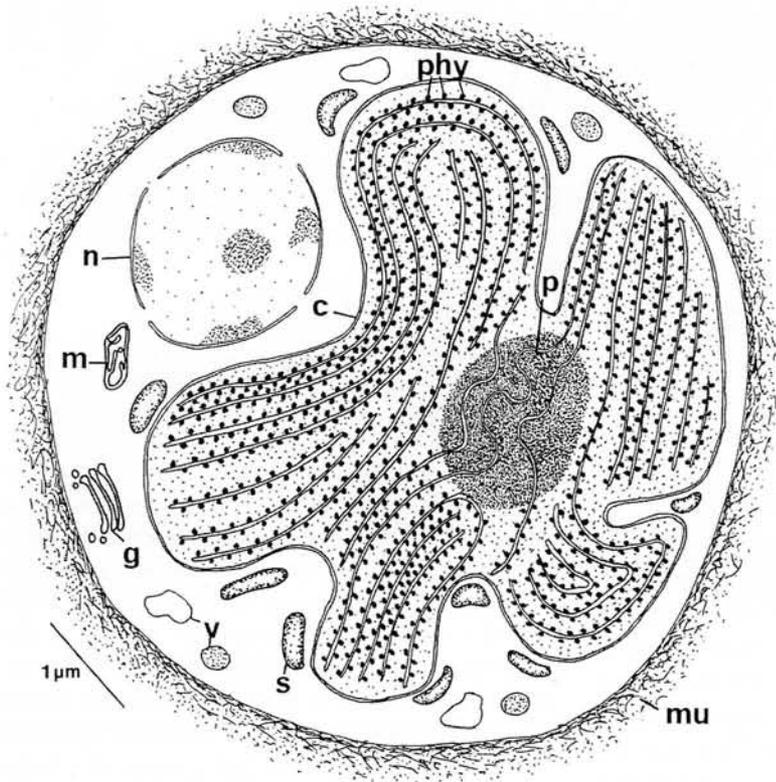
differs according to geographical region. The larger species of fleshy red algae occur in cool-temperate areas, whereas in tropical seas the Rhodophyceae (except for massive calcareous forms) are mostly small, filamentous plants. The Rhodophyceae also have the ability to live at greater depths in the ocean than do members of the other algal classes. They live at depths as great as 200 m, an ability related to the function of their accessory pigments in photosynthesis. About 200 species of Rhodophyceae are found in freshwater, where they do not reach as great a size as the red seaweeds (Skuja, 1938). The majority of freshwater red algae occur in running waters of small to mid-sized streams (Sheath and Hambrook, 1988). Few red algae occur at currents of less than  $30 \text{ cm s}^{-1}$ . This fast flow probably favors red algae because loosely attached competitors are washed out and because of a constant replenishment of nutrients and gases.

### Cell structure

The major features of a red algal cell (Fig. 4.1) are a chloroplast with one thylakoid per band and no chloroplast E.R., floridean starch grains in the cytoplasm outside the chloroplast, no flagella, pit connections between cells in filamentous genera, and a eukaryotic type of nucleus (Scott et al., 1980).

### Cell walls

Cellulose forms the microfibrillar framework in most rhodophycean cell walls, although in the



**Fig. 4.1** Semidiagrammatic drawing of a cell of *Porphyridium cruentum*. (c) Chloroplast; (g) Golgi; (m) mitochondrion; (mu) mucilage; (n) nucleus; (p) pyrenoid; (phy) phycobilisomes; (s) starch; (v) vesicle. (Adapted from Gantt and Conti, 1965.)

haploid phase of the Bangiales (*Bangia* and *Porphyra*) a  $\beta$ -1,3 linked xylan (polysaccharide composed of xylose residues) performs this function (Frei and Preston, 1964). Unicellular red algae have an amorphous matrix of sulfated polysaccharides without cellulose surrounding the cells (Arad et al., 1993). The amorphous polysaccharides or mucilages occur between the cellulose microfibrils in the rest of the red algae. The two largest groups of amorphous mucilages are the agars (Fig. 1.11) and the carrageenans (Fig. 4.15). These mucilages may constitute up to 70% of the dry weight of the cell wall. Cuticles, composed mostly of protein, can occur outside the cell wall (Craigie et al., 1992).

### Chloroplasts and storage products

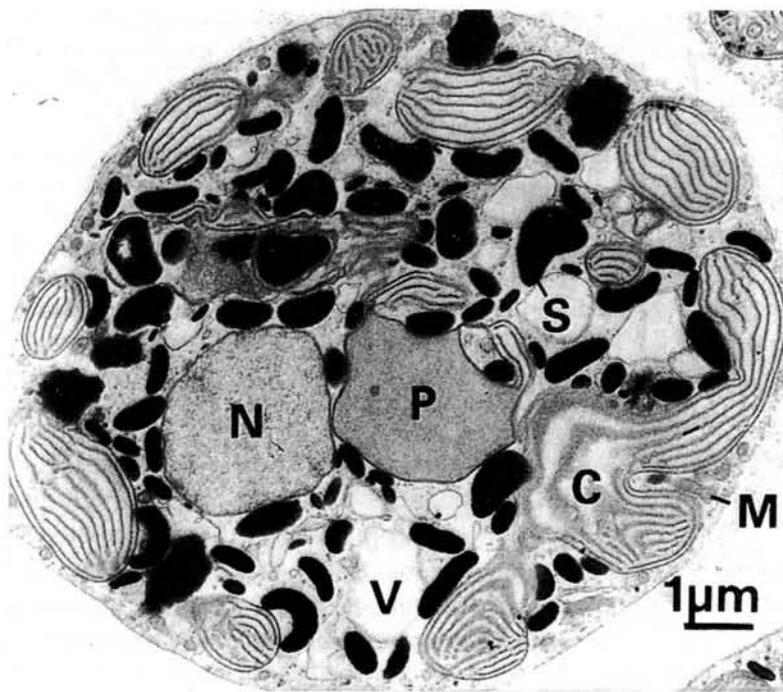
Chloroplasts are usually stellate with a central pyrenoid in the morphologically simple Rhodophyceae (Fig. 4.1), whereas in the remainder of the Rhodophyceae they are commonly discoid (Fig. 4.3). In the Rhodophyceae with apical growth, the chloroplasts usually originate from small colorless proplastids with few thylakoids in the apical

cell (Lichtlé and Giraud, 1969). Chloroplasts are surrounded by the two membranes of chloroplast envelope with no chloroplast endoplasmic reticulum present (Figs. 4.1, 4.2, 4.3). Thylakoids occur singly inside the chloroplasts. The phycobilin pigments are localized into phycobilisomes on the surface of the thylakoids, a situation similar to that in the cyanobacteria.

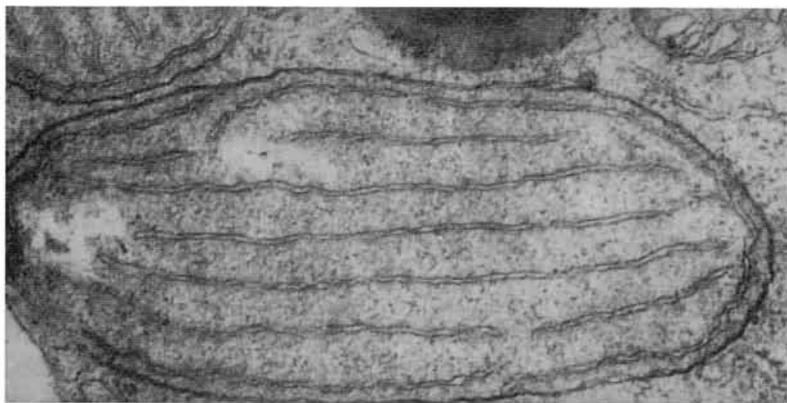
Chlorophyll *a* is in the chloroplasts. There have been erroneous reports of chlorophyll *d* occurring in the chloroplast. It has been shown that the chlorophyll *d* in these studies came from the cyanobacterium *Acaryochloris marina*, an epiphyte on red algae (Murakami et al., 2004).

The phycobiliproteins include R-phycoerythrin, allophycoerythrin, and three forms of phycoerythrin, the phycoerythrins being present in the greatest amount, giving the algae their pinkish color. B-phycoerythrin is present in the more primitive red algae and has been found in *Porphyridium* (Fig. 4.1), *Rhodorus* (Fig. 4.24 (a)), *Rhodochorton* (Fig. 4.31) and *Smithora*. R-phycoerythrin occurs in most higher red algae, and C-phycoerythrin occurs in

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**Fig. 4.2** Transmission electron micrograph of a section of a cell of *Rhodella violacea*. (C) Chloroplast; (M) mitochondrion; (N) nucleus; (P) pyrenoid; (S) starch; (V) vacuole. (From Marquardt et al., 1999.)

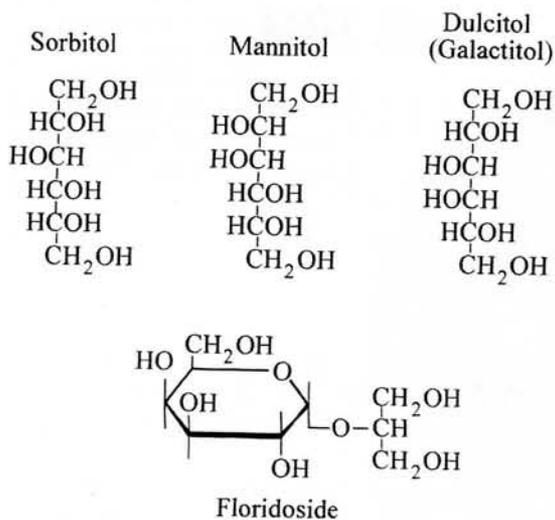


**Fig. 4.3** Chloroplast in a carpospore of *Polysiphonia*. (From Tripodi, 1974.)

*Porphyridium* (Fig. 4.1), *Porphyra* (Fig. 4.27), and *Polysiphonia* (Figs. 4.44, 4.45). The phycobiliproteins are in phycobilisomes on the surface of thylakoids (Fig. 4.1). The phycobilisomes are spherical if both phycoerythrin and phycocyanin are present. The phycobilisomes are discoid if only phycocyanin is present (Gantt, 1969).

**Complementary chromatic adaptation** occurs in the red algae. Orange and red light stimulate the production of long-wavelength absorbing phycoerythrin, while green light stimulates the formation of short-wavelength absorbing phycocyanin (Sagert and Schubert, 1995). The color will vary.

**Floridoside** (O- $\alpha$ -D-galactopyranosyl-(1,2)-glycerol) is the major product of photosynthesis in the red algae, although mannitol, sorbitol, digeneaside, and dulcitol also occur (Fig. 4.4) (Barrow et al., 1995; Karsten et al., 2003). The concentration of floridoside increases in red algal cells as the salinity of the medium increases (Reed, 1985). This change in floridoside concentration is thought to compensate, at least in part, for the changes in external osmolarity, thereby preventing water from leaving the algal cells as the salinity increases. The levels of floridoside can be as high as 10% of the tissue dry-weight in some



**Fig. 4.4** Chemical structure of low molecular polysaccharides that occur in the red algae.

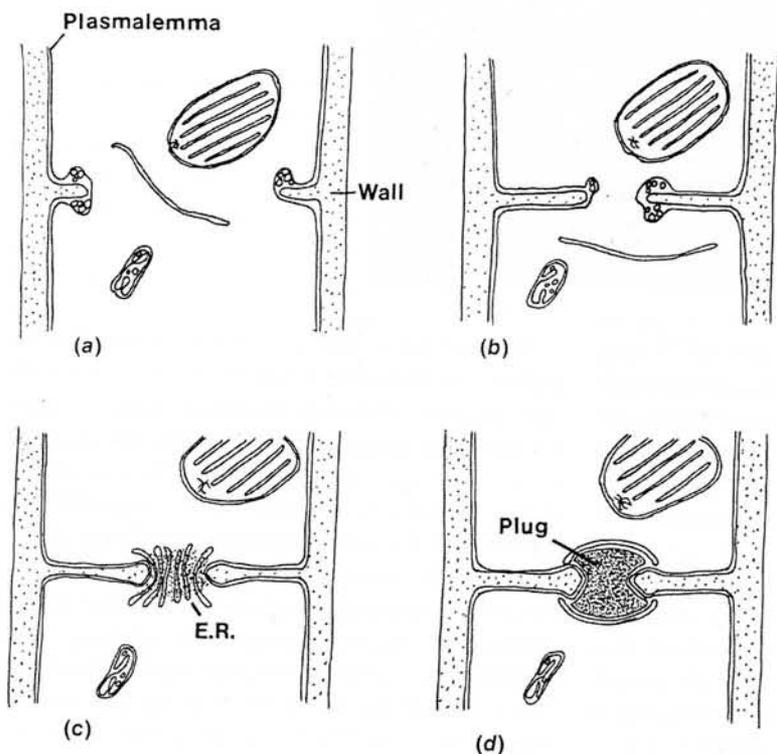
marine red-algal thalli. The first observable product of photosynthesis is phosphoglyceric acid, as is the case in higher plants. Floridoside appears after 30 seconds of illumination and after 2 hours floridoside is the major product of

photosynthesis. Floridoside apparently has the same function as sucrose, the common product of photosynthesis in green algae and higher plants.

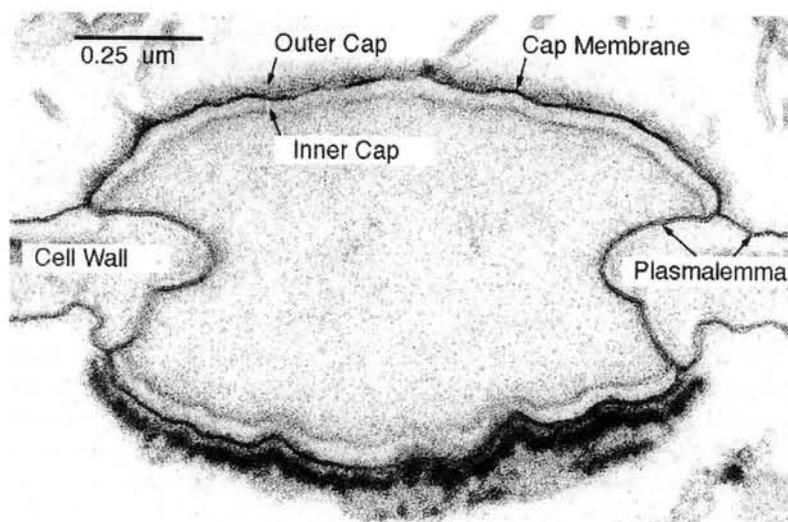
Floridean starch (Fig. 1.28) is the long-term storage product, occurring as grains in the cytoplasm outside of the chloroplast (Fig. 4.1). Floridean starch is similar to the amylopectin of higher plants, staining red-violet with iodine. In the more primitive Rhodophyceae the starch grains are clustered as a sheath around the pyrenoid of the chloroplast, whereas in the more advanced Rhodophyceae the starch grains are scattered in the cytoplasm (Hara, 1971; Lee, 1974).

### Pit connections

Pit connections occur between the cells in all of the orders except the Porphyridiales, and the haploid phase of the Bangiales. It has been pointed out that the term "pit connection" is inappropriate because the structure is neither a "pit" nor a "connection"; however, because the term has been used for so long, it is probably best to retain it. A pit connection consists of a proteinaceous plug core in between two thallus cells (Figs. 4.5, 4.6).



**Fig. 4.5** Semidiagrammatic drawing of the formation of a pit connection in a red alga. (a) The cross wall begins to furrow inward with the wall precursors found in vesicles derived from the cytoplasm; (b) the cross wall septum is complete, leaving an opening (aperture) in the center; (c) endoplasmic reticulum lies across the opening in the wall, and electron-dense material condenses in this area; (d) the pit connection is formed, consisting of a plug with the plasmalemma continuous from cell to cell. (Adapted from Ramus, 1969, 1971; Lee, 1971.)



**Fig. 4.6** A pit connection between cells of *Palmaria mollis*. The plasma membrane is continuous from cell to cell. The cap membrane is continuous with the plasma membrane. The inner and outer cap layers are on each side of the cap membrane. (From Pueschel, 1987.)

Cap membranes separate the plug core from the adjacent cytoplasm. The cap membrane is continuous with the plasma membrane, which in turn is continuous from one cell to the next. On the inside of the cap membrane can be an inner layer, while on the outside of the cap membrane can be an outer cap layer (Pueschel, 1987). The structure of the pit connection can vary. The more primitive red algae, such as *Rhodochaete* and *Compsopogon*, lack cap membranes and cap layers, with only a plug core present. It has been postulated that this represents the ancestral condition (Pueschel, 1989).

There are two types of pit connections. **Primary pit connections** are formed between two cells during cell division. **Secondary pit connections** result when two cells fuse. Both types of pit connections have the same structure (Kugrens and West, 1973). **Primary pit connections** are formed as follows (Fig. 4.5) (Ramus, 1969): soon after nuclear division, the cross wall grows inward from the lateral wall. When the cross wall is complete, there remains a hole (aperture) in the center through which the protoplasm of the two cells is continuous. A number of parallel vesicles traverse the hole, with electron-dense material condensing around the vesicles. Eventually the vesicles disappear, and the electron-dense material fills the hole. A membrane is formed around this material, producing a plug in the hole. The pit connection has been reported to contain proteins and polysaccharides (Pueschel

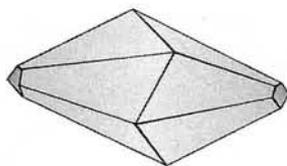
and Trick, 1991; Ramus, 1971). The pit connection may function as a site of structural strength on the thallus (Kugrens and West, 1973). In some algae the plugs of the pit connections become dislodged from between the cells of a developing gonimoblast, leaving the protoplasm continuous between the cells and allowing the passage of metabolites to the developing reproductive cells (Turner and Evans, 1978).

## Calcification

All members of the Corallinales and some of the Nemaliales (*Liagora* (Fig. 4.17 (a), (b)), *Galaxaura* (Fig. 4.34)) deposit  $\text{CaCO}_3$  extracellularly in the cell walls. Anhydrous calcium carbonate occurs in two crystalline forms, **calcite** (rhombohedral) and **aragonite** (orthorhombic) (Fig. 4.7). The two forms differ markedly in specific gravity, hardness, and solubility. The Corallinales deposit  $\text{CaCO}_3$  primarily as calcite, whereas the calcified members of the Nemaliales deposit  $\text{CaCO}_3$  primarily as aragonite. In *Liagora* (Fig. 4.17(a), (b)) (Nemaliales), the aragonite occurs as needle-like crystals in the wall, whereas in the Corallinales, the calcite occurs as massive deposits (Borowitzka et al., 1974). Calcified walls of living cells probably have a mucilaginous component that slows the loss of  $\text{Ca}^{2+}$  into the medium (Pearse, 1972). If a calcified thallus is killed, the dispersal of the calcified wall is greatly accelerated.



Aragonite



Calcite

**Fig. 4.7** The crystal structure of aragonite and calcite.

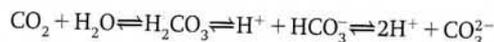
**Rhodoliths** are unattached biogenic (produced from living organisms) nodules composed at least partly of calcified red algae. A rhodolith begins as a central nucleus composed of a pebble or fragment of coral. Non-articulated coralline algae attach to the nucleus and grow. The shape of the rhodolith is determined by its environment, often being generally spherical because of frequent overturning due to water motion. Rhodoliths can reach 30 cm in diameter and be 500–800 years old. Sections of rhodoliths that reveal the banding of the coralline red algae can be used to determine the environment at the time of wall deposition (Halfar et al., 2000).

Skeletons of coralline algae are formed with little biological control, by impregnation of cell walls with magnesium and calcium at a ratio similar to the Mg/Ca in the water. Therefore, the Mg/Ca ratio in the cell walls reflects the Mg/Ca ratio in the water. Analysis of the Mg/Ca ratio in cell walls of fossil coralline red algae since the beginning of the Paleozoic Era have shown that there have been times of “aragonite seas” with relatively high Mg in seawater, resulting in coralline algae with cells walls contain high-Mg calcite and aragonite, and times of “calcite seas” with relatively low-Mg seawater, resulting in coralline algae with low-Mg calcite (Fig. 4.8) (Stanley et al., 2002). The differences in the Mg/Ca ratios in seawater are due to changes in the mid-ocean spreading rates.

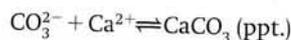
The coralline algae thrive in rock pools and on rocky shores exposed to very strong wave action and swift tidal currents. The red algae that have the highest rates of calcification also have the highest rates of photosynthesis and are usually found in waters less than 20 m deep (Goreau, 1963). Calcification of the thallus occurs about two to three times more rapidly in the light than in the dark, although significant calcification does occur in the dark (Okazaki et al., 1970). The above observations have led to the theory that

calcification may be linked to photosynthesis (Pearse, 1972). The most quoted theory on calcification is that calcium salts are precipitated from seawater by the alkalinity brought about by the extraction of carbon dioxide during photosynthesis, calcium carbonate being less soluble in alkaline waters than acid. The obvious and often mentioned drawback to this theory is that because all algae carry out photosynthesis, it is difficult to understand why they do not all calcify. Also the continued calcification of corallines in the dark is another argument against this theory.

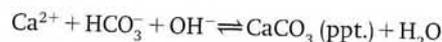
Seawater is more or less saturated with respect to calcium carbonate, and the addition of either calcium or carbonate will cause the carbonate to precipitate. The concentration of  $\text{CO}_3^{2-}$  is related through a complex series of equilibria (Digby, 1977a,b):



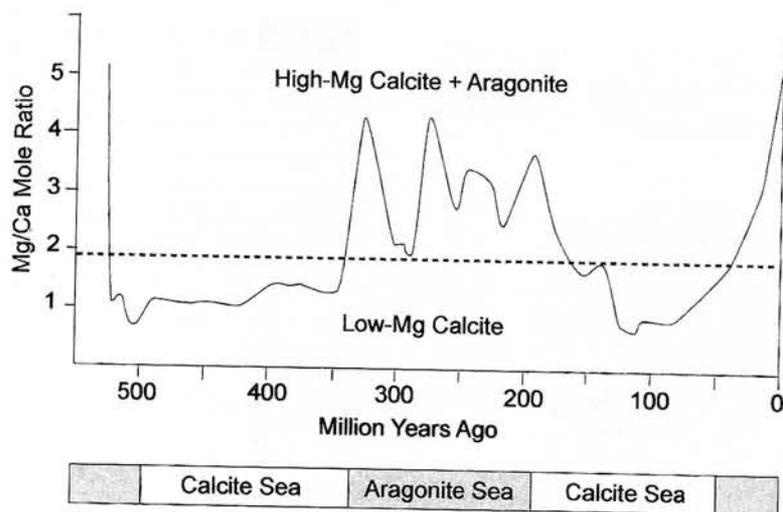
then



The addition of acid will drive the reactions to the left and cause carbonate to dissolve, whereas the addition of base will drive the reactions to the right and form more carbonate. At the pH of seawater (8.4), almost all of the  $\text{CO}_2$  in the water is in the form of bicarbonate ion,  $\text{HCO}_3^-$ . The addition of one equivalent of hydroxyl ions to seawater saturated with respect to calcium carbonate will precipitate one equivalent of calcium carbonate:

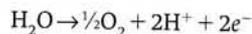


The fact that seawater is nearly saturated with calcium carbonate was demonstrated with seawater from the coast of Maine by Digby (1977a). By raising the pH of this seawater to 9.6, he caused precipitation of carbonates. Calcium carbonate precipitated first, being less soluble, followed by carbonate richer in magnesium.

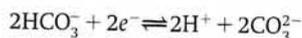


**Fig. 4.8** Effects of the Mg/Ca ratio of seawater on the mineralogy of carbonate deposition in coralline red algae. High Mg/Ca ratio in seawater results in the deposition of aragonite and calcite high in Mg, resulting in "aragonite seas." Low Mg/Ca ratio in seawater results in the deposition of calcite low in Mg and "calcite seas." (Modified from Stanley et al., 2002.)

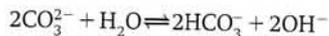
Digby (1977b) proposed a theory of calcification of red algae based on raising the pH of the seawater immediately outside the cells, causing precipitation of carbonates as outlined above. The first process is the normal photosynthetic splitting of water:



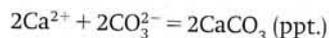
The oxygen then diffuses out of the cell. As mentioned above, in the sea most of the carbon dioxide is in the form of bicarbonate ions; these ions diffuse into the cells and receive the electrons freed initially by photosynthesis. The bicarbonate ions are then converted into carbonate ions and hydrogen according to the following reaction:



The carbonate ions diffuse out of the cell where they partially dissociate, forming bicarbonate and hydroxyl ions and thereby raising the pH:



When saturation with regard to calcium and carbonate is reached by a rise in pH outside the cells, calcium carbonate precipitates on the walls:



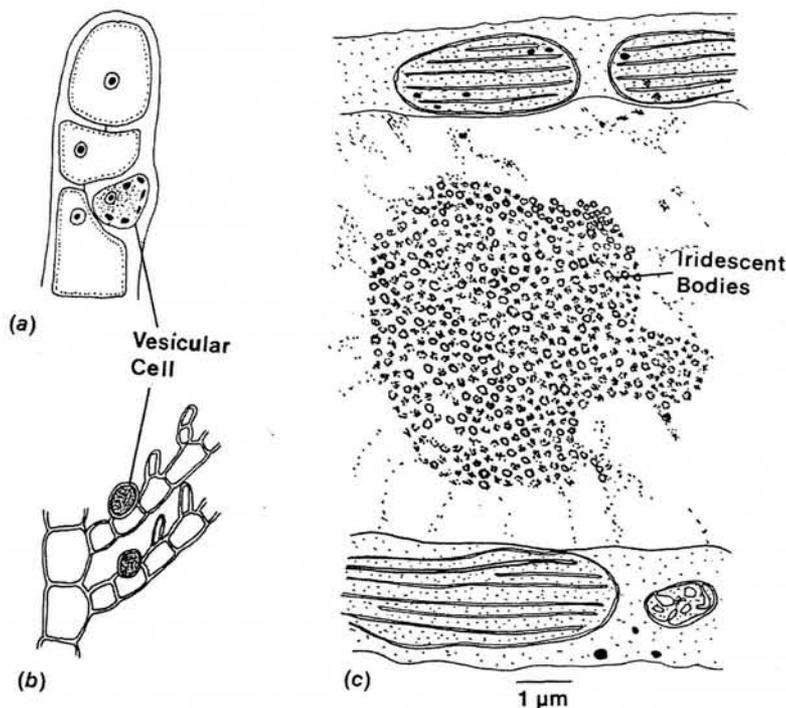
Continued precipitation of  $\text{CaCO}_3$  results in the calcified wall of the Rhodophyceae. Although the above theory explains the mechanism of calcification, it does not explain why calcification is specific to certain red algae.

It has been theorized that calcification of red algal thalli evolved as a protection against grazing by organisms such as limpets, although it has also been pointed out that grazing is beneficial to the coralline algae in that the grazers remove epiphytes from the red algal thallus (Pueschel and Miller, 1996).

## Secretory cells

Secretory cells (vesicular cells) occur in some Rhodophyceae (Fig. 4.9(a), (b)). These cells are colorless at maturity and commonly have a large central vacuole. The secretory cells in *Bonnemaisonia* are prominent and associated with high concentrations of iodine (Fig. 4.9(a)). The concentration of iodine can be high enough to produce a blue color in herbarium paper with starch as a filler (the chemical test for starch). Secretory cells are vestigial, lacking the large vacuole with its refractile contents, when these algae are grown in a medium without bromine (Wolk, 1968). Bromine can also occur as granular deposits in mucilage, such as in the thallus medulla of *Thysanocladia densa* (Pallaghy et al., 1983) or in the cuticle of *Polysiphonia nigrescens* (Peders'en et al., 1981).

Other types of secretory cells not associated with the accumulation of halogens occur. The cells are often called secretory cells, even though they are apparently not involved in secretion. In *Antithamnion* (Figs. 4.9(b), 4.10(a)), these cells



**Fig. 4.9** (a) Vesicular cell of the *Trilliella* stage of *Bonnemaisonia*. (b) Vesicular cells of *Antithamnion plumula*. (c) Iridescent bodies in the vacuole of a cell of *Chondria caerulescens*. ((a) after Kylin, 1956; (b) after Kylin, 1930; (c) adapted from Feldmann, 1970a.)

have a large central vacuole containing sulfated acidic polysaccharide (Young and West, 1979). In *Opuntia californica*, there are "gland cells" with a large vacuole containing a homogeneous proteinaceous material (Young, 1979) (Fig. 4.10(b)). These "secretory cells" and "gland cells" may have compounds that act as deterrents to grazing, or they may accumulate special reserves for metabolic use.

## Iridescence

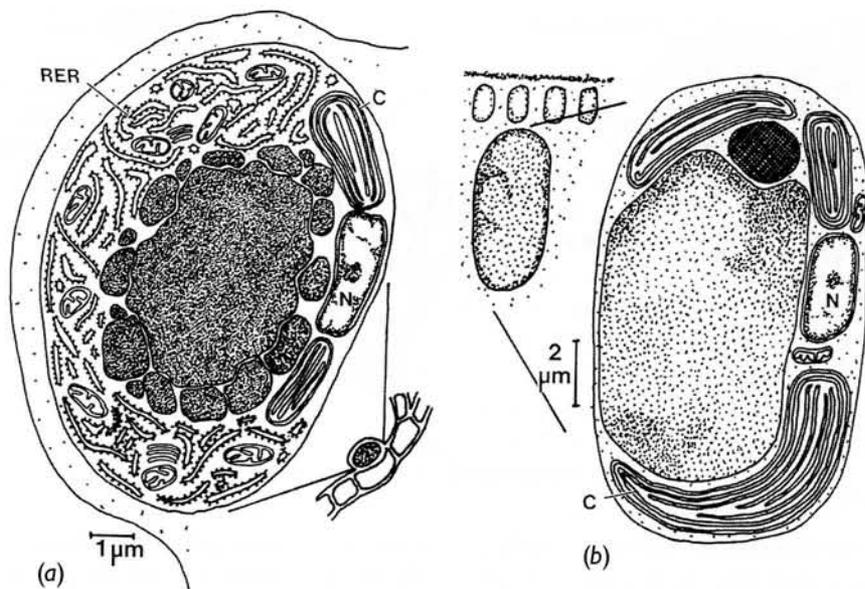
The thalli of some Rhodophyceae show a marked blue or green iridescence when observed in reflected light. **Iridescence** is solely a physical interference and is not related to any light-producing phenomena such as phosphorescence or bioluminescence (Gerwick and Lang, 1977). It results from the interference of light waves reflected from the surfaces of very thin multiple laminations separated by equally thin or thinner layers of material with a contrasting refractive index; the layers are uniform and produced by periodic secretion and deposition. Iridescence in the Rhodophyceae has been attributed to

different causes by different investigators. Feldmann (1970a,b) found iridescent bodies in *Chondria* (Fig. 4.9(c)) and *Gastroclonium*, whereas Gerwick and Lang (1977) attributed the iridescence in *Iridaea* to a multilayer cuticle.

## Epiphytes and parasites

Rhodophycean organisms range from autotrophic, independent plants to complete heterotrophic parasites. The spectrum includes non-obligate epiphytes (in the *Acrochaetium*-*Rhodochorton* complex), obligate epiphytes (*Polysiphonia lanosa* on *Ascophyllum* (Fig. 4.11)), semi parasites that have some photosynthetic pigments (*Choreocolax* (Fig. 4.13), *Gonimophyllum*), and parasites with no coloration (*Harveyella*, *Holmsella*).

The association between the obligate epiphyte red alga *P. lanosa* and its brown alga host *Ascophyllum* has been well studied. After the spore of *P. lanosa* germinates on the host, the red alga sends down a rhizoid that digests its way into the host tissue by means of enzymatic digestion of the host tissues. The enzymes are discharged from vesicles at the tip of the rhizoid. Once the rhizoid has

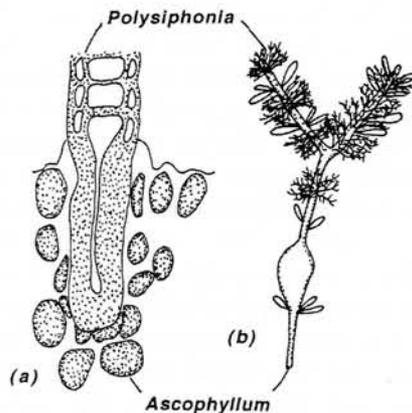


**Fig. 4.10** (a) Semidiagrammatic drawing of the fine structure of a vesicular cell of *Antithamnion*. The cell has a large central vacuole surrounded by protoplasm containing rough endoplasmic reticulum (RER), mitochondria, chloroplasts (C), and a nucleus (N). (b) Semidiagrammatic drawing of the fine structure of a gland cell of *Opuntiella californica*. The cell has a large central vacuole containing chloroplasts (C), a nucleus (N), and mitochondria. ((a) after Young and West, 1979; (b) after Young, 1979.)

established itself, intrusive cells form the basal parietal cells of the thallus (Fig. 4.11) (Rawlence, 1972). Although *P. lanosa* is an obligate epiphyte, there is no transfer of metabolites from the host to the epiphyte, the epiphyte manufacturing all of its own requirements through photosynthesis (Harlin and Craigie, 1975; Turner and Evans, 1978).

Parasitic red algae can be either adelphoparasites (*adelpho* = brother) or alloparasites (*allo* = other). **Adelphoparasites** are closely related to, or belong to the same family as their hosts and constitute 90% of parasitic red algae (Goff et al., 1996). **Alloparasites** are not closely related to their hosts. The parasitic habit apparently has been adapted more easily when the host is closely related to the parasite (adelphoparasites) than when it is not (alloparasites), partially because it is easier for the parasite to establish secondary pit connections with the host (and therefore transfer nutrients) if the host and parasite are related.

*Choreocolax polysiphoniae* is an example of a rhodophycean parasite (Fig. 4.12). The alga is a complete parasite and is interesting in that it is parasitic on *Polysiphonia fastigata*, which is itself epiphytic on *Ascophyllum* (Fig. 4.11). Because *Choreocolax* is in the Gigartinales, and *Polysiphonia* is in the Ceramiales, this is a case of alloparasitism. *Choreocolax* consists of a more or less hemispherical white external portion made up of subdichotomously branched filaments enclosed and surrounded by gelatinous matter, and a mass of haustorial cells growing inside the host (Sturch,

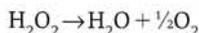


**Fig. 4.11** (a) The rhizoid of *Polysiphonia lanosa* penetrating tissue of *Ascophyllum nodosum*. (b) *Polysiphonia* epiphytic on *Ascophyllum*. ((a) after Rawlence, 1972.)

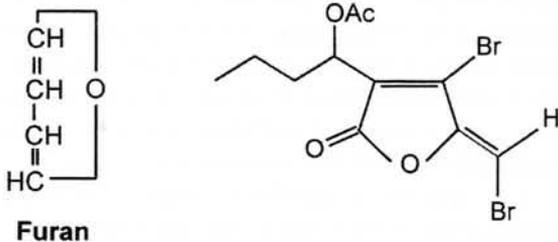
they are sessile and are restricted to the photic zone where conditions for fouling organisms are optimal. Epiphytes can significantly harm seaweeds by reducing the light, resulting in decreased photosynthesis and growth, by increasing drag and hence their susceptibility to breakage or being torn from the substrate, and by decreasing the reproductive output of the host.

Some red seaweeds secrete compounds that kill or retard the growth of epiphytes growing on them. *Delisea* secretes halogenated furones (Fig. 4.14) that affect the growth of epiphytes and keep the thallus clean (de Nys et al., 1995).

*Gracilaria conferta* (Fig. 4.42) has a defense mechanism that limits bacterial infection of the red alga. Invasive bacteria secrete agarases that break down the cell-wall agar of *Gracilaria* into shorter neogaroehexaose oligosaccharides. *Gracilaria* cells respond to nanomolar concentrations of the oligosaccharides by increasing respiration and producing active oxygen species such as hydrogen peroxide ( $H_2O_2$ ) and hydroxyl radicals ( $OH^-$ ) (Potin et al., 1999). The hydrogen peroxide is degraded to water and molecular oxygen:



Molecular oxygen is toxic and results in the elimination of 90% of the epiphytes within 15 minutes under experimental conditions (Weinberger and Friedlander, 2000). *Gracilaria conferta* has also been shown to release activated oxygen each morning after exposure to light. This short time release of activated oxygen, in addition to the defense related release of hydrogen peroxide,



**Fig. 4.14** Left: The chemical structure of furan, the basic building block of the furanones. Right: One of the halogenated furanones released by the red alga *Delisea pulchra*. Halogenated furanones inhibit the growth of epiphytes on this red alga.

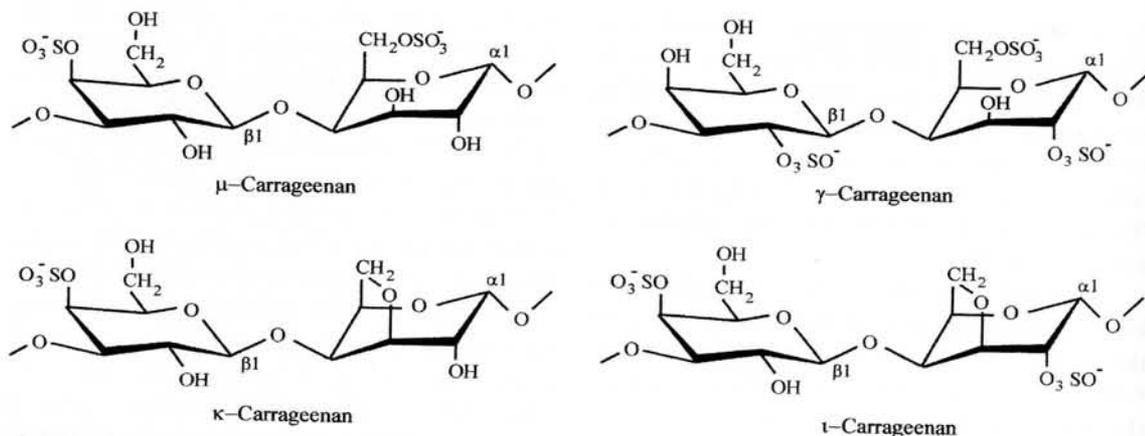
resulted in the selection of epiphytic bacteria that are relatively insensitive to these chemicals. *Corynebacterium-Arthrobacter* 1 bacteria were relatively resistant to hydrogen peroxide whereas *Vibrio* 1 and *Flavobacterium* 7 bacteria were sensitive (Bouarab et al., 1999; Potin, et al., 1999).

**Volatile halocarbons**, consisting of brominated, chlorinated or iodinated hydrocarbons, are also produced on exposure of *Gracilaria* cells to the oligosaccharide. These volatile hydrocarbons are electrophilic, attacking a variety of organic compounds and acting as natural **biocides** (pesticides). "White tip" disease of *Gracilaria* is due to the release of these biocides in response to bacterial infection. The bleaching of the tips of the alga is killing some of the algal cells while containing the pathogens at the site of attack (Largo et al., 1995).

## Commercial utilization of red algal mucilages

The two most important polysaccharides derived from the Rhodophyceae are agar and carrageenan. **Agar** is defined pharmaceutically as a phycocolloid of red algal origin that is insoluble in cold water but readily soluble in hot water; a 1.5% solution is clear and forms a solid and elastic gel on cooling to 32 to 39 °C, not dissolving again at a temperature below 85 °C. Agar is composed of two polysaccharides, agarose (Fig. 1.11) and agaropectin (Lahaye, 2001).

Agar is obtained commercially from species of *Gelidium* (Figs. 4.40, 4.41) and *Pterocladia* as well as from various other algae, such as *Acanthopeltis*, *Ahnfeltia*, and *Gracilaria* (Fig. 4.42) (Melo, 1998; Mollet et al., 1998). These algae are often loosely referred to as **agarophytes**. Commercial production of agar was a world monopoly of the Japanese for many years, and even in 1939 Japan was still the major producer. Wartime demands in areas deprived of Japanese agar led to the development of agar industries in many of the Allied countries, some of which have continued and prospered while others have declined or disappeared. The agarophytes are collected by diving, dragging, or raking them offshore at low tide. In the traditional processing procedure the



**Fig. 4.15** The chemical structures of the different types of carrageenans that occur in the red algae.

plants are then cleaned and bleached in the sun, with several washings in freshwater used to facilitate bleaching. The material is boiled for several hours, and the extract is acidified. This extract is then frozen and thawed. On thawing, water flows from the agar, carrying impurities with it. The agar that remains is dried and marketed as flakes or cakes. The more modern method extracts the agar under pressure in autoclaves. The agar is decolorized and deodorized with activated charcoal, filtered under pressure, and evaporated under reduced pressure. Further purification by freezing is then undertaken.

The greatest use of agar is in association with food preparation and technology, and in the pharmaceutical industry. It is used for gelling and thickening purposes, particularly in the canning of fish and meat, reducing the undesirable effects of the can and providing some protection against shaking of the product in transit. It is also used in the manufacture of processed cheese, mayonnaise, puddings, creams, and jellies. Pharmaceutically agar is used as a laxative, but more frequently it serves as an inert carrier for drug products where slow release of the drug is required, as a stabilizer for emulsions, and as a constituent of cosmetic skin preparations, ointments, and lotions. The use of agar as a stiffening agent for growth media in bacteriology and mycology, which was its main use almost a century ago, is still responsible for a very considerable part of the demand.

Carrageenan (Fig. 4.15) is a phycocolloid similar to agar but with a higher ash content and requiring higher concentrations to form gels. It is composed of varying amounts of the principal components,  $\kappa$ -carrageenan and  $\lambda$ -carrageenans, both negatively charged high-molecular-weight polymers (Chiovitti et al., 1995; Therkelsen, 1993).  $\kappa$ -Carrageenan is distributed throughout the wall while  $\lambda$ -carrageenan is localized to the cuticle (Vreeland et al., 1992).  $\kappa$ -carrageenan precipitates selectively from a cold, dilute solution in the presence of potassium ions. It forms a gel when heated and cooled with potassium ions and is therefore the gelling component.  $\lambda$ -Carrageenan is the non-gelling component and is not precipitated or gelled by potassium.  $\lambda$ -Carrageenan contains galactose-2,6-disulfate, whereas  $\kappa$ -carrageenan contains 3,6-anhydro-D-galactose. It has been shown in *Chondrus crispus* and *Gigartina stellata* that the proportion of  $\kappa$ - and  $\lambda$ -carrageenan in the cell wall varies according to the ploidy of the plant. In the tetrasporophyte the amount of  $\lambda$ -carrageenan present is high as compared with the amount of  $\kappa$ -carrageenan, whereas just the opposite is true in the gametophyte (Chen et al., 1973). Such results may prove valuable in determining the ploidy of Rhodophyceae that have unknown life cycles.

Carrageenan is usually obtained from wild populations of Irish moss, the name for a mixture of *Chondrus crispus* and the various species of *Gigartina*, particularly *G. stellata*. In the Philippines, *Euclima*, and in Vietnam and India, *Kappophycus* (Fig. 4.16) are extensively cultivated as a source of carrageenan (Reddy et al., 2003). Commercial extraction is similar to that for agar although



**Fig. 4.16** Cultivation of the carrageenan-containing *Kappophycus alvarezii* in an offshore area (left) and a shrimp pond (right) in Vietnam. (From Ohno et al., 1996.)



carrageenan cannot be purified by freezing. The dried alga is washed with freshwater to reduce the salt content and then boiled with 2 to 4 parts of alga to 100 parts of water. The soluble carrageenan is separated from the insoluble residue in a centrifuge. Following filtration and some evaporation under vacuum, the carrageenan is dried on a rotary drier.

Carrageenans are used extensively for many of the same purposes as agar; however, because of their lower gel strength, carrageenans are used less for stiffening purposes than is agar, although for stabilization of emulsions in paints, cosmetics, and other pharmaceutical preparations carrageenans are preferred to agar. Also, for the stiffening of milk and dairy products, such as ice cream, carrageenans have supplanted agar completely in recent years, and it is in this area that demands for these products are the greatest. One particular use is for instant puddings, sauces, and creams, made possible by the gelling action, which does not require refrigeration.

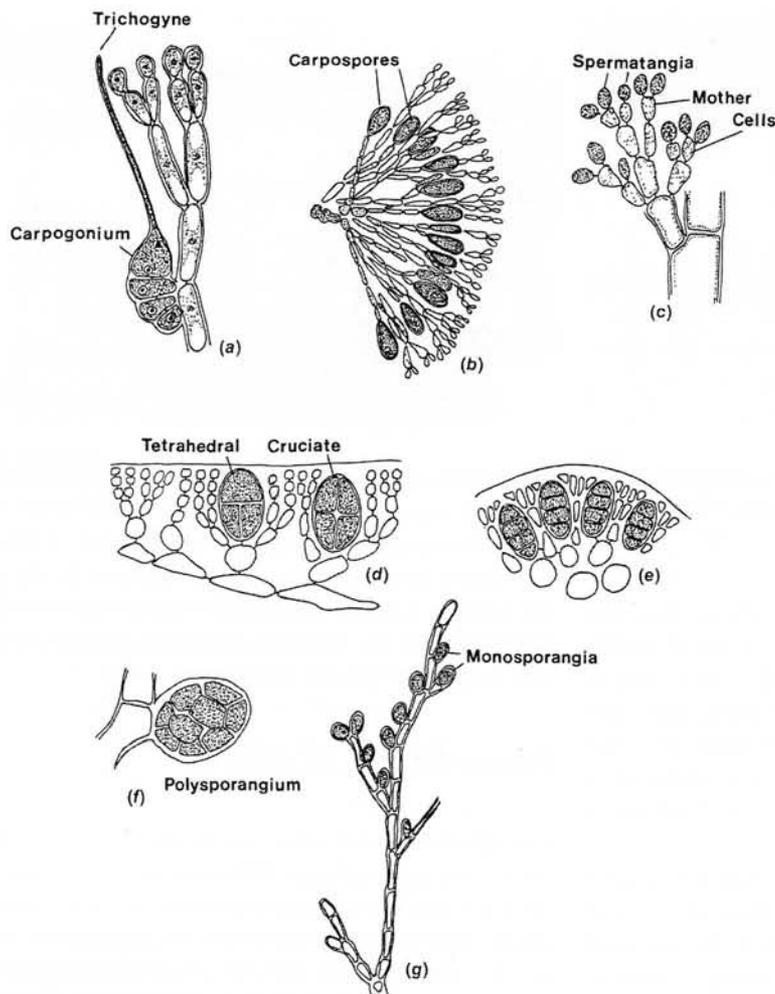
Carrageenans inhibit human immunodeficiency virus (HIV) replication and reverse transcriptionase *in vitro* (in the test tube) (Bourgougnon et al., 1996). Replication of the HIV virus depends on interaction of a glycoprotein on the HIV virus envelope with a receptor on the target cells in the human body. The sulfated carrageenans prevent attachment of the HIV virus to the target cells. This occurs by the stronger negative R-O-SO<sub>3</sub><sup>-</sup> groups on

the carrageenan binding to a loop on the HIV molecule. A carrageenan-based vaginal microbicide called Carraguard<sup>®</sup> has been shown to block HIV and other sexually transmitted diseases *in vitro*. Carraguard has entered clinical trials involving 600 non-pregnant, HIV-negative women in South Africa and Botswana (Spieler, 2002; Smit, 2004).

## Reproductive structures

The Rhodophyceae have no flagellated cells or cells with any vestigial structure of flagellation, such as basal bodies. In sexual reproduction, **spermatia** are produced which are carried passively by water currents to the female organ, the **carpogonium** (Figs. 4.17(a), 4.18). The fertilized carpogonium produces **gonimoblast filaments** that form **carposporangia** and diploid **carpospores** (Fig. 4.17(b)). The carpospores produce the diploid **tetrasporophyte** which subsequently gives rise to haploid **tetraspores**. Advanced red algae form chiefly tetrahedral tetrasporangia (Fig. 4.17(d)) with large spores, whereas less advanced groups generally form cruciate or zonate tetrasporangia (Fig. 4.17(d), (e)) with smaller spores (Ngan and Price, 1979). Tetraspores are generally larger than carpospores. The tetraspores complete the life cycle by germinating to form the gametophyte. Although this is the general life cycle of most Rhodophyceae, there are a number of modifications of it.

The postfertilization events vary from one order to another. The more advanced orders have **auxiliary cells** with which the fertilized



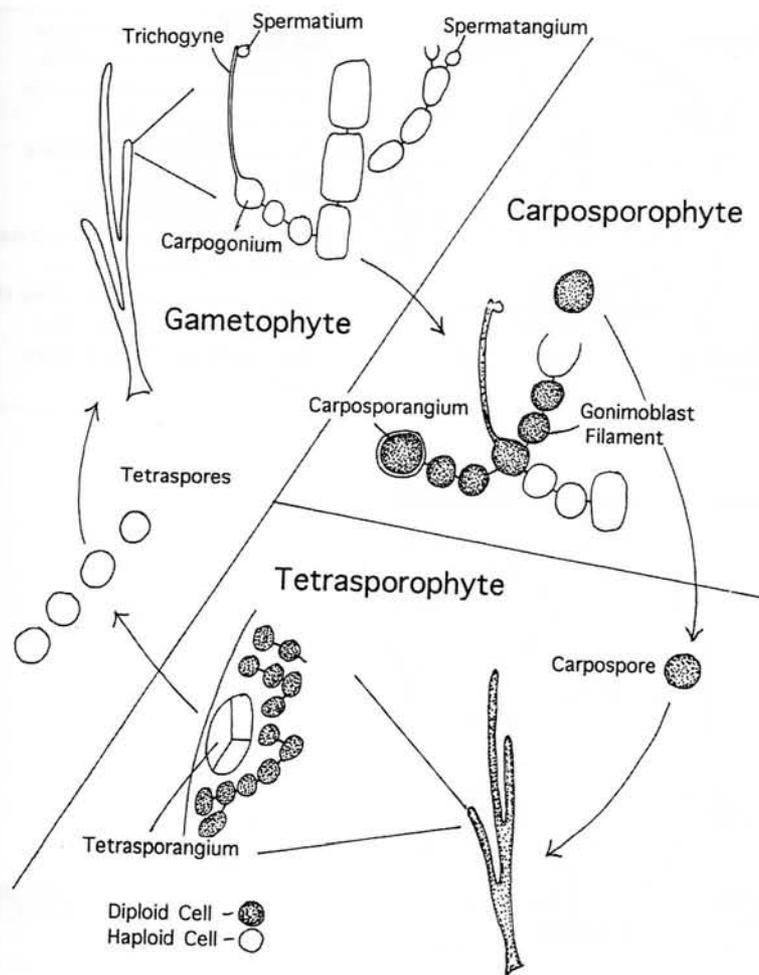
**Fig. 4.17** (a) A filament of *Liagora viscida* with a carpogonial branch. (b) Gonimoblast filaments of *L. viscida* with carpospores. (c) A spermangial branch of *Acrochaetium corymbiferum* with spermangia and spermangial mother cells. (d) Tetrahedral and cruciate tetrasporangia of *Nematostoma laingii*. (e) Zonate tetrasporangia of *Hypnea musciformis*. (f) Polysporangium of *Pleonosporium vancouverianum*. (g) Monosporangia of *Kylinia rhipidandra*. ((a), (b), (c), (e) after Kylin, 1930; (f) after Kylin, 1924; (g) after Kylin, 1928.)

carpegonium fuses to form a multinucleate fusion cell. Papenfuss (1966) recognizes two types of auxiliary cells, nutritive and generative. **Nutritive auxiliary cells** provide nutrients for the developing carposporophyte, whereas **generative auxiliary cells** give rise to gonimoblast filaments (Figs. 4.18, 4.33, 4.44). The diploid tissue formed from the fertilized carpegonium forms the gonimoblast filaments. The gonimoblast filaments produce terminal carposporangia, which in turn form the carpospores. The carposporangia enlarge considerably during their maturation because of the development of the chloroplasts and the vesicles containing wall precursors. The pit connection between the carposporangium and the gonimoblast breaks before release of the carpospore. Also during the development of the goni-

moblast filaments, the pit connections between the older gonimoblast cells usually dissolve (Kugrens and West, 1972a, 1973, 1974).

### Carpogonium

The female organ, or carpegonium, consists of a dilated basal portion and a usually narrow gelatinous elongate tip, the trichogyne, which receives the male cells (Figs. 4.6(a), 4.10). Usually there are two nuclei in a carpegonium, one in the trichogyne, which degenerates soon after the carpegonium matures, and one in the basal part of the carpegonium, which functions as the female gamete nucleus. In most Rhodophyceae the carpegonium terminates a short, often branched, three- to four-celled lateral called the carpogonial branch. The cell from which the carpogonial



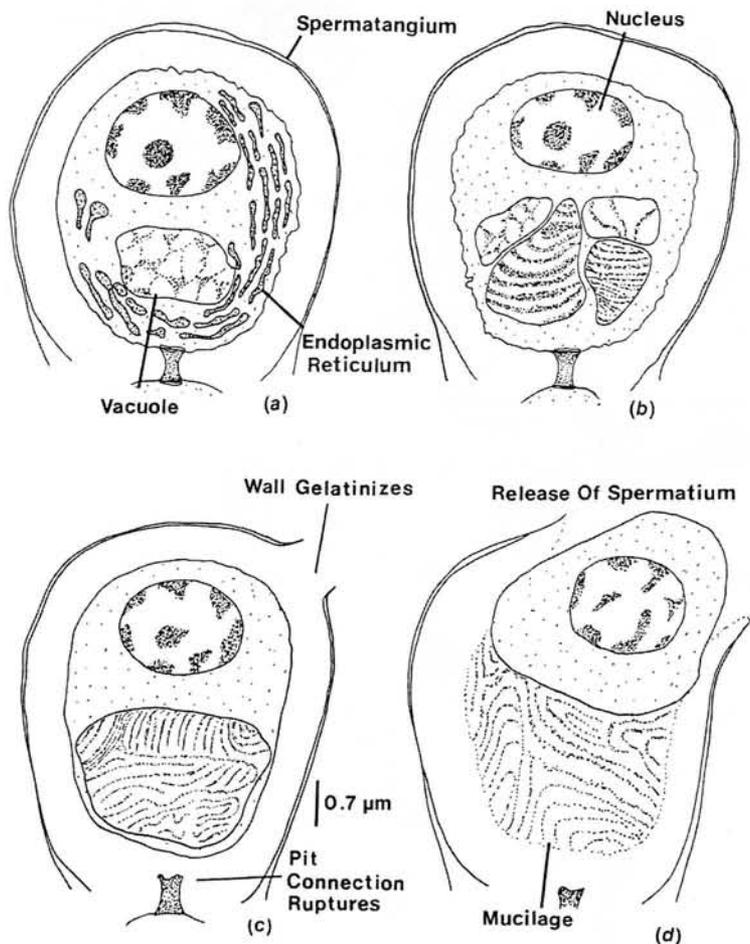
**Fig. 4.18** Simplified life cycle of a typical red alga.

branch arises is the **supporting cell**. The carpogonium and carpogonial branch are commonly colorless, although in some Nemaliales this is not true.

### Spermatium

The spermata of the Rhodophyceae are spherical or oblong cells produced in **spermatangia**, a single spermatium being formed in a spermatangium and then released, leaving the empty sporangium (Fig. 4.19). The spermatangia (Fig. 4.22) are formed on spermatangial mother cells (Fig. 4.17(c)). The young spermatangia frequently have a pronounced polar orientation, with the nucleus in the apical portion and one or more vacuoles in the basal portion (Scott and Dixon, 1973a). As the spermatangium ages, vacuoles form in the basal area. These vacuoles contain fibrous material (probably mucopolysaccharides)

and make up half the volume of the spermatangium. Subsequently the vacuoles fuse to form one large vacuole. The spermatium is released by the gelatinization of the spermatangial wall near the apex and the concurrent release of the fibrous material in the basal vacuole. The fibrous material presumably swells and pushes the spermatium out of the spermatangium (Fig. 4.19). The fibrous material is sticky, and some of it adheres to the spermatium, thereby facilitating attachment to the trichogyne (Fig. 4.22(c)). During the development of the spermatium the pit connection with the spermatium mother cell is severed. The mature spermatium is uninucleate, and wall-less, but surrounded by mucilage, and may (Simon-Bichard-Bréaud, 1971; Peyrière, 1971) or may not (Kugrens and West, 1972a; Kugrens, 1974) contain functional chloroplasts.



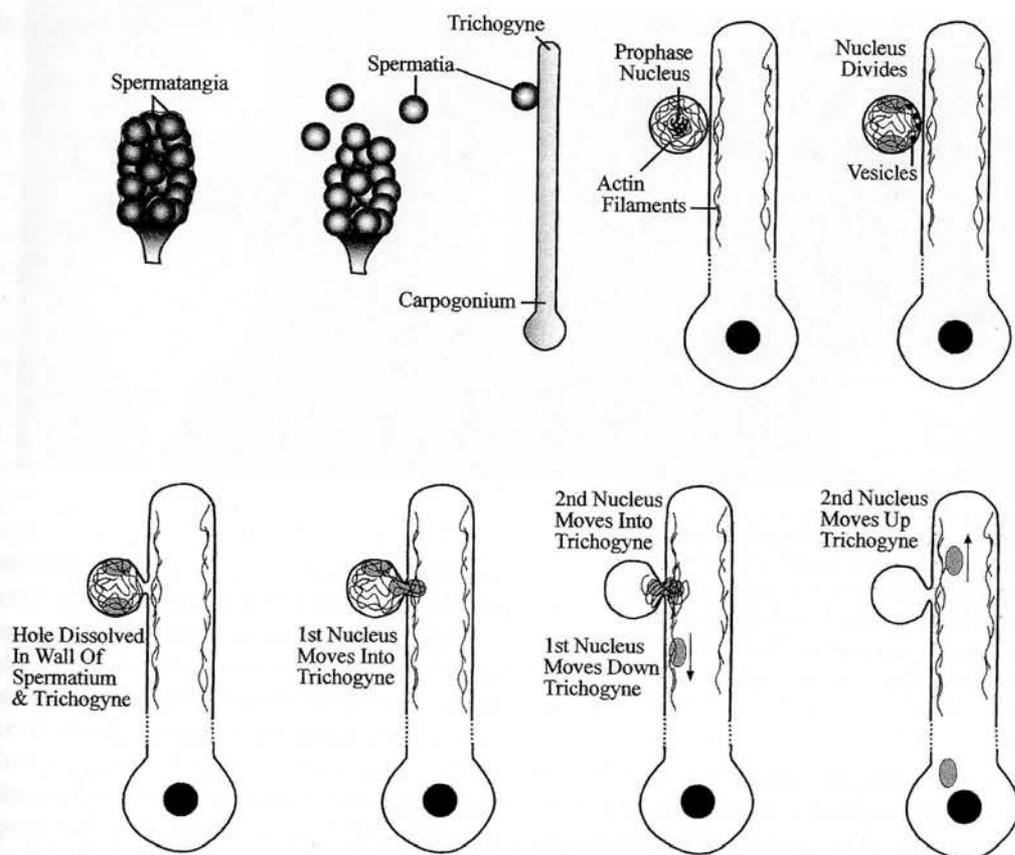
**Fig. 4.19** A semidiagrammatic drawing of the formation of the spermatium in the Rhodophyceae. (a) Young spermatium. (b) Formation of vacuoles containing fibrous material. (c) Fusion of vacuoles, breaking of the pit connection, and gelatinization of the wall of the spermatangium. (d) Extrusion of mucilage and release of the spermatium. (Adapted from Scott and Dixon, 1973a; Kugrens, 1974.)

### Fertilization

The spermatium usually is carried passively by water currents to the trichogyne of the carpogonium, although some spermata can glide in a manner similar to the gliding in *Porphyridium*. Actin filaments in the spermatium and carpogonium are involved in the subsequent steps (Fig. 4.20) (Kim and Kim, 1999; Pickett-Heaps et al., 2001). The wall of the spermatium and that of the carpogonium dissolve, the male nucleus divides, and the male nuclei move into the carpogonium. Fusion of one male nucleus and the carpogonial nucleus occurs in the basal portion of the carpogonium. Fertilization stimulates the production of polyamine spermine (Fig. 4.21) which steers the carpogonial branch toward the production of carpospores (Sacramento et al., 2004). The trichogyne will usually continue to grow until contact is made with a spermatium. After fertilization has

occurred, the trichogyne becomes separated at its base from the rest of the carpogonium by the progressive thickening of the cell wall.

There is a relatively low statistical probability that the non-motile spermata will be carried to receptive trichogynes of carpogonia. Some species have appendages on the spermata that extend the reach of the spermata five- to tenfold resulting in a better chance of attaching to a receptive carpogonium. The appendages are initially contained within vesicles within the spermatia and unfold when the spermata are released (Fig. 4.22). The appendages increase the surface area of the spermatium more than 30-fold, increasing the likelihood of interaction with a trichogyne of a carpogonium. Moieties of the sugar mannose cover the surface of the appendages. The surface of the trichogyne is covered with the lectin concanavalin A which binds the mannose



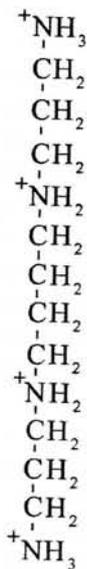
**Fig. 4.20** The behavior of the spermatium and its contents during fertilization in a typical red alga. (Modified from Wilson et al., 2003.)

moieties on the spermatangial appendages (Mine et al., 2003).

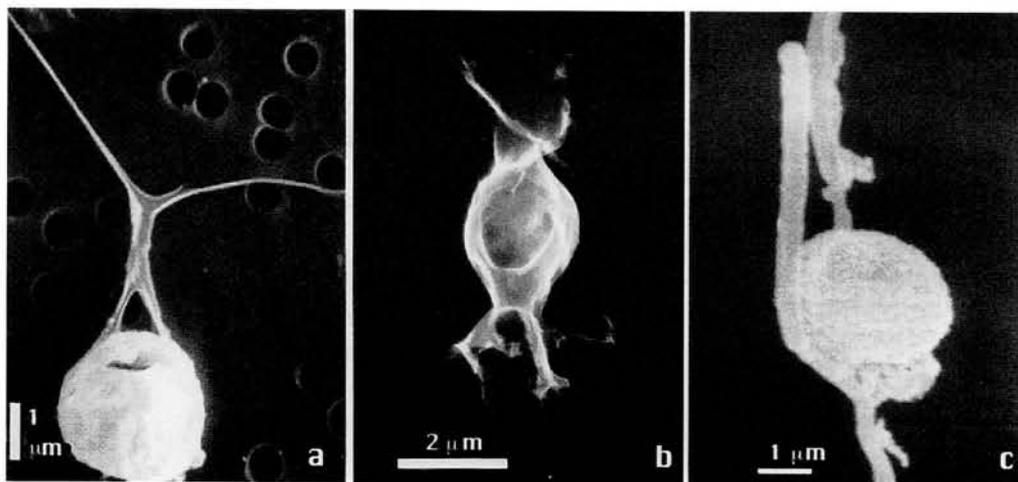
### Meiosporangia and meiospores

Tetrasporangia, polysporangia, and bisporangia formed on diploid plants are generally regarded as being the seat of meiosis although there are exceptions to this. The **tetrasporangia** (Figs. 4.17(e), 4.18) form four tetraspores either in a row (zonate), crosswise (cruciate), or most commonly in a tetrad (tetrahedral). In the formation of tetraspores a wall is laid down inside the tetrasporangia by the protoplast, which has prominent dictyosomes (each dictyosome associated with a mitochondrion as is common in the Rhodophyceae; Kugrens and West, 1972b; Scott and Dixon, 1973b). The tetraspores are not joined by pit connections.

### Spermine



**Fig. 4.21** The chemical structure of spermine.



**Fig. 4.22** Examples of spermatangial appendages. (a) Appendage of *Antithamnion nipponicum*. (b) Fimbriate cone-shaped appendages at each end of *Aglaothamnion neglectum*. (c) Fibrous strands attached to spermatia of *Tiffaniella snyderae*. ((a) from Kim and Fritz, 1993; (b) from Magruder, 1984; (c) from Fetter and Neushul, 1981.)

In some of the red algae it is possible to control tetrasporogenesis by varying the light period, but there is no general rule that can be applied to the response. In *Rhodochorton purpureum* (West, 1972; Dring and West, 1983) and *Acrochaetium asparagopsis* (Abdel-Rahman, 1982), tetrasporophytes produce tetrasporangia under short-day conditions. According to the physiological clock hypothesis, photoperiodism is controlled by an endogenous free-running circadian (approximately 24-hour) oscillation of some biochemical change. Each oscillation involves a regular alternation of two phases (each lasting approximately 12 hours) with a different sensitivity to light. The two phases are a **photophile** (light-loving) phase and a **skotophile** (dark-loving) phase. The initiation of a particular event depends on initiation or inhibition of metabolic changes of short-day or long-day organisms, respectively, by exposure to light at a particular point in the skotophile phase. In the case of *Rhodochorton purpureum* and *Acrochaetium asparagopsis*, light-breaks in the dark (skotophile) phase result in inhibition of tetrasporogenesis, whereas dark-breaks in the light (photophile) phase result in stimulation of tetrasporogenesis.

Tetrasporogenesis in these algae is therefore a short-day phenomenon (Abdel-Rahman, 1982).

**Polysporangia** contain more than four spores, usually in multiples of four (Fig. 4.17(f)). Polysporangia probably evolved from tetrasporangia because polysporangia occur predominantly in the most advanced order, the Ceramiales. **Bisporangia** are probably reduced tetrasporangia in which cell division has resulted in two spores after meiosis instead of four.

### Asexual spores

**Monosporangia** (one spore per sporangium) and **parasporangia** (more than one spore per sporangium) produce asexual spores that re-form the parent thallus. Monosporangia can be formed by the release of a vegetative cell from the thallus (*Goniotrichum*, Fig. 4.25(b), *Asterocystis*, Fig. 4.25(a)), or by the formation of sessile one-celled branches (*Kylinia*, Fig. 4.17(g)).

### Spore motility

Spores, whether monospores, tetraspores or carpospores, of almost all red algae are capable of motility by gliding. Some spores have smooth, directional and continuous gliding (e.g., *Batrachospermum* at  $2.2 \mu\text{m s}^{-1}$ ). In others, movement is non-continuous and unidirectional. Polysaccharide secretion appears to be responsible for the gliding (Pickett-Heaps et al., 2001).

## Classification

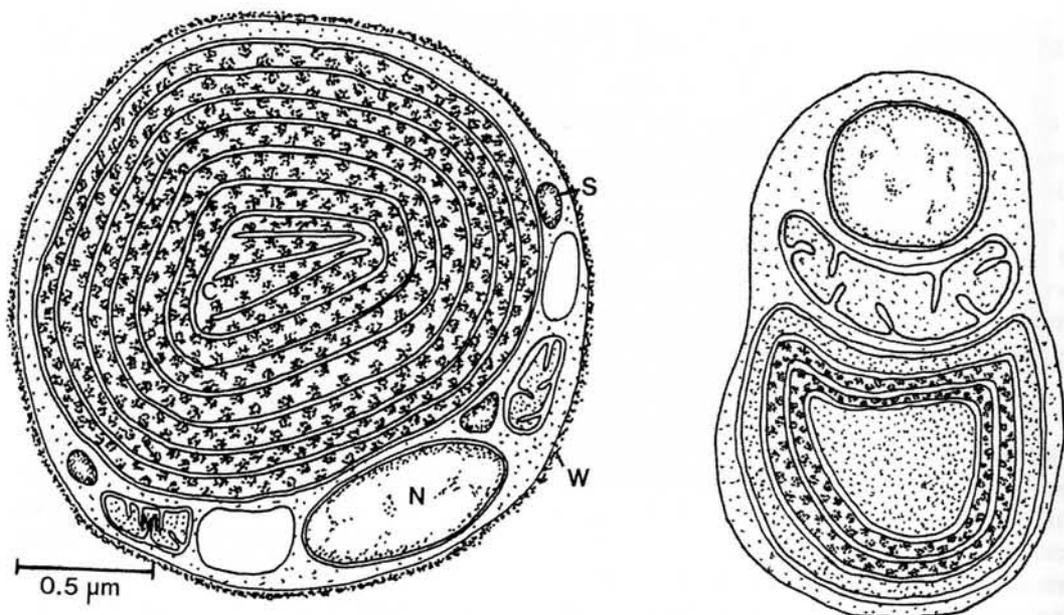
The Rhodophyta has a single class, the Rhodophyceae. In the past, the Rhodophyceae was divided into two subclasses, the Bangiophycidae and the Florideophycidae. The Bangiophycidae were supposed to lack pit connections, apical growth, and probably sexual reproduction, whereas the Florideophycidae had pit connections, apical growth, and sexual reproduction with a triphasic life cycle. The Bangiophycidae have since been found to have pit connections and apical growth in the *Conchocelis* filamentous stage of the Bangiaceae. Sexual reproduction also occurs in the Bangiaceae. In turn, the Florideophycidae do not necessarily have apical growth (intercalary growth occurs in the Corallinales (Dixon, 1973)), nor do they all have a triphasic life history (e.g., red algae in the Batrachospermales). For the above reasons, the two subclasses have been dropped in this treatment of the Rhodophyceae, as suggested by Gabrielson (Gabrielson, et al., 1985).

The classification of the more advanced orders of the red algae is based on complex characteristics of sexual reproduction. One of the more active fields of phycology in the last couple of decades has been in the application of nucleic-acid sequencing techniques in a delineation of the evolutionary relationships of these algae. While producing a more natural grouping of algae, these excellent studies have produced an even more complex classification system, which is difficult to present to a student taking a first course in phycology, to which this book is directed. In writing the current edition of the book, the author has spent some time trying to decide how to present the classification of the red algae, and has decided that a presentation of all of the more advanced orders would overwhelm the beginning student. As such, the author has selected those red algae that are commonly studied in phycology courses and/or are economically or ecologically important.

- Order 1 **Cyanidiales:** unicells that inhabit volcanic areas with pH values ranging from 0.5 to 3.
- Order 2 **Porphyridiales:** unicells, or multicellular algae that are held together by mucilage.
- Order 3 **Bangiales:** plants having a filamentous phase with pit connections and a macroscopic phase without pit connections.
- Order 4 **Acrochaetiales:** algae with a uniseriate filamentous gametophyte and tetrasporophyte (if both are present).
- Order 5 **Batrachospermales:** uniaxial (one apical cell per branch); gonimoblast usually develops from the carpogonium or hypogenous cell.
- Order 6 **Nemaliales:** multiaxial (more than one apical cell per branch); usually the gonimoblast develops from the carpogonium or the hypogenous cell.
- Order 7 **Corallinales:** heavily calcified algae with the reproductive organs in conceptacles.
- Order 8 **Gelidiales:** fleshy agarophytes, carpogonial branch consisting of a single cell, the carpogonium, no differentiated auxiliary cells.
- Order 9 **Gracilariales:** fleshy agarophytes, two-celled carpogonial branch, no auxiliary cells, or connecting cells.
- Order 10 **Ceramiales:** relatively delicate or filamentous forms with an auxiliary cell cut off after fertilization and borne on the supporting cell of a four-celled carpogonial filament.

Sequencing of nucleic acids have shown that the Cyanidiales and Bangiales represent separate natural groupings. The Porphyridiales are a grouping of three separate lines of unicells (Saunders and Hommersand, 2004). The Acrochaetiales, Batrachospermales, Nemaliales, and Corallinales are a natural grouping, as are the Gracilariales, Gelidiales, and Ceramiales (Harper and Saunders, 2001).

Using molecular data, it is estimated that the red algae diverged from other eukaryotes about 1400 million years ago (Yoon et al., 2004). The Cyanidiales diverged from the rest of the red algae soon after that, about 1370 million years ago. The Bangiales diverged from the remaining red algae



**Fig. 4.23** Left: *Cyanidium caldarum*. Right: *Cyanidioschyzon merolae*. (C) Chloroplast; (M) mitochondrion; (N) nucleus; (S) starch; (W) wall. (*Cyanidium* is after Seckbach and Ikan, 1972.)

about 1000 million years ago. The first fossil convincingly identified as a red alga is a 1200 million-year-old fossil similar to extant *Bangia* (Fig. 4.28) (Butterfield, 2000). Fossil coralline red algae have been recovered from the late Jurassic (160 million years ago) (Wray, 1977).

The relationship between freshwater and marine Rhodophyceae, as well as their evolution, was discussed in an interesting paper by Skuja (1938). He believed that the Rhodophyceae are a very old group (as is borne out by their fossil record) that originated in shallow coastal waters of primitive seas poor in salt. Living in shallow water, these plants had no need of a large quantity of phycoerythrins to absorb the blue-green light present at greater depths of water. Consequently these primitive Rhodophyceae were not pinkish-red but blue-green in color. These plants are represented by the freshwater Rhodophyceae of today, which are predominantly blue-green in color, and found primarily in the more primitive orders such as the Porphyridiales, Bangiales, Acrochaetiales, and Nemiales. Only later did the Rhodophyceae develop greater quantities of phycoerythrins, and a pinkish-red color, and pene-

trate into deeper waters where they attained their present state of development.

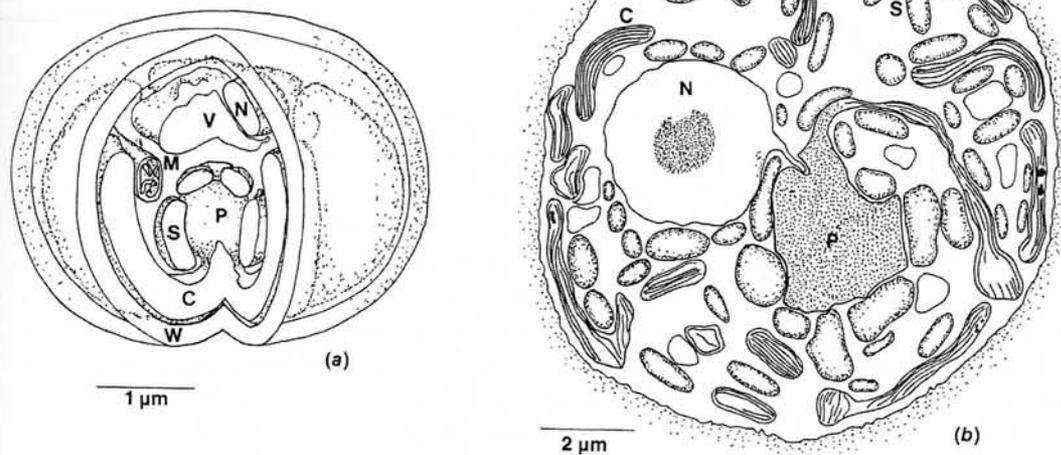
### Cyanidiales

This order contains three unicellular red algae: *Cyanidium caldarum*, *Cyanidioschyzon merolae*, and *Galderia sulphuraria* (Fig. 4.23). These algae inhabit volcanic areas with pH values ranging from 0.5 to 3 and temperatures up to 56°C (Gross et al., 2001).

*Cyanidium caldarum* and *Cyanidioschyzon merolae* are similar in that each of these unicells contains a single nucleus, mitochondrion, and plastid (Fig. 4.23). They differ in that *Cyanidium* is round, has a cell wall, and forms four endospores while *Cyanidioschyzon* is club shaped, has no cell wall, and divides by binary fission (Ohta et al., 1997). *Cyanidioschyzon* has the smallest genome size (16 520 305 base pairs and 5331 genes) so far recorded in eukaryotes and has had its genome sequence elucidated (Matsuzaki et al., 2004).

*Galderia sulphuraria* is morphologically similar to *Cyanidium caldarum*. *Galderia sulphuraria*, however, is able to grow heterotrophically while *Cyanidium caldarum* can not.

The algae in the Cyanidiales are probably the most primitive extant algae, evolving into an environment (acidic hot springs) that was an empty ecological niche at the time. The only other photosynthetic algae present at the time



**Fig. 4.24** (a) A diagrammatic drawing of a cell of *Rhodosorus marinus*. (b) A semidiagrammatic drawing of a section through a cell of *Rhodella maculata*. (C) Chloroplast; (M) mitochondrion; (N) nucleus; (P) pyrenoid; (S) starch grain; (V) vacuole; (W) wall. ((a) after Giraud, 1962; (b) adapted from Evans, 1970.)

were cyanobacteria. Cyanobacteria do not occur in ecological niches below a pH of 5 (Brock, 1973). It, therefore, makes sense that the first eukaryotic alga would have had an evolutionary advantage by evolving in an environment where there were no other photosynthetic algae to compete with.

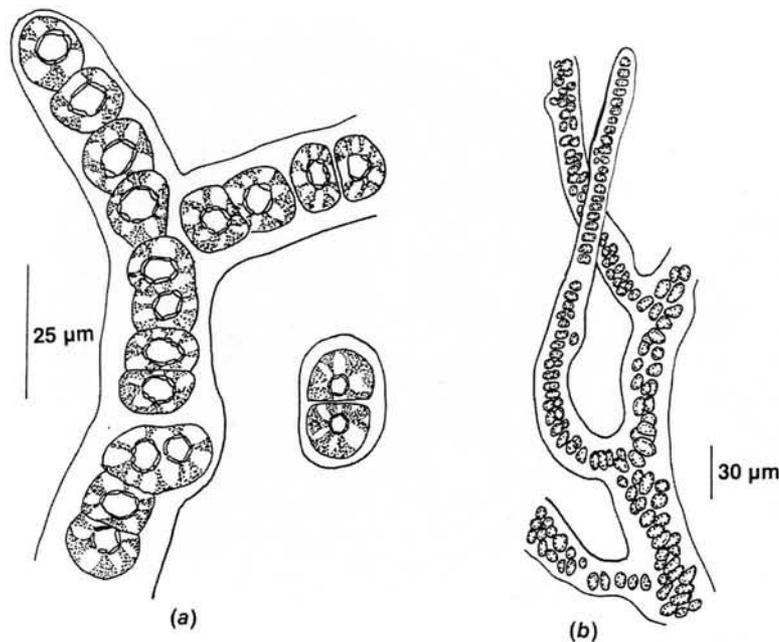
### Porphyridiales

These algae are either unicells or cells embedded in mucilage loosely organized into filaments. There are three evolutionary lines in the order (Oliveira and Bhattacharya, 2000; Karsten et al., 2003).

The unicells in the Porphyridiales are probably derived from monospores, carpospores or tetraspores of more evolutionarily advanced red algae (Ragan et al., 1994; Freshwater et al., 1994). These unicells are differentiated by cytological characteristics. Thus, *Porphyridium* (Fig. 4.1) has a single large stellate chloroplast with a central pyrenoid. *Rhodosorus* (Fig. 4.24(a)) has a lobed chloroplast with a basal pyrenoid, and *Rhodella* has a stellate chloroplast with a central pyrenoid, but with a

more dissected chloroplast than *Porphyridium* (Figs. 4.2, 4.24(b)).

*Porphyridium* is a common alga on soil and damp walls where it forms several-layered blood-red mucilaginous strata. Even though it is a soil alga, most species grow best in marine liquid media, indicating that it is probably of brackish or marine origin. *Porphyridium* has the ability to glide over a substrate it is in contact with. Overhead illumination results in random movement, whereas unilateral light causes movement toward the light source (Sommerfield and Nichols, 1970). The positively phototactic cells move by the extrusion of mucilage in vesicles in one direction, which results in the formation of a mucilage stalk behind the cells (Lin et al., 1975). *Porphyridium* releases different amounts of polysaccharides, depending on the environmental conditions it is living under (Ramus and Robins, 1975). During the log phase of growth, large Golgi bodies form polysaccharides, which are stored in vesicles under the cell membrane. During the stationary phase of growth in culture, the polysaccharide is secreted outside the cell, giving rise to a capsule. This behavior in culture can be related to the survival of the cells in nature. The rapid log phase of growth is equivalent to a soil environment that is moist with available nutrients. Here the polysaccharides are stored inside the cell, and there is



**Fig. 4.25** (a) *Asterocytis* sp. in the filamentous and bicellular form. (b) *Goniotrichum alsidii*. ((a) after Belcher and Swale, 1960; (b) after Taylor, 1957.)

only a thin mucilage layer around the cell. The stationary phase of growth is equivalent to a soil environment that is drying out with nutrients becoming limiting, thereby causing a cessation of cell growth. Here the polysaccharides are released to the outside of the cell, where they form a capsule that enables the cell to withstand the desiccation that follows.

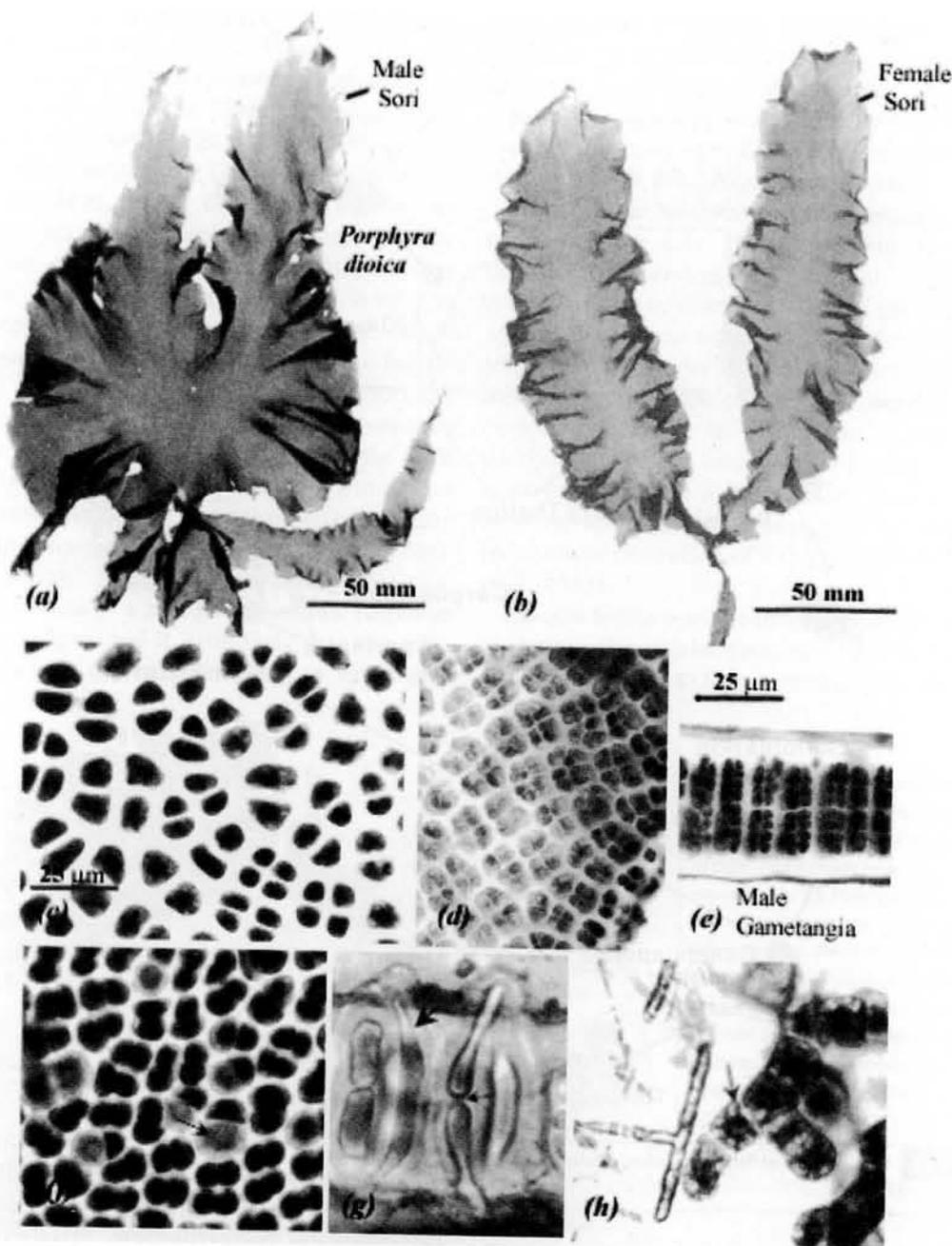
Also included in this order are algae that have cells joined together in thick mucilaginous filaments. *Goniotrichum* is a common marine epiphyte made up of branched mucilaginous filaments (Fig. 4.25(b)). *Goniotrichum* forms monospores simply by the release of a vegetative cell from a filament in photoperiods of over 12 hours of light (Fries, 1963). *Asterocytis* (Fig. 4.25(a)) exhibits what is probably an intermediate position in the evolution of a red unicell into a mucilaginous filamentous alga. In normal seawater *Asterocytis* forms branched filaments, whereas in seawater of one-fourth strength the organism forms unicells, which were previously classified in the genus *Chroothoece* (Lewin and Robertson, 1971).

### Bangiales

The algae in this order show alternation of a haploid thallus stage having no pit connections, with

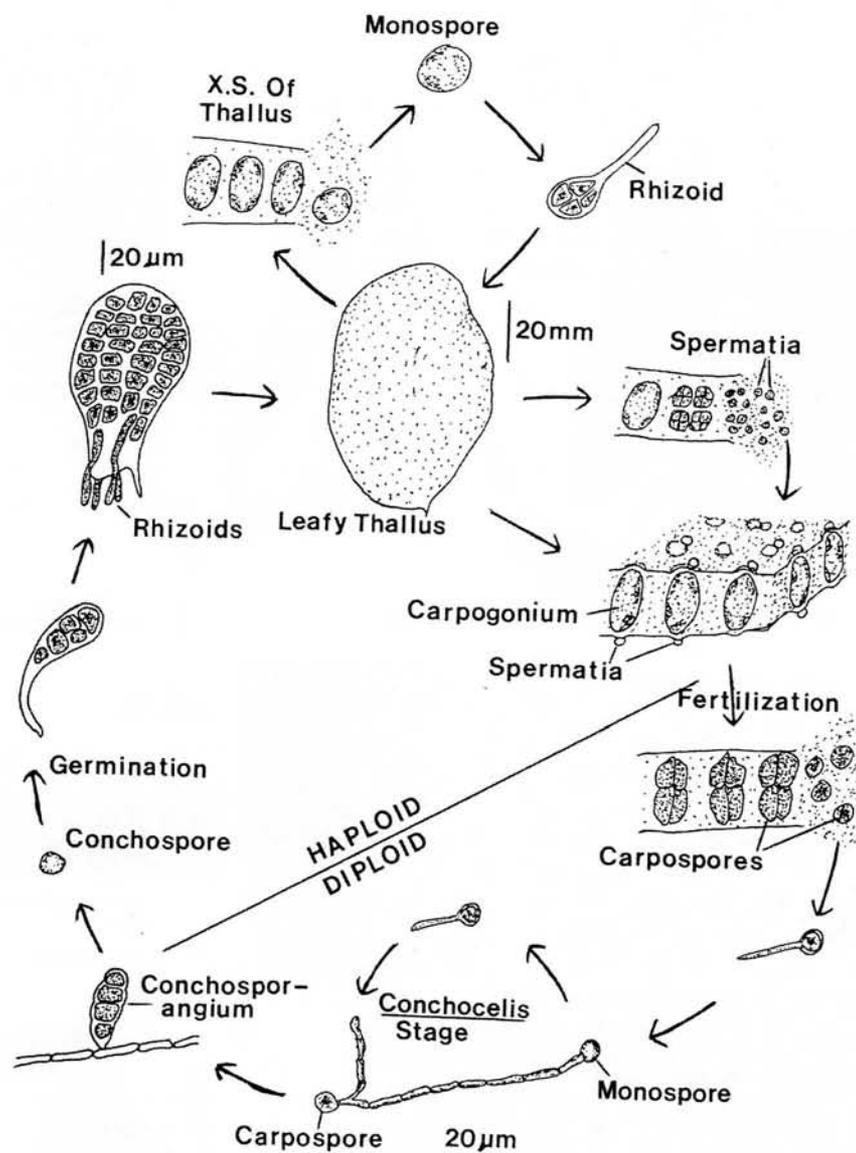
a diploid filamentous *Conchocelis* state that has pit connections (Lee and Fultz, 1970; Kornmann, 1994). The Bangiales is a monophyletic order and is a sister group to the higher red algae (Oliveira and Bhattacharya, 2000).

*Porphyra* (Figs. 4.26, 4.27) is an intertidal seaweed in the colder waters of the world. The thallus arises from a holdfast and is composed of a sheet of cells one to two layers thick. *Porphyra gardneri* (Fig. 4.27) is a foliose (leafy) monostromatic (single layer of cells) alga found growing epiphytically on several members of brown algae in the Laminariales. In British Columbia, Canada, the host *Laminaria setchellii* has its blade worn back almost to the stipe by November. During December, a new *Laminaria* blade is rapidly produced. The first thalli of *Porphyra gardneri* appear epiphytically on the *Laminaria* at the end of February. **Asexual reproduction** occurs soon after *Porphyra gardneri* appears in February. The margins of the thallus break down and release single-celled **monospores**. After 1 or 2 days, the monospores germinate by sending out long rhizoids that anchor the monospores in the host *Laminaria* tissue. From this, a new leafy thallus appears. Prolific monospore production results in a great increase of *Porphyra gardneri* during the spring months. **Sexual reproduction** begins



**Fig. 4.26** *Porphyra dioica*. (a) Male gametophyte with male gametangia in sori. (b) Female gametophyte with female gametangia in sori. (c) Surface view of vegetative cells in pairs. (d) Surface view of male gametangia. (e) Male gametangia in transverse section. (f) Gametangial mother cell (arrow) in surface view. (g) Carpogonium (large arrow) and first division of fertilized carpogonium (small arrow) in transverse section of thallus. (h) *Conchocelis* stage with conchosporangia (arrow). (From Holmes and Brodie, 2004.)

during late April. Spermatium mother cells in the thallus divide to form 64 spermatia. The spermatia contain a degenerate chloroplast with only a few thylakoids. Vesicles containing a fibrous material are discharged by the spermatia just before spermatia liberation. The released spermatia are 3 to 5  $\mu\text{m}$  in diameter, have no starch granules, and are surrounded only by the fibrous



**Fig. 4.27** The life cycle of *Porphyra gardneri*. (Adapted from Hawkes, 1978.)

material from the released vesicles. The spermatia are carried to the carpogonia by water currents. Carpogonia (with a chromosome number of 4) differentiate from vegetative cells by the production of a swollen area of the cell wall, the **prototrichogyne**, directly above the carpogonium. In a monostromatic species, such as *Porphyra gardneri*, two prototrichogynes are produced by each carpogonium, one on each surface. In dis-

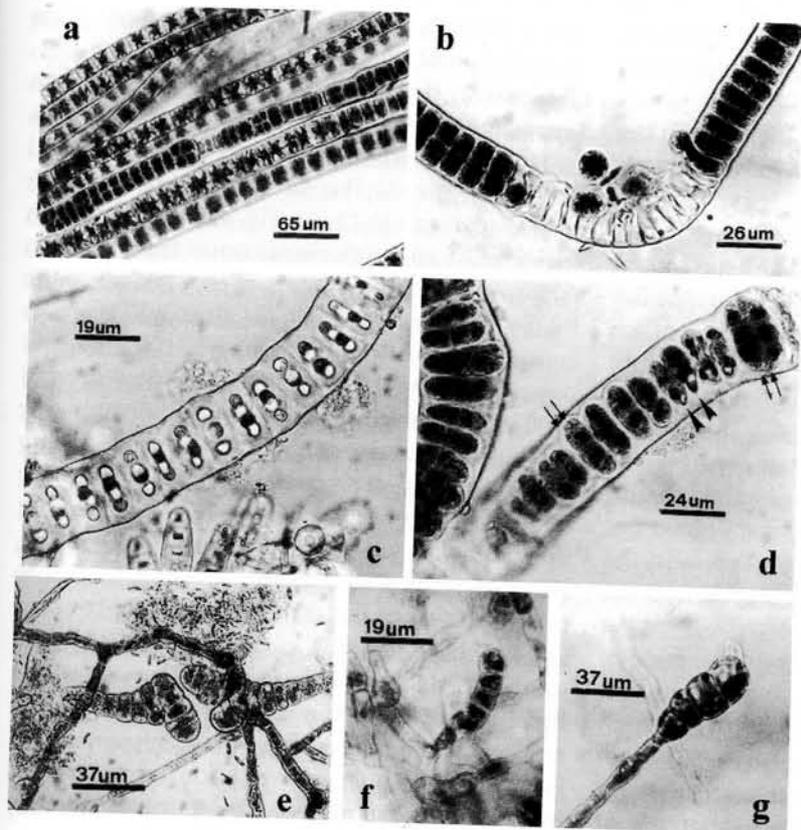
tromatic species, with two sheets of cells in the thallus, a single prototrichogyne is produced per carpogonium. A spermatium attaches to the prototrichogyne, a fertilization canal appears in the prototrichogyne, and the spermatial nucleus moves through the canal to fuse with the carpogonium. By the beginning of May, the fertilized carpogonia have divided to form two to four diploid carpospores (with a chromosome number of 8), 14 to 20 µm in diameter. Maximum carpospore production occurs during the months of June through August. The carpospores germi-

nate in 2 to 3 days to produce the diploid *Conchocelis* stage (Hawkes, 1978). The *Conchocelis* stage is filamentous and commonly lives in shells of dead marine animals. Under long-day conditions, the *Conchocelis* stage differentiates monospores, which re-form the *Conchocelis* stage (Dixon and Richardson, 1970). Under short days the *Conchocelis* stage forms conchosporangia (fertile cell rows), each cell of which produces a conchospore. Conchospores are released from the conchosporangia under low-temperature conditions (about 5 °C) (Chen et al., 1970). The formation of the conchosporangia under short-day conditions is a true photoperiodic response because a light break in the middle of the dark period is inhibitory (Dring, 1967a). A functional phytochrome system is operative, with red light being the most effective in breaking the dark period (Dring, 1967b). This is one of the few demonstrations of a true photoperiodic response in the red algae, and it is unlikely that this phytochrome type of response occurs in sublittoral

Rhodophyceae because far-red light penetrates to less than 1 m of seawater and red light no deeper than 10 m (Dixon and Richardson, 1970). On release, the conchospores germinate in a bipolar manner, forming a germling that grows into the thallus phase, completing the life cycle.

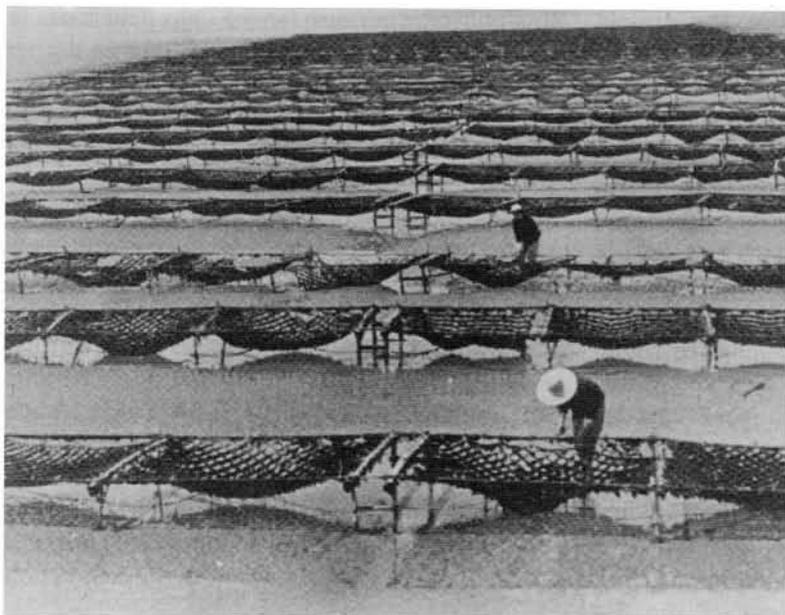
*Porphyra perforata* lives in the intertidal zone, where at low tide the plants are routinely exposed to air drying. As a result of evaporative water loss, the salt concentration of extracellular water can increase up to 10 times above normal levels. During desiccation at low tide, the alga can lose up to 90% of its fresh weight. Such desiccation results in inhibition of photosynthesis. Some of the inhibition of photosynthesis is probably due to a decrease in electron flow between water and photosystem II because of a reduced concentration of water in the cells (Sato et al., 1983).

*Bangia* forms upright threads that are at first uniseriate, the cells subsequently undergoing longitudinal division to form a multiseriate filament



**Fig. 4.28** *Bangia atropurpurea*.

(a) Uniseriate filaments becoming multiseriate by successive division of cells. (b) Filament releasing monospores. (c) Male gametophytes with spermatia. (d) Female gametophytes with spermatia. Arrowheads show a carpogonium with a single trichogyne. Arrows point to developing zygotes. (e) Conchosporangia. (f, g) Monosporangia on sporophytes. (From Gargiulo et al., 2001.)



**Fig. 4.29** Cultivation nets with *Porphyra* at low tide at Rudang, Jiangsu Province, People's Republic of China. (From Tseng, 1981.)

(Fig. 4.28). *Bangia* occurs in both marine and freshwater environments. *Bangia*-like fossils (*Bangiomorpha pubescens*) have been reported from the 1200 million-year-old Hunting formation on Somerset Island in Canada (Butterfield, 2000). It is possible to adapt freshwater *Bangia fuscopurpurea* to seawater by increasing the salinity by 10% of that of seawater every time the alga sporulates (den Hartog, 1971). If the thallus is moved directly from freshwater to seawater, the plant dies, illustrating that the spores have a better ability to adapt to changed salinity. Such an experiment shows the ease with which some of the smaller red algae can change from one habit to another. *Bangia* has a life cycle similar to that of *Porphyra* (Richardson, 1970; Sommerfeld and Nichols, 1973).

The diploid *Conchocelis* phase of *Porphyra* and *Bangia* differs chemically from the haploid thallus phase (Liu et al., 1996). The *Conchocelis* phase has cellulose in the wall of the cells, whereas in the thallus phase, cellulose is absent and, as the structural polysaccharide, is replaced by a xylan (polysaccharide composed of xylose residues) (Gretz et al., 1980; Mukai et al., 1981). The galactans in the *Conchocelis* phase are also different from those in the thallus phase (Gretz et al., 1983). These chemical differences are in addition to the structural differences, particularly the occurrence of

pit connections in the *Conchocelis* phase and their absence in the thallus phase.

The *Conchocelis* phase has been found as the fossil genus *Palaeoconchocelis starmachii* in the Upper Silurian of the Paleozoic (425 million years ago) (Campbell, 1980).

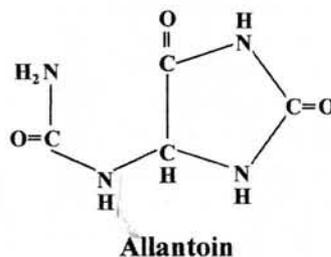
The leafy thallus phase of *Porphyra* is eaten as a vegetable in the Far East and Nova Scotia (Canada). In Japan, *Porphyra* is eaten as a vegetable called *nori*; in Nova Scotia, it is called *laver*. *Porphyra* is cultivated on farms in China (Fig. 4.29) and Japan. In Japan, most of the *Porphyra* comes from *Porphyra* farms in the shallow waters of such places as the Inland Sea and Tokyo Bay, although there is considerable collecting of plants from natural populations. *Porphyra* was first cultivated around 1700 in Tokyo Bay by placing bundles of bamboo or oak bushes (known as *hibi*) into the mud in early autumn, the usual procedure being to arrange the bundles in regular rows and at such a depth that the twigs were well covered by water at high tide. The modern method is to drive bamboo stakes into the mud in rows and then place netting between the stakes (Mumford and Miura, 1988). The *Conchocelis* stage growing in seashells releases the conchospores, which settle on the brush or nets and germinate to form the foliose *Porphyra* plant. From late November to March, the *Porphyra* plants (sometimes mixed with the green alga *Monostroma*)

are harvested by a person in a narrow boat who picks or scrapes the plants off by hand. The *Porphyra* is brought to the factory, where it is washed and chopped into small fragments. These fragments are stirred in a vat, from which measured amounts of the mixture are dipped by means of a small wooden container and poured over a stiff porous mat. As the liquid drains away, the nori fragments are spread evenly over the mat, which is hung on outdoor bamboo racks to dry. The thin film of dry nori is removed as a sheet from the mat, folded, and packaged for market. The food value of nori or laver lies in its high protein content (25% to 30% of the dry weight), vitamins, and mineral salts, especially iodine. The vitamin C content is about 1½ times that of oranges per unit weight, and it is also rich in vitamin B. Humans digest about 75% of the protein and carbohydrate, and in this respect it is much better than other seaweeds.

Prior to the discovery of the alternate *Conchocelis* phase of *Porphyra* by Drew, the yield of *Porphyra* fluctuated sharply from one year to the next. Up to this time, the number of *Porphyra* plants formed depended on the production of conchospores by the *Conchocelis* phase. These fluctuations in the production of spores have been overcome by the artificial cultivation of the *Conchocelis* phase, usually on shells. The shells containing the *Conchocelis* phase are attached to the nets, or the nets are dipped into baths to which crushed shells have been added. The best settlement of spores occurs in waters of high nitrogen, that is, near sewage outflows. Another way of seeding *Porphyra* is by monospores. Monosporangia have been induced in haploid thalli by three week exposure to allantoin (Fig. 4.30) followed by homogenization of the thalli. The resulting monospores reproduce the haploid thalli of *Porphyra* (Mizuta et al., 2003). Although the production of nori increased until the early 1960s, there has been no increase in production since then, mostly because of increasing pollution of the shallow waters in which *Porphyra* farming is carried out (Dixon, 1973).

### Acrochaetiales

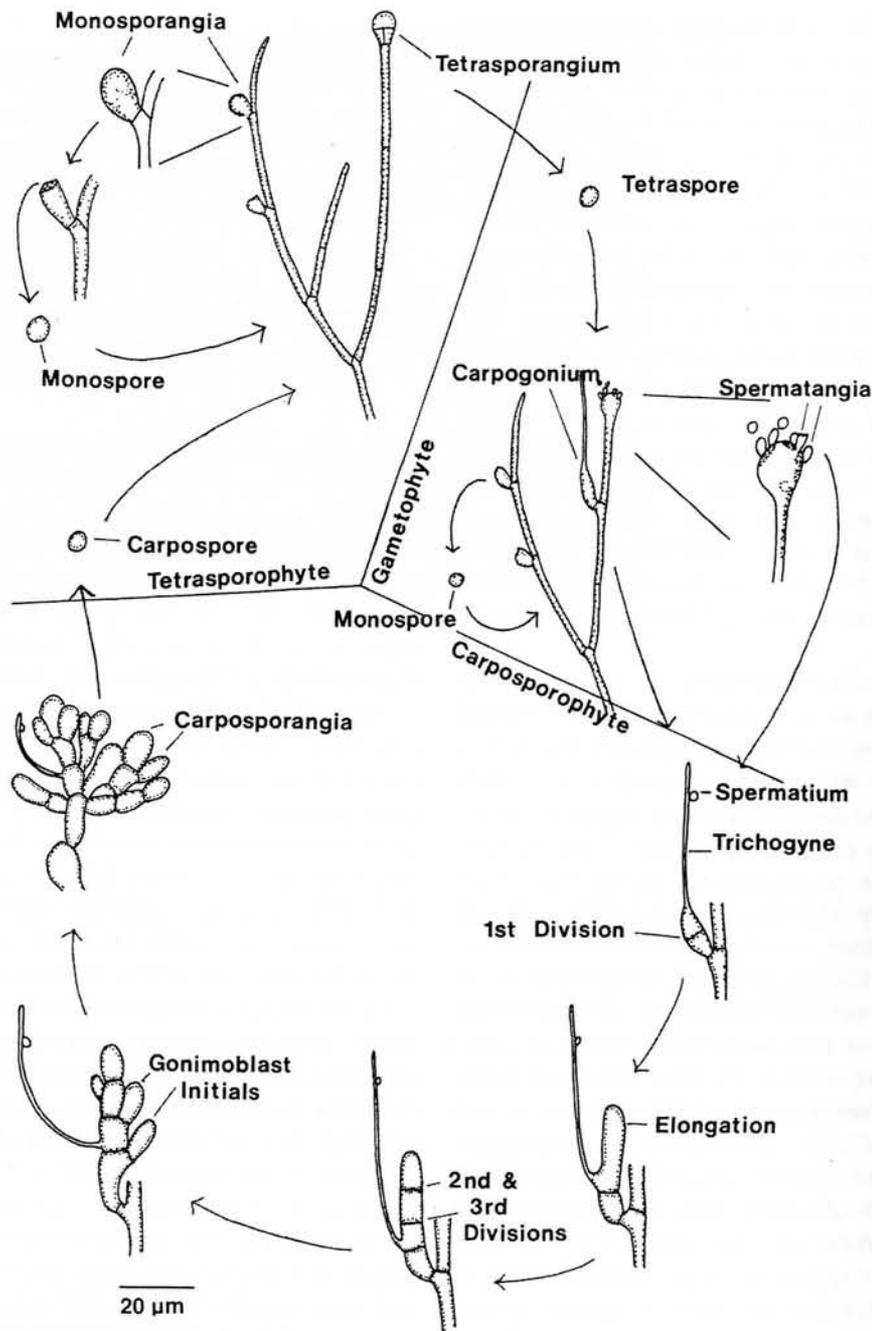
Algae with uniseriate filaments are in this order (Chemin, 1937; Feldman, 1953). Papenfuss (1945,



**Fig. 4.30** The chemical structure of allantoin, an inducer of monospore formation in *Porphyra*.

1947) recognizes four major genera in the order: (1) *Rhodochorton*, with each cell containing a few to many small discoid chloroplasts (Fig. 4.31); (2) *Acrochaetium*, with each cell having one parietal or laminate chloroplast (Fig. 4.17(c)); (3) *Audouinella*, with each cell having one or more spiral chloroplasts; (4) *Kylinia*, with each cell having one or more stellate chloroplasts (Fig. 4.17(g)).

Most of these algae are small epiphytes or endophytes. Some of them may still prove to be the alternate phase of more complex higher Rhodophyceae. *Rhodochorton investiens* can be used as an example of a triphasic life cycle (Fig. 4.31) (Swale and Belcher, 1963). Both the gametophyte and tetrasporophyte produce similar obovoid monospores in monosporangia arising just beneath a cross wall of the filament. The spore is liberated through the apex of the sporangial wall, which remains attached to the filament. After release, the monospores germinate without a resting phase to re-form the parent plant. The gametophyte is monoecious, with a filament ending in a cluster of spermatangia and a carpogonium being borne on the cell under the supporting cell of the spermatangia. The spermatangia occur in groups of four to six, emerging from the enlarged and flattened distal end of a terminal cell. The carpogonia are sessile and appear in the position of branch cells. At the distal end of the carpogonium is a narrow trichogyne. After fertilization, the carpogonium becomes divided by three cross walls into a row of four cells. The first transverse wall develops below the trichogyne, the upper cell then elongating and dividing into three cells. This results in the trichogyne emerging from the second cell of the row. Two-celled gonimoblast



**Fig. 4.31** The life cycle of *Rhodochorton investiens*. (Adapted from Swale and Belcher, 1963.)

filaments develop from each cell of the row, each gonimoblast filament producing two to three terminal carpospores. The carpospores germinate to form the tetrasporophyte, with larger cells of deeper color than those of the gametophyte.

Tetrasporangia either are sessile or terminate a one-celled branch. The tetraspores germinate to produce the gametophyte, and thus complete the life cycle.

#### Batrachospermales

This order includes the uniaxial (each filament with a single apical cell) freshwater Rhodophyceae.

The gonimoblasts usually arise from the fertilized carpogonium. No tetraspores are formed, and meiosis probably occurs when the diploid filamentous stage forms the thallus initials.

*Batrachospermum* (often called the "frog spawn" alga) is a freshwater alga that occurs in well-aerated, slow-moving streams. The gametophyte (Fig. 4.32) appears as delicate violet beads on a string. Each "bead" consists of whorls of branches arising at the cross walls of the elongated cells of the main axis. The gametophytes produce terminal carpogonia on short branches arising from the whorls of branches. Spherical spermatia are formed by small groups of antheridia at the tips of branches. The spermatia are carried to the carpogonium by water currents. After fertilization, the zygote cuts off gonimoblast initials which develop into gonimoblast filaments with terminal carposporangia. The carposporangia release diploid carpospores that germinate into filamentous prothalli. Monospores can be produced by the prothalli. The monospores germinate to re-form the parent plant. The prothalli also form erect filaments that elongate by apical growth. The apical cell of the erect filament cuts off three to five cells mitotically, then undergoes two meiotic divisions. The first meiotic division results in (1) a polar body and (2) a cell that divides again to form a second polar body and the apical cell of the haploid gametophyte. The macroscopic plant is thus composed of basal diploid cells on a haploid plant. The diploid portion of the plant has cells that are larger than those of the haploid portion (Hurdelbrink and Schwantes, 1972; von Stosch and Theil, 1979; Balakrishnan and Chaugle, 1980; Necchi, 2002).

### Nemaliales

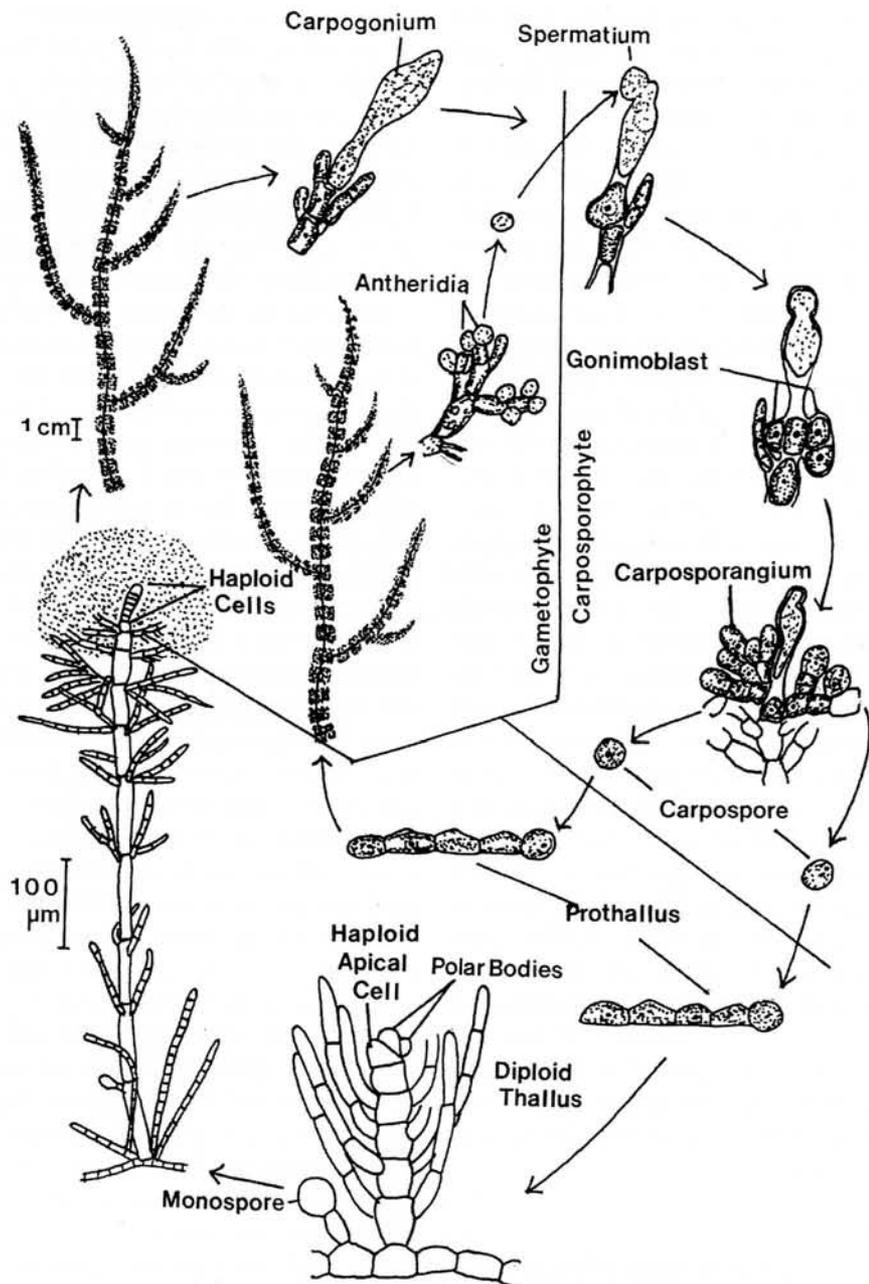
This order has multiaxial Rhodophyceae (with more than one apical cell), which usually have gonimoblasts developing from the carpogonium or hypogynous cell. There may be auxiliary cells present, but if there are, they are always nutritive auxiliary cells.

*Nemalion* is a common intertidal alga in north temperate seas. The thallus is a soft gelatinous cylinder reaching a length of 25 cm with a limited number of dichotomous branches (Fig. 4.33), being composed of a number of axial threads or filaments

in the center and richly branched laterals around the periphery. The laterals arise from the axial threads and grow out horizontally on all parts of the thallus except for the tip where they radiate out vertically. The laterals are all of about the same length, and their tips intercalate so as to give the thallus an even surface. The central axial cells are colorless, whereas the peripheral laterals usually have a stellate chloroplast with a central pyrenoid.

In *Nemalion*, the plants are homothallic. The carpogonial branch consists of an ordinary lateral of four to seven cells (Fig. 4.33). The elongate trichogyne projects slightly beyond the surface of the thallus. Spermatangial branches are produced from the terminal cells of the laterals, and at the tip of the two- to four-celled spermatangial branch are formed three to four spermatangia. Spermatangia produce spermatia that are released and pass to the trichogyne of the carpogonium where fertilization occurs. After fusion of the two gamete nuclei, the large zygote nucleus and the chloroplast divide into two. The carpogonium then divides transversely into two cells, the upper of which forms the gonimoblasts. The lower cell of the carpogonium gradually fuses with the **hypogynous cells** (those underneath the carpogonium), and eventually the upper carpogonial cell that has produced the gonimoblasts also fuses with these cells. These fusions probably have a nutritive function, providing the developing gonimoblasts and carposporangia with storage products. The gonimoblast threads hang downward, and each cell of the thread forms an upwardly curved two- to three-celled branchlet, the terminal cell of which enlarges to form the carposporangium. The carpospores give rise to a filamentous phase that produces tetraspores under short-day conditions (Cunningham and Guiry, 1989). The tetraspores produce filamentous gametophytes that form the erect axes under long-day conditions.

*Galaxaura* (Fig. 4.34) is a calcified alga that is widely distributed in the tropics. The calcification occurs as aragonite (Fig. 4.7) in the intercellular spaces of the cortex. *Galaxaura* has a gametophyte and tetrasporophyte that are similar in appearance. Male and female reproductive structures are borne in conceptacles deeply immersed in the medulla of the gametophytes, while tetraspores



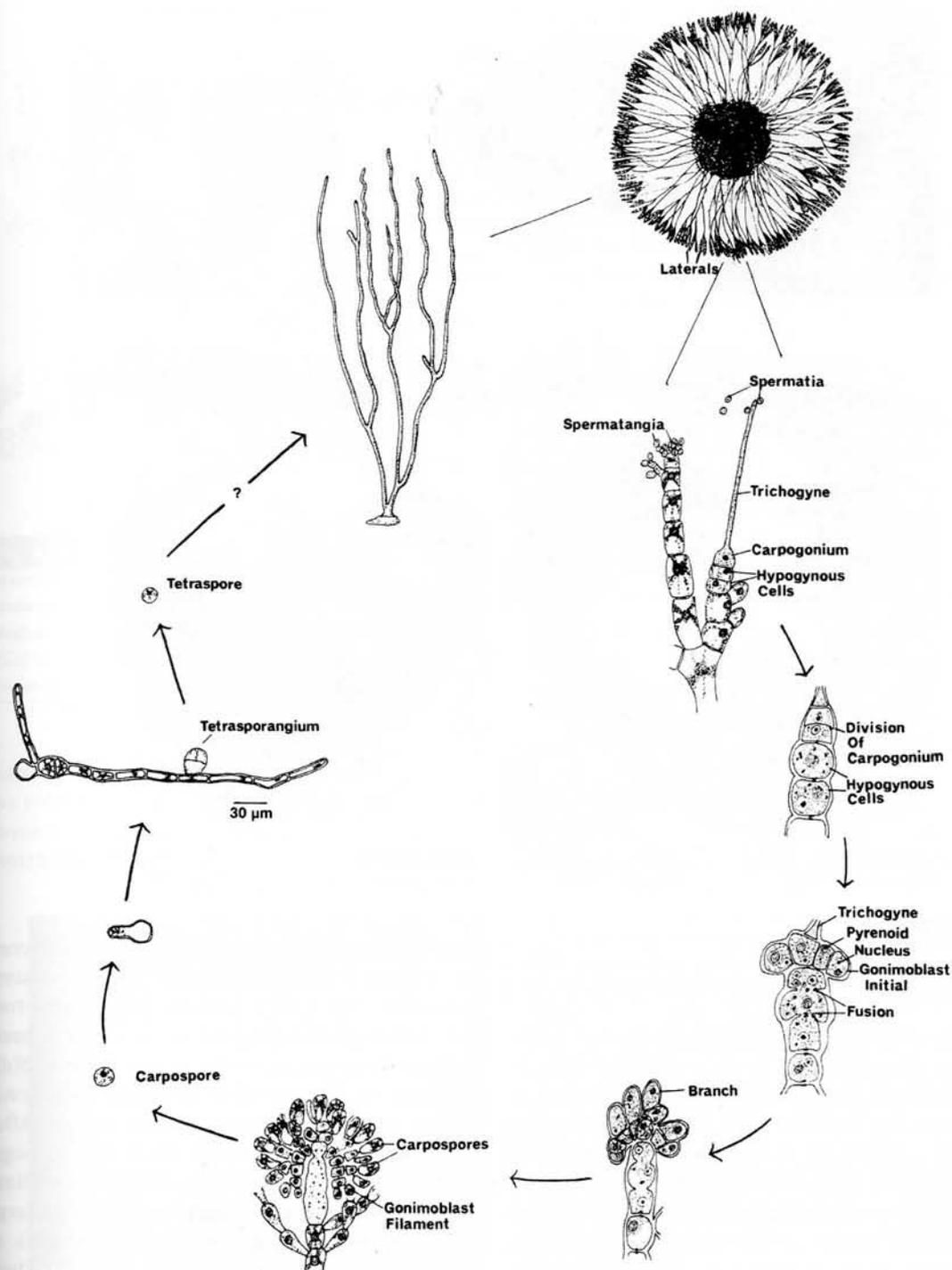
**Fig. 4.32** The life cycle of *Batrachospermum* sp. (Adapted from Balakrishnan and Chaugule, 1980; von Stosch and Thiel, 1979.)

occur scattered about the apical end of branches of the tetrasporophyte (Fig. 4.34). *Gymnocodium* and *Permocalculus* are two genera that arose in the Permian of the Paleozoic and became extinct during the Cretaceous of the Mesozoic (Johnson,

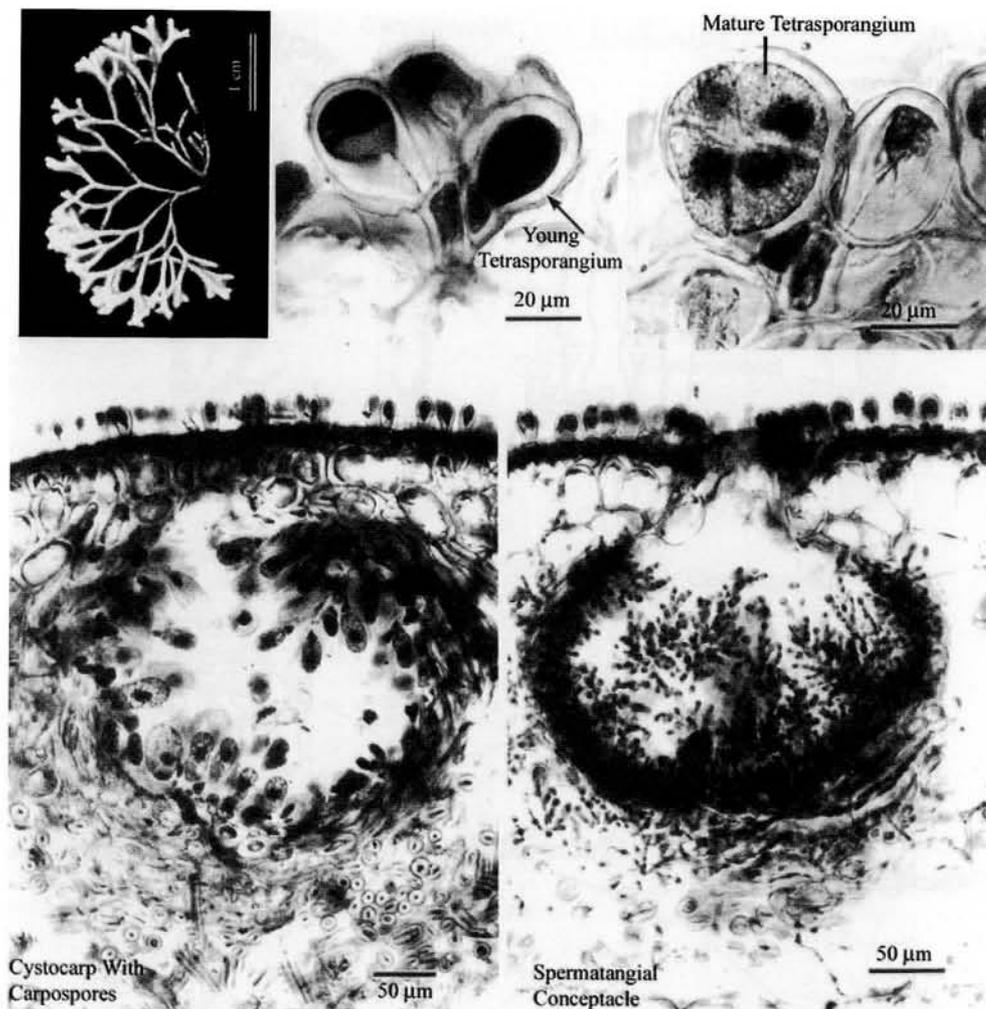
1961). The two genera were similar in morphology to *Galaxaura* with weak calcification restricted to an irregular outer zone.

### Corallinales

The Corallinales is an order of heavily calcified red algae (Figs. 4.35(a), 4.36(a), 4.37(a)) (Johansen, 1981; Silva and Johansen, 1986). Cytologically, the outer



**Fig. 4.33** The life cycle of *Nematium* sp. (Adapted from Oltmanns, 1904; Kylin, 1916; Fries, 1967; Umezaki, 1967.)

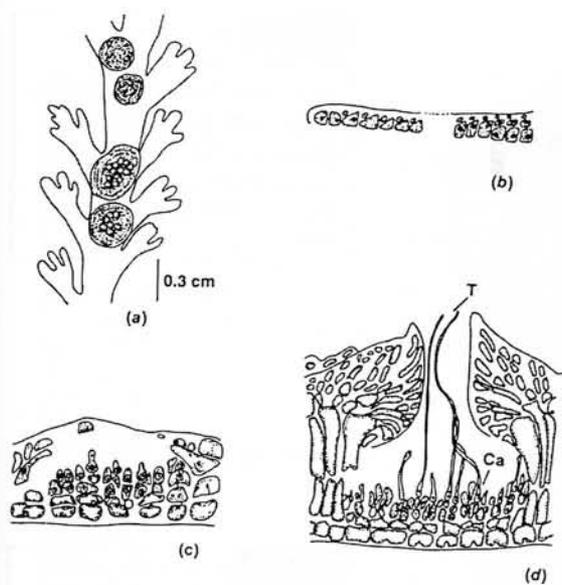


**Fig. 4.34** Photographs of vegetative and reproductive structures of *Galaxaura apiculata*. (From Kurihara et al., 2005.)

cap layer of the pit connections is large and dome-shaped (Pueschel and Trick, 1991). The order is characterized by having reproductive organs in **conceptacles** (cavities that open to the thallus surface) opening to the exterior by one or more pores (Figs. 4.35(d), 4.37(b)). In some genera, the tetrasporic conceptacles differ from sexual conceptacles in having numerous small pores in the roof rather than a single pore. The sexual plants are usually dioecious, with marked differences between male and female conceptacles. Both male and female organs are borne in **nemathecia** (wart-like elevations of the surface containing many reproductive organs), which develop on the

floor of the conceptacle. Spermatangia are formed abundantly from short filaments on the conceptacle floor. The female procarp consists of a two-celled carpogonial filament arising from a basal cell that functions as an auxiliary cell (Fig. 4.35(d)). The long trichogynes from the many carpogonia project through the conceptacular ostiole. After fertilization, a short ooblast from the carpogonium joins the auxiliary cell. All of the auxiliary cells of the conceptacle then fuse to form a large fusion or placental cell, from the margins of which issue the gonimoblast filaments with their carposporangia (Fig. 4.37(b)).

The thallus of the Corallinales is usually divided into two areas, the hypothallus and the perithallus. The **hypothallus** has relatively large cells and forms the basal part of the crustose



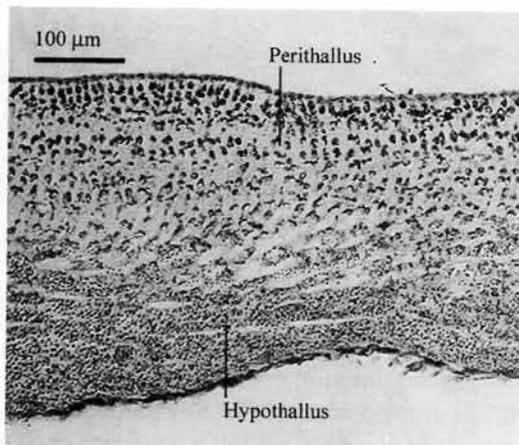
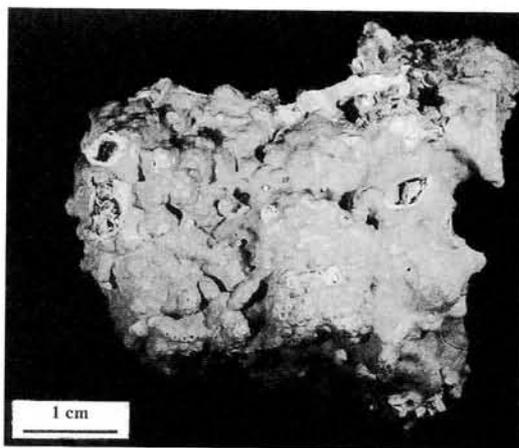
**Fig. 4.35** (a) *Melobesia marginata* epiphytic on *Laurencia spectabilis*. (b–d) *Melobesia lejolisii*: (b) section of sterile thallus showing cover cells and (c) section of immature fertile thallus. (d) *Melobesia limitata*: conceptacle with carpogonia (Ca) and trichogynes (T). ((a) after Smith, 1969; (b) after Suneson, 1937.)

plants (Figs. 4.36(b), 4.37(b)) and the central part of the erect branches. Also, in case of injury the scar tissue that develops is hypothallus tissue. The perithallus has smaller cells and is located above

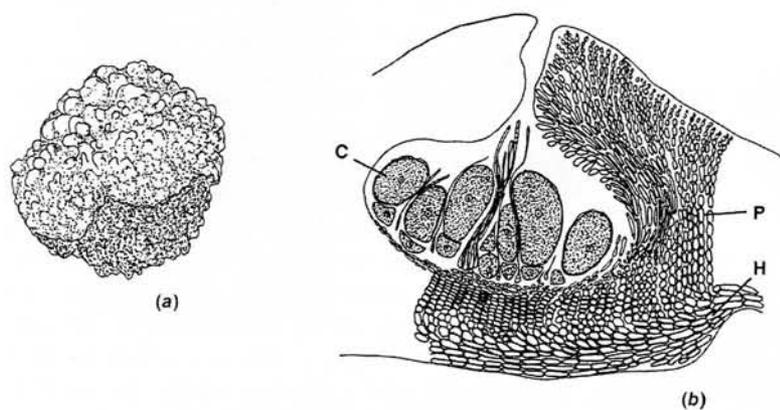
the hypothallus in crustose forms and outside of the medullar hypothallus in branched forms.

The Corallinaceae of the Corallinales has two subfamilies. The crustose and nodular forms (Figs. 4.35(a), 4.36(a), 4.37(a)) are in the Melobesoideae and the articulated or jointed forms (Fig. 4.38) are in the Corallinoideae (although recent investigations on gene sequences of rRNA have shown that these two subfamilies do not reflect the evolutionary history of the order (Bailey and Chapman, 1998)). In the Melobesoideae, the simplest type of thallus is in *Melobesia*, which has thin pink or red crusts that are widely distributed, especially as epiphytes on other algae and marine plants (Fig. 4.35(a)). The thallus consists of one to five layers of prostrate threads compacted to form a disc. A marker feature is the flat cover cells, which also occur in other Corallinales, forming the outer layer of cells (Fig. 4.35(b)). *Mesophyllum* and *Lithothamnion* are lithophytes that usually have considerably thicker crusts and sometimes nodules (Figs. 4.36, 4.37).

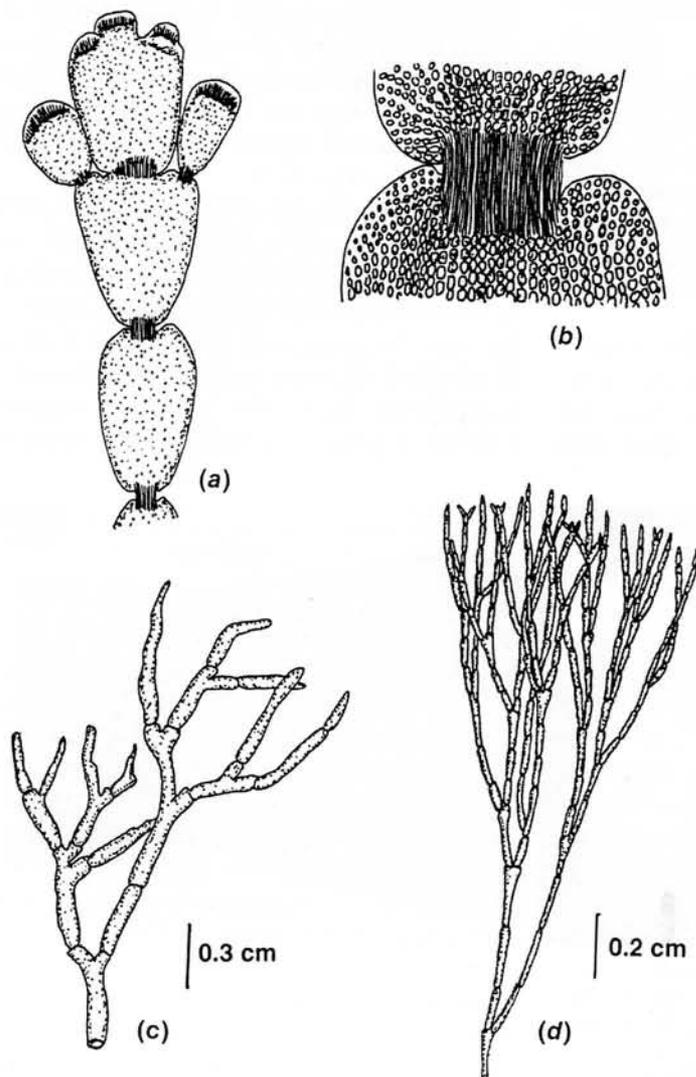
In the Corallinoideae the plants are multi-axial, having a medulla of elongated cells and a cortex of shorter cells (Fig. 4.38). Calcification normally occurs only in the cell walls of the cortical cells. The plants are composed of a number of calcified segments, each segment joined by a non-calcified joint. The segments consist of calcified cortical and non-calcified medullary



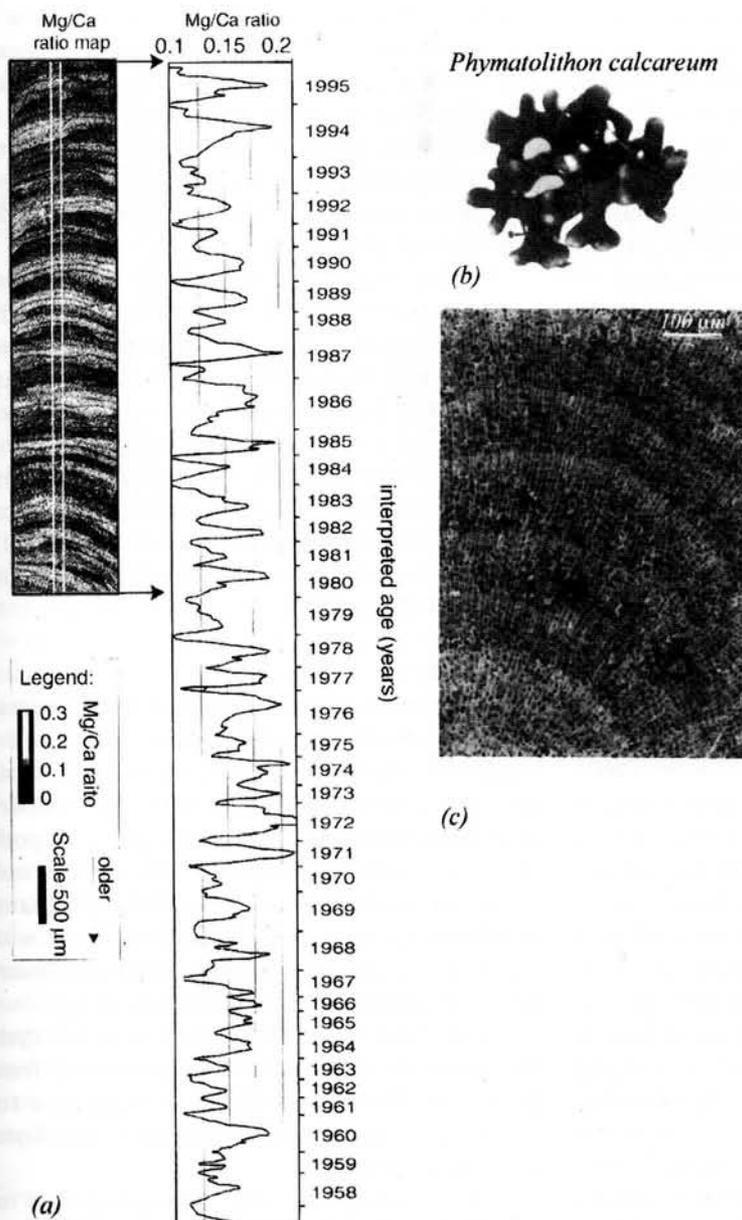
**Fig. 4.36** (Left) The coralline red alga *Mesophyllum alternans*. (Right) Section of the vegetative thallus showing the perithallus and hypothallus. (From Cabioch and Mendoza, 1998.)



**Fig. 4.37** (a) *Lithothamnion* sp.  
(b) *L. lenormandi*: drawing of a section of thallus with a hypothallus (H) and perithallus (P). The section includes a mature conceptacle and carposporangia (C). ((a) after Oltmanns, 1904; (b) after Suneson, 1943.)



**Fig. 4.38** (a) *Corallina* sp. (b) *Corallina* sp. showing non-calcified joints and calcified segments. (c) *Amphiroa rigida* var. *antillana*. (d) *Jania rubens*. ((a),(b) after Oltmanns, 1904; (c),(d) after Taylor, 1957.)



**Fig. 4.39** (a) Left: A micrograph of a section of the thallus of *Lithothamnion glaciale* showing 16 yearly growth bands. Right: A 38-year record showing the cycles in the ratio of Mg/Ca cycles. Greater amounts of Mg (e.g., higher Mg/Ca ratios) occur during the summer months. (b) Photograph of the coralline red alga *Phymatolithon calcareum*. (c) Scanning electron micrograph of a longitudinal section of *Phymatolithon calcareum* showing banding. ((a) from Halfar et al., 2000; (b),(c) from Blake and Maggs, 2003.)

tissue, the arrangement of tissues giving the plants a certain amount of flexibility.

The crustose Corallinaceae occur in the intertidal zone, but only in areas that are not exposed to excessive drying, either on exposed rocks where they are kept moist by spray from breakers or in well-shaded areas. In some places they occur near the high-tide mark but are well covered by other algae. The sublittoral zone is a more favorable area for crustose algal growth, especially on reefs from

the low-tide mark to a depth of 25 to 30 m. The depth and agitation of the water have a considerable influence on the growth form of the coralline algae. Crustose types are present at all depths, but the highly ramified or branching forms occur only near the surface, where they are most plentiful down to 30 m. In the crustose forms, the thickest crusts are formed in shallow waters; the crusts become thinner with depth (as a result of thinner hypothalli and smaller cells), probably as a result

temperature of the water where the reefs grow is among the deepest-growing algae, down to 125 m living, their life-span ranging from 10 to 50 years (Adey, 1970), probably as a result of their slow growth rate (0.3 to 3 mm year<sup>-1</sup>). The light saturation for photosynthesis for red crustose corallines was found by Adey (1970) to be between 700 and 1000 lux, which is considerably lower than the 4000- to 10000-lux saturation intensities found for other Rhodophyceae (Kanwisher, 1966; Brown and Richardson, 1968). These light saturation values are probably related to the great depth at which the crustose corallines are able to live.

Maerl is composed of shallow, subtidal deposits of calcareous red algae belonging to the Corallinales. Maerl has been obtained commercially for many years by dredging from the coast of Brittany in France, off Falmouth Harbor in England and Bantry Bay in Ireland. Maerl is placed on acidic soil to increase the pH of the soil for crops (Blunden et al., 1997).

The Corallinales form an important part of

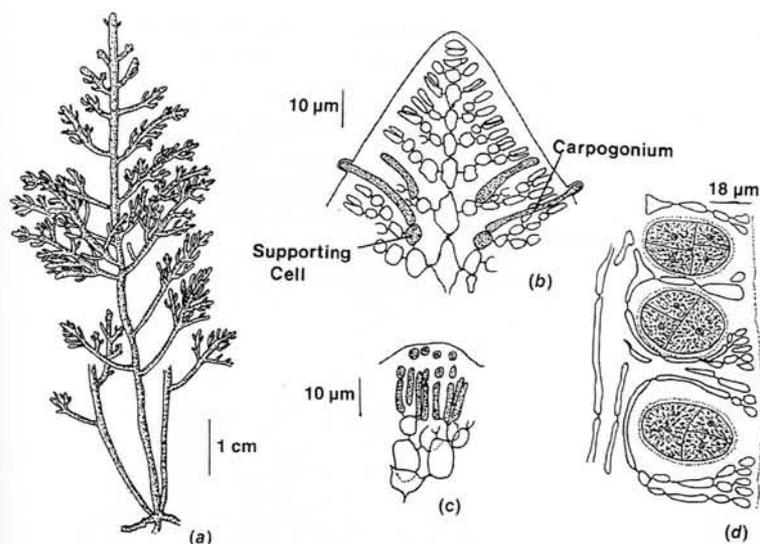
This is an order of uniaxial marine Rhodophyceae in which the carpogonial branch consists of a single cell, the carpogonium. After fertilization, the carpogonium may fuse with the supporting cell and/or nutritive filaments. The tetrasporophyte and the gametophyte are macroscopic plants, although not necessarily similar. The plants are commonly used in the production of agar, with almost half of the world supply coming from members of this order (Lewis and Haniask, 1996).

No member of the order has had its life cycle completed in culture, but it is presumed from plants collected in the field that there is a triphasic life cycle of gametophyte, tetrasporophyte, and carposporophyte.

The gametophyte and tetrasporophyte of *Gelidium* have a dome-shaped apical cell that cuts off daughter cells basipetally (Fig. 4.40). The daughter cells divide to form a thallus that soon loses its uniaxial nature in the mature parts. The carpogonia are usually formed on special ramuli (branches) with a deep apical notch (Fig. 4.41(a)), behind which there is a depression on both surfaces (Figs. 4.40(b), 4.41(a), (b)). The carpogonia are produced in these depressions. The carpogonium is cut off from a cell beneath the surface of the thallus and has a long trichogyne that reaches to the outside of the thallus. The carpogonial branch

to consist of sand and detritus cemented together by the plants and animals. Inside this rim of coralline Rhodophyceae, there is relative calm over the inner part of the reef. Within this inner area, carbonic acid, resulting from the solution of respiratory carbon dioxide produced by the plants and animals living there, tends to dissolve the solid calcareous materials. This dissolution of the inner part of the reef results in a central lagoon that stabilizes itself at a depth of 65 to 100 m.

The reef community is adapted to a low-stress environment characterized by the absence of significant seasonal change. The mean winter



**Fig. 4.40** *Gelidium cartilagineum* var. *robustum*. (a) Whole plant. (b) Section of fertile apex of branch showing apical cell, carpogonia, and supporting cells. (c) Section of spermatangial area. (d) Section of tetrasporangial area. ((a) after Smith, 1969; (b),(c) after Fan, 1961; (d) after Smith, 1938.)

thus consists of a single cell. Nutritive filaments are cut off from the cells at the base of each of the laterals in the fertile area. After fertilization, the carpogonium may fuse with the supporting cell and/or nutritive filaments, with the gonimoblast filaments and carposporangia developing from this fusion cell. Male plants are similar in morphology to female plants, with the spermatangial areas forming irregular patches on the thalli. The cortical cells of a fertile area elongate, fade in color, and become transformed into spermatangial mother cells (Fig. 4.40(c)). The colorless spermatangia are formed by transverse division of the mother cell. The tetrasporangial mother cell is a cortical cell that is terminal on a lateral. It divides to produce four tetraspores in either a cruciate or a tetrahedral arrangement (Fig. 4.40(d)).

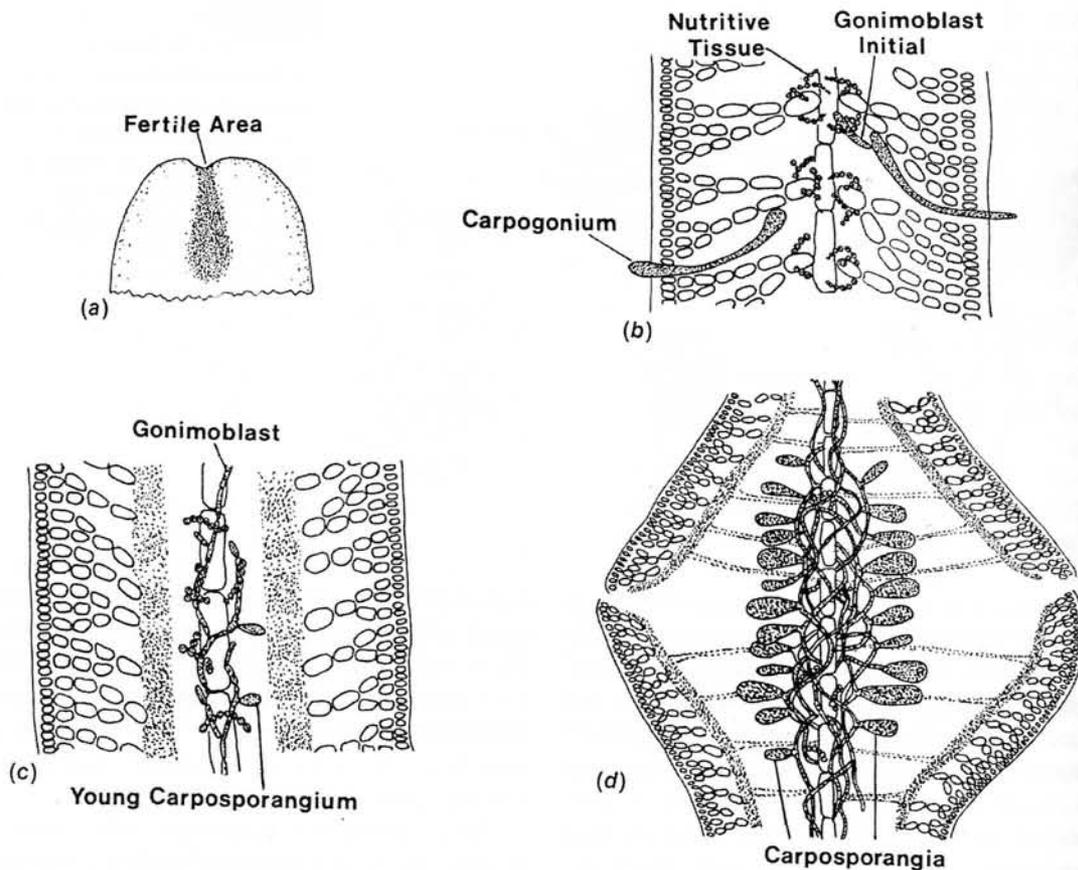
### Gracilariales

The Gracilariales are agarophytes that have a female reproductive system with a supporting cell of intercalary origin that bears a two-celled carpogonial branch flanked by two or more sterile branches (Fredericq and Hommersand, 1989).

The plants in the order are fleshy, having a tendency to be flattened or foliose with pseudo-parenchymatous tissues that lack filamentous cells in the mature vegetative thallus. The principal genus in the family is *Gracilaria*, a widely distributed northern lithophyte found at low-tide level and below, with about 100 species. The

dark-red thallus grows by means of a two-sided apical cell and has tapering branches (Fig. 4.42). There are large isodiametric cells in the medulla, with small cortical cells containing a number of ribbon-shaped chloroplasts. Unicellular hairs arise from enlarged peripheral cells that become multinucleate as they age.

The gametophytic plants are either male or female, and equal numbers of each are produced from tetraspores (Kain and Destombe, 1995). The male plants produce spermatia in antheridial pits over the surface of the thalli. The female plants form supporting cells from the outer layer of the large cells of the medulla (Kylin, 1930), the supporting cells producing the two-celled carpogonial branch and a number of laterals, a cell of which functions as the auxiliary cell. All of the cells of the procarp become multinucleate and develop into nutritive cells except for the carpogonium and the cell beneath it. After fertilization the carpogonium fuses with one of the nutritive cells that is acting as an auxiliary cell. Subsequently, this fusion cell fuses with the other multinucleate nutritive cells. At the same time, the cortical cells above the procarp divide to produce the cystocarp walls, the inner cells of which constitute nutritive cells. Gonimoblast initials are cut off from the fusion cell and develop into an inner sterile area that supports the outer carposporangia. The carposporangia ripen successively from the outside in. In some



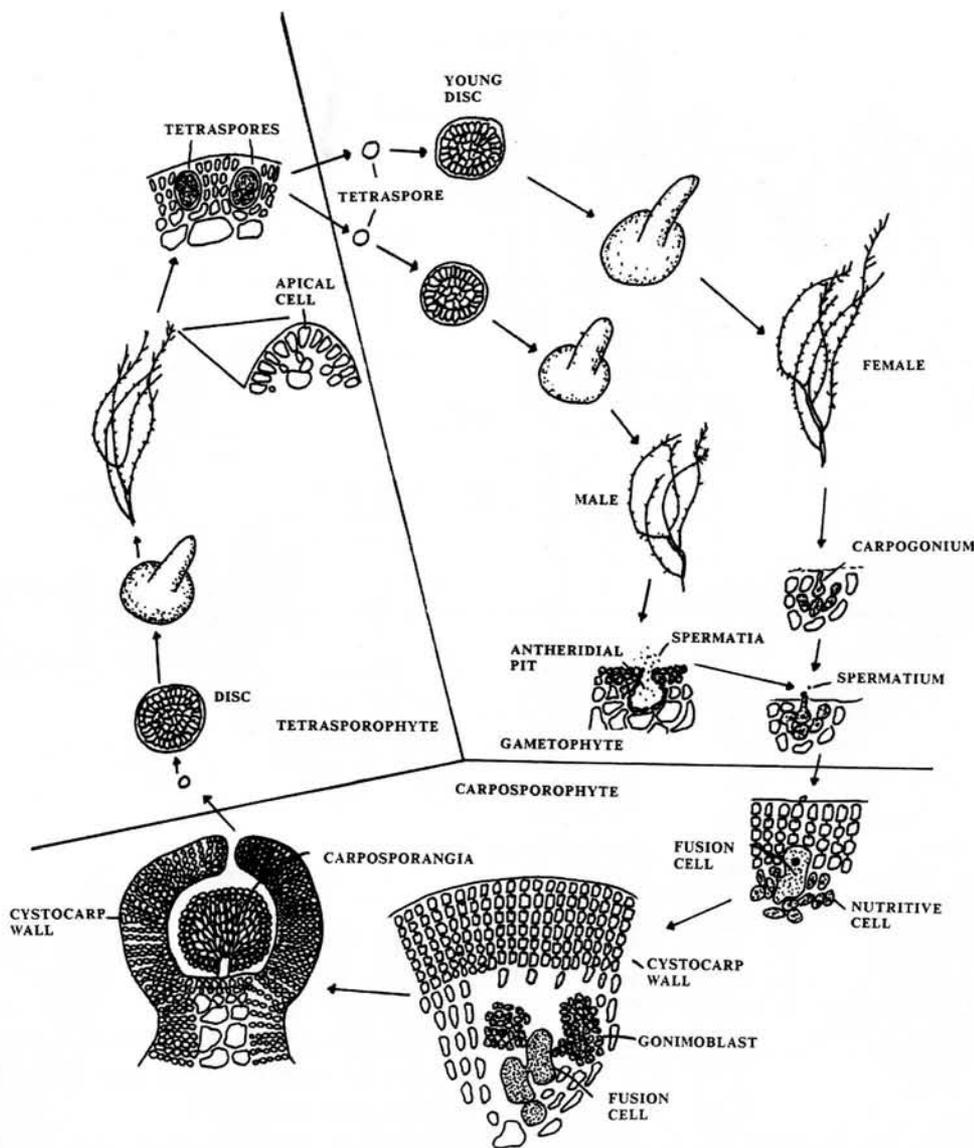
**Fig. 4.41** *Gelidium cartilagineum*. (a) Apex of fertile thallus. (b) Longitudinal section of thallus showing carposonium. (c) Gonimoblast producing young carposporangia. (d) Carposporophyte with mature carposporangia. ((a) after Kylin, 1928; (b–d) after Smith, 1938.)

species, elongate cells radiate from the compact regions of the gonimoblast, penetrating the **pericarp** (cystocarp wall), and become connected with the cells of the pericarp.

The carpospores germinate to produce a parenchymatous disc that forms the tetrasporophyte as an erect protuberance. The tetrasporophyte is morphologically similar to the gametophyte and about the same size as the female gametophyte. Cruciate tetrasporangia are formed terminally on laterals in the cortex and are embedded in the thallus. The tetraspores germinate to form a parenchymatous disc that produces the gametophyte as an erect protuberance (Ogata et al., 1972).

*Gracilaria* is a major agarophyte, currently providing greater than half of the world's supply of agar. The cultivation of *Gracilaria*, both in the sea and in tanks, has been a principal factor in making this genus a source of agar-containing seaweeds (Lewis and Hanisak, 1996). In Taiwan, *Gracilaria* is farmed in brackish-water ponds as a main food source for the cultivation of the small abalone *Haliotis* (Lee, 1999).

Human consumption of species of the red alga *Gracilaria* has been linked to "**ogonori**" **poisoning** (Noguchi et al., 1994; Smit, 2004). The symptoms are hypotension (abnormally low blood pressure), vomiting, nausea, and death resulting from hypotensive shock. Ogonori poisoning is caused by prostaglandin  $E_2$  (Fig. 4.43). Soaking *Gracilaria* in freshwater results in the production of prostaglandin  $E_2$ . This is usually compounded by eating seafood which is rich in prostaglandin  $E_2$ .

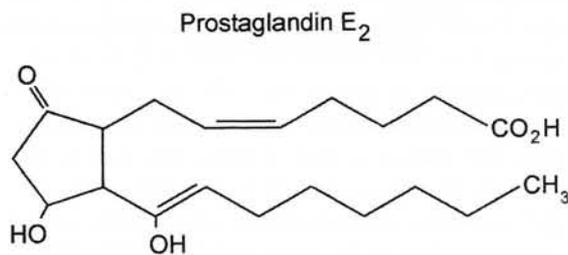


**Fig. 4.42** The life cycle of *Gracilaria* spp. (Adapted from Kylin, 1930; Ogata et al., 1972.)

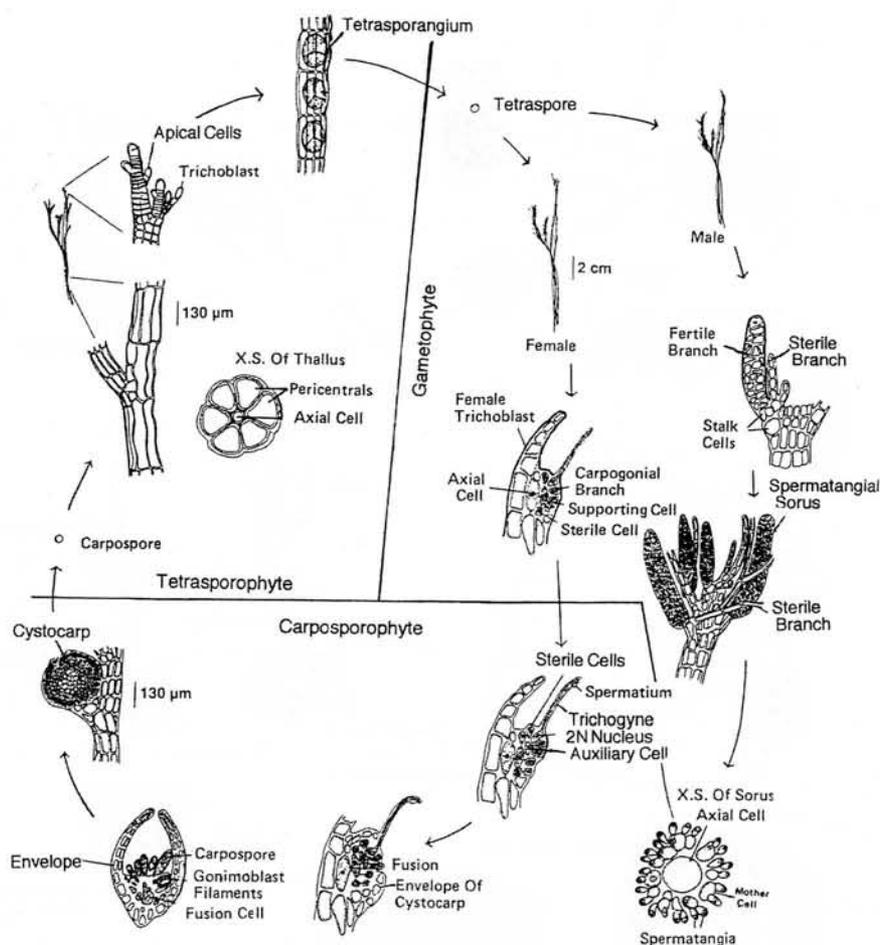
### Ceramiales

These plants have the auxiliary cell cut off after fertilization and borne on the supporting cell of the four-celled carposporangial filament. Most of the plants are relatively delicate filamentous or membranous forms.

In *Polysiphonia* the uninucleate, dome-shaped apical cell (Fig. 4.45(b)) is polyploid and contains 64 to 128 times the amount of DNA in most of the mature cells in the alga (Goff and Coleman, 1986).



**Fig. 4.43** The chemical structure of prostaglandin  $E_2$ .

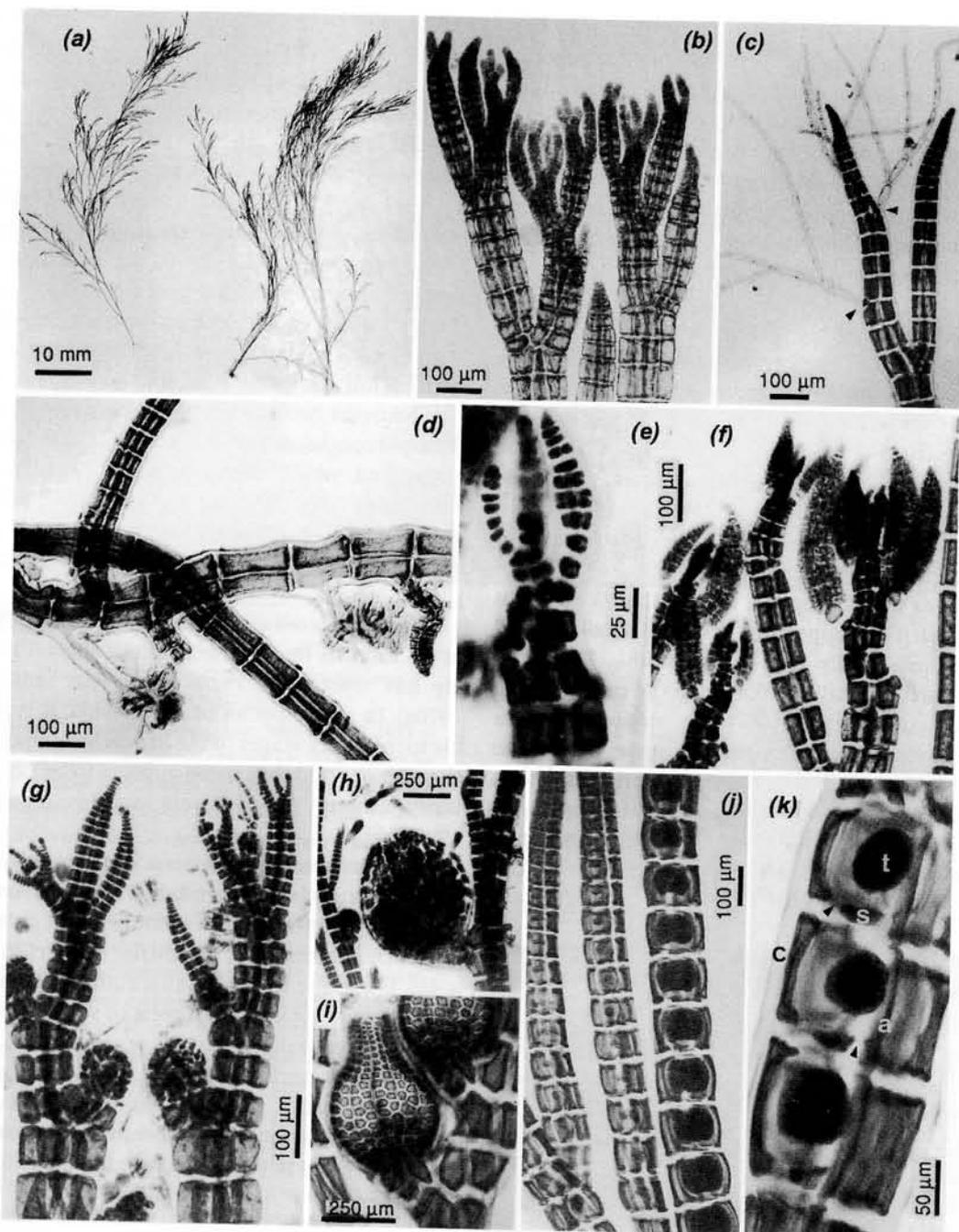


**Fig. 4.44** The life cycle of *Polysiphonia* sp. (Adapted from Kylin, 1923; Edwards, 1970a.)

Division of the cells derived from the apical cell is usually not accompanied by DNA replication; therefore, the farther the daughter cell is from the apical cell, the lower the ploidy of the cell, until the ploidy number stabilizes at  $1n$ . The apical cell forms daughter cells that produce lateral branches before dividing longitudinally into central and pericentral cells (Figs. 4.44, 4.45). The pericentrals are the same length as the axial cells. The lateral branches are of two kinds: the ordinary branches and the trichoblasts. The ordinary branches are polysiphonous with unlimited growth, similar to the main axis. The **trichoblasts** are uniseriate, usually colorless, and bear the sex organs (Fig. 4.45(c)). The trichoblasts progress

through a programmed cell death or apoptosis and drop off from the older parts of the thallus (Garbary and Clark, 2001).

*Polysiphonia* species occur either as lithophytes or as epiphytes on other algae. When the species grows on a solid substrate, some of the polysiphonous axes creep over the substratum to which they are firmly anchored by thick-walled, lobed rhizoids (Fig. 4.45(d)). When it grows as an epiphyte on another alga, the rhizoids penetrate that host tissue (Fig. 4.11). The procarys are produced near the base of a trichoblast (Figs. 4.44, 4.45(g)). The two basal cells of the trichoblast become polysiphonous, and a procarys develops from a pericentral of the upper of the two basal cells. The pericentral (supporting cell) produces in succession a lateral sterile cell, the four-celled carpoogonial branch, and, last, the second sterile cell. The



**Fig. 4.45** Vegetative and reproductive structures of *Polysiphonia stricta*. (a) Habit of thalli from shallow subtidal bedrock. (b) Vegetative apices showing large apical cells with oblique branching. (c) Trichoblasts, composed of uninucleate cells, attached by small scar cells (arrowheads). (d) Prostrate axis attached by unicellular rhizoids in open connection with pericentral cells. (e, f) Developing and mature spermatangial branches with sterile tips. (g) Tips

of female thallus with procarp and early postfertilization cystocarps. (h) Mature globose cystocarp, with extruded pyriform carposporangia. (i) Mature cystocarp. (j) Developing and mature tetrasporangia in long straight rows. (k) Tetrasporangia (t), showing pit connections (arrowheads) between tetrasporangial stalk cells (s), central axial cells (a), and cover cells (c). (From Kim et al., 2000.)

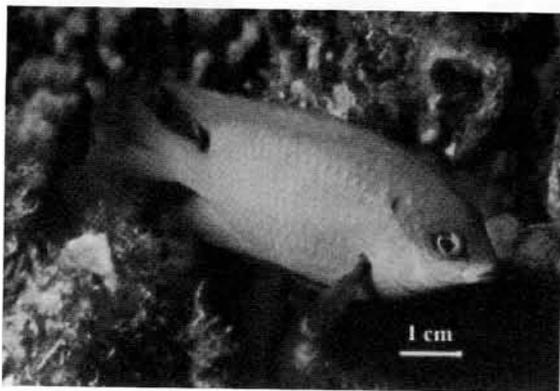
sterile cells divide after fertilization and may have a nutritive role. The cells of the carpogonial branch (with the exception of the carpogonium) are commonly binucleate (Kylin, 1923). A large area of endoplasmic reticulum extends from one pit connection to the other pit connection in each cell of the carpogonial branch. This may be how the message of fertilization is transmitted down the carpogonial branch (Broadwater and Scott, 1982).

The male plants of *Polysiphonia* bear spermatangial sori on a trichoblast consisting of a two-celled stalk surmounted by the fertile regions (Figs. 4.44, 4.45(e), (f)). The upper stalk cell frequently bears a branch. Fertile regions become polysiphonous, and the two pericentrals divide copiously to form a compact layer of mother cells, each of which gives rise to two or three spermatangia (Kylin, 1923). After the spermatium fertilizes the trichogyne, the auxiliary cell is cut off from the supporting cell. The auxiliary cell then fuses with the carpogonium. The male nucleus fuses with the female in the carpogonium (Yamanouchi, 1906), and the diploid nucleus divides once. One of the diploid nuclei passes into the auxiliary cell, which subsequently fuses with the supporting cell. The fusion cell also fuses with the axial cell of the fertile segment. The gonimoblast initials are cut off from the fusion cell

and develop into a number of gonimoblast filaments. The terminal cells of these filaments develop into pear-shaped carposporangia. In the meantime, the fusion cell unites with the gonimoblast initial and the fertile cells. The sterile outer envelope of the cystocarp (Fig. 4.45(b)) originates from the other pericentrals of the axial cell that gave rise to the fertile pericentral that acted as the supporting cell. The young envelope consists of two lateral valves, composed of fused threads, which enclose the procarp like the shells of an oyster, the trichogyne alone projecting. After fertilization the two valves unite, and the envelope becomes two-layered. The carpospores form a tetrasporophyte, which is similar to the gametophyte, and which forms tetrahedrally arranged tetraspores (Fig. 4.45(j), (k)) in polysiphonous branches called *stichidia*. The tetraspores then germinate to form the gametophyte (Edwards, 1969).

*Polysiphonia denudata* completes its life history in 1.5 months in culture; thus the species probably has several life cycles each year (Edwards, 1970a). In some species of *Polysiphonia*, it is possible to influence stages of the life cycle by changing the photoperiod, but there appears to be no regularity among the different species (Edwards, 1970a,b).

In the marine environment, herbivorous damselfish exclude other fish from their territories, and maintain dense stands of filamentous algae. One damselfish, the dusky farmerfish (Fig. 4.46), is unique in that it maintains a monoculture of *Polysiphonia* in coral reefs by selective weeding of other indigestible algae (Hata and Kato, 2003). The farmerfish grazes on the *Polysiphonia* sp. The relationship between the farmerfish and *Polysiphonia* is an example of **mutualism** (a situation where two populations benefit equally).



**Fig. 4.46** The dusky farmerfish *Stegastes nigricans*, a cultivator of *Polysiphonia* in coral reefs.



**Fig. 4.47** Left: Heinrichs Leonhards Skuja. Right: Harald Kylin. (Photograph of Skuja from Wilen and Wingqvist, 1986; photograph of Kylin from *Die Gattung der Rhodophyceen*, CWK Gleerups Forlag, Lund, Sweden.)

**Heinrichs Leonhards Skuja** Born September 8, 1892 in Majori, Rigas-Jurmula, Latvia. Died July 19, 1972. During his youth, Dr. Skuja lived close to the Latvian coast and took an early interest in aquatic plants and animals. During World War I, he lived in the Caucasus, where he was engaged in floristic studies on the Apsheron Peninsula. In 1922, he began his academic studies at the faculty of natural sciences at the University of Latvia, passed a *mag. rer. nat.* examination in 1929, and became *dr. rer. nat.* in 1943. In the autumn of 1944, Dr. Skuja arrived in Sweden, where in 1947 he obtained a position as research professor (*laborator*) and in 1958 he was awarded the degree of *doctor honoris causa* by the University of Uppsala. Besides his extensive publications on the algae, Dr. Skuja also published in the areas of general botany, mycology, and lichenology.

**Harald Kylin** Born Johan Harald Olsson February 5, 1879 near Gothenburg, Sweden. Died 1949. He changed his name to Harald Kylin when he entered the gymnasium (high school) because his father, who was chairman of the parish council, thought Olsson was too common a name. He graduated from Uppsala University in 1901 with a M.Sc. degree and in 1905 with a Licentiate of Philosophy. In 1907 he defended his thesis on algae and became a docent of the University. In 1917 he obtained a chair in botany at the University of Lund and remained there until he retired in 1944. He wrote a large number of publications on the red algae. The last of these was his book *Die Gattung der Rhodophyceen*, which was finished by his wife after his death.



**Fig. 4.48** Gary W. Saunders (right in photograph, with Dr. Gerry Kraft) Born June 30, 1962 in Halifax, Nova Scotia. Dr. Saunders received his B.Sc. in 1985 and his M.Sc. in 1987 from Acadia University. He received his Ph.D. in 1991 from Simon Fraser University. In 1995 he joined the faculty in the Department of Biology at the University of New Brunswick in Canada where he is Professor and Director and Algal Curator of the Connell Memorial Herbarium. Dr. Saunders has been a leader in the field of molecular systematics of the red algae.

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