Glaucophyta

- The Glaucophyta include those algae that have endosymbiotic cyanobacteria in the cytoplasm instead of chloroplasts.
- Because of the nature of their symbiotic association, they are thought to represent intermediates in the evolution of the chloroplast.

The endosymbiotic theory of chloroplast evolution is the one most widely accepted.

- According to this theory, a cyanobacterium was taken up by a phagocytic organism into a food vesicle.
- Normally the cyanobacterium would be digested by the flagellate as a source of food, but by chance a mutation occurred, with the flagellate being unable to digest the cyanobacterium.
- This was probably a beneficial mutation because the cyanobacterium, by virtue of its lack of feedback inhibition, secreted considerable amounts of metabolites to the host flagellate.
- The flagellate in turn gave the cyanobacterium a protected environment, and the composite organism was probably able to live in an ecological niche where there were no photosynthetic organisms (i.e., a slightly acid body of water where free-living cyanobacteria do not grow).

Although similar to cyanobacteria, the cyanelles should be regarded as organelles rather than endosymbiotic cyanobacteria.

- Cyanobacteria have over 3000 genes whereas cyanelles have about the same number of genes as plastids (about 200 genes). It is clear the cyanelles (and plastid) genomes have undergone substantial reduction during endosymbiosis.
- Many of the missing genes eventually relocated to the nucleus, while other genes were lost. For example, cyanobacteria have a respiratory electron-chain whereas plastids do not, the respiratory electron-chain is coded by the nucleus in eukaryotic algae.

There are a number of similarities between cyanobacteria and chloroplasts that support the endosymbiotic theory:

1. they are about the same size;
2. they evolve oxygen in photosynthesis;
3. they have 70S ribosomes;
4. they contain circular prokaryotic DNA without basic proteins;
5. nucleotide sequencing of rRNA or of DNA encoding rRNAs have shown similarities;
6. They have chlorophyll a as the primary photosynthetic pigment.
7. The cyanelles are surrounded by a peptidoglycan wall like cyanobacteria.

The pigments of the Glaucophyta are similar to those of the Cyanophyceae: both chlorophyll a and the phycobiliproteins (such as phycocyanin, phycoerythrocyanin, and allophycocyanin organized in phycobilisomes) are present, however, two of the cyanobacterial carotenoids, myxoxanthophyll and echinenone, are absent.
Thylakoids are not stacked.

Sexual reproduction is unknown in this division.

The organisms in the phylum represent a very old group.

The existence today of few extant members of the group.

Cyanophora paradoxa is a freshwater flagellate with two cyanelles (C) in the protoplasm, each cyanelle with a central dense body.

Nitrate reduction, photosynthesis, and respiration in the cyanelles of Cyanophora paradoxa are similar to the corresponding processes of chloroplasts and dissimilar to those of cyanobacteria.

This fact is cited as evidence that the cyanelles of Cyanophora paradoxa are close to chloroplasts.

However, the cyanelles of Cyanophora paradoxa are primitive in regard to where RuBisCo enzyme is produced.

RuBisCo, the carbon dioxide-fixing enzyme in photosynthesis, consists of 16 subunits, 8 large and 8 small.

In higher plants the large subunits are encoded by DNA of the plastids, whereas the small subunits are encoded by nuclear DNA.

In Cyanophora paradoxa, both sizes of subunits are encoded by cyanelle DNA.

Glaucocystis is also a fresh water organism, found sparingly in soft-water lakes (lakes low in calcium).

It has two groups of cyanelles, one on each side of the nucleus.

It has two reduced flagella found inside the cell wall.

Both of these organisms have starch formed in the cytoplasm, outside of the cyanelles, indicating that the host has accepted responsibility for the formation of the storage product.

There are other organisms that have endosymbiotic cyanobacteria that are not placed in the Glaucophyta.

These organisms have cyanelles that still have a cell wall and are cytologically similar to cyanobacteria, such as the cyanelles of the fungus Geosiphon.

The mechanism of division of cyanelles in Cyanophora paradoxa is different from that of plastids.

Plastids have an inner and outer ring of electron dense material in the area of the dividing organelle.

In division of cyanelles of Cyanophora paradoxa, however, there is only an inner ring in the “stroma” inside the plasma membrane (“inner envelope”) of the cyanelle.

The outer ring, normally outside the outer chloroplast envelope, is missing.

Evolution of the chloroplast

Diagrammatic representation of the uptake of a cyanobacterium by a protozoan into a food vesicle. This resulted in the establishment of an endosymbiosis between the cyanobacterium and the protozoan. Then, the endosymbiotic cyanobacterium evolved into a chloroplast surrounded by two membranes of the chloroplast envelope.
The Rhodophyta (red algae) and Chlorophyta (green algae) have chloroplasts surrounded by only the two membranes of the chloroplast envelope. The event that led to the chloroplast occurred as follows. 

– A phagocytotic protozoan took up a cyanobacterium into a food vesicle.
– Instead of being digested as a source of food, the cyanobacterium lived as an endosymbiont in the protozoan.
– This event benefited the protozoan because it received some of the photosynthate from the endosymbiotic alga, and it benefited the cyanobacterium because it received a protected stable environment.
– Through evolution the wall of the endosymbiotic cyanobacterium was lost.

• A mutation in the endosymbiont which resulted in a loss of the wall has facilitated the transfer of compounds between the host and the endosymbiont.
• The food vesicle membrane of the phagocytotic host became the outer membrane of the chloroplast envelope.
• The plasma membrane of the cyanobacterium endosymbiont became the inner membrane of the chloroplast envelope.
• Rearrangement of the thylakoid membranes and evolution of polyhedral bodies into a pyrenoid completed the transition to a true chloroplast such as occurs in extant green and red algae.

Rhodophyta (red algae)

• Rhodophyta, or red algae, are characterized by
  – the absence of flagellate cells. Flagella and centrioles are never present in any life stage.
  – Pit connections between cells in filamentous genera
  – simple plastids with free ungrouped (un-stacked) thylakoids (one thylakoid per band).
  – Thylakoids lie equidistant. In advanced members of the Rhodophyta peripheral thylakoids are present, which enclose the rest of the thylakoids.
  – Chloroplasts are surrounded only by the two chloroplast membranes (lack of chloroplast ER) and contain pyrenoids.

![Semidiagrammatic drawing of a cell of Porphyridium cruentum.](image)

### Chloroplast DNA

• Phycobilins play an important role in absorbing light for photosynthesis. These pigments can absorb the wavelengths of light that penetrate deep into the water. As a result, phycobilins allow red algae to live at depths where algae lacking these pigments cannot survive.

• Some species of red algae have been found at depths of nearly 270 m, which is about three times deeper than organisms from any other algal phylum have been found.

• Deepest photosynthetic organism is a coralline alga at 210 m depth.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Chromophylls</th>
<th>Phycobilins</th>
<th>Carotenoids</th>
<th>Anthophyllins</th>
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<tbody>
<tr>
<td>Rhodophyta</td>
<td>α, δ</td>
<td>Phycoerythrin, α-Phycocyanin and allophycocyanin</td>
<td>β-Carotene, Lutein</td>
<td></td>
</tr>
</tbody>
</table>
Rhodophyta are a morphologically diverse group.
- About 10 genera are unicellular (coccoid), while
  - the rest are multicellular with
    - simple filaments or
    - branched filaments, although
    - most are pseudoparenchymatous uniaxial or multiaxial thalli (Fig. 6).
- Cell walls have mucilages which compact the adjacent branched filaments and give consistency to the thallus.
- The parenchymatous organization is present in some genera of the order Bangiales, like Porphyra, and in some foliose thalli like Delesseria.

Despite their common name, not all red algae are reddish in appearance; parasitic forms white, cream or yellow; calcified species white, freshwater species often blue-green due to phycocyanin.

A majority of the seaweeds are red algae, and there are more red algae (about 4000 species) than all of the other major seaweed groups combined.

Red algae inhabit prevalently all marine ecosystems at all latitudes from polar to tropical waters but mostly distributed in temperate and tropical regions. There are few species in polar and subpolar regions where brown and green algae predominate.

The average size of the plants differs according to geographical region. The larger species of Rhodophyceae are found in temperate seas, whereas in tropical seas the Rhodophyceae (except for massive calcareous forms) are mostly small, filamentous plants.

They are also present in freshwater and terrestrial environment. About 200 species of Rhodophyceae are found in freshwater, where they do not reach as great a size as the red seaweeds. The majority of freshwater red algae occur in running waters of small to mid-sized streams. Few red algae occur at currents of less than 30 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.

In great majority of multicellular red algae, cytokinesis is incomplete, the cell wall formed during cell division usually leaves a pit in the center. In mature cells, the pits are occluded with a protein plug that looks like a biconvex lens when observed with transmission electron microscopy.

There are several types of protein plugs which have been used in the classification of red algae due to their systematic value.
- At maturity, some rhodophytes produce secondary pits between cells of adjacent filaments.
- The pit connection may function as a site of structural strength on the thallus.

The cell wall of most red algae is composed of microfibrillar framework of cellulose and a high percentage of amorphous polysaccharides or mucilage occur between the cellulose microfibrils which is the source of products of commercial interest, such as agar and carrageenan.

These mucilages may constitute up to 70% of the dry weight of the cell wall.

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A pit connection between cells of Palmaria ricaresis. 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.

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Figure 7. Diagrams of pit plug in the Rhodophyta. (a) The Palmaria type of pit plug, with cap membranes and two-layered plug cap. (b) The Rhodymenia type without cap layers. CM, cap membrane; CO, core of pit plug; IC, inner cap layer; OCL, outer cap layer; PM, plasma membrane; W, cell wall.
• Floridoside (O—α-D-galactopyranosyl-(1,2)-glycerol) is the major product of photosynthesis in the red algae, although mannitol, sorbitol, digalactoside, and dulcitol also occur.

• The concentration of floridoside increases in red algal cells as the salinity of the medium increases. 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.

![Chemical structure of floridoside](image)

- **Floridoside**
  - Floridoside is a major product of photosynthesis in red algae.
  - Increases in red algal cells as salinity increases.
  - Compensates for changes in external osmolarity.

![Floridoside structure](image)

• Corallinales, one of the most important groups of Rhodophyta, incorporate large amounts of calcium carbonate on the walls, as crystals of calcite or aragonite, which gives them an appearance of stone. Calcified "coralline" algae (support reefs)

![Corallinaceae](image)

• **Complementary chromatic adaptation** occurs in the red algae.
  - Orange and red light stimulate the production of long-wavelength absorbing phycoerythrin.
  - Green light stimulates the formation of short-wavelength absorbing phycocyanin.

• The color will vary.

![Floridean Starch Unit](image)

- **Floridean Starch**
  - α-1,4-glucan polysaccharide.
  - Produced in chloroplasts.

• Most rhodophytes live photoautotrophically and the most important storage product is **floridean starch**, an α-1,4-glucan polysaccharide.

- Grains of this starch are located only in the cytoplasm outside the chloroplast, unlike the starch grains produced in the Chlorophyta, which lie inside the chloroplasts.

- The color will vary.

![Iridescence](image)

- **Iridescence**
  - Blue or green iridescence in reflected light.
  - Not related to light producing phenomena such as phosphorescence or bioluminescence.

- 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.

- These "secretory cells" and "gland cells" may have compounds that act as deterrents to grazing, or they may accumulate special reserves for metabolic use.

- Secretory cells (vesicular cells) occur in some Rhodophyceae (Fig. (a), (b)). These cells are colorless at maturity and commonly have a large central vacuole. The secretory cells in one red alga are associated with high concentrations of iodine.

- In other algal species (Opuntiella californica), there are "gland cells" with a large vacuole containing a homogeneous proteinaceous material.

- Semidiagramatic 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.

- Secretory cells
  - Occur in some Rhodophyceae.
  - Colorless at maturity.
  - Have a large central vacuole.
  - Associated with high concentrations of iodine.

- Iridescence
  - Blue or green iridescence in reflected light.
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- Secretory cells
  - Vesicular cells.
  - Large central vacuole.
  - Associated with iodine.

- Gland cells
  - Large vacuole.
  - Proteinaceous material.

- Semidiagramatic drawing of gland cell.
Defense mechanisms of the red algae

- Benthic marine red seaweeds are particularly susceptible to being overgrown by epiphytes because 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.

Epiphytes and parasites

- Rhodophycean organisms range from autotrophic, independent plants to complete heterotrophic parasites.
- 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.
  - Alloparasites are not closely related to their hosts.

- Delisea secretes halogenated furanones (Fig. 4.14) that affect the growth of epiphytes and keep the thallus clean.
- Gracilaria conferta 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 neoagarosehexaose oligosaccharides.
- Gracilaria cells respond to nanomolar concentrations of the oligosaccharides by increasing respiration and producing active oxygen species such as hydrogen peroxide (H₂O₂) and hydroxyl radicals (OH⁻). The hydrogen peroxide is degraded to water and molecular oxygen:

  \[ \text{H}_2\text{O}_2 \rightarrow \text{H}_2\text{O} + \text{1/2O}_2 \]

- Molecular oxygen is toxic and results in the elimination of 90% of the epiphytes within 15 minutes under experimental conditions.

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 which containing the pathogens at the site of attack.

Commercial utilization of red algae

- Commercial utilization of red algae concerns the polysaccharidic mucilages of the cell wall, agar and carrageenan used for food processing, micro- and molecular biology.
- Agar
  - Agar is obtained commercially from species of Gelidium and Plocamium as well as from various other algae, such as Acarophyllum, Ahnfeltia, and Gracilaria.
- Carrageenan
  - Carrageenan is usually obtained from wild populations of Irish moss, the name for a mixture of Chondrus crispus and the various species of Gigartina. In the Philippines, Eucheuma, and in Vietnam and India, Kappaphycus are extensively cultivated as a source of carrageenan.
  - The red microalga Porphyridium is an important source of polyunsaturated fatty acids, such as arachidonic acid.
- Red seaweed (Porphyra) cultured for nutrition in Japan.
- Antimicrobial compounds and anti-grazing compounds; of interest to pharmaceutical research.
Asexual spores

- **Monosporangia** (one spore per sporangium) and **parasporangia** (more than one spore per sporangium) produce asexual spores that reform the parent thallus.

Living in extreme environments:
- The Rhodophyta have the ability to live at greater depths in the ocean than do members of the other algal classes.
- unicellular red algae can grow in acidic hot springs.

- The class Florideophyceae contains most of the Rhodophyta with a more complex morphology and is characterized by a life cycle of three generations:
  - a haploid stage, the gametophyte,
  - and two diploid stages.
- The diploid stages consist of a parasitic stage called carposporophyte which grows on the gametophyte and a second stage which is usually free, called tetrasporophyte, in which the tetrasporangia produce four motile spores or tetraspores.

Species in which sexual reproduction is known generally have an isomorphic or heteromorphic diplontic life cycle; haplontic life cycle is considered an exception.

Rhodophyta are grouped into seven classes.

The first six classes include the simplest forms with haplontic or haplo-diplontic life cycles like *Porphyra*, and most of them live in freshwater.

- **Florideophyceae** contains most of the Rhodophyta with a more complex morphology and is characterized by a life cycle of three generations:
  - a haploid stage, the gametophyte,
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Tetrasporophytes and gametophytes can be isomorphic or heteromorphic. The carposporophyte is considered a parasite of the gametophyte, since feeder cells from the gametophyte are frequently involved in its development.

In sexual reproduction, the female gametophyte, called carpogonium (1), are bottle-shaped with a narrow neck or trichogyne (2). The immobile male gametes, known as spermatia (3), are produced in spermatangia (4). The spermatia are passively transported by water currents until they contact the carpogonium. The fertilized carpogonium produces gonimoblast filaments (5) that form carposporangia (6) and diploid carpospores (7).

The carpospores produce the diploid tetrasporophyte which is subsequently separated by transverse wall fissions (8). The tetraspores complete the life cycle by germinating to form the gametophyte.

The tetrasporangia form the four tetraspores either in crosswise (cruciate), a row (zonate), or most commonly in a tetrad (tetrahedral).
Life cycle in *Polysiphonia* sp.

- Although this is the general life cycle of most *Rhodophyceae*, there are a number of modifications of it.

  - In Florideophyceae, the carpogonium (1) arises directly from a vegetative cell or appears at the apex of a specialized filament 2 to 5 cells long, the carpogonial branch (2).
  - Next to carpogonium, there may be one or more auxiliary cells (3) which the zygote is transferred to after fertilization.
  - Asexual reproduction occurs in tetrasporophytes through diploid monospores.
  - Spore motility: Spores, whether monospores, tetraspores or carpospores, of almost all red algae are capable of motility by gliding. Polysaccharide secretion appears to be responsible for the gliding.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Subphylum</th>
<th>Class</th>
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<tbody>
<tr>
<td>Rhodophyta</td>
<td>Cyanidiophytina</td>
<td>Cyanidiophyceae</td>
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<td></td>
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<td>Compsopogonophyceae</td>
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<td>Porphyridiophyceae</td>
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<td>Stylonematophyceae</td>
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<td></td>
<td></td>
<td>Bangiophyceae</td>
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<td></td>
<td></td>
<td>Porphyra</td>
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</tbody>
</table>

- Two subphyla are recognized: the subphylum Cyanidiophytina with only one class, *Cyanidiophyceae*, the most primitive group of red algae with unicellular, freshwater representatives, and the subphylum Eurhodophytina, which includes the rest of the red algae, with 6 classes.

**Bangiophyceae** are freshwater or marine.

Their thalli can be formed by:
- unbranched filaments, as in *Bangia*.
- branched filaments as in *Asterocystis* (Fig. 3f) or by a parenchymatous lamina as in *Porphyra*.

The blade of *Porphyra* is the gametophyte generation, which alternates with a sporophyte generation formed by branched filaments, known as the Conchocelis phase.

- The life cycle in *Porphyra* is controlled by photoperiod.
  - Under long-day conditions, the Conchocelis stage differentiates diploid spores or monospores (8), which reform the Conchocelis stage (7).
  - Under short days the Conchocelis stage forms carpospores (2), which generate a macroscopic gametophyte with a laminar appearance.

**Porphyra** is of great commercial importance. It is grown in large marine farms, and is known by the Japanese name Nori.

**Figure 8. Life cycle in *Porphyra* sp.**
Porphyra Cultivation

- Porphyra has an annual value of more than U.S. $1.8 billion and is considered the most valuable maricultured seaweed in the world. According to the Food and Agriculture Organization of the United Nations (FAO) (2003), nearly 1,011,000 metric tons (wet weight) of Porphyra were produced through mariculture.
- Porphyra has nearly 133 species distributed all over the world. Six species of Porphyra are usually cultivated.
- The plants can grow from 5 to 35 cm in length.
- The thalli are either one or two cells thick, and each cell has one or two stellate chloroplasts with a pyrenoid.

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Life cycles in class Florideophyceae are usually trigenetic with isomorphic or heteromorphic alternation or generations.
- Three generations or phases alternate in the cycle:
  - two diploid phases, the carposporophyte and tetrasporophyte, and
  - one haploid phase, the gametophyte.

Figure 11. Life cycle in Polysiphonia sp.

- The asexual life cycle of Porphyra comprises the following—the aplanospore (1), the gametophyte, and the bipolar sporeling (2).
The order Acrochaetiales is the simplest group, consisting of branched filaments. The carpogonium originates from a vegetative cell, and the carposporophyte develops directly from the fertilized carpogonium without an auxiliary cell. The life cycle is isomorphic alternation of generations, and tetrasporangia are cruciate. Protein bodies of pits plugs have a cap consisting of inner and outer layers which are similar in thickness.

Audouinella is a cosmopolitan genus living in fresh and marine waters. The thalli are small, uniseriate branched filaments formed by a few cells surrounded by mucilage. Asexual reproduction occurs by monospore formation.

Nemaliales have thalli of multiaxial structure. Pit plugs only present the inner layer of the cap. One of the cells of the nutritional branch acts as the auxiliary cell. Tetrasporangia are cruciate.

Nemalion, Liagora and the tropical genus Galaxaura are abundant in the sea shore. Nemalion is a mucilaginous rarely branched thallus with blunt apices. Liagora is a terete branched thallus with a lubricus texture, impregnated with carbonate calcium. Galaxaura, with subdichotomous thallus, is calcified and has similar gametophytes and tetrasporophytes.

Nemalion helminthoides Liagora Galaxaura

Coralinales is a cosmopolitan group which is very important in tropical seas as their representatives are actively involved in the formation of coral reefs. Its members are multiaxial and have calcium carbonate deposits on their walls. Pit plugs are characterized by their dome-shaped outer caps. The tetrasporangia are zonate. The basal cell or supporting cell of the two-celled carpogonial branch is the auxiliary cell. Reproductive organs are in conceptacles, cavities opening to the exterior by one or more pores.

It is a group with great morphological diversity with crustose species like Lithophyllum, Lithothamnion or Melobesia (Fig. 10D) and articulate species like Corallina, Jania or Amphiroa (Fig. 10C).

Coralina articulate species

The order Gigartinales and Ceramiales are the largest orders of red algae. Thalli of Gigartinales are uniaxial or multiaxial. Pit plugs are devoid of caps. The auxiliary cell is an intercalary cell of the nutritional branch, and it is generated before fertilization. Tetrasporangia can be cruciate or zonate.

In this group, some genera like Chondrus, Mastocarpus and Gigartina are of economic interest, since they are used for obtaining the phycocolloid carrageenan.

The most representative genus is Gelidium. In Gracilariales, the principal genus of the order is the agarophyte Gracilaria with uniaxial, terete or flattened thallus. In this group, the supporting cell originates a two-celled carpogonial branch and several sterile branches. The carposporangia are surrounded by a pericarp forming a surface cistocarp.
• The order Ceramiaceae differs from Rhodymeniales because
  – the auxiliary cell is generated after fertilization from the supporting cell of the four-celled carpogonial branch.
  – After fertilization, a cystocarp or gonimocarp is developed.
  – Tetrasporangia are cruciate or tetrahedral.
  – The pit plugs have no cap layers.

• The order contains more than 2,000 species and nine families which are widely distributed. Ceramiaceae include widely distributed genera of delicate filaments, such as Antithamnion, Ceramium or Callithamnion, and Rhodomelaceae include genera as common as Polysiphonia or Chondria.

• In Rhodymeniales,
  – pit plugs are also devoid of caps.
  – The auxiliary cell originates before carpogonium fertilization and is characterized by the formation of a cystocarp.
  – Tetrasporangia are cruciate or tetrahedral.
  – Many of its species, like Rhodymenia, have laminar shapes.

• The Halymeniales order is close to Rhodymeniales.
  – It consists of multiaxial thalli with isomorphic alternation of generations.
  – Carpogonial branches are of two or four cells, and auxiliary cells are intercalary.
  – Cystocarps are composed of carposporangia buried within rudimentary pericarps.
  – Tetrasporangia are cruciate.
  – The most numerous genera are Halymenia and Gratelapia.