

Wolfgang Frey (Editor)

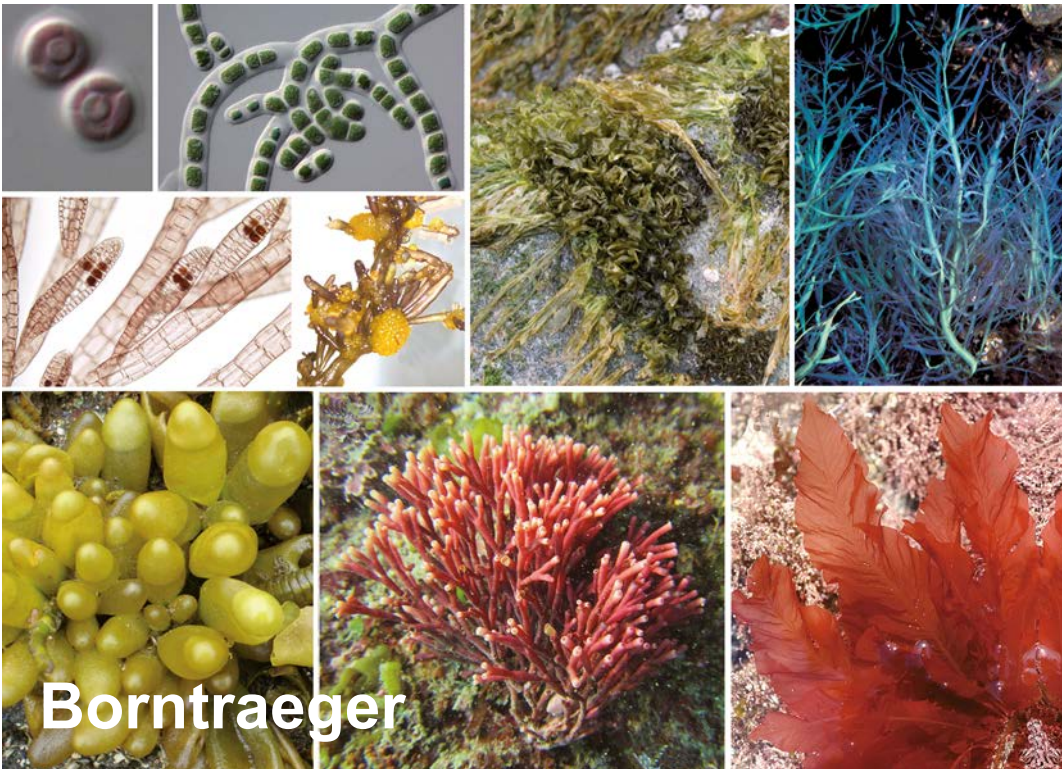
# Syllabus of Plant Families

13<sup>th</sup> ed.

A. Engler's Syllabus der Pflanzenfamilien

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## 2/2 Photoautotrophic eukaryotic Algae Rhodophyta



# Syllabus of Plant Families

## Adolf Engler's Syllabus der Pflanzenfamilien

13<sup>th</sup> edition by Wolfgang Frey

### Part 2/2      Photoautotrophic eukaryotic Algae Rhodophyta

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*Rhodorus marinus* Geitler (Stylonematophyceae, Stylonemataceae). Unicellular, multilobed parietal reddish chloroplast with pyrenoid. Photo: A. Yokoyama.

*Chroodactylon ornatum* (C.Agardh) Basson (Stylonematophyceae, Stylonemataceae). Pseudofilamentous, with false branching. Photo: A. Yokoyama.

*Platysiphonia delicata* (Clemente) Cremades (Rhodymeniophycidae, Sarcomeniaceae). Detail of branches with tetrasporangia. Photo: J.M. Huisman.

Parasitic *Benzaitenia yenoshimensis* Yendo on *Chondria crassicaulis* Harvey (both taxa Rhodymeniophycidae, Rhodomelaceae). Photo: M. Kamiya.

*Wildemanian norrisii* (V.Krishnamurthy) S.C.Lindstrom surrounded by *Pyropia pseudolanceolata* (V.Krishnamurthy) S.C.Lindstrom (Bangiophyceae, Bangiaceae). Photo: S.C. Lindstrom.

*Sarcomenia delesserioides* Sonder (Rhodymeniophycidae, Sarcomeniaceae). Thallus erect, with monopodial organization. Photo: J.M. Huisman.

*Halosaccion glandiforme* (S.G.Gmelin) Ruprecht (Nemaliophycidae, Palmariaceae). Thallus hollow, saccate. Photo credit: M. Lindeberg.

*Tricleocarpa* sp. (Nemaliophycidae, Galaxauraceae). Photo: S.-M. Lin & M.D. Guiry.

*Delesseria sanguinea* (Hudson) J.V.Lamouroux (Rhodymeniophycidae, Delesseriaceae). Tetrasporophyte. Photo: S.M. Lin & M.D. Guiry.

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# Preface

Half a century ago, in 1954, the 12<sup>th</sup> edition (vol. 1, 2) of Adolf Engler's well-known "Syllabus der Pflanzenfamilien" ("Syllabus of Plant Families"), ed. by H. Melchior and E. Werdermann was published. Later, a revision of the mosses (13<sup>th</sup> ed., Kapitel V,2 Bryophytina), by K. Walther, followed in 1983.

The 13<sup>th</sup> edition will be published in five parts, it started in 2009 with **Part 3 "Bryophytes and seedless Vascular Plants"** and was followed in 2012 by **Part 1/1 "Blue-green Algae, Myxomycetes and Myxomycete-like organisms, Phytoparasitic protists, Heterotrophic Heterokontobionta and Fungi p.p."**, in 2015 by **Part 2/1 "Photoautotrophic eukaryotic Algae" [Glaucobionta, Heterokontobionta p.p. (Cryptophyta, Dinophyta, Haptophyta, Heterokontophyta), Chlorarachniophyta, Euglenophyta, Chlorophyta, Streptophyta p.p. (except Rhodophyta)]** and **Part 4 "Pinopsida (Gymnosperms), Magnoliopsida (Angiosperms) p.p.: Subclass Magnoliidae [Amborellanae to Magnolianae, Lilianae p.p. (Acorales to Asparagales)]"** and in 2016 by **Part 1/2 "Ascomycota"**. Now **Part 2/2 "Rhodophyta"** is being published. Just as the other parts of the Syllabus this volume provides a basic treatise of the world-wide morphological and molecular diversity of the **Rhodophyta**.

Following the tradition of Engler, and incorporating the latest results from molecular phylogenetics and phylogenomics, this completely restructured and revised 13<sup>th</sup> edition provides an up-to-date evolutionary and systematic overview of the red algae groups. It is a mandatory reference for students, experts and researchers from all fields of biological sciences, particularly botany, phycology, and mycology.

The publisher, Dr. A. Nägele, and the editor are grateful to Professor Hiroshi Kawai, Kobe University, Rokko-dai, Nada-ku, who generously recommended several colleagues to contribute to this issue of the Syllabus and for the coordination of the authors. We are very grateful for this generous support.

The chapter "Rhodomelaceae" was contributed by the editor, following Algaebase.

The authors and the editor are grateful to the publisher, Dr. A. Nägele, for realizing this basic and fundamental systematic treatise "**Rhodophyta**" of the "**Syllabus of Plant Families**".

Berlin, September 2016

W. Frey





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# Abbreviations

acc.	according to
al.	see et al.
approx.	approximately
C	Central, central
c.	circa, about, approximately
class.	classes
cm	centimetre
cosmopol.	cosmopolitan
diam.	diameter
E	East, eastern
ed., eds.	editor, editors
e.g.	for example, <i>exempli gratia</i>
emend.	emendavit, emendation, amendment; correction of a taxon
ER	endoplasmatic reticulum
et al., & al.	et alia, and others
excl.	excluding
fam.	family, families
fig., figs	figure, figures
gen.	genus, genera
I., Is., i., is.	island, isle; islands, isles
i.e.	that is, <i>id est</i>
inc. sed.	incertae sedis, uncertain systematic position
incl.	including
ined.	inedited, not published
LMWC	Low molecular weight carbohydrate
max.	maximal, maximally
Ma	million years ago
medit., Medit.	mediterranean, Mediterranean region
µm	micrometer
N	North, northern
n	chromosome number
nom. cons.	nomen conservandum, conserved name
nom. rejic.	nomen rejiciendum, rejected name
NE	Northeast, northeast
NW	Northwest, northwest
NSW	New South Wales (Australia)
occ.	occasional, occasionally
ord.	order, orders
Orig., orig.	original, originally
pantrop.	pantropical, in all tropical areas
p., P., Pp., pp.	page, pages

---

pH	pH value
phot.	photograph, photographs
p.p.	pro parte
prob.	probably
Qld.	Queensland (Australia)
resp.	respectively
S	South, southern
SE	Southeast, southeastern
s. l.	sensu lato, in a wide sense
sp., spp.	species, species (plural)
s. str.	sensu stricto, in a strict sense
subclass.	subclasses
subdiv.	subdivision
subfam.	subfamily, subfamilies
subtrop.	subtropical, Subtropics
SW	Southwest, southwestern
syn.	synonym, synonymous
Tas.	Tasmania
tax.	taxon
temp.	temperate, in temperate zones
trop., Trop.	tropical, tropics, Tropic (geo)element, Tropics
U.K.	United Kingdom
USA	United States of America
Vic.	Victoria (Australia)
vol.	volume
W	West, western
warm-temp.	warm-temperate
(5)	number of species
°C	degree Celsius

# 1 Introduction

The last two and a half decades provided revolutionary new insights into the phylogeny and diversity of organisms on earth. This is particularly also true of the Red algae (Rhodophyta), where phylogenetic revisions have revolutionized the systematic classification of taxa from phylum to species level and a new understanding of algal evolution and species delimitation has emerged. These new insights are treated here, as well as in the other parts of the Syllabus in an integrated context of morphological and molecular data, providing an up-to-date synopsis of this plant group.

The present Part 2/2 of the 13<sup>th</sup> edition of “Engler’s Syllabus of Plant Families” gives an up-to-date review of the Rhodophyta, an algal group with an extremely great wealth of morphological and ecological diversity, and their relationships, integrating morphological-anatomical and molecular data. This synthesis includes a complete phylogenetic synopsis of all taxa down to genus level together with detailed descriptions for all families, and complete listings of genera per family, with estimates of species numbers at the family and genus level, combined with numerous new discoveries made during the last ten years.

“Red algae are a fascinating and diverse plant group”, as shown in Part Ecology (‘Characterization and systematic relationships’ of Rhodophyta), with a total of c. 7.000 species. “The majority of species is marine, diverse in pantropical regions. A small group is distributed in freshwater habitats, some species inhabit brackish regions. Most red algae live attached to rocks or solid substrata, some species grow free-floating or entangled in other vegetation. Many species occur as epiphytes, attached to other macroalgae or seagrasses. There are obligate epiphytes, species of small filamentous red algae ramify within the tissues of other seaweeds; some endophytes show host specificity, a small group are parasites (mostly adelphoparasites), occurring on red algal hosts and epizoic or endozoic red algae have been reported. *Porphyridium* spp. are photosynthetic endosymbionts within large tropical foraminifera, and thalli of *Ceratodictyon* species live symbiotic with a haplosclerid sponge”.

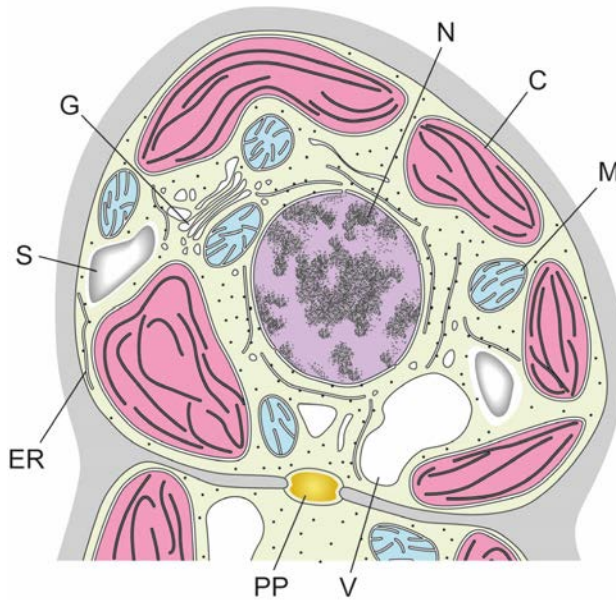
Engler’s Syllabus is an attempt to give an up-to-date evolutionary and systematic overview of the plant, algal and fungal groups. With Part 2/2 “**Rhodophyta**” the treatment of the algal groups has been completed. The remaining parts of the Syllabus, Part 1/3 “**Basidiomycota**” and Part 5 “**Angiospermae p.p.**” will follow in the near future.

## 2 Division Rhodophyta Wettstein

### Characterization and systematic relationships

The Rhodophyta belong to the Kingdom Plantae, which includes the glaucophyte (Glaucobionta, Glaucocystophyta, see Part 2/1 of the Syllabus), chlorophyte, charophyte, rhodophyte and land plants. The Plantae consist of primary plastid-bearing organisms that evolved via the endosymbiotic association between a heterotrophic eukaryote host cell and a cyanobacterial endosymbiont, approx. 1,600 Ma (Yoon et al. 2004). The red algae, including more than 7,000 species, form a monophyletic lineage and are characterized by some unique features: lack of flagella and centrioles in their entire life history, a special intercellular connection system (pit connections) seen in the most multicellular species, and triphasic sexual life history in the Florideophyceae. Many so called 'primitive' red algae occur as unicells, colonies, or small filaments or sheets of cells usually lacking intercellular connection and differentiation in the vegetative phase. More 'advanced' taxa have thalli of widely varying morphology, including more complex filaments, occasionally large terete, crustose, membranous or foliose thalli. Red macroalgae are abundant in tropical to cold seashores, where they are of economic and ecological significance. *Pyropia* and a few other red algae are cultured for use as human food, whereas carageenophytes (e.g., *Euचेuma*, *Kappaphycus* and *Chondrus*) and agarophytes (e.g., *Gelidium* and *Gracilaria*) are cultivated and/or harvested from natural populations to produce carrageenan and agar that are widely used in food products and laboratory experiments.

**Cell structure and component.** Golgi bodies are often tightly associated with other organelles, and 3 types of arrangement have been reported: 1) Golgi-nucleus association in *Dixonella* and *Glaucosphaera* (Rhodellophyceae); 2) Golgi-endoplasmic reticulum (ER) association in the Cyanidiophyceae, Compsopogonophyceae, Stylonematophyceae and *Rhodella* (Rhodellophyceae); and 3) Golgi-mitochondrion in the Porphyridiophyceae, Bangiophyceae and Florideophyceae (Fig. 2-1; van den Hoek et al. 1995, Saunders & Hommersand 2004, Scott et al. 2010, Yoon et al. 2010). The carbohydrate storage product floridean starch is deposited in the cytoplasm. Red algae also synthesize various Low molecular weight carbohydrates (LMWC), e.g., digeneaside, floridoside, trehalose, mannitol, sorbitol and dulcitol. These carbohydrates can be useful for some higher-level red algal classification (Karsten et al. 1999, 2003, 2007). Red algal cell walls are mainly composed with microfibrillar framework of cellulose, although haploid gametophytes of the Bangiophyceae contain  $\beta$ -1, 3 xylan (polysaccharide composed of xylose residues) instead of cellulose (Frei & Preston 1964). Some red algae contain sulphated polysaccharides such as agar and carrageenan between the cellulose microfibrils, and others deposit anhydrous calcium carbonate in their cell walls.



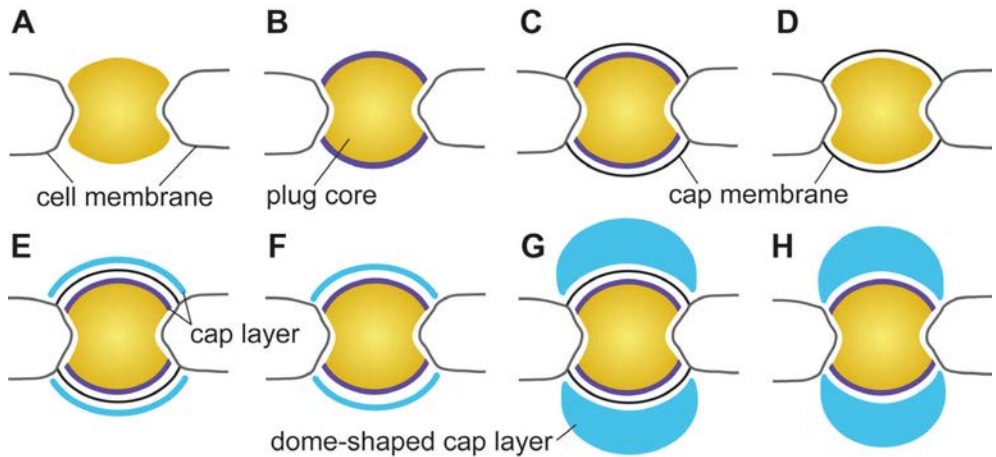
**Fig. 2-1. Diagram of the ultrastructure of a multicellular red alga *Agardhiella subulata* (Gigartinales, Florideophyceae).** [C chloroplast; ER endoplasmic reticulum; G Golgi body; M mitochondrion; N nucleus; PP pit plug; S starch granule; V vacuole]. (Klepacki et al. 1995 is modified by T. Nakayama and M. Kamiya; without scale).

**Chloroplast.** Chloroplasts can be with or without one or more pyrenoids and stellate to ribbon-like or discoid in shape. The chloroplast is surrounded by a double-membrane envelope, lacking any additional layers of ER. Thylakoids are unstacked, evenly spaced, and 1 or sometimes 2 thylakoids are present around the periphery of the chloroplast, running parallel to the chloroplast envelope, although such a peripheral encircling thylakoid is absent in Porphyridiophyceae, Bangiophyceae and some genera in Rhodellophyceae (Scott et al. 2010). Photosynthetic pigments are chlorophyll *a*, phycobiliproteins (phycoerythrin, phycocyanin and allophycocyanin), and several xanthophylls. The phycobiliproteins are located in hemidiscoidal, occasionally hemiellipsoidal or hemispherical, phycobilisomes, associated with light harvesting antennae of photosystem II, on the stromal surfaces of thylakoids (Gantt 1990).

**Motility.** Red algal cells have neither flagella nor any other specialized structures for locomotion in the entire life history. Nevertheless many unicellular red algae and spores (whether monospores, tetraspores, carpospores or zygospores) display various forms of motility: smooth, directional and continuous gliding, non-continuous and random movement, and amoeboid motion (Pickett-Heaps et al. 2001, Ackland et al. 2007).

**Cell division.** The nuclear envelope remains intact during mitosis (closed mitosis). At each pole of the spindle, a centriole is lacking but a darkly staining body, which is usually ring-shaped, is present in some species (polar ring; Scott & Broadwater 1990, van den Hoek et al. 1995). Cytokinesis starts with infurrowing, but an open protoplasmic connection (called pit

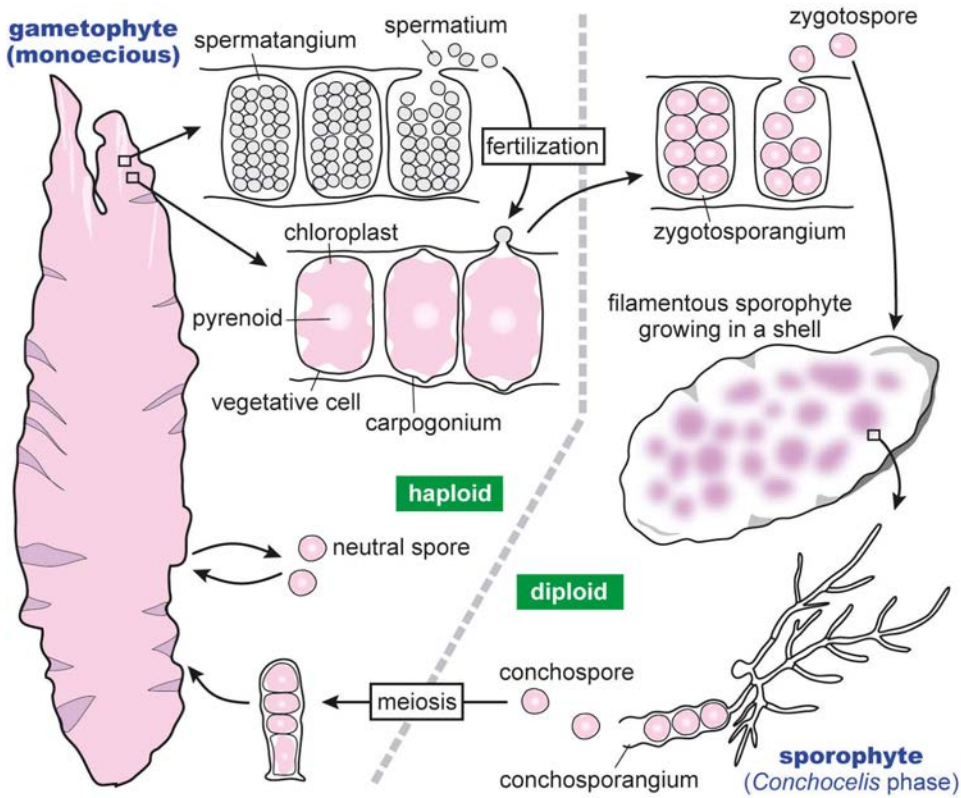




**Fig. 2-2. Diagram of pit plugs (Rhodophyta).** A. Plug core without any accessory structure; seen in the Compsopogonales, Rhodochaetales and Ahnfeltiales. B. Plug core with inner cap layers; seen in sporophytes of the Bangiales. C. Plug core with inner cap layers and cap membranes; seen in the Hildenbrandiales and Gelidiales. D. Plug core with cap membranes; seen in the Pihelliales and most orders of the Rhodymeniophycidae. E. Plug core with cap membranes sandwiched between inner and outer cap layers; seen in the Palmariales, Acrochaetales, Colaconematales, Entwisleiales and Nemaliales. F. Similar to type E but cap membranes are absent; seen in the Rhodachlyales and Thorealess. G. Similar to type E but outer cap layers are domed; seen in the Colaconematales. H. Similar to type G but cap membranes are absent; seen in the Balbianiales, Batrachospermales, and all orders of the Corallinophycidae. (Orig., illustration M. Kamiya).

connection) is retained between the daughter cells due to incomplete cleavage (Ramus 1969, Ueki et al. 2008). This pit connection is immediately plugged up by a pit plug. In addition to the pit connection produced by ordinary cell division (termed primary pit connection), 2 cells not derived from a common cell division can be linked by transfer of an uninucleate small conjuctor cell from one cell to another (secondary pit connection; Goff & Coleman 1990). A proteinaceous plug core is always seen at the center of pit plugs, and the presence of additional structural components at the cytoplasmic faces of pit plug, i.e., cap membrane and inner and outer cap layers, depends on the taxonomic group (Pueschel 1989). At least 8 different types of pit plug can be recognized and their distribution among the Rhodophyta is considered useful for ordinal or higher classification (Fig. 2-2; Saunders & Hommersand 2004).

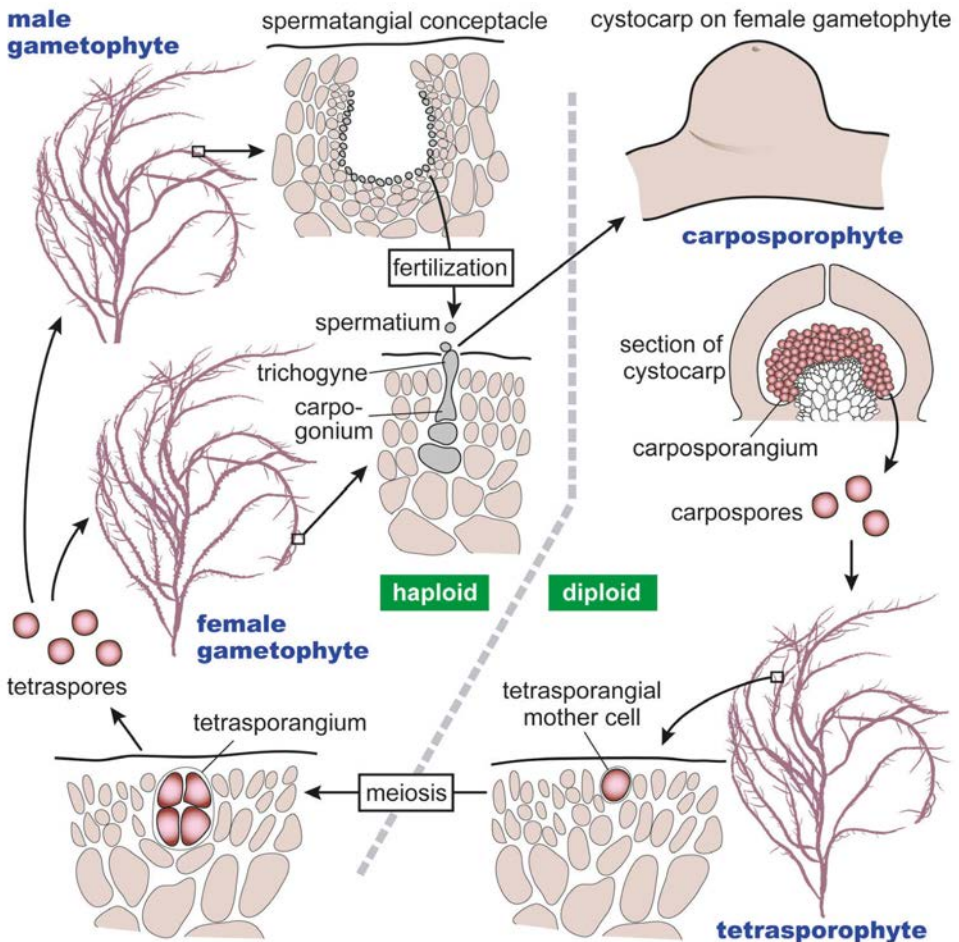
**Reproduction and life histories.** Sexual reproduction has been reported in members of the Compsopogonophyceae, Bangiophyceae and the Florideophyceae (van den Hoek et al. 1995). Fertilization is initiated by adhesion of a non-flagellated spermatium (male gamete) to a trichogyne, hair-like cytoplasmic extension of a carpogonium (egg cell) borne upon a female gametophyte. The Bangiophyceae show alternation of 2 generations, between a macroscopic gametophyte (haploid) and a microscopic sporophyte (diploid); a fertilized carpogonium divides into 4–32 zygospores that develop into sporophyte thalli (Fig. 2-3). In the Florideophyceae, the gametophyte is isomorphic or heteromorphic (but always larger than) to the sporophyte (Gabrielson & Garbary 1986, Hawkes 1990), and the fertilized carpogonium



**Fig. 2-3. Alternation of two generations in *Pyropia yezoensis* (Bangiaceae).** Macroscopic gametophyte is monoecious, producing spermatangia (male gametangia) and carpogonia (egg cells) on the same thallus. A fertilized carpogonium divides to form 16 zygospores, each of which develops into a microscopic sporophyte (called the “*Conchocelis*” phase). Diploid conchospores discharged from the sporophyte perform meiosis during germination and develop into haploid gametophytes. The terminology is based on Nelson et al. (1999). (Orig., illustration M. Kamiya).

nium develops into a microscopic tissue (carposporophyte), which is considered as third generation. This diploid carposporophyte tissue, frequently surrounded by a protective tissue (pericarp) of the parental female thallus (this combination is called the cystocarp), discharges large numbers of diploid carpospores (from carposporangia) which develop into free-living diploid tetrasporophytes (Fig. 2-4).

**Carposporophyte development.** The development pattern of the carposporophyte tissue varies and has been widely used to aid florideophycean classification and relationships (Hommersand & Fredericq 1990). In the Nemaliales, for instance, the carposporophyte tissue develops directly from a fertilized carpogonium or from a fusion cell that is produced by fusing a carpogonium with its adjacent carpogonial branch (Fig. 2-5.A). In the Corallinales, an order of heavily calcified red algae, a number of reproductive organs are produced within a chamber (conceptacle), the fertilized carpogonium fuses with adjacent carpogonial cells



**Fig. 2-4. Alternation of isomorphic generations in *Gracilaria* spp. (Gracilariaceae).** Dioecious gametophytes and tetrasporophytes are isomorphic. A fertilized carpogonium germinates on the female gametophyte and develops into a parasitic carposporophyte tissue. Numerous diploid carpospores released from the carposporophyte develop into free-living tetrasporophytes, and their tetraspores (meiospores) grow into gametophytes. (Orig., illustration M. Kamiya).

**Fig. 2-5. Variation of carposporophyte development in Florideophyceae.** **A. *Nemalion* spp.** A fertilized carpogonium directly produces diploid small filaments (called gonimoblast filaments), which form carposporangia at the apex. **B. *Corallina* spp.** Many gametangia are formed within a dome-shaped conceptacle. After fertilization, supporting cells and adjacent cells fuse to form a single fusion cell and produce gonimoblast filaments each with a terminal carposporangium. **C. *Dudresnaya* spp.** A fertilized carpogonium transfers its divided diploid nuclei to several auxiliary cells through connecting filaments, and each of the auxiliary cells develops gonimoblasts. **D. *Aglaothamnion* spp.** A supporting cell connected with a fertilized carpogonium cuts off an auxiliary cell, which fuses into the supporting cell and forms a gonimoblast initial. (AC auxiliary cell, CG carpogonium, CS carposporangium, FC fusion cell, GB gonimoblast, S spermatium, T trichogyne) (Orig., illustration M. Kamiya).