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Phaeophyceae—An Ultrastructural and Histochemical Overview

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In Phaeophyceae (brown algae) the cell walls are made up of microfibrils and are associated with alginic acid, fucoidin and cellulose. The eggs lack cell walls. In zygote, wall in response to fertilization is formed *de novo*. The various metabolites are incorporated at different time intervals in zygote wall only after fertilization. The chloroplasts are bound by limiting membrane and also possess chloroplast-endoplasmic reticulum (Chl-ER). The thylakoids are grouped into bands. The genophore is an area in the chloroplast that contains DNA-fibrils. The pyrenoid is associated with chloroplast and consists of proteinaceous matrix. Pyrenoids are present in primitive orders and absent in the advanced orders. Physodes contain phloroglucinol derivatives including tannins and/or terpenes. The two membranes of the nuclear envelope reveal distinct faces—(a) nonconvoluted with particles; (b) convoluted with few particles. Golgi bodies are found near nucleus in active cells and are involved in a number of secretion and transportation processes. The synaptonemal complexes and centrioles are associated with dividing nucleus. Ultrastructural studies have revealed that the flagella have mastigonemes, proboscis and flagellar roots. Plasmalemma proliferations show finger-like projections in *Sphacelaria tribuloides* and such wall projections are perhaps involved in short distance transport of metabolites.

Key words: Phaeophyceae, Ultrastructure, Histochemistry

Introduction

The phaeophyceae (brown algae) are complex forms whose plant body ranges between 1 mm and 70 m in length. Kylin (1933) sequestered all the families of phaeophyta into three groups based mainly on types of alternation of generations as isogeneratae, heterogeneratae and cyclosporeae. Fritsch (1945) and Scagel (1966), however, divided the phaeophyta into number of orders and families which can be treated independently. The phaeophyceae are widespread marine algae and grow luxuriantly in cold waters. The freshwater forms are *Pleurocladia*, *Heribaudiella*, *Bodanella* and *Sphacelaria fluviatilis*. The seaweeds are conspicuous in littoral or intertidal regions. The kelps are especially conspicuous in sublittoral waters.

In brown algae, diverse morphological forms occur ranging from simple filamentous, heterotrichous interwoven filaments and parenchymatous (both simple and complex) to cortication. This group lacks unicells, colonies and unbranched filaments. Further crustose forms like *Ralfsia*, free floating forms like *Sargassum* and attached forms like *Laminaria* are also known.

There large size demands many additional mechanical devices for support which are met by increased wall thickness, intertwining of threads and possession of haptera for anchorage. Even the smallest plants are branched and remain attached. A few taxa in addition, also exhibit stem-, and leaf-like appendages. The vascular tissues as seen in the higher plants are absent but the kelps do

show sieve tube-like structures which act as conduit of photosynthetic assimilates.

The important characteristic of brown algae is the pigmentation which consists of chlorophyll *a* and *c*; carotenes; and many xanthophylls (especially flavoxanthin and leutein). The products of assimilation are sugar alcohol, fats and complex polysaccharides namely Laminarin and Fucoidin. Many Phaeophyceae possess phenolic materials (Fucosan) in highly refractive vesicles usually called as physodes.

Sexual reproduction is of the three types namely isogamy, unisogamy and oogamy. Generally plurilocular structures are borne on both the diploid and the haploid plants. The unilocular structures normally occur on diploid plants and their presence indicate diploid thallus. Meiosis occurs in unilocular sporangia and the swarmers are therefore, haploid. The brown algae show flagellated gametes and zoospores which have laterally attached flagella. The brown algae are the source of alginic acid, iodine and bromine and are also used as fertilizer.

Cell Wall

The cell wall consists of different fibrillar layers and is associated with materials of various composition such as (a) alginic acid and cellulose that comprise the fibrillar material (b) fucoidin which comprises the amorphous wall material.

Orientation of Fibrils

In general, fibrils are randomly oriented in the cell wall. The cell wall is two layered in *Pylaiella irregulare* and is interrupted by spaces and vesicles. In the cell wall fibrils are arranged randomly in the outer layer and are parallel in the inner layer (Bourne & Cole 1968). In *Turbinaria conoides*, the outer wall of the receptacular meristoderm cell consists of two zones of microfibrils. In the outer zone microfibrils are reticulate whereas in the inner zone microfibrils are parallel. The cell wall is overarched by 1–5, extracellular layers made up of microfibrils (Sokhi & Vijayaraghavan 1985). In *Ectocarpus acutus* such fibrils are loosely interwoven and form a reticulum in the outer layer and are compactly arranged in the inner layer. Fibrils extend out from reticulum and form a pilose layer that periodically peels-off to maintain a clean surface (Bailey & Bisalputra 1969); and are reticulate in the thallus and apical cell walls of *Dictyota* (Dawes et al. 1961). The cell wall in *Elachista fucicola*, is 0.5–0.7 μm thick, smooth, and consists of longitudinally arranged microfibrils and is interrupted by Lacunae (Bailey & Bilasputra 1969). Vesicles situated beneath the cell wall secrete mucilage and thus help in maintaining clear and smooth surface.

A lamellated wall is present in the embryo of *Pelvetia*, wherein the microfibrils are oriented in more or less parallel fashion. In a lamella the fibrils are oriented at 35° (Peng & Jaffe 1976). A specialized orientation of the fibrils is seen in the pit-fields of Dictyotales and the trumpet cells of *Laminaria*. In these the microfibrils are so arranged that they skirt the circular and oval apertures of the pits, a situation similar to the primary pit-fields of angiosperm cell wall (Dodge 1973).

Plasmodesmatal Connections

Plasmodesmata, in the cell walls, allow cytoplasmic connections between adjacent cells. They are reported in *Laminaria*, *Alaria* (Fritsch 1945), *Fucus* (McCully 1968), *Dictyota* (Evans & Holligan 1972a). In the vegetative cells of *Sphacelaria tribuloides*, numerous plasmodesmata are present on the transverse walls but are absent from the longitudinal walls (Galatis et al. 1977). Plasmodesmata are tubular, single or sometimes bifurcated, and measure about 40 nm in diameter. In cross section, each one appears as a pore and contains a dense core about 20 nm in diameter, that partially fills the central portion of the pore. The central portion of the core is either electron dense or transparent. Pores of 50 nm diameter are also reported in the walls of meristematic cells of *Himanthalia* and each pore is transversed by a thin cytoplasmic strand (Berkaloff 1963). A group of plasmodesmata forming 'pit-fields' is present in meristoderm cells of *Fucus* and *Egregia*. These consist of pores of 37 nm diameter and tubes of plasmalemma pass through them (Bisalputra 1966).

Wall Materials

Cell walls of the brown algae in addition to cellulose consist of alginic acid and sulphated polysaccharides. Calcium incrustations are present in a few plants. The layers of alginic acid, sulphated materials and mixture of these two substances are present in the walls of thallus cells in *Fucus* (McCully 1966); *Turbinaria conoides* (Sokhi 1985); antheridia in *Fucus* (McCully 1968) and *Dictyota* (Evans & Holligan 1972a); oogonia in *Fucus, Dictyota, Zonaria farlowii*, and *Turbinaria conoides* (McCully 1968, Neushul & Liddle 1968, Evans & Holligan 1972a and Sokhi & Vijayaraghavan 1986); and unilocular and plurilocular sporangia in *Analipus japonicus* (Nelson 1982). In *Laminaria*, secretory cells

produce sulphated materials, which are discharged into the secretory canals and also on the surface (Evans et al. 1973, Evans & Callow 1974, Callow & Evans 1976).

In the cell wall of *Phaeostrophion irregulare* an inner layer of cellulose and an outer layer of alginic acid is present (Bourne & Cole 1968). Cellulosic wall is also reported in *Giffordia* and *Chorda* (Bouck 1965). Calcium incrustations are present in the thalli of *Padina* spp. (Fritsch 1945, Borowitzka et al. 1974, Miyata et al. 1977) and the crystals are made up of aragonite ($CaCO_3$). In *P. australis* and *P. pavonia* the needle-shaped crystals are 0.3–0.4 nm wide and 2–4 nm long (Borowitzka et al. 1974). Three kinds of crystals are present in *P. japonica*, the needle-shaped crystals 0.2 nm wide and 5 nm long; the rod-shaped crystals are predominant and are about 0.3 nm wide and 3 nm long, and crystals of intermediate shape are also present (Miyata et al. 1977).

Wall Formation in Zygote

Fucus eggs lack walls (Pollock 1970). In response to fertilization an extracellular structure is formed (Quatrano 1981) and various materials are incorporated in the wall of the zygote at different time intervals. The surfaces of the egg and the zygote appear different under SEM. The egg surface is rough due to the presence of vesicles just beneath the plasmamembrane (Callow et al. 1978a). These vesicles contain alginic acid and discharge their contents through exocytosis on the surface of the egg. The zygotes thus, have a secreted wall that is relatively smooth.

In *Fucus gardneri*, 24 hrs after fertilization, the main constituents of the zygote wall are alginic acid, cellulose and fucoidin (Novotny & Forman 1975). Alginic acid is the major component and comprises about 60% of the total wall, whereas the cellulose constitutes 20% and rest two are electrophoretically different forms of Fucan—F_1 and F_2 (Quatrano 1981). The first component deposited is the alginic acid followed by cellulose and the last component added is the sulphated polysaccharide. The sulphated polysaccharides are not localized in the zygote wall of *Fucus* spp. until 10 hrs (Quatrano & Crayton 1973) and 10 to 14 hrs after fertilization (Novotny & Forman 1974). F_1-Fucan with high level of xylose relative to fucose and a low level sulphate is present in the cell wall of a 4-hr zygote. F_2-fucan that contains 2 or 3 times more Fucose than that present in F_1-Fucan, and high level of sulphate appears 12 hrs after fertilization. F_2 is deposited in localized areas of the zygote wall that are the sites of presumptive rhizoid (Quatrano & Stevens 1976).

The preexisting, unsulphated fucan ploymer is sulphated after fertilization (Quatrano & Crayton 1973). Sugar chain of F_2-Fucan is preformed in the cytoplasm of egg or early zygote. The enzymatic sulphation begins at about 10 hrs after fertilization (Quatrano & Stevens 1976). Such enzymatic modification is necessary for polysaccharide localization into a specific region of the cell wall (Hogsett & Quatrano 1978). In zygote such sulphated polysaccharides are secreted throughout the cell both at the rhizoid and the thallus poles but with greater localization at the rhizoidal pole (Callow et al. 1978b, Brawley & Quatrano 1979). In the two-celled embryo, the sulphated polysaccharides are only localized in rhizoidal cell (Novotny & Forman 1974, 1975). Presence of a large number of active golgi bodies in the perinuclear region is perhaps responsible for large amount of sulphated polysaccharides in the rhizoidal cell. The golgi in the perinuclear region of the thallus cell are inactive, lack hypertrophied cisternae and associated vesicles.

Wall Structure of Two-Celled Embryo

The two-celled embryo wall of *Fucus vesiculosus* consists of fibrillar layers. The outer layer is composed of densely packed parallel fibrils, whereas the inner layer has an irregular and loose texture. The thickness of these wall layers varies at both the poles of the proembryo— the rhizoidal pole has thick and thin fibrillar layers whereas in the thallus pole the outer fibrillar layer is relatively thicker than the inner one. The amorphous layer, in the embryo wall covers both the fibrillar layers and is conspicuous at the rhizoidal pole (Vreugdenhil et al. 1976).

Significance of Polysaccharides Sulphation and its Subsequent Localization in Zygote Wall

Sulphation of fucoidin and its subsequent localization in the zygote marks the initiation of the rhizoidal site. The golgi derived vesicles are filled with fine fibrillar material. Further mitochondria, ribosomes and osmiophilic bodies; fucoidin, alginic acid and nucleic acids accumulate in the rhizoidal hemisphere of the zygote (Quatrano 1972). The differential localization of sulphated polysaccharides in the zygote wall results in the fixation of the polar axis (Novotny & Forman 1974). Crayton et al. (1974), however, consider that the establishment of a polar axis is independent of sulphation because normal rhizoids develop and protein synthesis is unaffected

although sulphation of fucoidin was prevented by zygotes developing in sea water lacking sulphate moiety. Attachment of zygotes to the substratum requires the formation of asymmetrical jelly layer in *Fucus* and *Pelvetia* (Schröter 1978), and an amorphous layer in *Fucus* (Callow et al. 1978b). In both the instances zygotes are unable to attach to the substratum sans sulphate. The localized wall changes result in the build up of internal osmotic forces and thus allow the germination and the expansion of the rhizoid (Novotny & Forman 1975).

Synthesizing Sites and Transportation of the Wall Materials

Alginic acid and fucoidin are initially found together in the cytoplasmic vesicles of *Fucus* and *Dictyota*. In *Pylaiella littoralis* the initial precursor of acid polysaccharide is synthesized within the photosynthetic apparatus. The transference of wall polymers from one type of organelle to the other occurs through the cytomembrane system found within the cell (Percival & McDowell 1967). In *P. littoralis* the initial precursor molecule of the acid polysaccharide is transported from the chloroplast to the golgi bodies through a series of membrane bound channels like chloroplast envelope, chloroplast-endoplasmic reticulum and nuclear envelope (Leepard 1974). Alginic acid is polymerized within the TBO particles. The particles stain with the basic dye like Toluidine blue O, and transport alginic acid (Leepard 1973). In *Dictyota*, the alginic acid contained in vesicles is deposited on the cell wall by reverse pinocytosis. The vesicle membrane fuses with the plasma membrane and releases its contents (Evans & Holligan 1972a). Alginate is found in vesicles and is deposited into the extracellular wall immediately after fertilization. The mechanism of cellulose deposition into the developing wall of *Fucus* zygotes appears to involve activation of preformed cellulose synthetase during fertilization. Source of energy for wall construction and polysaccharide deposition into the cell wall takes place in the absence of light and an exogenous carbon source. The zygotes possess a mechanism for Laminarin breakdown which in turn could provide glucose for cellulose and other polymer synthesis as well as for ATP formation (Quatrano 1981).

In *Fucus* the sulphation of fucoidin occurs in golgi derived vesicles (Callow et al. 1978b, Brawley & Quatrano 1979). The localization of sulphated polysaccharides, however, requires a cytochalasin sensitive process since the directional transport of golgi vesicles to the rhizoidal end is prevented in the zygotes treated with the cytochalasin (Brawley & Quatrano 1979).

Chloroplast

The chloroplast is a discrete organelle and represents photosynthetic unit of the cell. Various authors have used different terminologies for this organelle in the brown algae: chromatophores (Fritsch 1945, Evans 1968); phaeoplasts (Loiseaux 1976); and chloroplasts (Chi 1971, Hori & Ueda 1975, Buggeln & Bal 1977). The term chloroplast, however, is used in this review.

Chloroplasts in brown algae can be discussed under the following:

(a) Chloroplast envelope and its relation with endoplasmic reticulum and nuclear envelope
(b) Thylakoidal arrangement
(c) Chloroplast stroma and pigments
(d) Genophore
(e) Chloroplastic rRNA
(f) Chloroplast division and Genophore transmission
(g) Pyrenoid
(h) Physodes

(a) Chloroplast Envelope and its Relation with Endoplasmic Reticulum and Nuclear Envelope: Chloroplasts are bounded by two pair of membranes—the limiting membrane and the Chl-ER which forms a loosely fitting sac around the chloroplast (Gibbs 1962). The Chl-ER surface facing the chloroplast is smooth whereas the surface facing cytoplasm has ribosomes. The Chl-ER is continuous with nuclear envelope, golgi bodies and lysosomes. The chloroplast limiting membrane and Chl-ER are separated by a narrow perichloroplastic space occupied by tubules that probably originate from the underlying Chl-ER or from nuclear envelope. The chloroplast out-pocket is a large, non-lamellar area present between the thylakoids and the chloroplast limiting membrane in *Phaeostrophion irregulare* (Bourne & Cole 1968), *Leathesia difformis* (Cole & Lin 1968) and *Colpomenia sinuosa* (Cole 1970). The degree of association and contact between chloroplasts and ER not only varies but also is dependent upon the number of chloroplasts per cell. In *Sphacelaria, Egregia* and *Dictyota*, the chloroplast number per cell is high and Chl-ER is poorly developed (Bisalputra 1974). The Chl-ER collects diffused photosynthates, some of which are converted into secretory materials, and passes into the golgi bodies. Chl-ER serves as a channelling system for carbohydrate reserves and also plays an important

role in the transport of alginic acid precursors from chloroplasts to golgi bodies (Leepard 1973, 1974) and of polyphenolic precursors to physodes (Pellegrini 1980). Bisalputra (1974), considers that GERL (Golgi body-Endoplasmic Reticulum-Lysosome) system is associated with the transport of cellular products. The extent of this function depends upon degree of development of Chl-ER around the chloroplast.

(b) Thylakoidal Arrangement: In chloroplast the thylakoids are grouped into bands. A girdle of thylakoids surrounds the inner thylakoid bands (Bouck 1965, Brawley & Wetherbee 1981). The usual number of thylakoids per band is three in *Giffordia* (Bouck 1965); *Sphacelaria* (Evans 1966); *Phaeostrophion irregulare* (Bourne & Cole 1968); and *Heribaudiella fluviatilis* (Pueschel & Stein 1983) although two to four thylakoids per band are also seen in *Chorda filum* (Bouck 1965). Individual members, in each thylakoid band, are separated by a uniform space of 40Å (Gibbs 1970). The organization of thylakoids in chloroplasts of *Pylaiella littoralis* is disturbed when treated with antibiotics like chloramphenicol, lincomycin and rifampicin. These antibiotics affect protein synthesis (Loiseaux 1976). The effects of these antibiotics on chloroplasts are : (i) Chloramphenicol, at 25 g/ml, disturbs the normal arrangement of thylakoids in young chloroplasts. Irregular stacks of 3 to 25 thylakoids are formed. In both young and old chloroplasts the stroma becomes less dense, contains a few granules and ribosomes of normal size. (ii) Lincomycin, at 50 g/ml concentration, behaves like chloramphenicol and produces the same effects. (iii) Rifampicin, at 100g/ml, produces thylakoids that are arranged singly. lie parallel to one another and well-separated. The other effect is grouping of the thylakoids in large stacks and sometimes 25 such stacks unite.

The proteins coded by chloroplastic systems are thus, necessary for the normal arrangement and association of the thylakoids (Loiseaux 1976). The association between the thylakoids is due to H^+ bonds (Bisalputra 1974). In *Alaria* on treatment with naphthoxyacetic acid, the thylakoids become wavy and irregularly spaced whereas with phenoxyacetic acid, the thylakoid membrane bulges. Both the acids together cause chloroplast bulging. The alteration in chloroplast structure invariably reduces the photosynthetic efficiency and thus inhibits growth.

(c) Chloroplast Stroma and Pigments: Chloroplast stroma contains lipid droplets and patches of dense metabolites in *Dictyota* (Evans 1966) and electron opaque globules in *Giffordia* and *Chorda* (Bouck 1965). The main chloroplast pigments are β-Carotene, Violaxanthin, Fucoxanthin. Pigments like Chlorophyll a, c_1 and c_2, Zeaxanthin, Antheraxanthin and Mutatochrome are also present. Fucoxanthin imparts the characteristic olive yellow to deep brown colouration. Mixture of Fucoxanthin and Chlorophylls imparts olive green colour to the ova and the extra-chloroplastic accumulation of β-carotene imparts orange colour to the male gametes in *Fucus* and *Ascophyllum*. The amount of fucoxanthin varies in different taxa and is relatively high in *Laminaria, Dictyota, Petalonia, Pylaiella* and *Ectocarpous*. On the contrary fucoxanthin quantity in *Fucus* is low (Fritsch 1945).

(d) Genophore: Genophore is a gene containin body. It is a ring shaped, electron translucent area and contains DNA-fibrils located inside the gridle lamella (Bisalputra 1974). There is difference of buoyant densities between the chloroplastic and nuclear DNA. The DNAs in chloroplasts of *Pylaiella littoralis* and *Sphacelaria* are, however, same. The chloroplastic DNA is double stranded. Both strands contain an equal distribution of purine and pyrimidine bases (Dalmon & Loiseaux 1981).

(e) Chloroplastic rRNA: Two 23S rRNA are present in the chloroplasts of *Pylaiella littoralis* and have apparent molecular weights of 1.05×10^6 and 1.15×10^6 daltons. The 1.05×10^6 dalton species consists of unbroken, newly synthesized polynucleotide chains with a molecular weight of 1.07×10^6 dalton and constitutes fifty per cent of the total 23S. The 1.15×10^6 dalton species, is composed of post-matured, nicked molecules that cleave into two products having molecular weights of 0.58×10^6 and 0.48×10^6 daltons respectively. The post-maturational cleavage occurs at least twenty hours after the synthesis of the mature 23S (Loiseaux et al. 1979). Two large precursor molecules of rRNA originate in the chloroplasts of *Pylaiella littoralis*. The precursor molecules isolated have apparent molecular weights of $1.\mathcal{E}8 \times 10^6$ and 2.3×10^6. The former is the precursor for both 23S and 16S ribosomal species. The 2.3×10^6 species is labile and is inhibited by Camptothecin—an inhibitor of cytoplasmic rRNA synthesis. The RNA synthesis, in both cytoplasm and chloroplast, is dependent on photosynthesis. In the chloroplast during rRNA synthesis a repressing agent of proteinaceous nature is synthesized that exerts a negative control on the cytoplasmic rRNA (Loiseaux & Mache 1980). The synthesis of rRNA precursor is temperature and light dependent. At 4°C the precursor molecule accumulates than at

12–14°C indicating that the processing of rRNA is slowed down at low temperature. In cytoplasm and chloroplasts of *Pylaiella littoralis*, light is also necessary for the processing and synthesis of rRNA suggesting that light is important for the synthesis and regulation of the specific (?) RNAse (s?) which cuts the precursor rRNA molecules.

(f) Chloroplast Division and Genophore Transmission: The chloroplast and genophore elongate, constrict and result in a double loop configuration. In *Sphacelaria* the chloroplast separates into two and each daughter chloroplast possesses its own genophore-loop. The attachment of DNA molecules to thylakoid membranes is essential for the segregation of replicated DNA molecules (Bisalputra & Bisalputra 1970). This mode of genophore segregation also indicates that the multiple nature of chloroplast DNA helps in the transmission of all genes to daughter chloroplasts especially when unequal fusion of chloroplasts occurs (Bisalputra 1974). In *Colpomenia sinuosa*, *Petalonia debilis* and *Scytosiphon sinuosa* during chloroplast division the parental chloroplast form protrusions 'or arms into which the lamellae project. As the arms separate from the parental chloroplast the lamellae do push apart (Cole 1970). The chloroplast division in *Leathesia difformis* is of the unique type. It involves formation of the thylakoid-stalk in central portion which is accompanied by a projection of thickened part of the chloroplast into cytoplasm. A bifurcation finally divides the chloroplast evagination into two arms (Bourne & Cole 1968).

(g) Pyrenoid: Pyrenoid is the differentiated region of the chloroplast, consists of proteinaceous matrix, and is projected from the chloroplast by a thin, small stalk (Dodge 1973). One pyrenoid per chloroplast is reported in *Giffordia* (Bouck 1965), *Bifurcaria*, *Himanthalia* (Evans 1968), *Dictyota* and *Macrocystis* (Chi 1971) and two, in *Chorda* (Bouck 1965) and *Cystoseira tamariscifolia* (Evans 1968). In *C. tamariscifolia* the two pyrenoids lie roughly parallel to the chloroplast and are placed one above the other facing in opposite direction. The inner pyrenoid is larger than the outer. The pyrenoid, in most of the brown algae, measure 1.5–3.0 μm in width and 1.5–2.5 μm in length. The rudimentary pyrenoid found in *Cutleria cylindrica* is 0.5 μm in width and 0.9 μm in length. The pyrenoid is surrounded by three pairs of membranes (figure 1A) in *Chorda*, *Giffordia*, *Dictyota* and *Macrocystis*. The inner membrane is continuous, with the chloroplast envelope; the middle one with Chl-ER; the outer one is dilated and forms a cap that extends over the pyrenoid surface terminating at its neck (Bouck 1965, Evans 1966, Chi 1971). This cap contains either translucent storage material or is empty. The cap is absent in *Sphacelaria*, *Cystoseira*, *Bifurcaria Himanthalia*, *Pylaiella littoralis*, *Elachista fucicola*, and *Hecatonema streblonematoides*. The matrix of pyrenoid is coarsely granular or fibrous in *Chorda* and *Giffordia* and is uniformly dense in *Phaeostrophion irregulare*. Pyrenoid matrix is free of thylakoids and ribosomes.

Pyrenoid does not divide along with the chloroplast and is formed *de novo* (figures 2A–C). In *Pylaiella littoralis*, *Elachista fucicola*, *Hecatonema streblonematoides*, the granular material accumulates in lamellar free space of the chloroplast. The membrane of chloroplast bulges out and dense material is pushed out into the growing pyrenoid until it becomes an adult, pear-shaped pyrenoid (Loiseaux 1973). A new pyrenoid bulges from the point of attachment of the old one just before chloroplast division. A plane of fission then passes between the old and the new pyrenoid (Evans 1966).

(h) Physodes: Physodes are refractive, colourless, and variously sized inclusions called 'Fucosan vesicles' by the earlier workers. Ragan (1976) suggested that the term 'fucosan' should be avoided for denoting the physodes contents, and further emphasized that the 'fucosan vesicles' are not *pro parte* physodes. Recent studies reveal that the physodes contain phloroglucinol derivatives including tannins and/or terpenes but not fucosan. Physodes are abundant in vacuolated and non-vacuolated cells of *Phaeostrophion irregulare* (Bourne & Cole 1968); in both the vegetative and the reproductive cells of *Dictyota* (Evans & Holligan 1962b). In *Dictyota*, the apical cells and their immediate derivatives contain a large number of physodes. In the epidermal and the medullary cells, physodes are evenly distributed. In *Cystoseira stricta*, the physodes are confined to external pole of meristoderm cells and are scattered throughout the cytoplasm of promeristematic cells (Pellegrini 1980). In released eggs of *Dictyota* physodes lie around the nucleus but the unreleased eggs lack them. Physodes are absent in antheridia. A large number of physodes are present during the precleavage stage of the tetraspore development but decrease in the released tetraspores (Evans & Holligan 1972b) and are also reported to disappear during zooidogenesis in *Pylaiella littoralis*, *Elachista fucicola*, *Hecatonema streblonematoides* (Loiseaux 1973). Physodes, in certain taxa accumulate in special cells like the ascocysts of *Ascocyclus;* and glands of certain Laminariales. The fucosan vesicles, in

Sphacelaria, consist of tanniniferous matter and are abundant in the apical cells (Fritsch 1945). Physodes in the apical cell of *Dictyota* (Evans & Holligan 1972b) and *Durvillea* (Roberts 1979) are resistant to treatments of organic solvents, acids and alkalis. Interestingly, those that are away from the apex lyse rapidly when treated with above chemicals including distilled water. The unstable physodes pass probably through the plasmamembrane and extrude through the cell walls into the surrounding water.

Classification of Physodes: Chadefaud (1932) classified physodes into four types. Type A, are refractive and contain fucosan. These are found in most brown algae and also in unhealthy *Laminaria.* Type B, less refractory, contain fucosan and present in *Laminaria.* Type C, slightly refractive, lack fucosan, react with cresyl-blue and present in *Laminaria.* Type D, slightly refractive, lack fucosan, unreactive with cresyl-blue and present in *Laminaria* and *Desmarestia.* Likewise Ando (1958a, b) also described four types of physodes. Type A, contains alginic acid in addition to fucosan but mainly corresponds to type A of Chadefaud. Type AY is mucilaginous body. In Type B tannins are present and in Type C physodes sesquiterpene alcohol exists.

Three kinds of physode-like inclusions are present in *Dictyota dichotoma* (Feldmann & Guglielmi 1972). P_1 physodes, are phenolic impregnated membranous structures with numerous infoldings; P_2 physodes, are membranous bodies probably phenolic, and of irregular osmophily; and P_3 physodes, appear to consist of spiral bodies produced by mitochondria.

Aging of Physodes: Aging is an irreversible chemical process in physodes and is characterized by a progressive loss (Letouzé 1912), or increase (Kylin 1918) of the osmiophily, and by decreasing solubility in alcohols. In *Dictyota* the physodes in younger cells stain turquoise or green with TBO and are also electron transparent. In the older cells they stain dark-blue with TBO and are electron dense (Evans & Holligan 1972b). In *Cutleria hancockii* the appearance of physodes changes during gametogenesis. In early gametogenesis the osmiophilic masses appear as small, electron-opaque granules, and as gametangial maturation proceeds the osmiophilic materials become more electron-dense. These two types represent physodes of different age. Golgi bodies may be involved in the aging process as these were seen fusing with osmiophilic masses (LaClaire II & West 1978). In extracts of *Fucus vesiculosus,* a homologous group of phloroglucinol-based polymers are present (Ragan & Craigie 1976). The aging of physodes may be due to polymerization of phloroglucinol units. The appearance and nature of physodes have been viewed differently by various authors. (a) There probably exists biochemical classes of physodes within brown algal orders and also between various species (Pellegrini 1980), in *Dictyota* (Evans & Holligan 1972b) and *Durvillea* (Roberts 1979). (b) The various appearances of physodes are due to mechanism inolved in formation, synthesis, secretion and transformation of phenolic compounds into the vacuoles.

Structure: Presence of fluid content in the physode is accepted by a number of authors but whether physode is a membrane bound structure is not clear. Evans and Holligan (1972b) speculate that a membrane not the usual unit membrane probably surrounds the physodes. Loiseaux (1973), however, defined physodes as membrane bound, osmiophilic granules whereas Pellegrini (1974, 1980) described it as vesicles surrounded by single unit membrane. Ultrastructural evidences do account for a membrane-bound structure yet the nature of this membrane is poorly understood.

Genesis: Physodes originate in the chloroplasts of *Dictyota* (Evans & Holligan 1972b), *Cystoseira* (Pellegrini 1980); and in *Fucus* (McCully 1968) and *Durvillea* (Roberts 1979) from the nucleus. In *Durvillea* the medullary hyphae lack chloroplasts but are full of physodes. The oosphere contains numerous chloroplasts but not physodes. In *Laminaria,* endoplasmic reticulum is probably the site of physode origin (Davies et al. 1973). Pellegrini (1980), studied the origin of physodes in *Cystoseira stricta* and described different phases during their formation: (a) The origin and development of vacuoles involve the fusion of small provacuoles, and the sequestration of cytoplasmic materials that are probably formed from GERL. A few of these vacuoles accumulate phenolic materials; (b) Secretion includes successive phases; (c) Osmiophilic inclusions of irregular shape are phenolic precursors (Evans & Holligan 1972b, Pellegrini 1980). The osmiophilic inclusion is surrounded by a membrane in *Dictyota* (Evans & Holligan 1972b), but lacks a membrane in *Cystoseira* (Pellegrini 1980); (d) Chloroplastidial exudations are dense globules which are ejected out of chloroplasts (Pellegrini 1980), into Chl-ER or directly into the physodes which are intimately associated with chloroplasts; (e) Dense material is carried and accumulated sparsely or in large quantities in the physodes. Lysosome-like vesicles empty lytic enzymes and lead phosphatase inside the physodes. The products

after lysis appear as compact masses and/or unfurled membrane configurations.

Physodes are by-products and are expelled from the cytoplasm during zooidogenesis in *Pylaiella littoralis, Elachista fucicola, Hecatonema streblonematoides* (Loiseaux 1973), and are diffused through the wall of the female gametangia in *Cutleria adspersa* (Caram 1977). In maturing female gametes of *C. hancockii*, the bulk of phenolic material secreted into the extraplasmic space eventually escape through the walls suggesting that the phenolic material is a metabolic waste product and is of little use to the zygote. The release of this material may aid the gametes to round up and pull away from the walls (LaClaire II & West 1978). The physode content, in *Cystoseira stricta* is also excreted from the cell toward the cell wall by exocytosis. In this process the physode envelope fuses with the plasmalemma and then the contents are discharged against the walls that lie on both the sides of the middle lamella. Interestingly physodes are known to secrete antigrazing products.

Nucleus

The uninucleate condition is prevalent in most of the cells whereas the multinucleate condition is an exception and is found in a few Laminariales and in older cells of *Halopteris* (Fritsch 1945). In *Durvillea*, the vegetative cell usually contains two or more nuclei, and rarely clusters of five nuclei are also found (Roberts 1979). The nuclear envelope in unilocular sporangia *Phaeostrophion irregulare* (Bourne & Cole 1968); Plurilocular sporangia of *Pylaiella littoralis* (Markey & Wilce 1975); sieve elements of *Laminaria groenlandica* and *Nereocystis lutkeana* (Schmitz & Srivastava 1974, 1976) is a double membrane structure and contains pores. In *Padina* three dimensional view of the nuclear envelope was studied by the freeze-etching technique. The two membranes of the nuclear envelope show distinct faces. One has many particles and is non-convoluted, whereas the other has a fewer particles and is convoluted. Nuclear pores aggregate into bands which alternate with the bands lacking pores. The latter band has more or less regular particle arrays that are not present around the nuclear pore (Neushul & Dahl 1972b). In *Zonaria* the pores are few in the dormant nucleus than in the active one. The presence or absence of the nuclear pores, is probably related to differences in the subcellular morphogenetic activities. Such differences influence the relative positions of golgi bodies in the cytoplasm. In active cells golgi bodies are near the nucleus whereas in the inactive ones they are away. In *Fucus vesiculosus*, the sperm pronucleus envelope lacks pores (Brawley et al. 1976a), whereas, they are present in the egg pronucleus. The envelope of sperm pronucleus degenerates after the sperm penetration into the egg. A new envelope regenerates on the sperm pronucleus surface facing the egg pronucleus during fertilization. The regenerated portion of the envelope is perhaps formed from the ER elements present near the sperm pronucleus. In the released egg the pronucleus is convoluted and during the pronuclear fusion the egg pronuclear envelope convolutions are on the side that is near to the approaching sperm pronucleus. After fertilization the convolutions in egg nucleus are particularly marked and enclose electron-opapue material (Brawley et al. 1976a, b). In *Zonaria* (Neushul & Dahl 1972a, b) and *Chorda* (Toth 1974) the nuclear membrane at the apical region is indented due to the presence of the centrioles which are associated with the microtubules. In the cell, the nucleus is anchored in a precise position probably due to the array of microtubules. At the time of division, the apical and the basal ends of the nuclear envelope become fenestrated, from where the microtubules along with the small vacuoles penetrate the nucleoplasm. In *Fucus serratus*, during metaphase, the microtubules also extend into the nucleoplasm (Berkaloff & Rousseau 1979).

The nucleoplasm is, granular in *Phaeostrophion irregulare* (Bourne & Cole 1968); reticulate in *Sphacelaria tribuloides* (Galatis et al. (1977); and *Durvillea* (Roberts 1979). In *Macrocystis* dark and light stained regions are present in the nucleus (Chi & Neushul 1971). The nucleoplasm, in *Laminaria groenlandica*, contains a few condensed patches and evenly distributed chromatin (Schmitz & Srivastava 1974).

The nucleolus in *Sphacelaria tribuloides* has distinct granular and fibrillar zones (Galatis et al. 1977) whereas in *Pylaiella littoralis*, it is characterized by a homogenous central and an outer granular regions. In both regions internucleolar vacuoles are present. In *Nereocystis lutkeana* the internucleolar chromatin consists of small patches of condensed chromatin (Schmitz & Srivastava 1976).

In *Zonaria* and *Dictyopteris* the dormant nucleus is characterized by spherical shape, smooth outline, presence of a centriole at the apical end, and occurrence of nuclear pores all around the nuclear envelope except at the place near the centriolar depression. Microtubule organizing centre is present around the active nucleus. (a) A region occupied by microtubules and granular material, (b) layers of ER (c) zones occupied by

golgi bodies (Neushul & Dahl 1972b). The nucleus, of multinucleate zoosporangium in *Macrocystis*, also shows the layers of ER (Chi & Neushul 1971). The perinuclear region perhaps acts as a channel through which products of nuclear activity are moved by the microtubules.

Synaptonemal complexes are present during meiosis in *Chorda tomentosa* (Toth & Markey 1973); *Pylaiella littoralis* (Toth & Markey 1973, Markey & Wilce 1976a); *Fucus serratus* (Berkaloff & Rousseau 1979). In *Chorda tomentosa* the synaptonemal complex has the characteristic structure of three parallel electron-dense elements which are separated by less dense regions. The two side elements vary in width from 60-110 nm and are separated by 60-70 nm region which contains a central element. The central element consists of two parallel narrow bands. In *Pylaiella littoralis* the synaptonemal complexes consist of two side elements, 25–50 nm wide and a central element 25 nm wide. The central space between the two side elements is approximately 50–75 mm wide. These synaptonemal complexes are found close to the nuclear envelope. In *Fucus serratus*, they are attached to the nuclear envelope (Berkaloff & Rousseau 1979), and their lateral components sometimes exhibit distinct transverse thickenings. The presence of synaptonemal complexes in the nuclei of *Chorda* and *Pylaiella* substantiate the concept that meiosis occurs in unilocular sporangia (Toth & Markey 1973), and in *Fucus*, during the formation of spermatozoids (Berkaloff & Rousseau 1979).

Centriole

The centriole is a complex and cylindrical body It is made up of nine outer triplet tubules and lack core tubule. In *Pylaiella*, centriole is 300–350 μm in length and 130–180 μm in width. In *Zonaria* (Neushul & Dahl 1972b), *Pylaiella* (Markey & Wilce 1975), and *Cutleria* (LaClaire II & West 1979) the centrioles are surrounded by a darkly staining amorphous material from which the microtubules extend into the cytoplasm. In *Fucus*, also a high density of microtubules surround the centrioles (Berkaloff & Rousseau 1979). The centrioles apparently serve as a focal point, for both microtubules that form the aster, and those that run around the adjacent nucleus (Neushul & Dahl 1972b). The paired centrioles are present in interphase cells of plurilocular gametangia of *Pylaiella* (Markey & Wilce 1975). Each centriole prior to its migration to spindle pole divides into two daughter centrioles. The microtubules are present between and also emanate from the migrating centrioles. Centrioles are conspicuous in the apical cells of Sphacelariales, Dictyotales and Fucales (Fritsch 1945) in sporelings of *Petalonia* (Bourne & Cole 1968); in apical cells of *Zonaria* (Neushul & Dahl 1972a, b), in meristoderm cells of *Laminaria* (Davies et al. 1973), and in plurilocular gametangia and unilocular sporangia of *Pylaiella* (Markey & Wilce 1975, 1976a). In *Chorda* centrioles are present both in the developing and the mature plurilocular sporangia but not in the sterile and non-dividing paraphyses. The centriolar material is thus not present throughout the entire life of the sporangia or the vegetative cells. Toth (1974) considers that centrioles are probably formed *de novo* just before nuclear division and prior to flagellar initiation. In *Pylaiella*, centrioles are present in vegetative cells, plurilocular gametangia, and unilocular sporangia (Markey & Wilce 1975). Their formation is, however, not traced. Centriolar formation and distribution in various vegetative and reproductive cells need critical ultrastructural examination. Centrioles serve as an organization centre for the spindle and basal body development in *Chorda* (Toth 1974) and *Cutleria* (LaClaire II & West 1978).

Mitochondria

The mitochondria in brown algae exhibit the same basic structure having an outer, smooth membrane and an inner, folded membrane forming cristae that extend into the central lumen or matrix. Mitochondria also contain intercristal inclusions and DNA-like fibrils. The mitochondrial location and shape varies in different genera.

The inner mitochondrial membrane invaginates to form tubular cristae, in *Giffordia, Fucus* and *Chorda* (Bouck 1965); *Laminaria groenlandica, Nereocystis lutkeana* (Schmitz & Srivastava 1974, 1976), *Laminaria saccharina* (Sideman & Scheirer 1977); *Cutleria hancockii* (LaClaire II & West 1978, 1979), and *Pylaiella littoralis* (Markey & Wilce 1976a). The tubular intercristal inclusions are also found in the developing zoospores of *Pylaiella littoralis* and spermatozoids of *Fucus* (Pollock & Cassell 1977). The fibrous elements in the mitochondrial cristae, however, are only found in the female gametes of *Cutleria hancockii* (LaClaire II & West 1978). The tubular intercristal inclusions of *Pylaiella littoralis* are 5–10 nm in diameter and are present either singly or in groups of three. The occurrence and significance of these intercristal inclusions are still an enigma.

In mitochondria, the DNA-like fibrils are reported in *Nereocystis lutkeana* (Schmitz & Srivastava 1976), and *Egregia menziesii*

(Bisalputra & Bisalputra 1967). These fibrils measure 1.0–2.5 nm in diameter and can be removed with DNase. Mitochondria in sieve elements of *Nereocystis lutkeana* (Schmitz & Srivastava 1976) are variously shaped like spherical, lobed, dumb-bell, and cup-shaped. Elongated mitochondria are observed in differentiating sieve-elements of *Laminaria groenlandica* (Schmitz & Srivastava 1974), and female gametes of *Cutleria hancockii* ((LaClaire II & West 1978). In the plurilocular gametangia of *Pylaiella littoralis*, during meiosis, mitochondria are constricted at the mid-region and often appear cup-shaped with enclosed cytoplasm (Markey & Wilce 1976b). The mitochondrial shape is, thus, influenced by the divisional stages. In the cell mitochondria are randomly distributed and also lie along the cell periphery in *Giffordia, Fucus* and *Chorda* (Bouck 1965) and in the vegetative cells of *Sphacelaria tribuloides* (Galatis et al. 1977). In the male gamete of *Cutleria hancockii* they are clustered at the anterior end and at the flagellar basal body (LaClaire II & West 1979). Mitochondria are abundant in the sieve-elements of *Laminaria saccharina* (Sideman & Scheirer 1977). The translocation of metabolites, thus, requires a high level of oxidative metabolism and an energy requiring mechanism.

Golgi Bodies

The golgi bodies are found both near the perinuclear region and in the cytoplasm, and are involved in a number of secretion and transportation functions (Brawley & Wetherbee 1981). In active cells the perinuclear position of golgi bodies is common. In *Cystoseira stricta*, during differentiation of vegetative apex, morphological changes in golgi bodies occur. In primary meristematic apical cells the golgi bodies are small in size and lack vesicles whereas in meristoderm cells they are hypertrophied. Those present in the inner promeristematic cells are non-secretory (Pellegrini 1976). In *Pylaiella littoralis* (Markey & Wilce 1975) and *C. stricta* (Pellegrini 1976), 'C'-shaped golgi bodies are reported and these are normally functioning structures (figure 1B). In *C. stricta*, the golgi bodies are also altered by various environmental conditions. The treatments —prolonged immersion of thallus, placing of algae in atmosphere with reduced oxygen level, absence of light, and decrease in salinity do alter the shape of golgi but do not interfere with the number of golgi cisternae (Pellegrini 1976). In prolonged immersion the ultrastructural modifications are not conspicuous. The perinuclear golgi bodies consist of approximately ten stacks of cisternae. These cisternae have swollen ends and have vesicles at their periphery. The contents of these vesicles are incorporated into the cell wall by inverse pinocytosis. Significant ultrastructural changes are brought about in the reduced oxygen atmosphere where the golgi cisternae expand and dilate uniformly. The perinuclear golgi bodies assume an U-shape. In total darkness, within three days the typical appearance of golgi bodies is lost and the cisternae dilate. On the fifth day (in total darkness), the cisternae swell and on the tenth day they merge and form large vesicles. The normal structure and functions of golgi bodies are, thus, affected not only by ontogeny but also by environmental factors.

Flagellum and Its Structure

The motile reproductive cells of brown algae possess two flagella that are laterally inserted. One, of the two flagella, possesses mastigonemes whereas the other lacks them as seen in *Fucus* (Manton & Clarke 1951) and *Chorda* (Toth 1976). In *Chorda* the flagellum in addition to mastigonemes possess also a highly coiled terminal region which helps the zoospores in attachment to the substratum. The flagella, in addition to mastigonemes, may bear appendages like spines. In *Himanthalia*, the anterior flagellum bears one micron long spine near the distal base on one fibril of the peripheral series. In *Dictyota*, the flagella has a row of 12 blunt spines, on a median line, between the two lateral rows of flimmers (Manton 1959). In *Hormosira*, the mastigoneme bearing flagellum also has a scale near the distal end (Forbes & Hallam 1978).

Proboscis: Proboscis is funnel-shaped membranous structure traversed by 13 concentric bands of thickenings. In *Fucus serratus* proboscis partially covers the mastigonemes bearing flagellum. Proboscis is an important organ and is characteristic of the Fucaceae (Manton & Clarke 1951). The functional significance of proboscis is not known. Manton and Clarke (1951), consider that either it is a part of swimming mechanism or has some sensory and copulation functions connected with oogamous reproduction.

Flagellar Root: The flagellar root is a flat sheet of microtubules, as in *Ectocarpus* (Baker & Evans 1973a, b) and *Cutleria hancockii* (LaClaire II & West 1978). In *Ectocarpus* the flagellar root originates near the front of flagellum and consists of 6 or 7 microtubules that lie in one plane and are perpendicular to the plasmalemma (Baker & Evans 1973a).

Flagellar Formation: Three basic patterns of flagellar formation has been described.

(a) In *Dictyota*, entire axoneme in the cytoplasm is without coils. The axoneme is pushed out of the plasmalemma, as it uncoils, and plasmamembrane forms a sheath around it.
(b) In *Chorda*, flagella are formed on the cell surface and not in the cytoplasmic vesicles. The centrioles migrate to the plasmalemma to function as basal bodies.
(c) In *Pylaiella littoralis* (Markey & Wilce 1976a) a basal plate develops on the basal body. This plate acts as a marker for the orientation of the primary flagellar vesicles that arise from the golgi bodies. These vesicles fuse to form large vesicle which are present near the basal body. The flagellar vesicle along with the enclosed axoneme elongate in the cytoplasm and eventually reach the plasmamembrane. The plasmamebrane and flagellar vesicle membrane fuse and flagella is released in the cleavage space.

Mastigonemes: Mastigonemes are fine hair-like structures that extend from the flagellar surface. In *Ascophyllum* and *Fucus*, it is a tripartite structure consisting of a tapered basal region, a closed microtubular shaft and a group of two or three filaments (Bouck 1969). Each part is made up of globular subunits. In *Leptonematella* mastigonemes similarly possess an expanded base of 650 Å in diameter. The base is a shallow cone on a hemisphere with a hollow center, with an anchoring device inserted beneath the flagellar sheath. A shaft consisting of two differentiated zones is present on the basal region. The short proximal fibrillar zone is 180 Å in diameter and 1500–3000 Å in length and lies outside the flagellar membrane. The distal tubular region of the shaft is 1 μ long and 150 Å in diameter and is terminated by two hairs. The hair consists of a single row, 30 Å wide, of globular subunits (Loiseaux & West 1970). In *Chorda* mastigonemes lack terminal hairs and consist of a solid base and tubular shaft. The mastigonemes are attached on one side of the flagellum (Toth 1976).

Mastigonemes are reported to be formed in different regions of the cell. They are present in perinuclear continum (Bouck 1969, Markey & Wilce 1976a). The mastigonemes, in the developing antherozoids are formed in membrane bounded sacs in *Fucus* and *Ascophyllum* (Bouck 1969); in developing zoospores of *Pylaiella littoralis*, *Elachista fucicola*, *Hecatonema streblonematoides* in golgi vesicles (Loiseaux 1973), and in *P. littoralis* in the developing zoospores of unilocular sporangia are formed in ER cisternae (Markey & Wilce 1976a).

Loiseaux (1973) considers that the mastigonemes are formed in perinuclear region and are carried in membrane bound vesicles through the cytoplasm to a special golgi body that is present near the developing flagellum. Mastigonemes are then liberated in parallel rows at the base of the flagellum. Markey and Wilce (1976a), suggested a similar process of mastigoneme formation and also added that the mastigonemes after elaboration in perinuclear continum are found in ER and then golgi cisternae.

Microbodies

Microbodies are membrane bounded, roughly spherical to elongated structures, seen in the vegetative cells of *Sphacelaria tribuloides* (Galatis et al. 1977). These structures are associated with mitochondria and chloroplasts. The membrane of the microbody is darkly stained at the junction where it is attached to the chloroplast.

Plasmalemma Proliferations and Plasmalemmasomes

Numerous finger-like projections, 1 μm in length and 1 or 2 μm in width, or plasmamembrane are present along the longitudinal walls of the vegetative cells of *Sphacelaria tribuloides* (Galatis et al. 1977). The contour of the ingrowth is either smooth or undulated. The threads of cell wall project into the undulations (figure 1C). Mitochondria are seen associated with the plasmalemma proliferations which probably are involved in the physiological activity of cells.

Plasmalemmasomes are structures that probably originate by an elaboration of plasmalemma. They are present in sporelings of *Petalonia* (Cole & Lin 1970), and in developing plurilocular sporangium of *Ectocarpus* (Lofthouse & Capon 1975). The *Petalonia* plasmalemmasomes are present between the plasmalemma and the cell wall. In *Ectocarpus*, during cell wall formation and the time when cell divisions are at peak they are abundant suggesting their involvement in the cell wall formation (Lofthouse & Capon 1975). In *Pylaiella* cells during plasmamembrane formation and cell wall synthesis, paramural bodies are present (Markey & Wilce 1976b). It is inferred that such bodies are *pro-parte* plasmalemmasomes.

Plaques

Plaques are structural units consisting of fine fibrillar materials and a rim of electron dense granules. In zoospores still enclosed in the zoosporangium, plaques are produced by golgi bodies. In *Laminaria saccharina* and *Nereocystis lutkeana* zoospores are naked but the newly settled ones have a covering layer of plaque material. The individual-plaques do not fuse with one another

(Oliveira et al. 1980). The main component of plaques is protein but carbohydrates are also present. The polysaccharides perhaps participate in the adhesion of zoospores to the substratum. In *Chorda*, the grey staining bodies contain fibrillar material, and are involved in accumulation of the adhesive material of the zoospores (Toth 1976). Similarly in *Ectocarpus* zoospores the fibrillar material is the adhesive substance and is not organized into plaque-like structures (Baker & Evan 1973a).

Virus Particles

Virus-like particles are reported to be present in both vegetative and reproductive cells. They vary in shape and size. In *Ectocarpus fasciculatus* (Clitheroe & Evans 1974), and *Streblonema* (LaClaire II & West 1977), these particles show a dense core and a shell. The osmiophilic coat is 7–12 nm thick which surrounds an electron translucent region and an opaque fibrillar core (LaClaire II & West 1977). The presence of virus-like particles causes lysis of various organelles. In *Ectocarpus*, the electron-transparent vesicles precipitate their contents as a dense mass, and thus prevent ultimate attachment of the zoospores (Baker & Evans 1973a). The lysis of *E. fasciculatus*, zoospores occurs if they contain large number of virus-particles (Clitheroe & Evans 1974). In *Streblonema* sp. the nucleus of the infected vegetative cell is lysed, and the "virogenic stroma" consists of numerous fibrillar material probably representing DNA strands from the lysed nucleus and ribosomes. The nucleus in infected sporangia of *Pylaiella littoralis*, however, exhibits dark staining areas and membranous components in the cytoplasm. The membranous structures may be involved in the development of the particle (Markey 1974).

The terminal cells of the branch which develop unilocular sporangia get infected, suggesting that the infection is probably systematic. The virus particles are transmitted to each zoospore within sporangium during subsequent cleavage (Clitheroe & Evans 1974). In *Pylaiella* virus particles perhaps enter either through damaged-cells or sporangia and move through plasmodesmata in the adjacent structures.

The infected zoospores of *Ectocarpus*, are unable to attach to the substratum (Baker & Evans 1973a). The growth of infected *Streblonema* (in *vitro* conditions) is, however, not affected. This suggests that infection is not harmful (LaClaire II & West 1977).

Sieve Filament

Sieve filaments are present in the medulla of the kelp thallus, and consist of cells with simple sieve plates on their cross walls. The individual cell of such a filament represents the sieve filament member. The sieve elements in *Laminaria* differentiate from the inner cortical cells by addition of large number of organelles and vacuoles (Schmitz & Srivastava 1974). The sieve elements are characterized by presence of vacuoles, many mitochondria, plastids, nuclei, golgi bodies (figure 3A) and ribosomes as in *Laminaria groenlandica*. The pores are in the end walls of the sieve elements (figure 3B and facilitate interconnections between the adjacent sieve elements. The pores are formed by enzymatic digestion of the parts of the cross wall, and have different sizes in various genera. The anatomical specialization of sieve elements suggests that they acts as a pathway for translocation of metabolites.

The older sieve elements show a general pattern of the organelles disorganization. In *Laminaria groenlandica* the chloroplasts and the mitochondria membrane vesiculate (Schmitz & Srivastava 1974). In *L. saccharina* the chloroplasts, contain either a single or a double thylakoid; irregularly shaped discs, exhibit different shapes and dispersed plasto-globuli (Sideman & Scheirer 1977). The ribosomes, golgi bodies also disappear, vesicular structures appear at the cross walls and in addition the plasmalemma and cytoplasmic connections are lost. There is large deposit of callose in sieve plates of older sieve elements as in *L. groenlandica* and *Nereocystis lutkeana* (Schmitz & Srivastava 1974, 1976).

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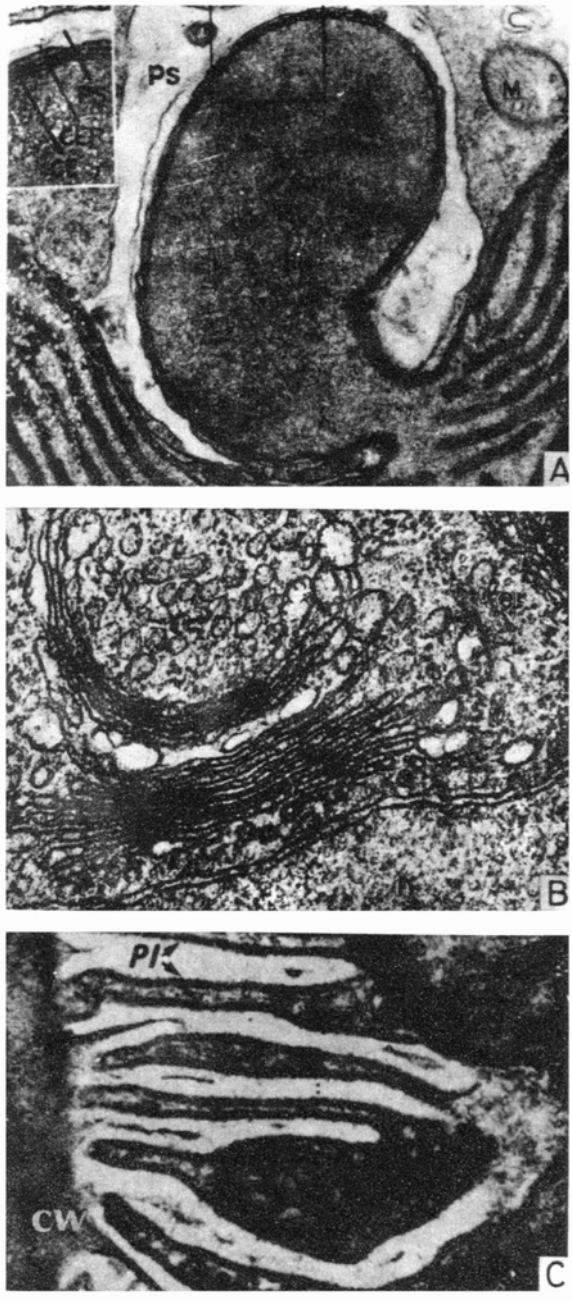

Figure 1A–C, A, *Chorda* (after Hori 1972), Pyrenoid (P) with electron transparent cap (PS). The cap extends all over the pyrenoid except at its neck. In the inset, the various envelops of the pyrenoid are evident. The chloroplast envelope (CE) limits the pyrenoid whereas the chloroplast-endoplasmic reticulum (CER) constitutes the middle pair of membrane. Mitochondria (M) is also present near the pyrenoid· **B,** *Pylaiella littoralis* (after Markey & Wilce 1975). C' shaped golgi body is present near the nucleus (n). Endoplasmic reticulum (er) is also present; **C,** *Sphacelaria tribuloides* (after Galatis et al. 1977). Threads from the cell wall (CW) project into plasmalemma proliferations (PI)

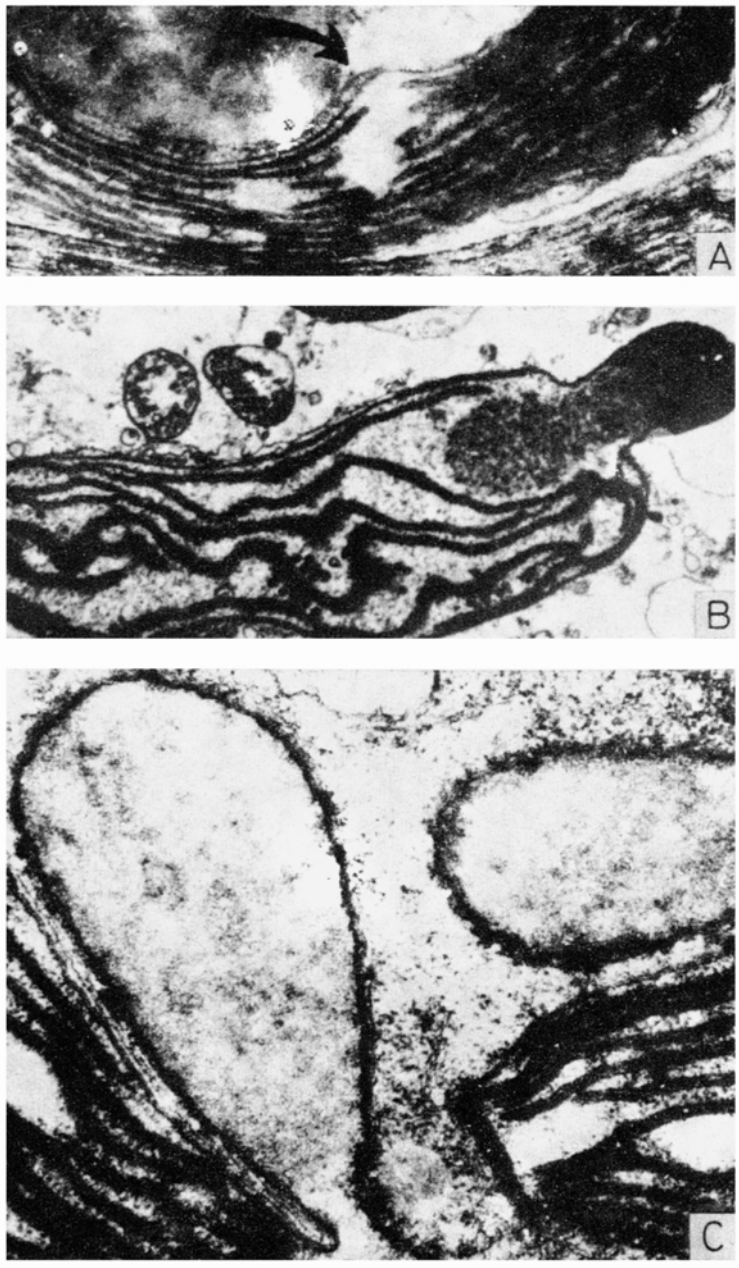

Figure 2 A–C. Stages in *de novo* formation of pyrenoid (after Loiseaux 1973); **A,** *Hecatonema streblonematiodes* lamellar-free space in the chloroplast (arrow); **B,** *Elachista fucicola* showing granular material condensed in the chloroplast's lamellar-free space; **C,** *E. fucicola* mature pear-shaped pyrenoid. The pedicle is attached to lamellar-free portion of the chloroplast. The pyrenoid is limited by chloroplast double membrane and endoplasmic reticulum

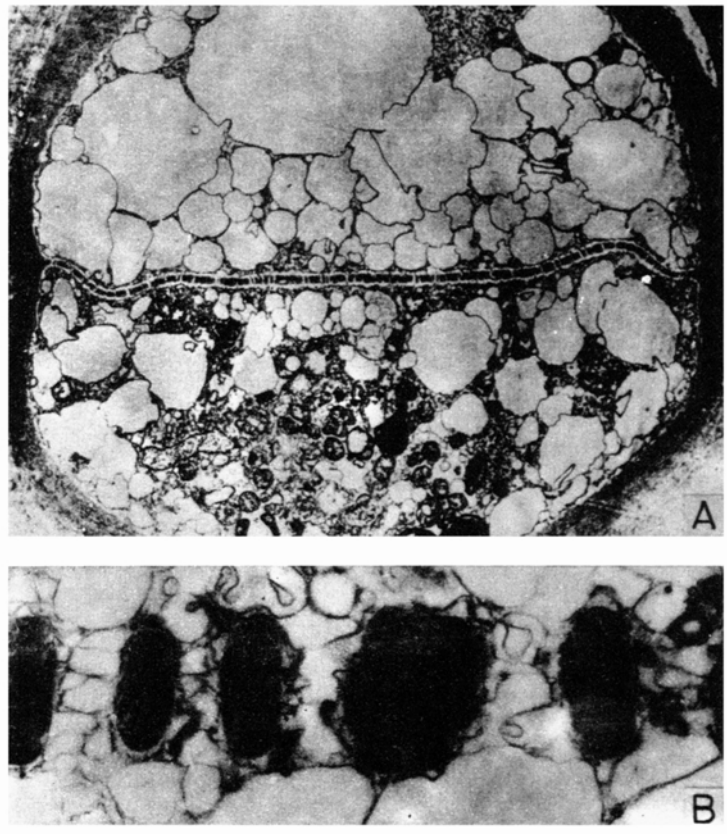

Figure 3 A–B. Sieve element and pores. **A,** *Laminaria groenlandica* (after Schmitz & Srivastava 1974). The primary and secondary walls are clear. Vacuoles, chloroplasts and a large number of mitochondria are present; **B,** *Nereocystis lutkeana* (after Schmitz & Srivastava 1976). Pores are present in the cross wall of the sieve element

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