ULTRASTRUCTURE OF THE FUSION CELL IN 
FAUCHEOCOLAX ATTENUATA SETCH. 
(RHODOPHYTA, RHODYMENIALES) 

STYLIANOS G. DELIVOPOULOS* AND PAUL KUGRENS 
Department of Botany, Colorado State University, 
Fort Collins, Colorado 80523, U.S.A. 

SUMMARY 

The fusion cell in Faucheocolax attenuata Setch. is a highly lobed, thick-walled, multinucleate and irregularly shaped cell originating from the basal cell of the auxiliary cell branch. The formation of the fusion cell occurs by an incorporation of vegetative cells into the basal cell, after dissolution of septal plugs between these cell types. Thus the fusion cell is a syncytium containing only haploid nuclei, as well as unusual mitochondria and plastids. Mitochondria lack cristae and instead contain a tubular helical structure. Plastids are atypical with regard to thylakoid organization in red algae, because they lack the peripheral thylakoid and their photosynthetic thylakoids are aggregated to one side. In addition, they contain large osmiophilic bodies. Nuclear envelopes appear to produce large quantities of membrane cisternae. Floridean starch is absent and the cytoplasm contains few ribosomes. The plasma membrane is irregular and endoplasmic reticulum cisternae are situated parallel to it. Bundles of putative microfilaments were commonly found in nuclei and the cytoplasm. Structural evidence does not support any meristematic, nutritive or secretory functions previously ascribed to fusion cells in other genera.

INTRODUCTION 

Following fertilization, Florideophycean red algae form a diploid phase termed the carposporophyte. This stage remains attached to the female gametophyte and consists of three different cell types: the fusion cell, gonimoblast cells and carpospores. The most unusual component is the fusion cell, which is generally considered to be an important structure, because apparently it can give rise to gonimoblast filaments (Sjöstedt, 1926; Oza, 1976; Kugrens, 1982; Delivopoulos & Tsekos, 1983). The fusion cell reportedly is formed from repeated fusions of diploid and haploid cells (Wetherbee, 1980; Kugrens & Arif, 1981; Kugrens, 1982; Ramm-Anderson & Wetherbee, 1982; Delivopoulos & Tsekos, 1983), resulting in a large, irregularly shaped syncytium. 

Despite its significance and general occurrence in the Class Florideophyceae, the fusion cell remains one of the least investigated structures of the carposporophyte. Most ultrastructural studies of this cell have been incidental in papers describing carposporogenesis (Kugrens & West, 1973, 1974; Kugrens, 1982; Ramm-Anderson & Wetherbee, 1982) and with two exceptions (Kugrens, 1982; Ramm-Anderson &
G. Delivopoulos and P. Kugrens (Wetherbee, 1982) they have been confined to members of the Ceramiales (Kugrens & West, 1973, 1974; Wetherbee, West & Wynne, 1974; Tripodi & De Masi, 1977, 1978; Wetherbee, 1980; Kugrens & Arif, 1981). As a result of this taxonomic selectivity, the extent of variation in structure and function of fusion cells among other orders of red algae remains enigmatic. To date only three papers have provided detailed descriptions of the fine structure of fusion cells (Tripodi & De Masi, 1977, 1978; Kugrens & Arif, 1981) and only two considered the fusion cell as a developmental system (Wetherbee, 1980; Kugrens & Arif, 1981).

There remain numerous unresolved problems and ambiguities regarding the ultrastructure of fusion cells. These include: (1) fusion cell function; (2) the process and reason(s) for vegetative and gonimoblast cell incorporation into the fusion cell; (3) the fate of haploid nuclei within fusion cells; (4) the functional significance of different organelles and/or structures existing within fusion cells; (5) the presence of any unusual fusion cell structures; and (6) the timing and extent of fusion cell degeneration that often takes place.

Therefore, studies on Faucheocolax fusion cells were initiated to provide additional information in a representative of the Rhodymeniales, Faucheocolax attenuata Setch. The information from this study provides some interesting contrasts and comparisons with the descriptions of fusion cells from Ceramialean genera (Tripodi & De Masi, 1977, 1978; Wetherbee, 1980; Kugrens & Arif, 1981).

MATERIALS AND METHODS

Thalli of Faucheocolax attenuata bearing cystocarps of varying sizes, were collected near Salmon Bank, San Juan Island, Washington and by SCUBA diving north of the Bodega Marine Laboratories, Sonoma County, California. The parasitic thalli were excised (from Fauchea) and fixed immediately for light and electron microscopy according to previously described procedures (Kugrens, 1974). Thin sections were examined with either an AEI-6B or AEI-801 electron microscope.

OBSERVATIONS

Faucheocolax is a parasitic red alga that is related to its host Fauchea (Kylin, 1956) and this is considered an adelphoparasite. The thallus is reduced in size and has a light pink coloration. The carposporophyte of Faucheocolax appears typical of other genera in the Order Rhodymeniales of the Florideophyceae, because it is subtended by a large fusion cell (Kylin, 1956). Fig. 1 summarizes the post-fertilization events leading to the formation of this unusual fusion cell, which originates from the basal cell of a two-celled auxiliary cell branch. Subsequently, adjacent cells become incorporated to form a larger, more irregularly shaped fusion cell. Incorporated cells always include vegetative cells and sometimes carpogonial branch cells, as well as the supporting cell, but never the auxiliary cell. Therefore, only haploid nuclei occur in this fusion cell.

From the earliest to the oldest developmental stages, the nature of the fusion cell remains unchanged, except that additional incorporation of vegetative cells increases its size. Even before any cell incorporation is initiated, the fusion cell precursor (the
of development. The plug is dark staining and has a mottled appearance. In addition, it exhibits an irregular or crenulate profile on the side of the fusion cell, whereas it is smooth on the side toward the auxiliary cell.

Fusion cell nuclei usually occur in proximity to each other (Figs 2, 3) and are generally situated in the peripheral cytoplasm (Fig. 4), often in contact with the plasma membrane or the endoplasmic reticulum cisternae beneath the plasma membrane (Fig. 4). Furthermore, the nuclear envelopes in newly incorporated cells generally become irregular and highly lobed (Fig. 4). Numerous stacked membrane cisternae are characteristically associated with nuclei (Figs 2–4), their appearance suggesting that they are derived from the nuclear envelope. These membranes are parallel to each other in longitudinal view but appear reticulate in cross-section (Figs 3, 4).

One of the more unusual structures in these fusion cells are the clusters of small parallel rods having dimensions and aggregations reminiscent of microfilaments. They are tentatively designated as such. These microfilaments occur in both the cytoplasm (Fig. 5) and nuclei (Figs 4, 6).

Fusion cell plastids are atypical of red algae (Fig. 7). The thylakoids are aggregated to one side and large osmiophilic bodies are found in the stroma. The peripheral thylakoid is absent.

Mitochondria, likewise, are atypical (Fig. 8). Instead of possessing identifiable cristae, most either lack any internal membranes or they contain a tubular helical membrane that is located in the centre of the stroma.

The incorporation of vegetative cells into the fusion cell requires the dissolution of septal plugs between the respective cells. Fig. 9 shows the features of the auxiliary-fusion cell septal plug, which appears to be undergoing some degradation on the fusion cell side, as indicated by material being removed from the plug. This plug, however, is never degraded completely, so the auxiliary cell retains its integrity throughout development.

Septal plugs between fusion and vegetative cells are smaller (Fig. 10) and readily undergo dissolution. Even before the actual fusion is accomplished, the adjacent cells begin to deposit wall material, forming a thick wall (Fig. 10). The vegetative cell septal plugs have densely staining peripheries with a less-dense core (Figs 10, 11). Plug degradation generally is initiated on the fusion cell side and the first indication of degeneration is the swelling of the septal plug on that side (Figs 11, 12). Microtubules are in the proximity of the swollen plug (Fig. 12). With continued swelling, the plug eventually breaks down into smaller dark-staining pieces (Figs 13, 14), until the entire plug has been fragmented (Fig. 15). The septal plug fragments are often associated with a reticulate membrane system, possibly endoplasmic

Fig. 2. Overview of the fusion cell. Numerous fused vegetative cells are incorporated, as indicated by wall remnants (arrows). Note the absence of floridean starch and the paucity of organelles, as well as the disposition of nuclei and organelles toward the peripheral cytoplasm. A thickened wall surrounds the components of the fusion cell. X2950.

Fig. 3. The fusion and auxiliary cells connected by a large basal septal plug (sp). Note the irregular outline of the plug on the fusion cell side. X7750.
Faucheocolax *fusion cell*

reticulum (Figs 14–16), that may have been formed by the nuclear envelopes. Cytoplasmic continuity is now established between the cells that contain numerous dark-staining masses of material, probably representing septal plug remnants (Fig. 16). Thus the fusion cell now has increased its size and numbers of nuclei, all of which are haploid. This incorporation of nuclei through cytoplasmic fusions creates a syncytium.

**DISCUSSION**

Fusion-cell formation and carposporophyte development in *Faucheocolax* do not match the descriptions of Setchell (1923) and Kylin (1956), although the diagrams of the mature carposporophyte are similar. Both state that post-fertilization development in *Faucheocolax* is identical to *Fauchea* but details of this development were provided only for *Fauchea*. We must, therefore, assume that either the descriptions were erroneous or we are dealing with a different species from the one described by Setchell (1923). This contradiction points out the necessity for a critical re-evaluation of fusion cells in different taxa, so that we can correctly assess the roles assigned to them by light microscopists.

Studies on *Polysiphonia novae-angliae* Taylor (Wetherbee, 1980), *Asterocolax gardneri* Setch. (Kugrens & Arif, 1981) and *Leachiella pacifica* (Kugrens, 1982) demonstrated that fusion cells change during carposporophyte development. Therefore, all developmental stages should be examined, so that accurate interpretations of fusion cell structure and function can be made (Brawley & Wetherbee, 1981). This is particularly true in the light of some reports that indicated that fusion cells contained unusual organelles (Tripodi & De Masi, 1977, 1978) or appeared to be degenerating (Kugrens & West, 1974). Some important functions are usually ascribed to the fusion cell (Yamanouchi, 1906; Drew, 1954; Fritsch, 1965; Wetherbee, 1979, 1980; Kugrens & Arif, 1981; Kugrens, 1982), but apparently some of the ideas regarding this cell must be modified, on the basis of our findings in *Faucheocolax*.

The fusion cells in some species may not be the important components of the carposporophyte that previous investigators had presumed. Rather, this cell in some of these organisms appears degenerate and seemingly does not play any role in carposporophyte development, thus merely representing a vestigial cell. The degradative enzymes that may form in this cell might initiate fusions with adjacent cells, also

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**Fig. 4.** Fusion cell nucleus showing the apparent production of numerous membranes from the nuclear envelope. An expansion of these membranes forms a reticulate network of endoplasmic reticulum. Note the intranuclear microfilaments (arrows). ×16,000.

**Fig. 5.** Cytoplasmic microfilaments in the fusion cell. ×40,000.

**Fig. 6.** Higher magnification of intranuclear microfilament cluster. ×70,450.

**Fig. 7.** Degenerating plastids and proplastids in the fusion cell. ×15,000.

**Fig. 8.** Typical fusion cell mitochondria. Tubular helical membranes (arrows) occur in the stroma. ×32,150.
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Figs 9–16
causing them to assume a similar degenerate appearance. Cytoplasmic fusions occur through the dissolution of septal plugs between the fusion cell and adjacent cells, thereby increasing the cytoplasmic volume of the fusion cell and giving it more prominence in the carposporophytic system than is justified through light-microscopic observations.

Fusion cells in other genera, regardless of their initial functions, apparently also degenerate with an accompanying incorporation of gonimoblast and vegetative cells. In these fusion cells, however, degeneration begins only after the carposporophyte is well formed. On the other hand, Faucheocolax fusion cells begin degeneration during the earliest stages of carposporophyte development and never participate in forming any products of the carposporophyte. Faucheocolax gonimoblast cells apparently are protected from incorporation by the large, basal septal plug between the auxiliary cell and the fusion cell. This plug shows some degeneration on the fusion cell side but a cytoplasmic connection is never created. In addition, the auxiliary cell could act as a buffer cell, intervening between the meristematic gonimoblast cells and the fusion cell.

Since the multinucleate condition of fusion cells arises from the fusions of haploid and diploid cells (Wetherbee, 1980; Kugrens & Arif, 1981; Kugrens, 1982; Ramm-Anderson & Wetherbee, 1982; Delivopoulos & Tsekos, 1983), it is assumed that there is some means of isolating or inactivating the haploid nuclei (Kugrens & Arif, 1981). To date the only isolating mechanism reported is a cytoplasmic barrier (Kugrens & Arif, 1981), which thus far is unique for the Rhodomelaceae. Obviously there is no need for nuclear degeneration or inactivation in Faucheocolax fusion cells, since only haploid nuclei are present. Nevertheless, nuclear envelopes seem to produce large numbers of membranes, which usually aggregate into stacks. These membranes often completely surround the nuclei and are sometimes associated with septal plug fragments. Similar

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Fig. 9. Portion of the large septal plug between the fusion and the auxiliary cell. Note the crenulated profile of the plug on the fusion cell side and the smooth outline on the auxiliary cell side. Dark staining masses (arrows), representing material being removed from the plug, are present in the fusion cell close to the plug, as well as on its surface. ×15,700.

Fig. 10. Young fusion cell connected to two intact vegetative cells. The septal plugs between the fusion cell and vegetative cells are in various stages of dissolution. ×4,570.

Fig. 11. Septal plug showing incipient dissolution indicated by plug enlargement in the fusion cell side. ×13,750.

Fig. 12. Septal plug exhibiting additional dissolution. Microtubules are present near the plug. ×18,400.

Fig. 13. Septal plug showing further degeneration. ×11,250.

Fig. 14. Higher magnification of an advanced stage of septal plug dissolution. Note the reticulate endoplasmic reticulum near the septal plug. ×25,000.

Fig. 15. Final stage of septal plug dissolution. The plug remnants occur to one side of the cytoplasmic channel that has been created. The vegetative cell now takes on the characteristics of the fusion cell. ×16,875.

Fig. 16. Fusion cell and its newly incorporated vegetative cell. Masses of septal plug material are dispersed in the cytoplasm. Arrows indicate wall remnants from fused cells. ×11,785.
stacking of endoplasmic reticulum (ER) has been reported in developing and/or mature sieve elements (Melaragno & Walsh, 1976; Singh, 1980). In these instances it was suggested that the stacked ER may participate in the autolytic process by providing enzymes for this activity (Esau & Gill, 1972, 1973). The localization of acid phosphatase (Catesson, 1973; Esau & Charvat, 1975) and ATPase (Gilder & Cronshaw, 1973a,b) on stacked ER support such a view. Although it is difficult to identify the observed features with certainty, it is possible that a similar function could be ascribed to the membranes of Faucheocolax fusion cells, since these cells have some additional features in common with differentiating and/or mature sieve elements, such as the absence of dictyosomes and ribosomes (Esau, 1977).

The study of Tripodi & De Masi (1977) on Erythrocystis montagnei (Derb. et Sol.) Silva fusion cells revealed numerous 'unusual or peculiar' structures, similar to the ones in Faucheocolax. These included unusual nuclei, mitochondria with helical internal membranes, dense cytoplasmic bodies surrounded by endoplasmic reticulum, crystalline endoplasmic reticulum, large concentrations of membranes and sheets of electron-transparent material. One of the most unusual, however, was a cylindrical structure consisting of coiled sheets of electron-dense material that in longitudinal section vaguely resembled a basal body, and in fact was interpreted by Tripodi & De Masi (1978) as 'a vestige of a flagellum'. However, it does not actually resemble any structure that can be construed as part of a basal body, because there are no microtubular remnants. A serious effort was made to find these or similar structures in Faucheocolax, but we failed to locate them.

Plastids of the Faucheocolax fusion cell, as those of Erythrocystis (Tripodi & De Masi, 1977), lack a peripheral thylakoid and exhibit a degenerate appearance. Furthermore, the twisted or helical membranes in mitochondria, previously interpreted as mitochondrial DNA (Tripodi, Pizzolongo & Giannattasio, 1972; Tripodi, 1974; Tripodi & De Masi, 1977; Tsekos, 1983), are identical to the helical membranes found in degenerating mitochondria of the Faucheocolax fusion cell. Therefore, we believe that these structures represent disorganized membranes in a degenerating mitochondrion.

These previous studies apparently were based on late ontogenetic stages in fusion cell development; it is therefore difficult to ascribe functional significance to many of their observed features. Consequently, it seems plausible that the organelles are becoming disorganized in an aging fusion cell, since similarly structured organelles and membranes were also found in Faucheocolax fusion cells, which we interpreted as aging or degenerating cells.

Plant cells have cytoskeletons composed of actin microfilaments and microtubules that are indistinguishable from those found in animal cells (Alberts et al. 1983). The occurrence of microfilaments in plant cells and their possible function have been discussed by Parthasarathy & Mühlethaler (1972) and reviewed recently by Jackson (1982). In another investigation (Parthasarathy, 1974) microfilament bundles were observed in differentiating sieve elements whose protoplasts undergo a profound change during ontogeny (Esau, 1977). Electron-microscopic studies of cells undergoing changes in shape have shown that microtubules and microfilaments are involved
in these processes (Wessels, 1971). In addition, formation of the actin filaments in the fertilization tubule of *Chlamydomonas reinhardii* Dan. is clearly dependent upon receipt of intracellular signals generated by adhesion of flagellar membranes (Goodenough, 1977; Solter & Gibor, 1977). Since the fusion cell in *Faucheocolax* changes its shape rapidly and expands outwardly by fusions with adjacent cells, it seems possible that the cytoplasmic microfilaments are somehow involved in cellular fusions. Similar structures were found in nuclei of *Porphyridium purpureum* (Bory) Drew et Ross (Bronchart & Demoulin, 1977) and *Rhodella reticulata* (Deason, Butler & Rhyne, 1983), as well as in *Faucheocolax* nuclei, but the role of these intranuclear microfilaments remains to be demonstrated. Whether cytoplasmic and intranuclear microfilaments of *Faucheocolax* fusion cells are composed of actin needs further investigation.

A generally held view (Yamanouchi, 1906; Drew, 1954; Fritsch, 1965; Wetherbee, 1979, 1980; Kugrens, 1982) is that the fusion cell and any cells incorporated into the fusion cell provide nutrients to the remainder of the developing carposporophyte, since large quantities of floridean starch are found in some fusion cells (Kugrens & Arif, 1981; Kugrens, 1982; Delivopoulos & Tsekos, 1983). Wetherbee (1980) observed that the main body of the *Polysiphonia* fusion cell was devoid of starch grains and ribosome concentrations were greatly diminished in that cell. Consequently, its function as a nutrient source for the developing carposporophyte is limited. Nevertheless, Wetherbee (1980) embraced the idea of a nutritive role for the fusion cell. Meristematic activity (Tripodi & De Masi, 1977; Duckett & Peel, 1978; Kugrens, 1982; Delivopoulos & Tsekos, 1983) or secretory functions (Kugrens & Arif, 1981) also were ascribed to the fusion cell. Structural evidence in *Faucheocolax*, however, does not support a nutritive, secretory or meristematic function for the fusion cell. Thus the fusion cell, while taxonomically important, does not play any active or obvious role in carposporophyte development in *Faucheocolax* and we suspect that the same may apply to other genera where fusion cells are given a prominent role in carposporophyte development.

The lighter and degenerate appearance of the fusion cell is not artifactual or due to poor fixation. Carpospores (Delivopoulos & Kugrens, 1984), as well as auxiliary and gonimoblast cells, were properly preserved and displayed a variety of developmental features in the carposporophyte. Rather, the *Faucheocolax* fusion cell has the characteristics of a disorganized cell similar in structure to differentiating and/or mature sieve elements (Esau, 1977). Therefore, we conclude that the fusion cell remains alive throughout carposporophyte development but its function in relation to the female reproductive system remains enigmatic.

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