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The ultrastructure of tetrasporogenesis in *Dictyota dichotoma* (Hudson) Lamouroux (Dictyotales, Phaeophyceae)

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The first sign of tetrasporogenesis in *Dictyota dichotoma* (Hudson) Lamouroux is the outgrowth of certain epidermal cells that follow a characteristic differentiation process. These cells soon become polarized and constitute the tetrasporangium mother cells (TMCs). Three distinct zones are established along their growth axis: one apical, full of small vesicles, one central, in which most of the organelles are aggregated, and a basal one with large vacuoles and peripheral chloroplasts. The nucleus is displaced towards the basal zone and, as the cell grows outwards, the thick multilayered external wall breaks while new layers are deposited on its internal surface. An asymmetrical division of the TMC results in the formation of the tetrasporangium, which is obviously larger than the stalk cell(s), with more dense cytoplasm and numerous organelles distributed along its anticlinal axis. This cell undergoes a characteristic differentiation proccess, the polarity pattern changing from axial to radial. Finally, it becomes almost spherical. After meiosis, four haploid nuclei are formed and the organelles are arranged in groups around them. During these stages many active dictyosomes are observed, secreting an amorphous material, that is deposited between the membranous septa separating the tetraspores, as well as in the inner side of the external wall. This material is probably mucilagenous and may help, by absorbing water, in the breaking of the external wall, thus facilitating the release of the spores.

Key Index Words: asymmetrical division—Dictyota—*Phaeophyceae—polarity—tetrasporogenesis—ultrastructure.*

The study of the reproductive processes of algae has been proved a significant tool for the understanding of many cytological, taxonomical and physiological problems. Moreover, these studies, combined with the fine structural investigation of thallus development and differentiation, give answers to some important morphogenetic problems.

Within the brown algal order Dictyotales the study of the reproduction has started very early, with the pioneer work of Williams (1897, 1904a, b, 1905). More than fifty years later a number of light microscope studies appeared, dealing with tetraspore formation in some members of Dictyotales, like *Dictyota dichotoma* (Hudson) Lamouroux, *Dictyopteris divaricata* (Okamura) Okamura, *Padina japonica* Yamada and *P. crassa* Yamada (Ishii *et al.* 1959, Kumagae *et al.* 1960). On an ultrastructural level, there are detailed studies on thallus structure and development of *D. dichotoma* and *Dictyopteris membranacea* (Stackh.) Batt. (Katsaros 1980, Katsaros and Galatis 1985, 1988, Gaillard *et al.* 1986). However, only a few ultrastructural studies have been published, dealing with reproductive stages. These describe the structure of sperms of *D. dichotoma* (Manton *et al.* 1953, Manton 1959) and eggs of *Dictyota binghamiae* J. Agardh (Neushul and Liddle 1968), as well as oogonia and eggs of *Zonaria farlowii* S. & G. (Neushul and Liddle 1968, Liddle and Neushul 1969). In addition, the sexual reproduction of *Dictyota diemensis* Kützing was recently studied in detail by means of both, light and electron microscopy (Philips *et al.* 1990). As far as we know, there is no ultrastructural information on tetrasporogenesis of any member of this class.

The aim of the present study is to inves-

tigate the ultrastructural changes accompanying the tetrasporogenesis in *D. dichotoma*, with particular attention to those preceding, accompanying and/or following the establishment of a new polarity axis and the shift in the differentiation process.

Materials and Methods

Thalli of *Dictyota dichotoma* were collected between April and June at a depth of 1-3 m at "Rafina", about 30 km from Athens, Greece. Small pieces of mature thallus portions bearing tetrasporangia and unreleased tetraspores were fixed and processed for EM according to Katsaros and Galatis (1986), with a more prolonged (up to three days) infiltration time (see also Hallam and Luff 1988). Thin sections were examined and photographed with a Philips 300 electron microscope.

Results

Tetrasporangium mother cell (TMC)

Tetrasporogenesis in *D. dichotoma* is not synchronous. Therefore, all the developmental stages can be traced on a limited thallus area. Tetrasporangia occur alone or in small groups along the central part of the thallus, at some distance from the apex.

The first sign of TMC formation is the outgrowth of certain epidermal cells (Fig. 1). Sometimes two or more adjacent cells are observed swelling in parallel. These cells are devoid of large vacuoles and have a more dense cytoplasm compared to their neighbouring cells. The swelling grows outwards resulting in a pear-like form (Fig. 3). The structural polarization of this cell is further expressed by the deposition of additional layers of wall material in the external periclinal wall (Figs. 1, 2) and the gradual distribution of the cell elements in three distinct zones along the cell axis: 1) an apical zone with numerous dictyosomes, vesicles and small vacuoles, 2) a subapical zone in which the nucleus and most of the organelles around it are localized, and 3) a basal one with well developed vacuoles and peripherally distributed chloroplasts (Figs. 2, 3).

As the cell grows outwards, the thick multilayered external wall breaks and new, less dense layers are deposited on its internal surface. A large number of vesicles and small vacuoles are observed in the apical region (Fig. 2). The nucleus is larger than that of typical epidermal cells and is usually lobed. A centriole is usually displaced in a depression of the nuclear envelope (Fig. 6). The chloroplasts are smaller than those of typical epidermal cells, with poor internal membrane organization (cf. Figs. 4 and 5). Small vacuoles, dictyosomes, physodes and endoplasmic reticulum (ER) membranes are observed among them (Fig. 5).

TMC-surrounding epidermal and stalk cells

The epidermal cells surrounding the TMC follow a characteristic differentiation process parallel to TMC formation. This process results in a polar organization of these cells which is expressed by: 1) Cell outgrowth that is parallel to that of the TMC, but not so extensive (Figs. 1, 3). 2) Zonation of the organelles in a way similar to that of the

Fig. 1. Light micrograph showing two TMCs and the surrounding epidermal cells, as appear in transverse thallus section. TMC: tetrasporangium mother cell. Scale bar=30 μm.

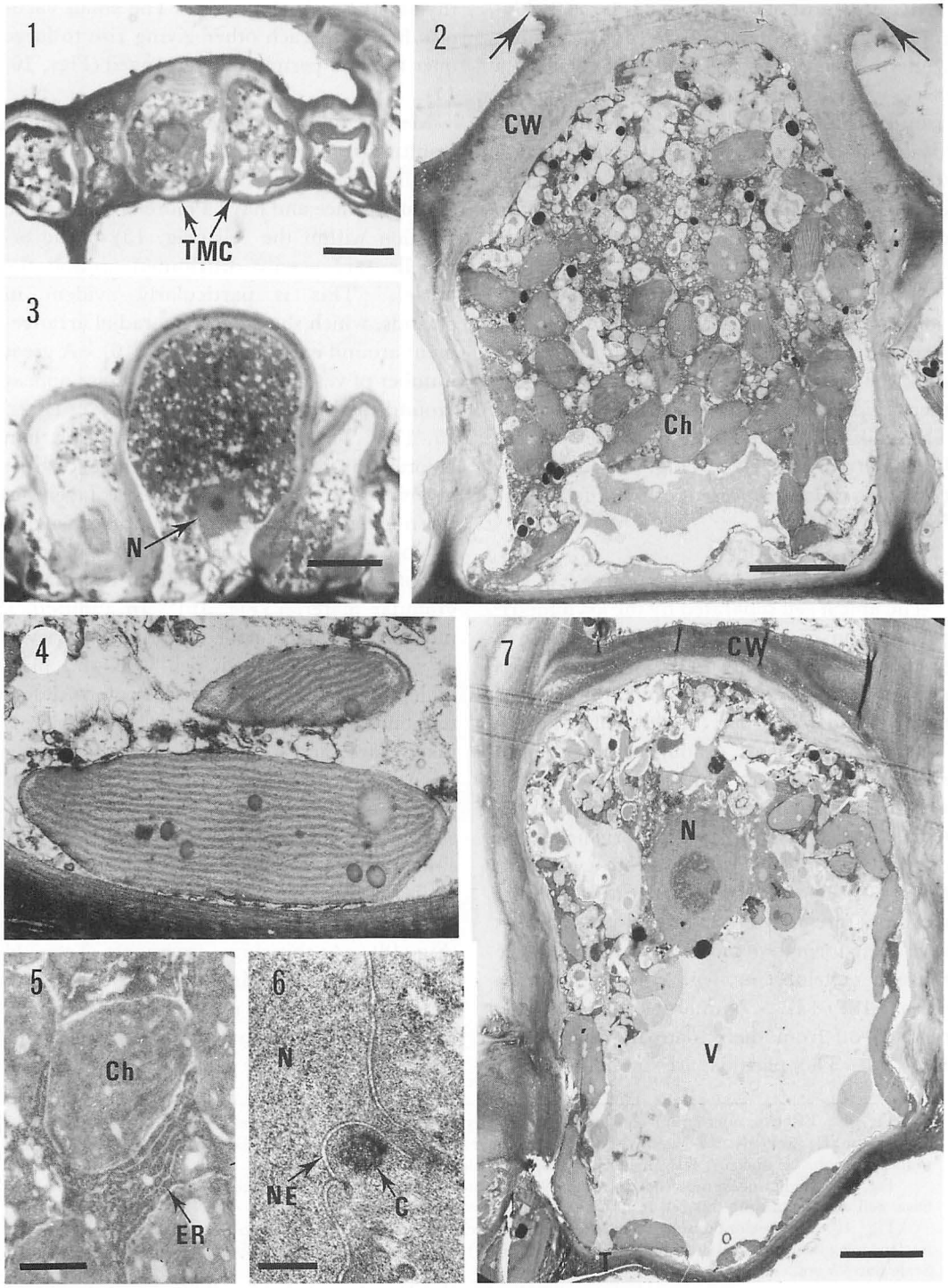
Fig. 2. Transverse thallus section passing through the cortical cytoplasm of a TMC at an early developmental stage. The distribution of cell elements varies gradually along its anticlinal axis. Note the break of the external layers of the cell wall at the apical dome area (arrows). Ch: chloroplast, CW: cell wall. Scale bar=5 μm.

Fig. 3. Light micrograph of a TMC at a more advanced developmental stage. The polarization is further expressed by the position of the nucleus towards the basal part of the cell. N: nucleus. Scale bar=25 μm.

Figs. 4, 5. Plastids of a typical epidermal cell (Fig. 4) and of a TMC (Fig. 5). Ch: chloroplast, ER: endoplasmic reticulum. Scale bar=1 μm.

Fig. 6. Part of the nucleus and the perinuclear cytoplasm of a TMC. The nuclear envelope shows invaginations and the centriole is located in a deep depression of it. C: centriole, N: nucleus, NE: nuclear envelope. Scale bar=0.5 μm.

Fig. 7. Epidermal cell surrounding a TMC. CW: cell wall, N: nucleus, V: vacuole. Scale bar=5 μm.


1
TMC
2
CW
Ch
3
N
4
5
Ch
ER
6
N
NE
C
7
CW
N
V

TMC, i.e. most of the organelles (except chloroplasts) are gathered in the apical region, while the basal part is usually occupied by a large vacuole and typical peripherally distributed chloroplasts (Fig. 7). The nucleus is located in the central region with many dictyosomes and mitochondria around it (Figs. 7, 8). 3) The cell wall structure is similar to that of the TMC with thick multiple layers (Fig. 7).

After the completion of TMC differentiation, an asymmetrical division results in the formation of the tetrasporangium and one stalk cell (Figs. 9, 10). The latter can be further divided, giving rise to a two-celled stalk. The stalk cell is similar in structure with the basal part of the TMC (Fig. 10) and when two stalk cells are present, this difference is further amplified.

Tetrasporangium and tetraspore formation

The apical cell separated by the asymmetrical division of the TMC continues growth further, symmetrically in all directions. Its nucleus is large and lobed, and is positioned towards the basal part of the cell (Fig. 9). This cell undergoes gradual differentiation and finally becomes almost spherical (Fig. 11). The nucleus migrates towards the centre of the cell and most of the organelles are distributed in the perinuclear cytoplasm (Figs. 10, 11). A large number of active dictyosomes are observed around the nucleus with their formative faces associated with the nuclear envelope or with ER membranes (Figs. 12, 13). Numerous vesicles are pinched off from their maturing face (Figs. 12, 13). The plastids are small with few thylakoid bands (Fig. 14). The small vacuoles fuse with each other giving rise to large ones that are peripherally arranged (Figs. 10, 11).

Meiotic division takes place at this stage, resulting in four haploid nuclei. They are usually arranged in one plane parallel to the thallus surface and have a more or less central position within the cell (Fig. 15). The organelles are evenly distributed around the nuclei. This is particularly evident in plastids, which show a strictly radial arrangement around each nucleus (Fig. 16). A great number of vesicles and small vacuoles appear around the nuclei-organelle complexes (Figs. 15, 17). The cell wall appears thicker than before, consisting of at least three distinct layers: an external electron dense layer, an intermediate more transparent one consisting of loose fibrils, and an internal one consisting of both dense fibrillar and more transparent granular material (Fig. 16). In addition, a more or less amorphous material is observed in some areas between cell wall and plasmalemma (Fig. 16). After the complete formation of the four haploid nuclei, cytokinesis takes place, and a thin membranous septum separates the tetraspores (Figs. 17, 18). This septum at the first stages of its formation consists of two more or less parallel membranes similar to those of the surrounding vesicles, while in more advanced stages an electron dense material is deposited between them (Fig. 18). At this stage, fragments of the old external excised wall layers are observed (Fig. 17). The amorphous material along the internal face of the external cell wall appears increased, while similar material occurs on both

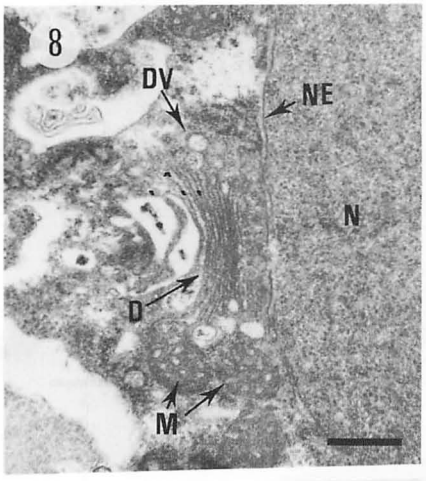
Fig. 8. Electron micrograph showing a part of the perinuclear cytoplasm of a cell surrounding a TMC. A dictyosome (D) is closely associated with the nuclear envelope by its formative face. DV: dictyosome vesicle, M: mitochondrion, N: nucleus, NE: nuclear envelope. Scale bar=0.5 μm.

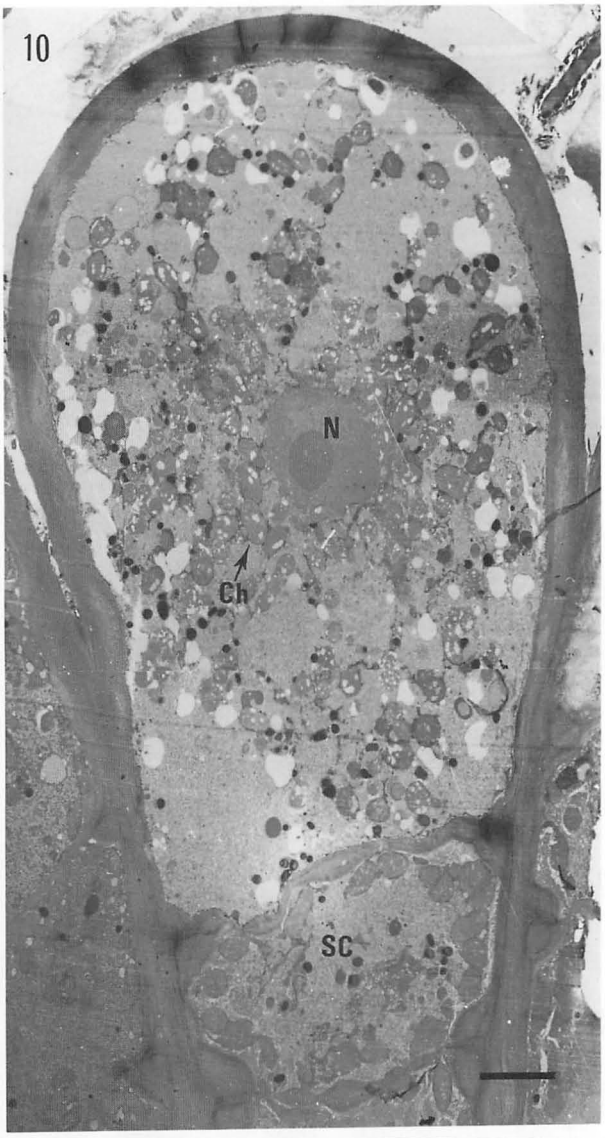
Fig. 9. Light micrograph showing a newly-formed tetrasporangium. The nucleus (N) is located close to the basal cell wall separating this cell from the stalk cell. Scale bar=25 μm.

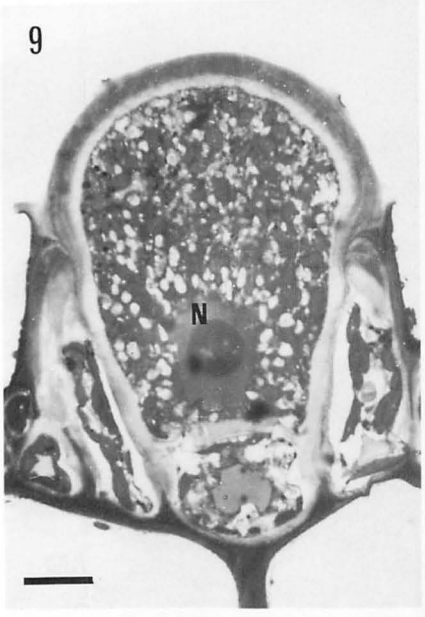
Fig. 10. Tetrasporangium at a more advanced developmental stage compared to that shown in Fig. 9. The nucleus has taken a central position and the stalk cell (SC) has been further divided. Ch: chloroplast, N: nucleus. Scale bar=5 μm.

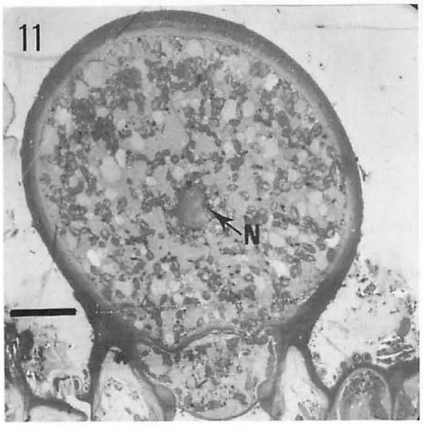
Fig. 11. Tetrasporangium before meiosis. Its shape is spherical and the nucleus (N) is centrally positioned. Scale bar=10 μm.

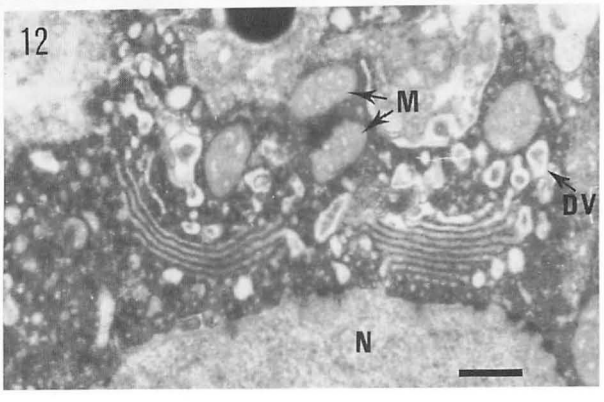
Fig. 12. Part of the nucleus and the perinuclear cytoplasm of a tetrasporangium. Two dictyosomes are closely associated with the nuclear envelope. DV: dictyosome vesicles, M: mitochondrion, N: nucleus. Scale bar=0.4 μm.


8
DV
NE
N
D
M


10
N
Ch
SC


9
N


11
N


12
M
DV
N

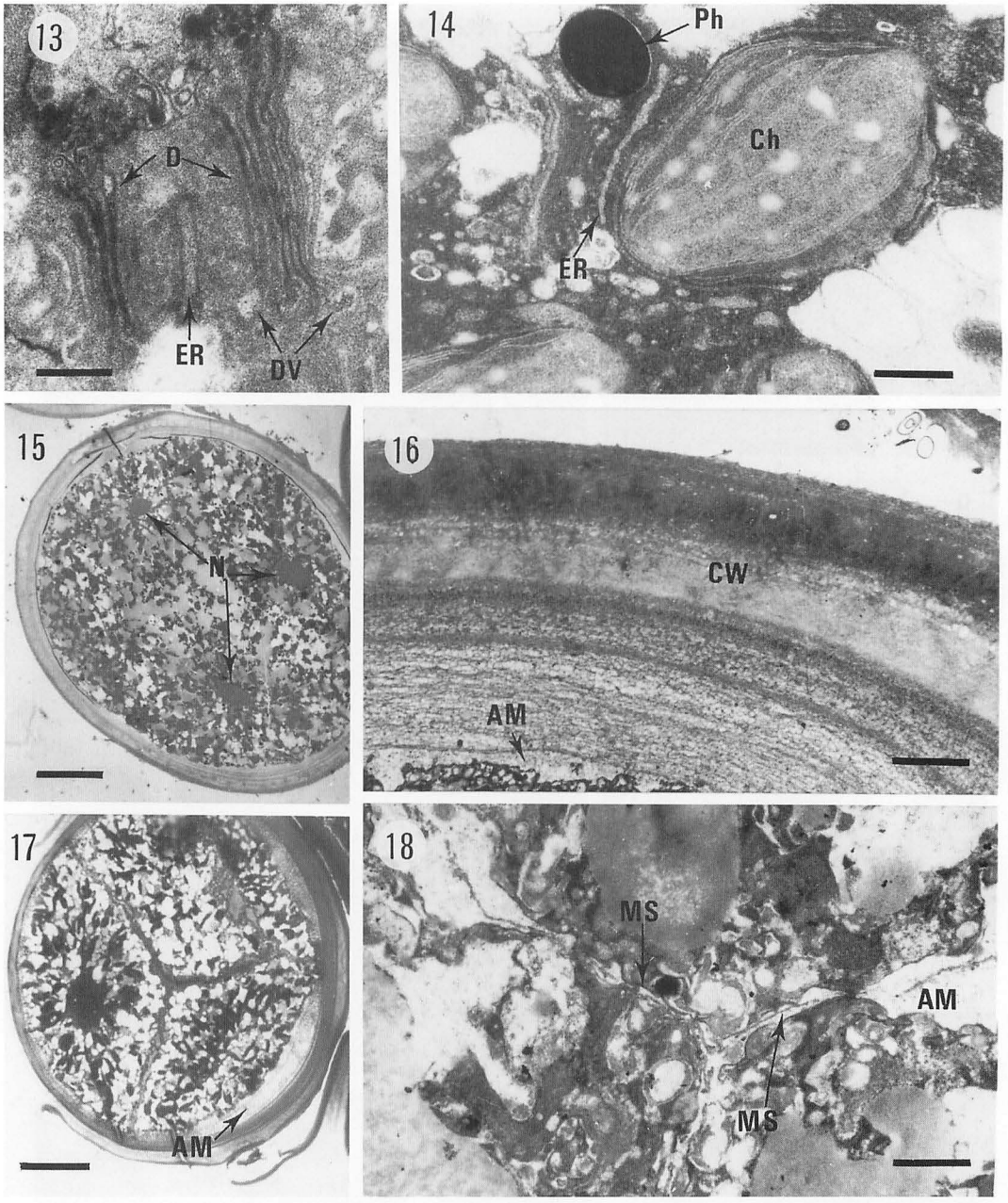


Fig. 13. Two active dictyosomes (D) of a young tetrasporangium. DV: dictyosome vesicle, ER: endoplasmic reticulum. Scale bar=0.3 μm.

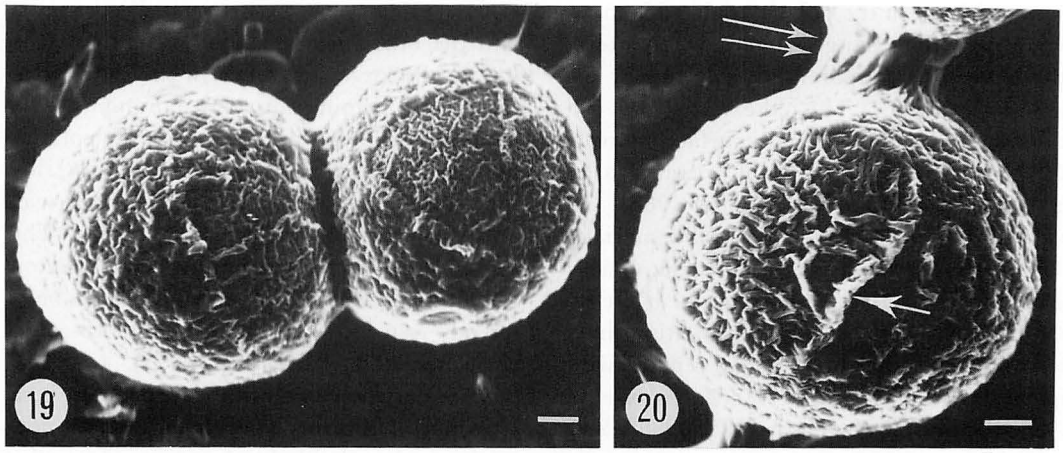
Fig. 14. Plastids of a tetrasporangium. Ch: chloroplast, ER: endoplasmic reticulum, Ph: physode. Scale bar=0.4 μm.

Fig. 15. Pre-cytokinetic tetrasporangium. Meiosis has already taken place. Three of the four haploid nuclei (N) are visible. Scale bar=10 μm.

Fig. 16. Part of the wall of a tetrasporangium at the stage of the meiotic division. AM: amorphous material, CW: cell wall. Scale bar=3 μm.

Fig. 17. Light micrograph showing a post-cytokinetic tetrasporangium. Three tetraspores are observed. AM: amorphous material. Scale bar=10 μm.

Fig. 18. Detail of the membranous septum (MS) separating the young tetraspores. AM: amorphous material. Scale bar=1 μm.



Figs. 19, 20. Scanning electron micrographs of young tetrasporangia. Their surface exhibits a shrink-like appearance. Arrow in 20 indicates the possible trace of the wall separating the tetraspores. Double arrows show amorphous material connecting two neighbouring tetrasporangia. Scale bar=10 μm.

sides of the partition membranes (Figs. 17, 18). Examination of material under the scanning electron microscope, reveals that the tetrasporangia at the stage before tetraspore release, appear spherical, with an irregular and shrinked external surface (Figs. 19, 20). Sometimes neighbouring tetrasporangia appear sticked together by an amorphous material (Fig. 20). In the tetrasporangium of Fig. 20 the cytokinesis of the meiotic division is probably finished, and the wall separating the tetraspores can be seen as an intense shrinkage on the external surface of the tetrasporangium.

Discussion

The present observations on the sequence of cell divisions that result in tetraspore formation, confirm those made with light microscope by Williams (1904a), Ishii *et al.* (1959) and Kumagae *et al.* (1960). The first ultrastructural change in the process of tetrasporogenesis is the de-differentiation of certain epidermal cells, the TMCs. The increased metabolic activity of these cells, compared to typical epidermal cells, is expressed by the dense cytoplasm and numerous small vacuoles. The chloroplasts, due to repeated divisions, become small and undifferentiated. This process is similar to that already described during branch or propagule mother cell formation in *Sphacelaria tribuloides* Meneghini (Katsaros 1980) and unilocular sporangium development in *Halopteris filicina* (Grateloup) Kützing (Katsaros and Galatis 1986). These changes are accompanied by outgrowth of the TMC, followed by the establishment of a new polar axis in it. Polarization is further expressed by the distribution of the organelles in particular zones. A similar organization occurs in apical cells of *Zonaria farlowii* (Neushul and Dahl 1972), *Dictyopteris membranacea* (Katsaros 1980, Katsaros and Galatis 1988), and *Sphacelaria tribuloides* (Katsaros 1980, Katsaros *et al.* 1983). It seems that at this stage the TMC behaves like an apical cell, showing a kind of tip growth. However, after the asymmetrical division of the TMC the polarity pattern changes from axial to radial. This results in the formation of the tetrasporangium, which gradually becomes almost spherical, with a radial distribution of the organelles around the centrally located nucleus. The cell organization at this stage is comparable to that of the sporangium of *H. filicina* before meiosis (Katsaros and Galatis 1986). However, ultimately the organelles in the tetrasporangium of *D. dichotoma* show a perinuclear distribution, whereas in *H. filicina* they are more or less evenly distributed throughout the sporangium volume.

The change in the polarity pattern is in accordance with a change in the growth pattern, which becomes apparent by the evenly expanding cell wall. The old external wall layers cannot accomodate the surface increase and break under the internal pressure, as in *H. filicina* (Katsaros and Galatis 1986). In parallel, the deposition of new wall material is carried out by numerous dictyosome vesicles released from active dictyosomes near the expanding cell wall. Similar observations have been made in other brown algal cells showing apical growth (Katsaros 1980, Katsaros *et al.* 1983, Katsaros and Galatis 1985, 1988, 1990, Gaillard *et al.* 1986).

The presence of specialized sterile cells surrounding the sporangial sori is not a general feature of Dictyotales, but it has also been observed in *D. diemensis* (Philips *et al.* 1990). Their fine structure is different from the typical epidermal cells, showing polar growth and increased metabolic activity. This activity is indicated by the shape and size of the nucleus, as well as the abundance of dictyosomes and dictyosome vesicles. Since the differentiation of the cells surrounding the TMCs in *D. dichotoma* is limited and stops before the completion of tetraspore formation, their particular activity can be attributed to a coordination with the TMCs.

After meiosis, the four haploid nuclei occupy a more or less central area of the cell and do not divide further, in contrast to *H. filicina* zoospore formation (Katsaros and Galatis 1986). The organelles are re-arranged, in order to give a full organelle complement to each nucleus. This is the "coenocytic tetranucleated stage", in which the organelles show radial arrangement around each of the nuclei. It is noteworthy that occasionally the four nuclei are arranged in one plane, usually parallel to that of the thallus. This protoplast reorganization is different from that observed in developing sporangia of Ectocarpales (Baker and Evans 1973a, b, Loiseaux 1973, Markey and Wilce 1976) and *H. filicina* (Katsaros and Galatis 1986), and was not observed in Laminariales (Toth 1974, Henry and Cole 1982). The differences in the pattern of protoplast reorganization between *D. dichotoma* and the other groups already mentioned, is due to the large difference in the number of the spores forming into the sporangia. Organelle movements and change in the polarity pattern are supposed to be based on interactions of cellular elements, like the cell wall and the cytoskeleton (Schnepf 1986). The organization of the microtubule cytoskeleton in polarized cell types of brown algae has been already studied by immunofluorescence (Katsaros 1992, Rusig *et al.* 1993).

The partition membrane separating the tetraspores, is formed after the protoplast reorganization, probably by the fusion of vesicles that have been aggregated around the nuclei-organelle complexes. A similar process has been described during zoosporogenesis in different brown algal orders (Loiseaux 1973, Toth 1974, Markey and Wilce 1976, Katsaros and Galatis 1986). The external cell wall of the post-cytokinetic tetrasporangium is usually thicker than that of the tetrasporangium mother cell. It appears similar to the three-layered cell wall of the *Fucus* zygote, which consists of an external rather amorphous layer, mainly of alginic acid and sulphated fucoidan, a median layer of cellulose and alginic acid, and an inner layer of sulphated fucoidan fibrils (Callow *et al.* 1978). Inside the external cell wall, and also on both sides of the membranous septa that separate the tetraspores, the amorphous deposits of granular material increase significantly. This material is possibly mucilagenous and may help, by absorbing water, in the breaking of the external cell wall and the release of the tetraspores. It has been reported that in various algal species a mucilagenous material secreted among zoospores generates pressure that forces the sporangial wall to break down locally (Loiseaux, 1973, Toth 1974, 1976a, b, Markey and Wilce 1976, Katsaros and Galatis 1986). However, a local digestion of the internal cell wall cannot be excluded (Markey and Wilce 1976, Toth 1976a, b), although Kumagae *et al.* (1960) have noticed that the four tetraspores are released together bounded by intact inner layers of cell wall.

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References

Baker, J. R. J. and Evans, L. V. 1973a. The ship fouling alga *Ectocarpus*. I. Ultrastructure and cytochemistry of plurilocular reproductive stages. Protoplasma **77:** 1–13.

Baker, J. R. J. and Evans, L. V. 1973b. The ship fouling alga *Ectocarpus*. II. Ultrastructure of unilocular reproductive stages. Protoplasma **77:** 181–189.

Callow, E. M., Coughland, S. J. and Evans, L. V. 1978. The role of Golgi bodies in polysaccharide sulphation in *Fucus* zygotes. J. Cell Sci. **32:** 337–356.

Gaillard, J., L' Hardy-Halos, M. TH. and Pellegrini, L. 1986. Morphogenèse du *Dictyota dichotoma* (Huds.) Lamouroux (Phaeophyta). II. Ontogenèse du thalle et cytologie ultrastrucurale des différents types de cellules. Phycologia **25:** 340–357.

Hallam, N. D. and Luff, S. E. 1988. The fixation and infiltration of larger brown algae (Phaeophyta) for electron microscopy. Br. Phycol. J. **23:** 337–346.

Henry, E. C. and Cole, K. M. 1982. Ultrastructure of swarmers in the Laminariales (Phaeophyceae). I. Zoospores. J. Phycol. **18:** 550–569.

Ishii, K., Nishibayashi, T. and Inoh, S. 1959. Morphogenesis in Dictyotales. 1. Comparative studies of tetraspore formation in *Dictyota dichotoma* (Huds.) Lamour., *Dictyopteris divaricata* (Okam.) Okam., *Padina japonica* Yamada and *P. crassa* Yamada. Bull. Jpn. Soc. Physiol. **7:** 37–45.

Katsaros, Chr. 1980. An ultrastructural study on the morphogenesis of the thallus of five brown algal species. Ph.D. thesis, Athens.

Katsaros, Chr. 1992. Immunofluorescence study of microtubule organization in some polarized cell types of selected brown algae. Bot. Acta **105:** 400–406.

Katsaros, Chr., Galatis, B. and Mitrakos, K. 1983. Fine structural studies on the interphase and dividing apical cells of *Sphacelaria tribuloides* (Phaeophyta). J. Phycol. **19:** 16–30.

Katsaros, Chr. and Galatis, B. 1985. Ultrastructural studies on thallus development in *Dictyota dichotoma* (Phaeophyta, Dictyotales). Br. Phycol. J. **20:** 263–276.

Katsaros, Chr. and Galatis, B. 1986. Ultrastructural studies on zoosporogenesis of *Halopteris filicina* (Sphacelariales, Phaeophyta). Phycologia **25:** 358–370.

Katsaros, Chr. and Galatis, B. 1988. Thallus development in *Dictyopteris membranacea* (Phaeophyta, Dictyotales). Br. Phycol. J. **23:** 71–88.

Katsaros, Chr. and Galatis, B. 1990. Thallus development in *Halopteris filicina* (Phaeophyceae, Sphacelariales). Br. Phycol. J. **25:** 63–74.

Kumagae, N., Inoh, S. and Nishibayashi, T. 1960. Morphogenesis in Dictyotales. II. On the meiosis of the tetraspore mother cell in *Dictyota dichotoma* (Hudson) Lamouroux and *Padina japonica* Yamada. Biol. Journ. Okayama Univ. **6:** 91–102.

Liddle, L. B. and Neushul, M. 1969. Reproduction in *Zonaria farrlowii*. II. Cytology and ultrastructure. J. Phycol. **5:** 4–12.

Loiseaux, S. 1973. Ultrastructure of zoidogenesis in unilocular zoidocysts of several brown algae. J. Phycol. **9:** 277–289.

Manton, I., Clarke, B. and Greenwood, A. D. 1953. Further observations with the electron microscope on the spermatozoids in the brown algae. J. Exp. Bot. **4:** 319–329.

Manton, I. 1959. Observations on the internal structure of the spermatozoid of *Dictyota*. J. Exper. Bot. **10:** 448–461.

Markey, D. R. and Wilce, R. T. 1976. The ultrastructure of reproduction in the brown alga *Pylaiella littoralis*. II. Zoosporogenesis in the unilocular sporangia. Protoplasma **88:** 147–173.

Neushul, M. and Liddle, L. 1968. A light- and electron-microscopic study of primary heterogeneity in the eggs of two brown algae. Amer. J. Bot. **55:** 1068–1073.

Neushul, M. and Dahl, A. L. 1972. Zonation in the apical cell of *Zonaria*. Amer. J. Bot. **59:** 393–400.

Philips, J. A., Clayton, M. N., Maier, I., Boland, W. and Müller, D. G. 1990. Sexual reproduction in *Dictyota diemensis* (Dictyotales, Phaeophyta). Phycologia **29:** 367–379.

Rusig, A.-M., Le Guyader, H. and Ducreux, G. 1993. Microtubule organization in the apical cell of *Sphacelaria* (Phaeophyceae) and its related protoplast. Hydrobiologia **260/261:** 167–172 (XIVth International seaweed symposium, Britanny, France).

Schnepf, E. 1986. Cellular polarity. Ann. Rev. Plant Physiol. **37:** 23–47.

Toth, R. 1974. Sporangial structure and zoosporogenesis in *Chorda tomentosa* (Laminariales). J. Phycol. **10:** 170–185.

Toth, R. 1976a. The release, settlement and germination of zoospores in *Chorda tomentosa* (Phaeophyceae, Laminariales). J. Phycol. **12:** 222–233.

Toth, R. 1976b. A mechanism of propagule release from unilocular reproductive structure in brown algae. Protoplasma **89:** 263–278.

Williams, J. L. 1897. The antherozoids of *Dictyota* and *Taonia*. Ann. Bot. **11:** 545–553.

Williams, J. L. 1904a. Studies in the Dictyotaceae. I.

The cytology of the tetrasporangium and the germinating tetraspore. Ann. Bot. **18:** 141–160.
Williams, J. L. 1904b. Studies in the Dictyotaceae. II. The cytology of the gametophyte generation. Ann. Bot. **18:** 183–204.
Williams, J. L. 1905. Studies in the Dictyotaceae. III. The periodicity of the gametophyte generation. Ann. Bot. **18:** 531–560.

Christos I. Katsaros・Konstantinos Pentaris：褐藻アミジグサ *Dictyota dichotoma* (Hudson) Lamouroux（アミジグサ目）の四分胞子形成における微細構造

アミジグサの四分胞子形成は，ある表層細胞の外側への発達により始まり，それに引き続き特徴的な分化がみられる。これらの細胞はすぐに極性を持つにいたり，四分胞子嚢母細胞になる。これらの細胞の成長の軸において三つの顕著な領域が生じる。すなわち小さな小胞に満たされた頂端領域，ほとんどの細胞内小器官が集合した中心領域，大きな液胞と表面に集まった葉緑体がみられる基部領域である。核は細胞が外側に向けて成長するにつれ基部領域に移動し，厚い多層の外側の細胞壁は，新しい層が内側に向け形成されるにつれて崩壊する。四分胞子嚢母細胞の非相称分裂により四分胞子嚢が形成されるが，これは柄細胞よりはるかに大きく，またより密度の高い細胞質と背軸にそって分布する多くの細胞内小器官を有する。この細胞は特徴的な分化過程を経て極性が軸にそう方向から放射状に変化する。最終的にそれはほとんど球状になる。減数分裂の後，4つの単相の核が形成され細胞内小器官はそれらの回りに集まって配置する。この段階では多くの活動的なディクティオソームがみられ，不定形の物質を分泌している。これらは4分胞子を隔てている膜状の隔壁の間や外側の細胞壁の内側に蓄積する。この物質は多分粘質で，水分を吸収することで外側の細胞壁の崩壊を助け，それにより胞子の放出を引き起こしていると考えられる。(Institute of General Botany, University of Athens, Athens 157 84, Greece)

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