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Vegetative Anatomy and Tetrasporogenesis in *Stoechospermum marginatum* (C. Agardh) Kützing (Dictyotales, Phaeophyceae)

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Anatomical organization of *Stoechospermum marginatum* reveals small cortical cells with moderately dense cytoplasm, overlying a multilayered medulla comparatively poor in cytoplasmic contents. The anticlinal walls of cortical cells show local thickenings rich in alginic acids. Sori form on both thallus surfaces and show tetrasporangia, paraphyses and sterile-cells. The unicellular paraphyses are rich in sulphated polysaccharides whereas multicellular ones have abundance of not only polysaccharides, but also of vacuoles and phenols. The sterile-cells are modified cortical cells present on either side of the tetrasporangium and bear cytoplasmic strands towards soral cavity. Various stages of tetrasporogenesis are seen in a single sorus. The developing tetrasporangium shows a two layered wall, where the outer one is rich in alginic acid and inner has sulphated polysaccharides. An apical pad aids tetraspore release. Also involved in the release process are sterile-cells, paraphyses and polysaccharides.

Key Words: alginic acid, apical pad, paraphyses, sterile-cells, *Stoechospermum*, sulphated polysaccharides, tetrasporangium

INTRODUCTION

Morphology, development and reproduction in three members of Dictyotales has been extensively studied. Detailed ultrastructural and histochemical studies have been carried out in *Dictyota* sp. (Evans and Holligan 1972; Gaillard *et al.* 1986; Katsaros and Pentaris 1994), *Padina* sp. (Fagerberg and Dawes 1973; Mshigeni and Mkwizu 1978; Ampili *et al.* 1987), and *Dictyopteris* sp. (Womersley 1987; Tanaka 1992; Phillips 1998; Bhamrah and Kaur 2000). Besides these three large genera, considerable work has also been done on *Zonaria* (Haupt 1932; Liddle and Neushul 1969; Phillips and Clayton 1991). A few reports are also available on *Taonia* sp. (Robinson 1932; Mathieson 1966), *Spatoglossum* sp. (Gayral 1958; Tanaka 1991; Babbar *et al.* 1999), *Lobophora* sp. (Kaur and Kumari 1998) and *Stoechospermum* sp. (Wevers and Mshigeni 1979; Phillips *et al.* 1993).

The aim of the present work was to study the vegetative anatomy and tetrasporogenesis with a special emphasis on the occurrence of alginic acids and sulphated polysaccharides in a lesser studied member of the group.

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MATERIAL AND METHODS

The material was collected from Port Okha, Gujarat (India). Selected parts of the plants were fixed on spot in 10% (v/v) aqueous acrolein for 24 hrs, washed in distilled water and post-fixed in 1% $HgCl_2$ for 24 hrs to stabilize polyphenols. Later the material was rinsed three times in distilled water at an interval of 15 minutes. Dehydration was carried out at room temperature by transferring material to 2-methoxy ethanol (2 times for 48 hrs); 100% ethanol (24 hrs); n-propanol (24 hrs) and n-butanol (24 hrs). Infiltration and embedding was done in glycol methacrylate. Embedded samples were sectioned on Spencer rotary microtome fitted with a specially designed adaptor to hold glass knives. Two micron thick serial sections were cut and transferred to small drops of distilled water kept on pre-cleaned slide. Sections were stained with Periodic Acid Schiff (PAS) reagent to localize insoluble polysaccharides (Feder and O'Brien 1968) for 30 minutes and with Toluidine Blue O (TBO) for sulphated and carboxylated polysaccharides (Mc Cully 1966) for 5 minutes. 0.05% TBO at pH 4.4 was used to localize both alginic acid and sulphated polysachharides. TBO at pH 4.4 stains both carboxylated and sulphated polysaccharides pink to reddish violet (the former is PAS positive whereas the latter is PAS

Table 1. Staining intensities with PAS & TBO

S. No.	Regions	PAS	TBO	Contents
1.	Cortical cell cytoplasm	+	+	SP
2.	Marginal cells	+++	+++	SP, AA
3.	Medullary cell walls	+	+	SP
4.	Paraphysis walls	+++	++	AA
5.	Paraphysis cytoplasm	-	++	Phenols

+: Feebly
++: Moderately
+++: Intensely
SP: Sulphated polysaccharides
AA : Alginic acid

negative). TBO also stains phenols turquoise green or green blue (Sokhi and Vijayaraghavan 1986 see also Table 1). The photomicrographs were taken using B/W ORWO film on Reichert photoscope. For Scanning Electron Microscopy (SEM), the plants were fixed in 4% formalin, dehydrated in graded acetone series, critical point dried and scanned for topographical details.

OBSERVATIONS

Morphology

Stoechospermum marginatum occurs in rock pools in clear water of the lower parts of littoral zone. The plants are yellowish brown in colour, forming tufts that are 7-20 cm in height. The thallus is erect, flat and repeatedly branched. At the base the branches are irregularly ramified, bent and interwoven giving way to a fibrous holdfast. Thin rhizoids arise from it assisting in anchorage. Each frond in the tuft is cuneate at the base, spathulate near margins and lacks a midrib. The apices are terminated by an involute curl across the entire apical region. Growth of the plant is by means of marginal meristem which is present in the involute curl of the thallus (Fig. 1A). During vegetative phase, the fronds show bundles of sterile hairs near the margins. The asexual reproductive phase is marked by marginal sori bearing sporangia amongst the paraphyses.

Anatomical and Histochemical Studies

Thallus is multilayered, being 5 or 6 celled a little away from the apex becoming 9 or 10 celled in the midrib region. The marginal meristem occupies the straight front edge. The upper cell and basal cell contribute to cortical and medullary region respectively (Fig. 1B). The marginal cells or the cortical cells are rectangular with rounded edges (Fig. 1C). They are placed at right angles to the medullary cells, are smaller in size and have local thickenings half way in the anticlinal walls (Fig. 1D). The centrally placed medullary cells are large, rectangular with sinuous walls and lack local thickenings (Fig. 1D).

The cortical cell cytoplasm is dense, rich in polysaccharides that stain feebly with PAS reagent and light pink with TBO indicating presence of sulphated groups. The marginal cells are covered with a thick layer of polysaccharides. These polysaccharides stain intense violet with TBO and dark magenta with PAS reagent, indicating the richness of alginic acids. The material in local thickenings is also rich in alginic acids (Fig 1C, D). The medullary cells appear almost empty with only a small proportion of cytoplasm containing sulphated polysaccharides. The walls stain similar to those of the cortical cells (Fig. 1D).

Sterile Hairs

Bundles of unbranched, uniseriate hairs, originate from the cortical cells of both the surfaces. The hair initial has a dense cytoplasm and a large nucleus. The hair develops a basal meristem. The hairs develop inside the cuticle, which gets ruptured as the hairs grow within (Fig. 1E). The cell size varies throughout the length of the hairs. The lower cells are small and narrow, further up the cells appear squarish and those placed in the distal region are large appearing more long than broad. All the cells are uninucleate and have dense cytoplasm. The walls are thin, rich in alginic acid and are without any extracellular deposition (Fig. 1F).

TETRASPOROGENESIS

One of the cortical cells acts as a tetrasporangial initial, becomes enlarged and protrudes a little above the cortical layer. An unequal transverse division in the initial cuts off a small lower cell or the stalk cell and a large upper cell or the tetrasporangial mother cell (TMC) (Fig. 2A). The stalk cell with moderately dense cytoplasm does not divide further.

The TMC gradually matures into a tetrasporangium and the stalk cell forms only a small portion of the entire structure. During enlargement, in TMC, fibrous wall material gets deposited at the apical end. The lobed nucleus lies towards the base of a developing tetrasporangium (Fig. 2A). The young tetrasporangium has a thin unilayered wall rich in alginic acid. The nucleus at this stage is centrally placed, is lobed and the cytoplasm is divided into two regions. The perinuclear

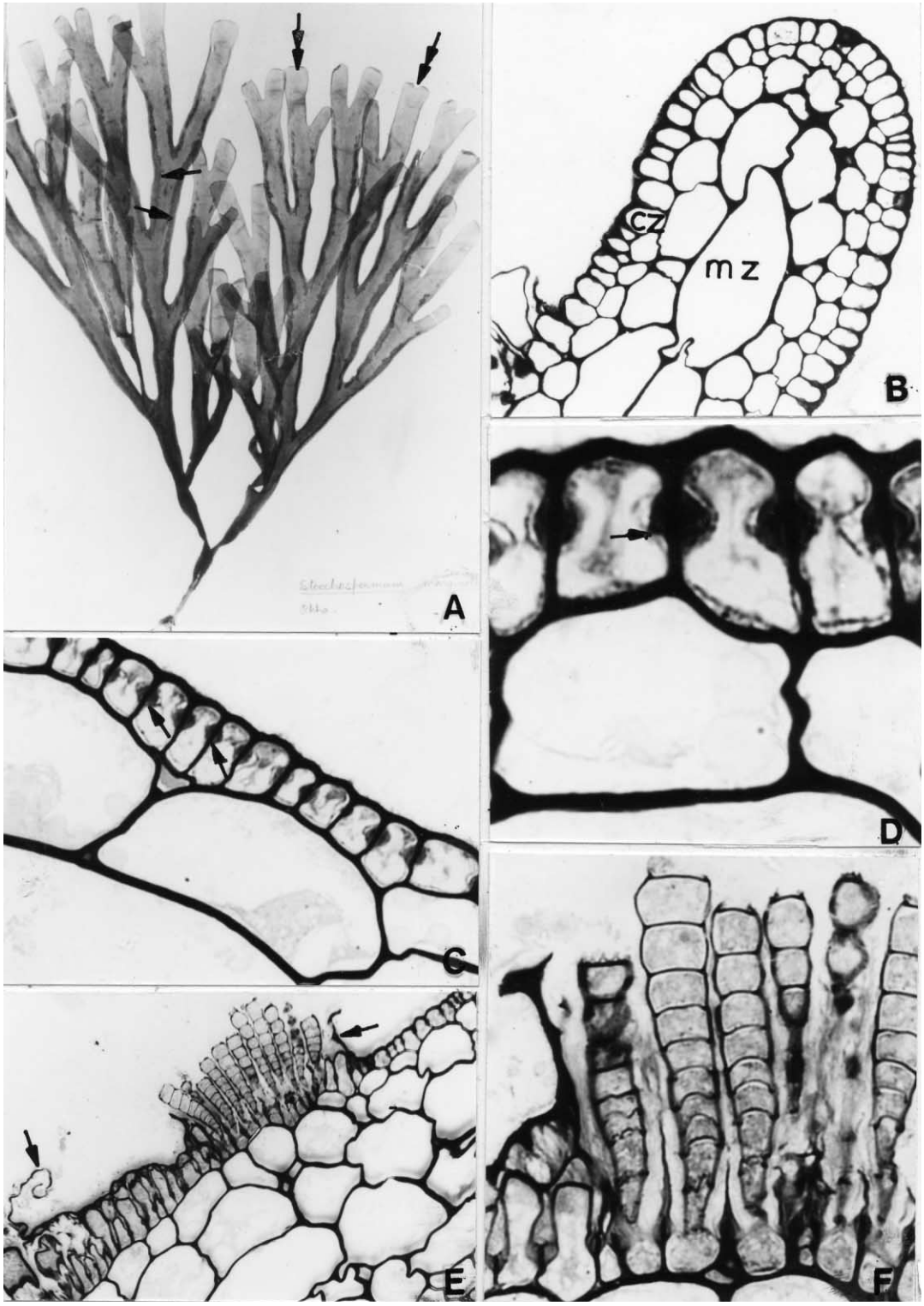
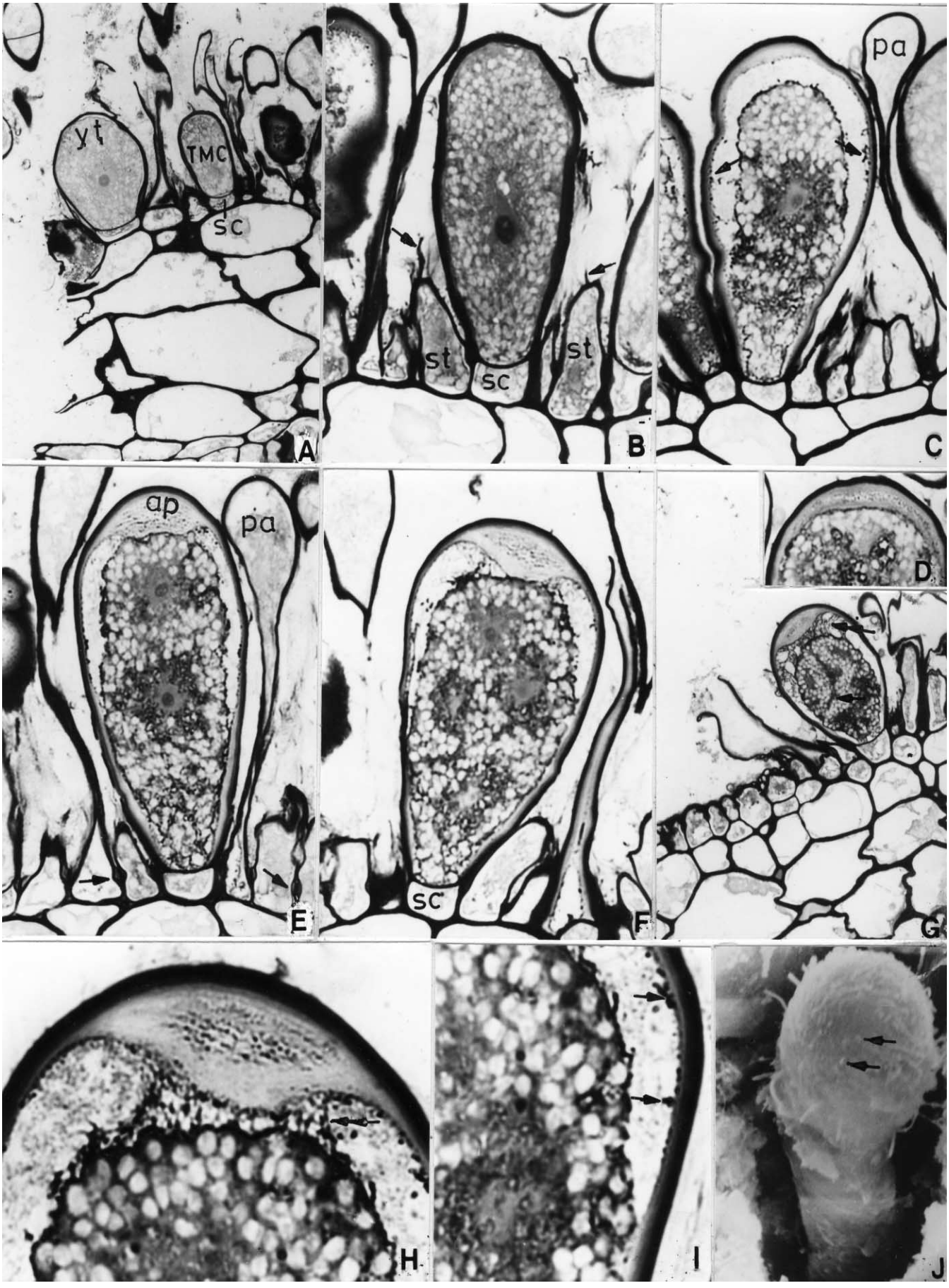


Fig. 1A-F. *Stoechospermum marginatum*. Thallus organization. B-F. TBO stained. A. The plant is flat, dichotomously branched and forms small tufts attached to the substratum by means of a holdfast from which arise small rhizoids. Each frond in the tuft shows marginally placed sori and/or hairs (arrows) and the incurved apical ends (double arrows). X 1. B. Vertical section through apical region showing a single layered cortical zone (cz) and a multilayered medullary zone (mz). X 500. C, D. Same, the cortical cells are placed at right angles to the medulla. The former possess local thickenings (arrows) rich in alginic acids. Moderate amounts of sulphated polysaccharides are present in the cytoplasm of cortical cells. The medullary cells are large and appear empty. C X 1575; D X 2000. E, F. Bundles of sterile hairs. The hairs aggregate under cuticle which ruptures (arrows) as the hairs inside grow. In F, the hairs are unbranched, uniseriate with thin walls and the cell size varies through the length of the hair. E: X 500; F: X 1575.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cytoplasm that occupies a small volume, is rich in sulphated polysaccharides. A few vacuoles are also present. The peripheral cytoplasm occupies rest of the cell volume and contains a sulphated polysaccharide matrix with phenolic grains (Fig. 2A). As the tetrasporangium grows, from pear-shaped structure it becomes somewhat elongate (Fig. 2B). The wall at this stage appears thick (Fig. 2B). The developing tetrasporangia are sandwiched by modified cortical cells which during early tetrasporogenesis resemble TMCs but as the development progresses, they lag behind in growth. These are the sterile-cells with a dense cytoplasm, centrally placed nucleus and thread-like extensions on the wall facing the soral cavity (Fig. 2B). The sterile-cells also possess local thickenings.

Further development of tetrasporangium leads to changes both in the cytoplasm and wall composition. The wall becomes two layered, where the newly formed second layer is rich in sulphated polysaccharides staining light pink with TBO and feebly with PAS reagent. Grains resembling the outer wall in composition appear next to this layer. The centrally placed nucleus shows a distinct nucleolus. The perinuclear cytoplasm at this stage possesses a few vacuoles that give it a reticulate appearance. Physodes appear in both cytoplasmic regions and the stalk cell appears almost empty (Fig. 2C).

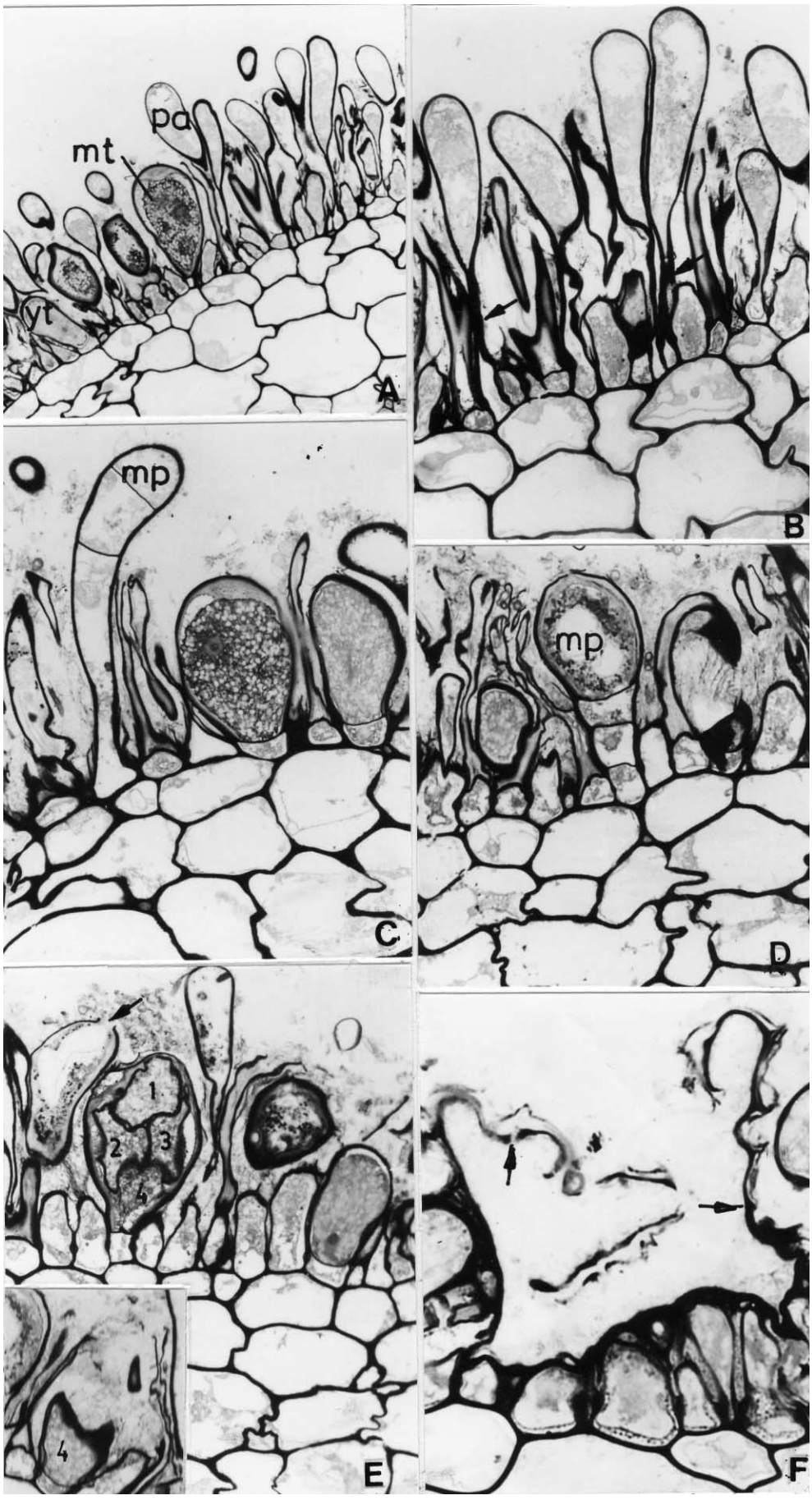
The mature tetrasporangium is 2 or 3 times the size of young sporangium. It organizes an apical cap (Fig. 2D) rich in sulphated polysaccharidic matrix and small alginic acid grains. It undergoes a reduction division. The first nuclear division results in a binucleate condition (Fig. 2E). The second reduction division leads to a 4-nucleate condition (Fig. 2F). The nuclei arrange themselves in an isobilateral manner and acquire their own perinuclear cytoplasm which shows small vacuoles, sulphated polysaccharides and physodes. Cytokinesis later sets in cutting four tetraspores (Fig. 2G).

With further development, the apical pad becomes more granular in texture and gets demarcated from the rest of the sporangium (Figs. 2F, G). The pad is in contact with the cytoplasm below through the cytoplasmic threads forming a reticulate network. The network meshes have grains rich in alginic acid (Fig. 2H). These grains are also present in cytoplasmic vacuoles (Fig. 2I).

Paraphyses and Tetraspore Release

In a sorus, some specialized cells, the paraphyses, are present alongwith the tetrasporangium (Figs 2J, 3A). The paraphyses, which are single celled have a swollen distal end and a proximal narrow end. The wall extends at certain regions into fibrils (Fig. 2J) and a proximal narrow end. The wall is identical to that of the young tetrasporangium being rich in alginic acid. The cell is uninucleate and the cytoplasm besides a few vacuoles shows sulphated polysaccharides (Fig. 3B). Occassionally, multicellular paraphyses are also seen with a large terminal cell extending beyond the tetrasporangium (Fig. 3C). The terminal cell has a large centrally placed vacuole and a peripheral cytoplasm.

Fig. 2A-J. *Stoechospermum marginatum*. Tetrasporogenesis. TBO stained. A. Vertical section of the thallus to show tetrasporangium mother cell (tmc) and a stalk cell (sc). Both cells have a moderately dense cytoplasm. Young tetrasporangium (yt) has a single layered wall, is pear-shaped and uninucleate. The wall stains intensely for alginic acid. The stalk cell is an embedded structure with little cytoplasmic contents. X 1575. B. Developing tetrasporangium is an elongate structure with a thick single layered wall. The stalk cell (sc) appears more vacuolate. The perinuclear cytoplasm has a few small vacuoles. The sterile-cells (st) contain dense cytoplasm and a centrally placed nucleus. The thin strands (arrows) placed towards the soral cavity are prominent. X 2000. C. Tetrasporangium prior to reduction division shows a two layered wall, where the second layer is rich in sulphated polysaccharides. A space appears between the cytoplasmic contents and the cell wall towards the apical and lateral regions being absent from the basal region. Small grains rich in alginic acids aggregate inner to the second layer (arrows). Paraphysis (pa) is vacuolate. X 2000. D. Portion of the tetrasporangium to show deposition of sulphated polysaccharides in the apical region. X 2000. E. Two-nucleate stage. Both the nuclei organize their perinuclear cytoplasm. Apical pad (ap) rich in sulphated polysaccharides becomes prominent and the paraphysis (pa) shows dense cytoplasmic contents. Local thickenings in the cortical cells are distinct (arrows). Also seen are the sterile-cells with thread-like projections towards the soral cavity. F. Four-nucleate stage. The apical pad becomes more prominent and shows alginic acid-rich grains. The cytoplasm is full of vacuoles and fusion amongst vacuoles is common. Stalk cell (sc) is seen with scanty cytoplasmic contents. X 2000. G, H. At cytokinesis, walls are laid down (arrow). Cortical cells are seen with dense cytoplasm and local thickenings. Apical pad maintains contact with cytoplasm through a reticular network of cytoplasmic threads (double arrows). In G, network is distinctly studded with polysaccharide grains rich in alginic acids. G: X 500; H: X 2500. I. Portion of a tetrasporangium prior to release of contents. The aligning of alginic acid-rich grains is distinct (arrows) on the lateral walls. The texture of sulphated materials in the space between cytoplasm and second layer appears granular. X 2500. J. Scanning Electron Micrograph of a multicellular paraphysis showing rough wall of the terminal cell. X 160.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Sulphated polysaccharides with interspersed grains rich in alginic acids co-occur with physodes occur in this thin layer of cytoplasm (Fig. 3D). The paraphysial head ruptures to release its cytoplasmic contents into soral cavity. Simultaneously apical pad also ruptures, adding polysaccharide material to the soral cavity (Fig. 3E*). It is followed by tetraspore release from the sporangium (Fig 3E inset). Upon release the soral cavity shows ruptured indusium and paraphysis (Fig. 3F). The indusial remnants stain differentially with TBO. The released tetraspore is retained for sometime in the cavity where it grows in size and acquires a thick wall. One such released tetraspore is seen in the sorus (Fig. 3E).

The tetraspore release is also assisted by the sterile-cells that retain their shape growing in size and generate pressure, pushing tetraspores out of the soral cavity. Tetraspore release is a well coordinated phenomenon where a joint effort of paraphysis, sterile-cells and apical pad ensures a successive release of the propagules (Fig. 4).

DISCUSSION

Local Thickenings

In *Dictyota dichotoma* (Huds.) Lamour.(Katsaros and Galatis 1985), *Dictyopteris membranacea* (Stackhouse) Batters (Katsaros and Galatis 1988) and *Dictyopteris australis* (Sonder) Askensay (Bhamrah and Kaur 2000) local thickenings have been observed in the anticlinal walls of the outer most layer of cells. The thickenings in these taxa have been observed only in the differentiated cells but the significance and mode of their formation remains unknown. Present work on *Stoechospermum marginatum* (C. Ag) Kützing is a detailed report on the nature and occurrence of these thickenings. Alginic acid-rich thickenings occur not only during the vegetative growth but also throughout tetrasporogenesis. They may help in retaining the shape of the cortical cells even during tetraspore release when the cells are stretched. This rigidity is an important adaptive strategy in ribbon-like thalli of *Stoechospermum* where no other mechanical tissue is seen.

Paraphyses

Paraphyses undergo histochemical changes during tetrasporogenesis and may be assigned both structural and protective roles. There has been a great deal of inconsistency regarding the nature of paraphyses in *Stoechospermum marginatum*. The type specimen of *S. marginatum* has unicellular hairs in the sporangial sori (Kützing 1859). Durairatnam (1961) reported multicellular paraphyses in *S. marginatum* from Sri Lanka. Papenfuss (1977) also observed sporangial paraphyses in this plant but did not comment on their structure. Nizamuddin and Perveen (1986) however, did not report paraphyses in the sporangial sori of this species from Pakistan. Present investigation on this plant from Port Okha, India reports two types of paraphyses in the same sorus. Prior to tetraspore release, the multicellular paraphyses in *S. marginatum* rupture at the tip, and the sulphates and phenols contained in their cytoplasm are given into the soral cavity. The contents are protective in function with physodes possessing antibacterial properties and sulphates known to prevent dessication. The tetrasporangia which lie exposed to the environment once the indusium breaks are thus, protected from adverse environmental conditions.

The function of unicellular paraphyses in *Stoechospermum marginatum* is to facilitate tetraspore release by providing polysaccharide material. Histochemical changes and rupture of unicellular paraphyses was not observed. But as they are not deciduous being present till maturity, they can be assigned either structural or evolutionary significance. Additional pressure is probably exerted on sporangia by the tightly packed unicellular paraphyses which are

Fig. 3A-F. *Stoechospermum marginatum*. Paraphyses. TBO stained. A. In a sorus, besides tetrasporangia are present tightly packed paraphyses (pa) with fibrillar material (fm) in the distal region. The nucleus resides at the base. Various stages of tetrasporogenesis are seen where young tetrasporangium (yt) and mature tetrasporangium (mt) develop in the same sorus. X 250. B. Single celled paraphyses are elongate, sac-like at the distal end and thin towards cortex (arrows). The wall stains intensely for alginic acid and the cytoplasm is rich in sulphated polysaccharides. X 500. C, D. Multicellular paraphyses (mp) are 3 or 4 celled structures with a large terminal cell. In D, this terminal cell is seen to possess large vacuoles in the centre and the cytoplasm is restricted towards periphery. C, D: X 1575. E. When tetraspores (1-4) have matured, the paraphysis ruptures at the tip (arrow) releasing its contents into the cavity. This polysaccharide matrix is seen near the exit point of the tetrasporangium. Just prior to tetraspore release, the sporangium shows ruptured apical pad whose contents are given to the soral cavity (*). Inset shows tetraspores exit at the apical end in a successive manner. A released tetraspore is seen in the vicinity of a tetrasporangium with tetraspores. X 1575. F. Once the tetraspores are released, the remnants of the indusium (arrows) are seen to stain differentially. The cortical cells with local thickenings and dense cytoplasm are well defined. X 2000.

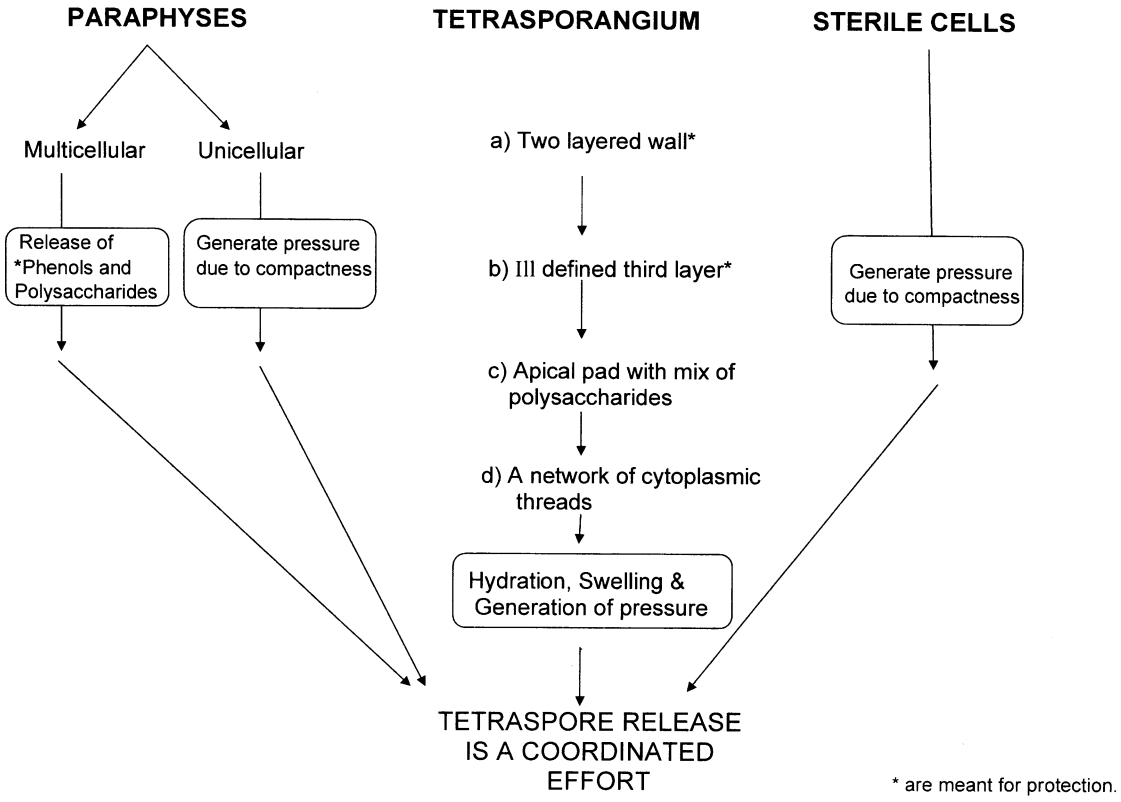

Fig. 4. Various developmental changes that occur inside a normal sorus. The tetraspore release is a highly coordinated phenomenon in which each cell of the sorus plays an important role.

interspersed with sporangia as also seen in *Chorda tomentosa* Lyngb.(Toth 1976).

Sterile-cells

Though the presence of specialized sterile-cells surrounding the sporangia is not a general feature of Dictyotales but such cells have been observed in *Dictyota dichotoma* (Katsaros and Pentaris 1994) and in *D. diemensis* Kütz (Phillips *et al.* 1990). It is believed that their activity is coordinated with tetrasporogenesis in these plants. In *Elachista* sp. and *Chorda tomentosa* (Toth 1974), sporangial release may be aided by side pressure from the tightly packed surrounding cells. Though, all the cortical cells of the sorus do not participate in tetraspore production, yet they are committed to the production of paraphyses and sterile-cells which play an important accessory role in tetraspore formation and release.

Release

Another interesting feature observed in *Stoechospermum marginatum* is the presence of an apical pad in the tetrasporangium. Such apical pads have earlier been reported during antheridial release in Fucalean members, *Turbinaria conoides* (Sokhi and Vijayaraghavan 1990) and *Sargassum vulgare* (Vijayaraghavan and Kaur 1992). Additional reticular structures appear in form of a network of cytoplasmic polysaccharides. These perhaps help to push away the apical pad and create an exit point for tetraspores. Similar observations have also been made by Toth (1974, 76). Toth (1976) observed a 'beak' in mature sporangia of a simple brown alga *Pylaiella littoralis* (L.) Kjellm. (Ectocarpales). It is through this 'beak' that the mass of zoospores is released. In *Chorda tomentosa* (Laminariales), apical cap is entirely composed of sulphated polysaccharides (Toth 1974). The materials rich in sulphated polysaccharides accumulate in the apical pad in the antheridium. They absorb water and an internal pressure is created by partial degradation of the material pushing spermatozoids out (Maier and Müller 1982). The present work reports for the first time an apical pad in a member of Dictyotales suggesting apical pad to be a constant feature of reproduction in Phaeophyceae. However, some more orders have to be investigated to confirm it.

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