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MORPHOLOGY AND SHEATH ARCHITECTURE IN THE FILAMENTOUS GREEN ALGA *PLANCTONEMA LAUTERBORNII* (CHLOROPHYCEAE, ULOTRICHALES)

by

OLIVIER REYMOND AND FRANTIŠEK HINDÁK

WITH 18 FIGURES

Key words: ultrastructure, cell wall, pyrenoid, green algae, Ulotrichales, *Planctonema*.

Abstract: Some morphological characteristics of the ulotrichacean green alga *Planctonema lauterbornii* Schmidle are examined under the light microscope (LM) and transmission/scanning electron microscope (TEM/SEM).

LM observations of field material show filaments of about 16 to 170 cells (mean number 62.3); they are covered with an unequal layer of mucilage. All the cells are side by side, slightly distant from one another or joined in pairs. Cultured filaments have 1 to 46 cells (mean number 14.6). Their multiplication is by liberation of hypertrophied cells and by filament rupture. These results, complete or confirm in different points those of previous authors (i.e. SKUJA, 1956; BOURRELLY, 1962, 1966; HÄLLFORS, 1984; HEYNIG, 1988; HINDÁK & MOUSTAKA-GOUNI, 1990).

The present TEM micrographs, complete or differ from the previous results of AKIYAMA & HORI (1977) and WATANABE *et al.* (1986): the outline of the filament is formed by tubular pieces made of current cell wall and former mother cell walls of successive generations. These tubular pieces show a gross or slight overlapping between each other. In the case of nonsynchronously dividing cells or ruptured filaments, the lineage of the tubular pieces cannot be determined precisely; i.e. an eight celled filament is the result of four or more successive generations. Contrary to TEM results of previous reports, no pyrenoids have been found. The taxonomical value of this feature cannot be interpreted satisfactorily. The existence of poorly documented but very closely related genera *Geminellopsis, Geminella, Binuclearia, Gloeotila*, and *Psephonema*, places a doubt on the taxonomical limits of *Planctonema*.

INTRODUCTION

The ulotrichaceaen alga *Planctonema lauterbornii* SCHMIDLE (1903) consists of small to long filaments made of tiny, side by side, distant, or arranged in pairs, cylindrical cells enclosed in a sheath made of overlapping tubular pieces.

A review of the literature concerning this alga shows that the morphology of material determined as *P. lauterbornii* depends on its origins (i.e. SKUJA, 1956; BOURRELLY, 1962, 1966; HÄLLFORS, 1984; HINDÁK & MOUSTAKA-GOUNI, 1990). Differences can be noted in the filament length, the cell shape, and the presence/absence of pyrenoids, aplanospores, zoospores, mucilaginous sheath, and other details of less importance.

Recently, the questions concerning polymorphism and taxonomy were presented by HEYNIG (1988) in a description of German collections of *P. lauterbornii*, and a presentation and assessment of the existing literature on *Planctonema* and the closely related genera, *Geminella* Turpin, *Binuclearia* Wittrock, *Gloeotila* Kützing, *Geminellopsis* Korsikov and *Psephonema* Skuja (these two last genera are presented as synonyms of *Planctonema* by most of the authors). This report by Heynig was preceded by an abstract by AKIYAMA & HORI (1977) and a well documented article by WATANABE *et al.* (1986) concerning Japanese material.

However, it seemed to us that the taxonomical limits of the species and genus were not yet satisfactorily clarified and more basic information regarding some morphological aspects, like the presence/absence of the pyrenoid were still needed. The present report deals with field collected, and cultured material of *P. lauterbornii* originating from Lake Tahoe (USA). Our results are compared with those of the previous authors cited above.

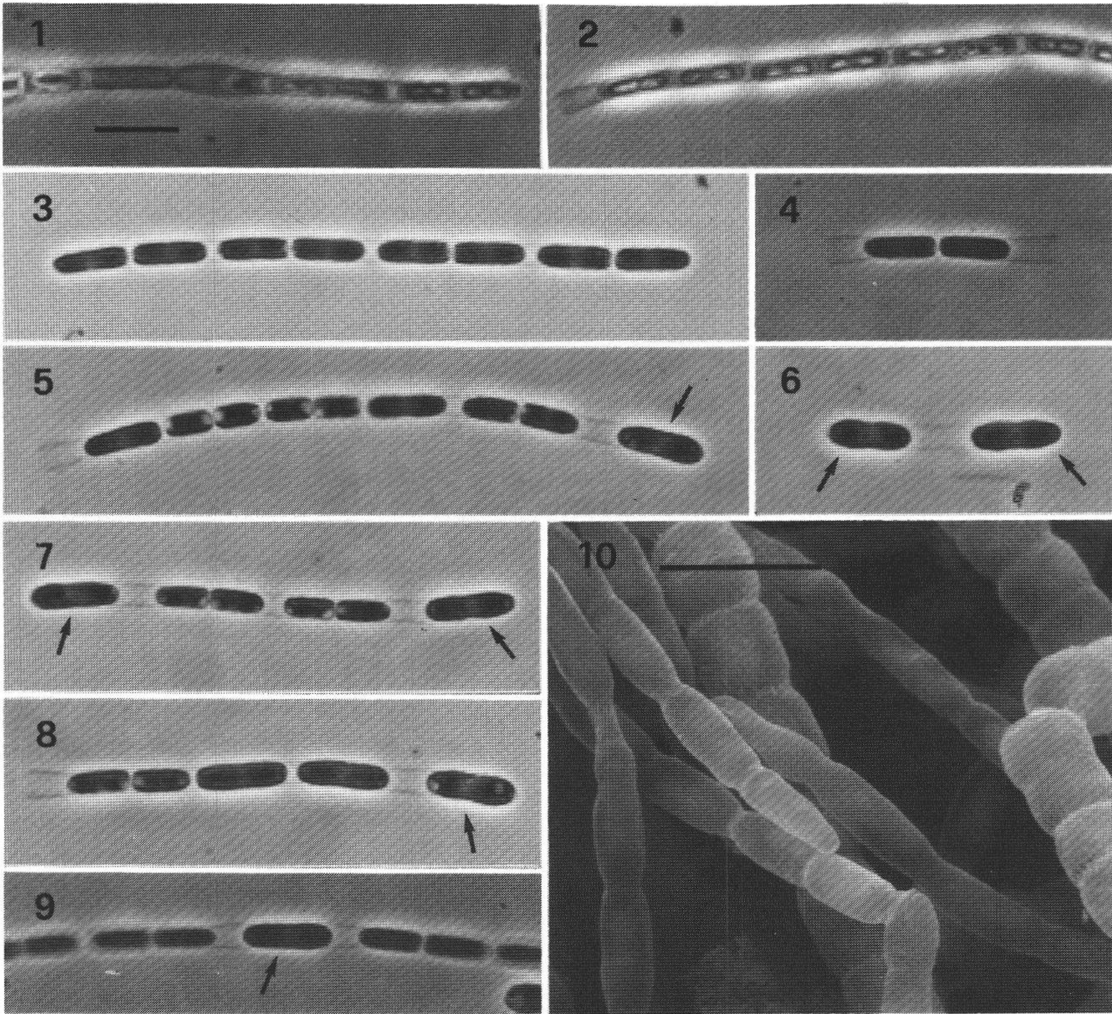
MATERIALS AND METHODS

Field and cultured material. Field material of *Planctonema lauterbornii* was collected by Dr. H.-R. Buergi, EAWAG, Dübendorf (Switzerland), from the plankton of Lake Tahoe (California, USA) in April 1991. A first subsample was immediately preserved in formaldehyde, and a culture was later isolated from a second subsample by the second author of this article. The cultured strain HINDÁK 1991/353 was originally deposited at the EAWAG but is presently maintained at the Botanical Institute, Bratislava, Slovak Republic. The strain was cultured in the liquid medium Z after ZEHNDER (in STAUB, 1961) in a 250 ml flask with a light cycle of 12/12 hrs and an intensity of about 1300 Lux.

Light microscopy. The tubular elements of the cell wall (Figs. 1-9), have been documented with a Zeiss plan-Neofluar 63x phase contrast objective. Due to their small size, the other features (i.e., the nucleus and the chloroplast) are shortly presented in "Results, Light microscopy (LM)" but illustrated with electron micrographs only in "Results, Transmission electron microscopy (TEM)".

Scanning electron microscopy (SEM). Filaments, of cultured material, were dehydrated by critical point drying and coated with gold prior to observations with a LEITZ 1000 A electron microscope at the EAWAG, Dübendorf.

Transmission electron microscopy (TEM). Field material was originally fixed for LM in formaldehyde at about 3% but was later used for TEM without further fixation. Cultured material was fixed in osmium tetroxide and glutaraldehyde, following PICKETT-HEAPS *et al.* (1978). Both materials were flat embedded in Spurr's resin between two microscope slides (REYMOND & PICKETT-HEAPS, 1983). Several *Planctonema* filaments were selected with a phase-contrast microscope (see LM above) then longitudinally and serially sectioned for TEM. All the sections were collected on formvar coated slot grids, stained with uranyl acetate and lead citrate and then carbon coated prior to observations on a TEM ZEISS EM 10 at the Institute of Histology and Embryology at the University of Lausanne.



Figs. 1, 2. Field collected filaments. Note the empty cells in Fig. 1 and the apical tubular empty piece in Fig. 2. Bar: 10 μm, fit also for Figs. 2 to 9.
Figs. 3 to 9. Cultured filaments. Tubular pieces are visible on each figure. Hypertrophied cells are indicated by arrows. Some vacuoles (white spots) are visible in cells of Figs. 5, 7. Scale: see Fig. 1.
Fig. 10. SEM micrograph of cultured *P. lauterbornii* (narrow and elongated cells) and *Microspora* (broad cells). Bar: 10 μm.

RESULTS

Number of cells per filament. Field collected filaments of *P. lauterbornii* are composed of about 16 to 170 cells. Mean number on 70 observed filaments is 62.3, standard deviation 34.37. Cultured filaments are composed of about 1 to 46 cells. Mean number on 300 observed filaments is 14.6, standard deviation 5.97.

Light microscopy (LM)

Field material (Figs. 1, 2). Cells are slightly distant from each other or in pairs when division just occurred. Some translucent gaps in the filament reveal empty cell walls. Cells are 6.5 to 9.5 μm long, 2 to 2.8 μm wide

(including the sheath). They shows a thin and irregular layer of mucilage around the filament They contain one/two chloroplast and a central nucleus; no pyrenoids or thickening of the cell apex could be clearly observed.

Cultured material (Figs. 3-9). Cells are in slight contact or distant from each other, sometimes in pairs when division has just occurred. Cell dimensions are a little bit larger in cultured than in field material: 7 to 10.9 µm long, 2.8 to 3.5 µm wide (minimum size of a young cell: 5.6 µm long, 2.9 µm wide). The apices of the filaments show three distinct morphologies: 1) a vegetative cell with an hemispherical tip (Fig. 3); 2) a short empty tube (Figs. 4, 5, 8); 3) one (sometimes two or more) hypertrophied cell of about 11.2 µm long and 3.5 µm wide, often with a light constriction in the median region (Figs. 5-9).

Up to now, these hypertrophied cells have not been observed in field material, but are frequent in our cultures. Their diameters are slightly greater than those of the algal filaments and consequently are most often attached by one of their ends to the tip of the filament. An empty space is often visible between the last vegetative cell and the hypertrophied one. After an undetermined period of time, the hypertrophied cell is finally released in the medium where it can be found alone. Later it will divide and give a two-celled filament.

In addition to the above description of field and cultured material, one can note in both cases a thin layer of mucilage on the cell wall, and one to two chloroplasts as well as a central nucleus. Often conspicuous vacuole occupy the distal ends of the cells (Figs. 5, 7). No pyrenoids or thickening of the cell apex can be observed.

Scanning electron microscopy (SEM)

SEM micrographs of cultured *Planctonema* (Fig.10) reveal a smooth surface with some attenuated narrowing in the diameter of the filament (it contrasts with the filamentous green alga *Microspora* THURET present on the same figure). Field material has not been investigated with this method.

Transmission electron microscopy (TEM)

The cover of the cells constitutes the filament. It is formed of two similar components: the proper cell wall and mother cell walls originating from several filiation ranks (Figs.11-14, 16). Both have a similar fibrilar structure, and up to now, the exact filiation rank of the mother cell walls cannot be deduced with TEM. The cell wall and the mother cell walls are so firmly overlapped that they give the algal filament its rigidity. Depending on the life cycle and the physiological state of a filament, the tubular pieces more or less overlap with each other with the result that filaments, with the same number of cells can have various lengths (Fig.16).

The elongation of a single cell, prior to its division, is by the apical rupture of its cell wall and the formation of a new one. Before the rupture, the cell thickens at each end due to the local disaggregation of cell wall fibers (Fig. 13). Contrary to reports on some other filamentous green algae (i.e.,

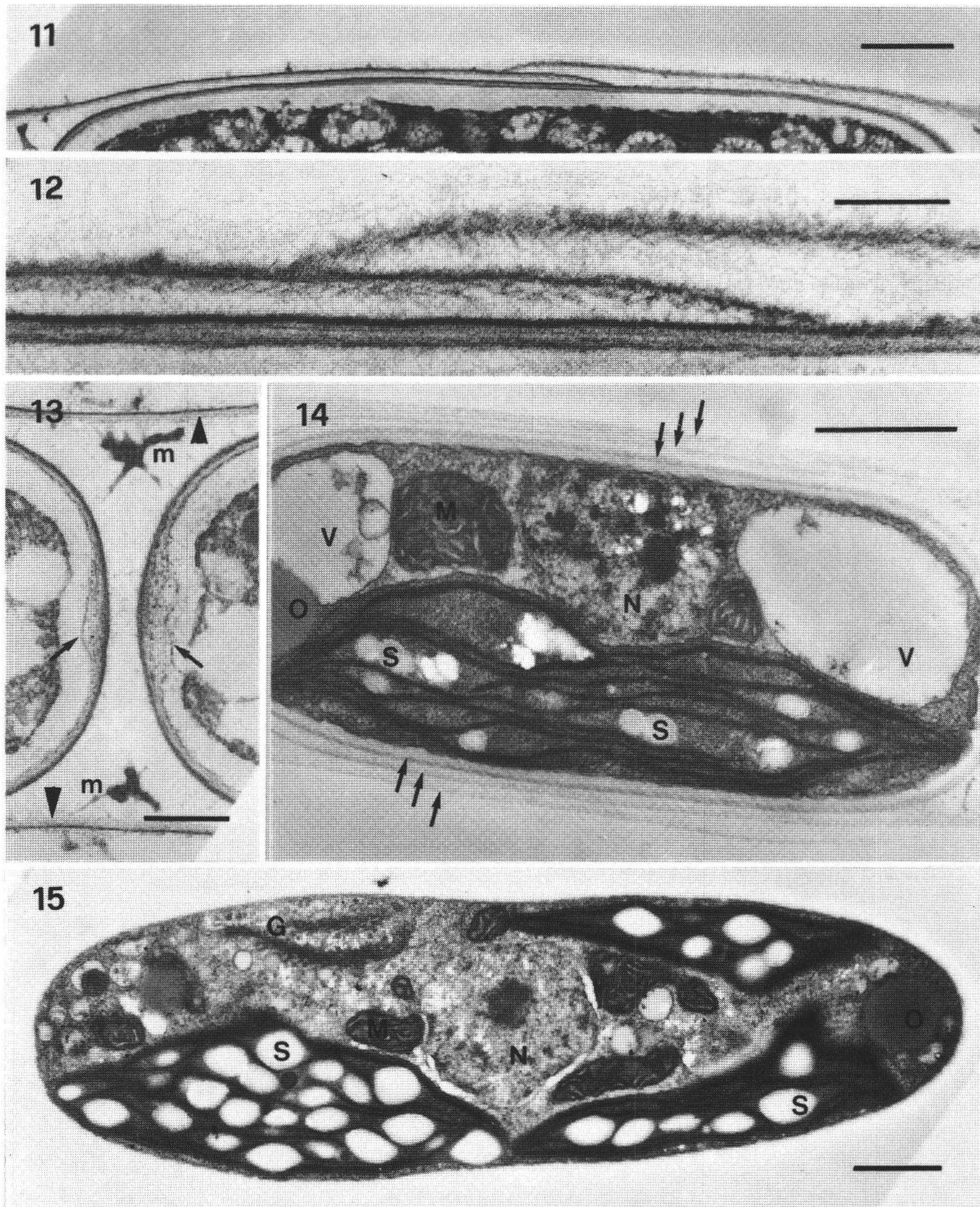


Fig. 11. TEM micrograph. Cell wall and two overlapping mother cell walls *P. lauterbornii* (field material, cytoplasm not well preserved). Bar: 1 µm.

Fig. 12. Detail of Fig. 11. Bar: 0.2 µm.

Fig. 13. Apices of two close cells. Field collected material. A thickening is visible on each cell wall (arrows). Both cells are bounded by a tubular piece made of the mother cell wall (arrowhead). Some mucilage (m) is present between the cells. Bar: 0.5 µm.

Fig. 14. Young cell of cultured *P. lauterbornii*. Nucleus (N), mitochondria (M), oil (O), starch (S), vacuole (V). The cell wall and two surrounding mother cell walls are indicated by arrows. Bar: 1 µm.

Fig. 15. Hypertrophied cell. Note the slight cell constriction in the equatorial region. The cell wall is not visible here. Golgi (G). For other abbreviations see Fig. 14. Bar: 1 µm.

Microspora studied by PICKETT-HEAPS, 1973), the space between two adjacent cells is never occupied by a H-shaped piece, only some mucilage can be observed (Fig. 13).

TEM longitudinal sections (Figs. 14, 15) of the cells (including the hypertrophied ones) reveal one central and laterally positioned nucleus associated with a Golgi apparatus, mitochondria, oil droplets, parietal chloroplasts, and in young cells, huge and apical vacuoles. The chloroplast always contains starch granules but no pyrenoids at all.

In addition to these morphological results, we can mention that a HPLC analysis of the pigments (EAWAG, Dübendorf) confirms the presence of chlorophyll *a* and *b* as already stated by WATANABE *et al.* (1986).

DISCUSSION

The pyrenoid. As it was stated in the introduction, *P. lauterbornii* has been observed under LM without or with a pyrenoid. SCHMIDLE (1903), the author of the genus, as well BOURRELLY (1966), HEYNIG (1988), and HINDÁK & MOUSTAKA-GOUNI (1990) do not observe a pyrenoid in the chloroplast. Our TEM results based on serial sections of several field and cultured filaments confirm these former LM reports.

In contrast, SKUJA (1956) and HÄLLFORS (1984) found the presence of a pyrenoid in *P. lauterbornii* from Sweden and Finland respectively. Their reports are corroborated by TEM observations of a pyrenoid with a starch cap in Japanese material by AKIYAMA & HORI (1977) and WATANABE *et al.* (1986).

In the taxonomy of green algae, the presence or absence of pyrenoids has been mostly used as a generic feature (e.g. in Volvocales: *Chlamydomonas* Ehrenb. (with a pyrenoid) – *Chloromonas* Gobi em. Wille (without a pyrenoid), similarly *Carteria* Diesing em. Francé – *Provasoliella* A.R. Loeblich (see ETTL 1983); in Chlorococcales: *Macrochloris* Kors. – *Pseudodictyochloris* Vinatz; in Ulotrichales: *Gloeotila* Kütz. – *Geminella* Turp (see BOURRELLY 1972). But there are still some genera including species with or without a pyrenoid (e.g. *Chlorella* Beij, *Tetrastrum* Chod). However, this very feature has been applied to taxonomic classifications of Chlorophyta at least at the species level.

Now the question should be asked as to how *P. lauterbornii* from Sweden, Finland and Japan should be taxonomically evaluated. According to the original diagnosis of this species, our alga without a pyrenoid is a "typical" *P. lauterbornii*, while Skuja's, Hällfors's and Watanabe *et al.* algae are different in this very respect. It is not clear how to solve this problem because our knowledge on the genetic stability of the pyrenoid in cells of the Chlorophyta is rather poor.

The apical thickenings of the cell wall. These features are mentioned for *P. lauterbornii* by SKUJA (1956) or in the closely related genus *Binuclearia* WITTROCK (1886). Our TEM results as well those of WATANABE *et al.* (1986) confirm these previous reports. The thickenings are a stage in the preparation of the cell wall aperture. Indeed, they are positioned at the place

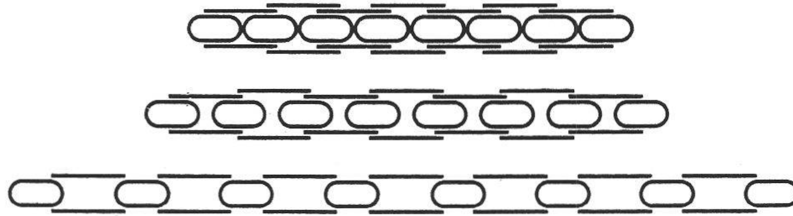


Fig. 16. The filaments of *P. lauterbornii* stay very rigid by the firm overlapping of cell wall and tubular pieces made of the mother cell wall of successive generations. Depending on the life cycle and the physiological state of a filament, the tubular pieces are more or less overlapping with each others. It results that filaments with the same number of cells can have various lengths.

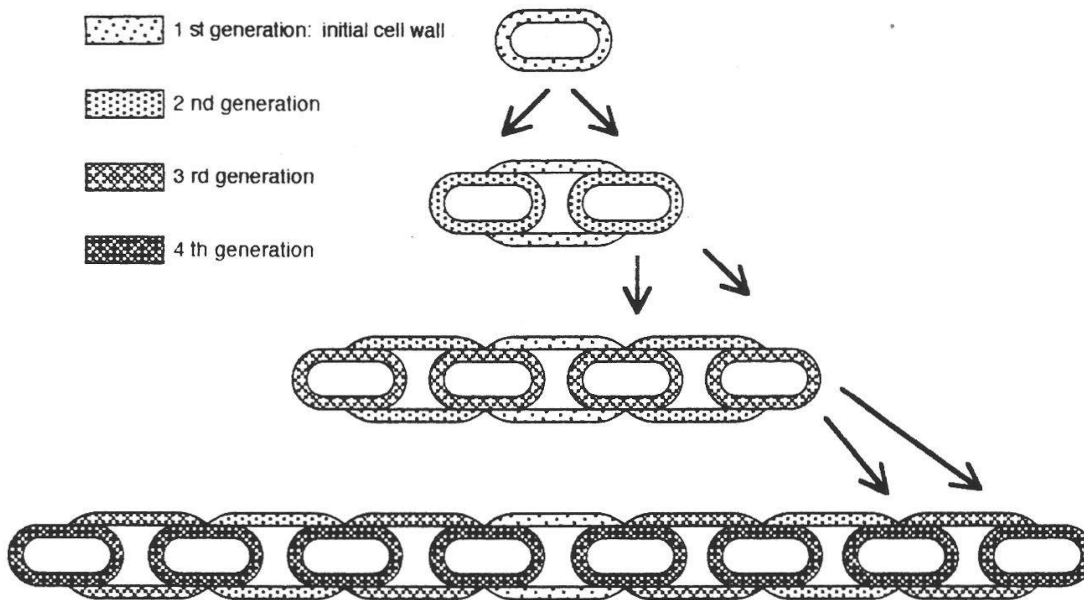


Fig. 17. Representation of a theoretical case of a simultaneous division of all the cells of a filament. The eight-celled filament is made of cells which all belong to the fourth generation. The cylindrical pieces (mother cell wall) which surround the cells belong to the following generations: 3-2-3-1-3-2-3. Compare with Fig. 18.

where the cell wall will rupture to form a new tubular piece of the filament around two daughter cells.

The hypertrophied cells. They have been encountered and described from our material only. However hypertrophied, apical, but drop-shaped or spherical cells have been observed in German *P. lauterbornii* by HEYNIG (1988) and were considered to be aplanospores. Identical observations have been made in the closely related genus *Geminellopsis* by KORSIKOV (1939). In both cases, zoospore formation and liberation has been looked for, but never observed. A close relationship between our hypertrophied cells and those cited above is still premature without further reports.

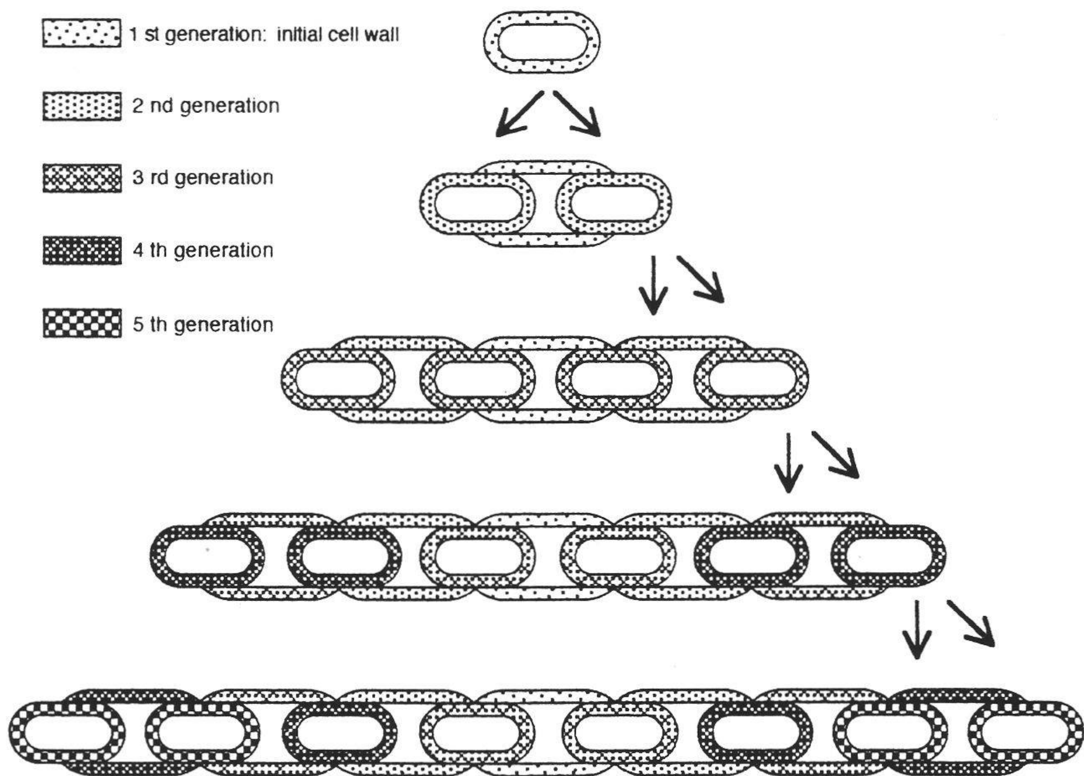


Fig. 18. Another theoretical case in which only the apical cells divide simultaneously (other cells do not divide). The eight-celled filament belongs to generation 3, 4 and 5. The cylindrical pieces which surround the cell walls belong to the generations: 4-3-2-1-2-3-4. Compare with Fig. 17.

The filament development. As supposed by AKIYAMA & HORI (1977), discussed by HÄLLFORS (1984) and demonstrated by WATANABE *et al.* (1986), each of the tubular pieces which form the frame of the filament is made of the proper cell wall or mother cell walls originating from several filiation ranks.

In the case that all cells of a filament divide at the same time (Fig. 17), all the tubular pieces emanating from a same generation will be ordered regularly along the filament and allows the observer to determine the age (degree of filiation) of each part of the sheath (see also WATANABE *et al.*, 1986, Figs. 1g and 4).

However, this firstcase seems to be very theoretical: light microscopy observations of our cultured material show that the cells of a filament do not divide synchronously. In addition, the filaments can break or release hypertrophied cells. In these cases, the ordered distribution of tubular segments of different filiation ranks is disturbed, and consequently their lineage is difficult or impossible to resolve (Fig. 18). In the present case, 8-celled or 14-15-celled filaments are the most common in our culture, which means about four, five or more generations of overlapping tubular pieces. In field material which can include up to 170 cells, we can expect nine or more generations of tubular pieces involved in the organization of the filament.

Taxonomy. The present report describes American material determined as *P. lauterbornii*, and apart from the generic or specific concepts concerning pyrenoid absence/presence, it does not have a detailed taxonomical goal. Taxonomical problems are especially treated by SKUJA (1956), BOURRELLY (1962), HÄLLFORS (1984) and HEYNIG (1988), who considered the genera *Geminellopsis, Geminella, Binuclearia, Gloeotila* and *Psephonema* in their study. However, as concluded by LOKHORST (1991) "(the) taxonomic position of *Planctonema* (is) uncertain, with contradictory reports based on light microscopy..." (loc. cit.). The present LM and TEM report, in complementarity with the results of WATANABE *et al.* (1986), sustains the hypothesis of several taxa in the genus, as suggested by BOURRELLY (1962) and proposed by HÄLLFORS (1984).

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Résumé

Architecture de l'enveloppe cellulaire et morphologie de l'algue verte filamenteuse Planctonema lauterbornii (Chlorophyceae, Ulotrichales). — Cette algue se compose de chaînes de cellules cylindriques et arrondies à chaque extrémité (7 µm long. — 2,5 µm dia., environ). Chaque chaîne est entourée d'une gaine tubulaire formée de nombreux éléments emboîtés les uns dans les autres.

Le matériel examiné sous sa forme naturelle ou en culture provient du lac Tahoe (USA). Les observations ont été réalisées au microscope à lumière (LM) ainsi qu'aux microscopes électroniques à transmission (TEM) et à balayage (SEM).

Le matériel provenant directement du lac est formé de filaments de 16 à 170 cellules (moyenne: 62,3), et le matériel mis en culture, de 1 à 46 cellules (moyenne: 14,6). Ces cellules sont placées, soit côte à côte, soit légèrement distantes les unes des autres, soit encore en paires. La dissémination de l'espèce se fait par libération de cellules hypertrophiées situées à l'extrémité des filaments ainsi que par ruptures des chaînes de cellules. Ces résultats de microscopie optique complètent ou confirment en différents points ceux d'auteurs précédents (SKUJA, 1956; BOURRELLY, 1962, 1966; HÄLLFORS, 1984; HEYNIG, 1988; HINDÁK & MOUSTAKA-GOUNI, 1990, etc.).

En microscopie électronique, les résultats complètent ou au contraire se différencient de ceux obtenus antérieurement par AKIYAMA & HORI (1977) ainsi que WATANABE *et al.* (1986). Une gaine composée d'éléments tubulaires se chevauchant entoure les cellules et donne sa rigidité aux filaments. Ces éléments tubulaires sont formés des parois de cellules issues de plusieurs générations successives (Figs. 16 à 18). Il en résulte que si toutes les cellules d'un filament de *Planctonema* ne se divisent pas de façon synchrone, il sera extrêmement difficile de déterminer à quelle génération appartient tel ou tel élément tubulaire; par exemple les éléments tubulaires d'un filament de 8 cellules seulement peuvent provenir de 4 générations successives ou plus de cellules.

La présence d'un pyrénoïde dans les cellules est difficile à observer en microscopie optique, et les rapports concernant ce sujet sont contradictoires. La présence de cet organite a finalement été démontrée en microscopie électronique par AKIYAMA & HORI (1977) ainsi que WATANABE *et al.* (1986) sur du matériel japonais. Cependant, contrairement à ces auteurs, cet organite est absent du matériel du lac Tahoe. Les résultats actuels sont encore trop fragmentaires pour évaluer dans ce cas précis la valeur taxonomique du pyrénoïde et affirmer par ce moyen que le matériel japonais et américain constitue deux espèces distinctes.

Au niveau générique, on peut noter que *Geminellopsis, Geminella, Binuclearia, Gloeotila*, et *Psephonema* sont des algues extrêmement peu étudiées mais citées comme proches ou très proches de *Planctonema* (HEYNIG, 1988; LOKHORST, 1991). Les limites taxonomiques de *Planctonema* ne pourront donc être mieux établies tant que ces autres genres ne seront pas mieux connus.

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