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Aspects of asexual and sexual differentiation in *Vaucheria*

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Vaucheria species have good developmental features allowing morphogenetic studies. One of these features is the transition from siphonal, apically elongating vegetative structures to differentiation of a terminal, large synzoospore. The second is the sequential inception of sexual organs in a subterminal location.

Concerning both these morphogenetic aspects, Klebs (1896) has been a pioneer. He first got a controlled zoospore induction based on his concept of nutritive level and the effect of dark-light alternative; after photosynthetic, initial growth, a transfer to darkness induces in 24 hours at the optimum temperature of 22°C, transformation of the apices to synzoospores, as a consequence of limited photosynthesis (League and Greulich, 1955). Transfer from moving to still water is another effective way to induce sporulation. Noteworthy, Klebs also obtained multiple generations of zoospores from successively germinated zoospores.

Chemical factors are certainly involved in this differentiation; among them, tryptophane derivatives are inducers even in the presence of light (Denffer and Hustede, 1955); some indolyl-derivatives (indolyl-3-aldehyde and – carboxylic acid), on the contrary, inhibit the process (Hustede, 1957).

Since Klebs (1896), we know that factors which stimulate sexual differentiation act as inhibitors of the vegetative development and vice versa. Such antagonism can indeed be mediated by indolyl compounds (Hustede, 1957). *Vaucheria* species which are normally sterile in nature can be brought to sexual reproduction under laboratory controlled conditions. Klebs (1896) also showed that media enriched in organic substances such as raw sugar (2–4%) and in good light exposure provide adequate conditions to get antheridia and oogonia. Keeping the sugar high but lowering the intensity of light may lead to sexual malformation. Interestingly enough, Denffer and Hustede (1955) showed in *V. sessilis* a sharp increase in the proportion of developing antheridia which redifferentiate into zoosporangia in the presence of a higher concentration of indolyl-3-acetic acid.

From the above general considerations, it seemed to us that *Vaucheria* especially with its apical growth provides an excellent experimental material to try to unravel ultrastructural and functional aspects of the fate of the apex. This apical evolution is in strong analogy with the situation described in apically sporulating Fungi (Turian, 1969). Moreover, the monoecious sexual differentiation reminiscent of many aquatic Fungi can also be found in the *Vaucheria* species.

Materials and Methods

We have used an axenic strain of *Vaucheria sessilis* isolated by M. Keil and kindly sent from the Algenkultur Collection by Dr. W. Koch der Universität Göttingen (Germany). It has been grown in a Pringsheim (1954) semi-synthetic medium enriched with vitamin B₁₂ (0.001 mg %) which we found to stimulate vegetative growth, at 23°C, under 2700 or 1600 lux of white light. After harvesting by filtration, fresh weights have been measured.

Zoospore induction has been obtained by transferring vegetative filaments from light to darkness and zoospores were counted under binocular microscope. Sexual organs obtained on solidified medium have also been microscopically counted in squares randomly selected.

For electron microscopy, filaments outgrown from freshly germinating zoospores have been fixed in glutaraldehyde 2.5% – OsO₄ 1%, buffered with phosphates at pH 7.3. After Epon embedding for thin-sectioning, observations were made with an Hitachi HS-7 electron microscope.

Results

a) Vegetative stage

The optimum conditions for growth of *V. sessilis* were found to be 23°C at 2700 lux in the Pringsheim medium without sugar. A supplement of glucose 2% slows down that growth. Acetate as single C source (0.5–1.0 and 2.0%) does not support and even inhibits growth. Higher concentration of nitrate (up to 5%) increased growth without consequences on differentiation.

Young filaments issued from germinated zoospores always show an apical clear zone in optical microscopy (Fig. 1). We could recently get documents about this tip structure in electron microscope pictures (Fig. 2). In the best ones yet obtained, we confirm the lack of chloroplasts and the impoverishment in mitochondria while noticing a concentration of vesicular-like bodies as the only structures reaching the ultimate tip. This last one is characterized by its thinner wall material.

b) Asexual differentiation

Induction is best obtained with transfer of young vegetative cultures from 2700 lux of light to darkness in the usual medium. As first morphological sign we observe a club-like enlargement (Fig. 3a), secondarily followed by a cytoplasmic displacement (Fig. 3b) preceding the basal septation (Fig. 3c).

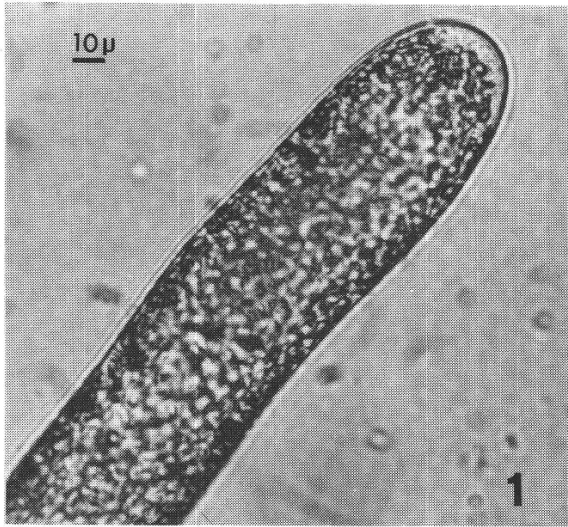


Fig. 1:
 Apex of a vegetative filament showing the restrictive zone without chloroplasts as seen in vivo with the optical microscope.

Fig. 2:
 Longitudinal thin section of the apex of a vegetative filament as seen in electron microscopy.

- ch = chloroplast
- w = wall
- v = vacuole
- ve = vesicula

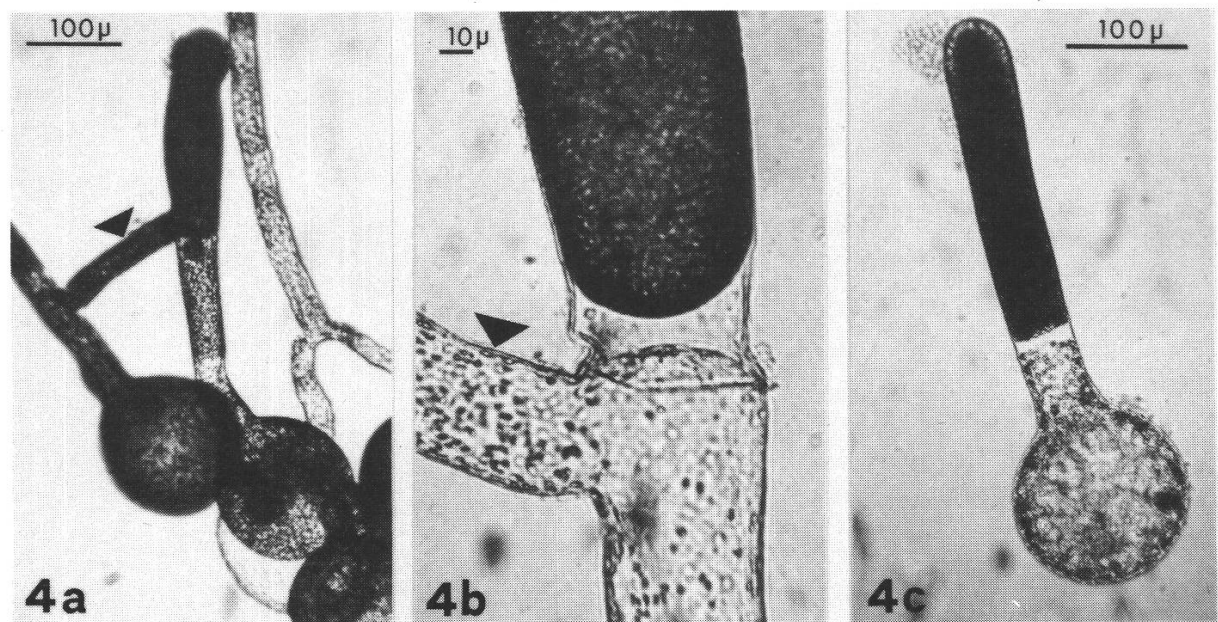
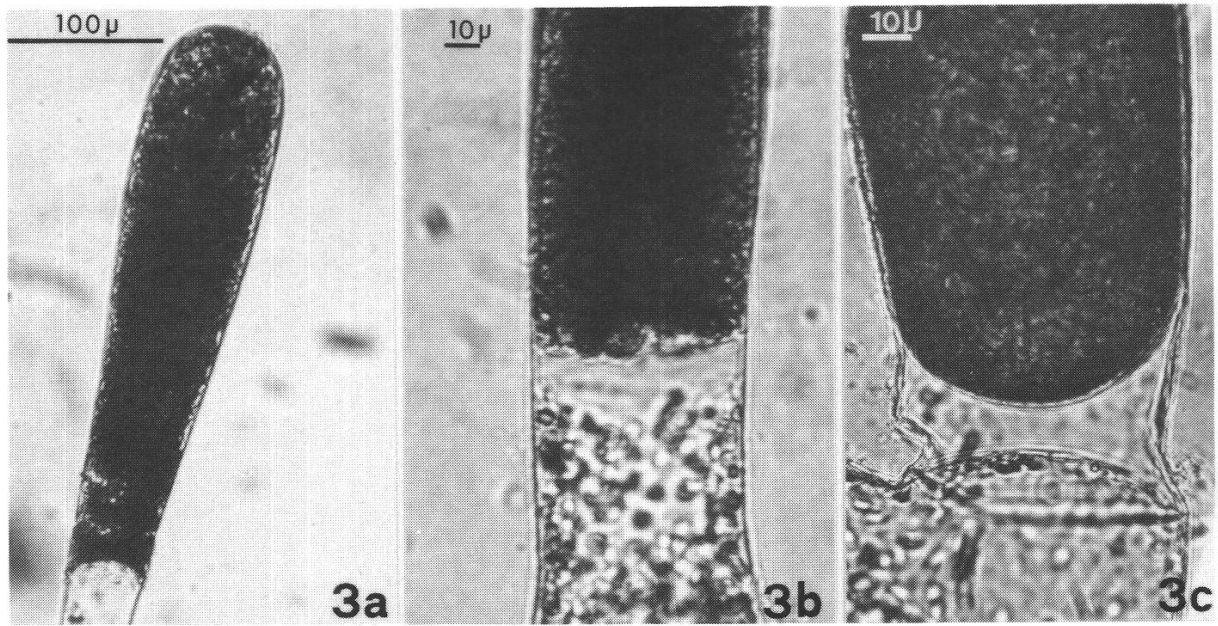


Fig. 3:

Stages of zoosporangium differentiation.

- a) Terminal differentiation of the zoosporangium.
- b) Cytoplasmic displacement.
- c) Basal septation of the zoosporangium.

Fig. 4:

Germinations of synzoospores of *V. sessilis*.

- a) New synzoospore laterally germinating (arrow).
- b) Lateral vegetative elongation (arrow) after zoospore formation.
- c) The shortest span obtained between the zoospore and the zoosporangium.

Physiologically, we noticed that short-day conditions (6h light – 18 h darkness) favour the zoospore formation. The span between one generation and the next can even be reduced (microcycle) to a short tube as we have obtained in total darkness (Fig. 4a, b, c).

It is of interest to add that too low nitrate concentrations in the synthetic medium did not allow any zoospore formation.

c) Sexual differentiation

Light and organic substrates as glucose have been used as controlling exogenous factors. Long-day conditions (18h light – 6h darkness) stimulate sexual differentiation.

Insufficient light (820 lux) in the long-day conditions without glucose in the medium, does not allow sexual differentiation. When increased to 2700 lux it provides conditions to get differentiation with a sex ratio of around 40 ♂ : 60 ♀.

Introducing glucose under low light (820 lux) induces the appearance of a few male and female organs. Introducing 2% glucose and increasing light intensity (2700 lux) speeds up the process with more fertility (Table I).

Table I

Factors controlling sexual differentiation.

The gametangia are counted in 5 mm square fields and are expressed as number of antheridia-oogonia groups.

| Days | 23° C – 2700 lux (18h/day) | |
|------|----------------------------|------------|
| | 0 glucose | 2% glucose |
| 1 | | |
| 3 | | |
| 5 | | |
| 7 | | + |
| 9 | | + |
| 11 | | ++++ |
| 13 | + | ++++ |
| 15 | + | +++ |
| 17 | ++ | ++ |
| 19 | +++ | + |
| 21 | ++++ | ++ |
| 23 | ++++ | + |
| 25 | ++ | |
| 27 | + | |
| 29 | ++ | |
| 31 | + | |

| | |
|------|--------------------------|
| + | less than 3 groups |
| ++ | between 3 and 10 groups |
| +++ | between 10 and 18 groups |
| ++++ | more than 18 groups |

Discussion

Vaucheria is a very common filamentous „yellow-green“ algal genus widely distributed in the damp and aquatic biotopes of the surroundings of Geneva where it has been described for the first time by Vaucher as *Ectosperma* (1803). De Candolle (1805) described it and renamed it as *Vaucheria* in the honour of the genevian algologist.

However, the systematic and phylogenetic position of *Vaucheria* has long been in question because of its specific characters (Venkataraman, 1961). It was placed formerly in the Siphonales of Chlorophyceae (Heering, 1921) but it was replaced in Xanthophyceae by Chadeffaud (1945) because of the color of the chromatophores and the lack of starch. Since then, additional evidence has been accumulated to show that *Vaucheria* belongs to Xanthophyceae (Soma, 1960).

Recently Sagromsky and Rieth (1972) have extracted chlorophylls a and c from *V. woroniniana* Heer. Concerning carotenoids, Egger et al., (1969) have studied them in *Vaucheria* sp. and found diatoxanthin and diadinoxanthin. Other xanthophylls of *Vaucheria* have been characterized by Strain et al., (1971), and Stransky and Hager (1970) have recently proposed a structure formula for the newly discovered vaucheriaxanthin (Kleinig and Egger, 1967).

From the cytological point of view and since conventional preliminary studies with the optical microscope (Mundie, 1929; Gross, 1937; Küster, 1956) interest has concentrated on the ultrastructure of the flagellar apparatus from antherozoids (Koch, 1951) and from synzoospores (Greenwood et al., 1957; Greenwood, 1959) as well as on chloroplasts (Schulte, 1964) with their newly electron microscopically described pyrenoid in *V. sphaerospora* grown under continuous light (Descomps, 1972).

Our preliminary results show that the apex of *Vaucheria* filaments has some analogies with that of Fungi as it also presents a restrictive zone at its tip showing no organelles such as nuclei, mitochondria and chloroplasts. At asexual, zoospore induction, there is a reorganization of the apex which mingles organelles and other materials. It is already well known that an inversion of positioning of chloroplast *versus* nuclei occurs at the transition vegetative filaments *versus* zoosporangia i.e. the nuclei move close to the cytoplasmic membrane when the flagellar system appears in the young zoospore (see Smith, 1965).

As far as sexual differentiation is concerned, it is interesting to note the interrelationships between light and carbon substrate in the complex mechanisms controlling this morphogenetic orientation.

Summary

Tips of vegetative filaments of *Vaucheria* lack chloroplasts, are impoverished in mitochondria and are rich in vesicula-like bodies. This apically polarized organization is lost at spore induction. In total darkness, filaments outgrown from synzoospores prematurely induce new synzoospores (microcyclic development). Sexual differentiation is accelerated by glucose and high light intensity.

Résumé

Différenciation asexuée et sexuée de *Vaucheria*.

Les extrémités des filaments végétatifs de *Vaucheria* sont dépourvues de chloroplastes, sont pauvres en mitochondries et riches en corps vésiculaires. Cette organisation à polarité apicale est perdue lors de l'induction de la spore. A l'obscurité totale, les filaments émis par les synzoospores induisent de nouvelles synzoospores (développement microcyclique). La différenciation sexuelle est accélérée par l'apport de glucose et par une forte intensité lumineuse.

Zusammenfassung

Asexuelle und sexuelle Differenzierung bei *Vaucheria*.

Die Spitzen vegetativer Fäden von *Vaucheria* enthalten keine Chloroplasten und wenige Mitochondrien, aber viele vesikuläre Körper. Bei der Sporeninduktion geht diese Spitzenpolarität verloren. Bei vollständiger Dunkelheit induzieren die aus Synzoosporen auswachsenden Fäden neue Synzoosporen (mikrozyklische Entwicklung). Die geschlechtliche Differenzierung wird durch Zugabe von Glucose und durch starke Belichtung beschleunigt.

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