Viewer's Guide[1]

"*Remarkable Plants: the Oedogoniales (Green Algae)*"

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The Oedogoniales comprise a very unusual, highly circumscribed Order of green algae, exclusively freshwater. The three genera, *Oedogonium*, *Oedocladium* and *Bulbochaete*, are markedly different from each other morphologically, but all share the several characteristics that distinguish the Oedogoniales from all other green algae. Their unusual and fascinating features were well known to early phycologists (e.g., references in Fritsch, 1945). While they have no obvious ancestors, several other features common to other greens (e.g., possession of the phycoplast) place them in the Chlorophyta (*sensu* Mattox & Stewart, 1984). Preliminary molecular data (Booton et al., 1998) confirm that they constitute a monophyletic, taxonomically isolated clade. This data also suggest that *Bulbochaete* could be more basally situated phylogenetically than the other two genera.

Oedogonium (from the Gk: *oedos* = swelling + Gk: *gonos* = reproductive structure/offspring) is very widespread and common, and it is often a dominant organism; I have found one or more species in almost every freshwater sample I have ever collected . Many species are very hardy, living years, for example, in aquaria. *Oedocladium* is a terrestrial genus and apparently quite rare; *Bulbochaete* is also uncommon. The number of species described by two authorities are:

Oedogonium: 465 (Mrozinska, (1985) to 531 (Gonzales, 1981);
Bulbochaete: 109 (Gonzales, 1981) to 113 (Mrozinska, (1985);
Oedocladium: 13 (Gonzales, 1981) to 15 (Mrozinska, (1985).
More recently, Mrozinska (1991) has analysed 442 species of *Oedogonium* phylogenetically.

All three genera lend themselves to light microscopy: for example, the unusually large chromosomes makes observations of live mitosis very rewarding (Chap. 2.1). Ultrastructural and cytological observations on *Oedogonium* and *Bulbochaete* are summarised in Pickett-Heaps (1975a).

Summary of the Most Distinctive Morphological Features of the Oedogoniales

i) Following mitosis, their mechanism of cell elongation is unique (Chap. 2.1). Before and during mitosis, a "donut ring" of soft, primary wall material is secreted at the apical end of the cell, attached firmly to the wall. Telophase is followed by a preliminary cytokinesis where the components of the future cross wall are assembled in the phycoplast; then the wall splits circumferentially and this ring is stretched to enclose a new daughter cell. The nascent crosswall in the phycoplast slides along the cell and consolidates into a wall when just past the end of the older wall. This extraordinary behaviour creates a series of wall scars characteristic of the family (Chap. 1).

ii) The highly motile zoospores differentiate singly in parental cells and display a ring of flagella (the "stephanokont" condition: Chap. 3), a morphology displayed elsewhere only by a few members of the unrelated Caulerpales (e.g., *Derbesia*).

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[1] This text is not a comprehensive review but is designed to introduce the user of the video to relevant background material.

ii) oogamous sexual reproduction is distinctive and of two types: macrandrous (Chaps. 4.1, 4.2) and nannandrous (Chaps. 5.1, 5.2).

All three genera display strong apical/basal polarity and the cells are interconnected by numerous, complex plasmodesmata (Fraser & Gunning, 1969).

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Chap. 1. Morphology of the Three Genera: *Oedogonium*, *Bulbochaete*, *Oedocladium*

i) *Oedogonium* is a simple unbranched filament, usually attached by a strong holdfast to a substrate. In a few species, the apical terminal cell is elongated into a hair-like tip (e.g., Fritsch, 1902).

ii) *Oedocladium* is a simple branched filament; the basal terminal cell is not differentiated into a holdfast (presumably because the organism is terrestrial and often lives in mud).

ii) *Bulbochaete* is a branched filament in which terminal cells and many interstitial cells bear very long hair cells with a bulbous base (hence the name). This filament, like that of *Oedogonium*, is attached by a holdfast cell.

Chaps. 2.1 - 2.3. Mitosis and Cell Growth

Mitosis in *Oedogonium*

Mitosis in *Oedogonium* has been well described by early workers (e.g., Strasburger, 1880; Ohashi, 1930; Tuttle, 1910; van Wisselingh, 1908a). Large species such as *O. cardiacum* offer numerous advantages for research into the mechanisms of mitosis, for example, ease of culture, invariable indication of impending division (the wall ring), large and active chromosomes, rapidity of mitosis (e.g., Coss & Pickett-Heaps, 1974b; Sampson, Pickett-Heaps & Forer, 1996; Sampson & Pickett-Heaps, 2001), and spectacular spindles under the electron microscope (Pickett-Heaps & Fowke, 1969, 1970a; Schibler & Pickett-Heaps, 1980, 1987); the layered kinetochores are particularly striking (Pickett-Heaps & Carpenter, 1993). For optimal observations, exponentially growing cells are needed to minimise the number of pyrenoids which can often interfere with images of the spindle.

Cell Elongation (Growth) by Ring Formation

The very peculiar method of cell expansion after mitosis was well known to early investigators and van Wisselingh (1908b) gives an accurate description of the wall rings and their relationship to the division scars characteristic of this genus. The pattern of these scars precisely reflects the division history of each cell (Fig. 13 in Pickett-Heaps & Fowke, 1970b; Pickett-Heaps, 1971).

By using the wall ring for growth, the cell undergoes elongation in a single discrete, short period immediately after mitosis. The particular innovation that this group has evolved is to secrete primary wall material (by definition, that which allows cellular growth) all at once, and in the one place, the division ring (Hill & Machlis, 1968: Pickett-Heaps & Fowke, 1969; 1970b; Pickett-Heaps, 1973). Only when cells have subsequently achieved full length does secondary wall deposition takes place. (A somewhat similar sequence of events is seen in desmids which double in size immediately after cytokinesis by expansion of a soft primary wall; the rigid secondary wall is deposited quite separately after expansion). By building a preweakened breakage point into the secondary wall (Pickett-Heaps & Fowke, 1970b), the cell can use turgor pressure to escape the confines of this wall when needed for growth or zoospore release (Pickett-Heaps, 1971, 1972a). For this unusual system to work, the wall weakness has to, and indeed does, absolutely determine the position of the division ring.

The evolutionary origin of this unique mechanism of elongation may lie in the modification of a wound response and the evidence for this suggestion has been given in Pickett-Heaps (1972c).

Branching in *Oedocladium*

The origin of branching in *Oedocladium* is simple to understand (Pickett-Heaps, 1977). Electron microscopy shows that interphase cells have a frequent propensity to prematurely break their wall at the weakening; these breakages are subsequently repaired by polysaccharide secretion (i.e., the normal wound response; Pickett-Heaps, 1972c). Given the absolute predetermination of the siting of the wall ring by the wall weakness (prev. para.), cells with these wall repairs cannot undergo cell growth using the wall ring. Instead, they revert to the simpler, more primitive mechanism of tip growth in a bulging cell pushed through the weakest part of the repair. One might argue that this genus illustrates a more primitive condition, wall breakage being relatively uncontrolled.

Branching in *Bulbochaete*

Electron microscopy also shows why the more complex morphology of this genus evolved. Wall rings are present in many dividing cells, and these are invariably situated at the wall weakness as usual (Pickett-Heaps, 1973). When a cell has already formed a hair cell, there is invariably a circular wall weakness under the base of the hair. This is where the wall ring forms for the next division, and in turn, this determines why a branch grows out at this site (Fraser & Gunning, 1973; Pickett-Heaps, 1973). Thus, the basic mechanism of division seems consistent, but why should the wall weakness come to lie in that situation in cells with hairs?

The explanation lies in a number of irregularly appearing interphase cells which bulge on one side (Pickett-Heaps, 1974). Close inspection reveals that these do **not** have a normal wall weakness. Instead, the wall is thinned out over the bulge, in the middle of which is a weakening of limited extent. Clearly, these cells cannot form a normal wall ring either. They undergo a reduced version of the wound response accompanying an asymmetric division with one spindle pole directed into the bulge. Unlike normal division, the phycoplast hardly moves after mitosis and it lays down a cross wall under the base of the hair cell that will extend through the split now formed in the apical daughter cell (Chap. 2.3). Built into this cross wall is the circular weakening needed for resumption of normal cell division. Thus, the next normal division grows a branch under the hair. The hair is always colourless (Fraser & Gunning, 1973) because the phycoplast eliminates the chloroplast from it before cytokinesis.

Why the bulging wall with the partial weakening? Comparison of these vegetative cells with developing oogonial cells demonstrates that both have the altered type of weakening which the cell breaks open to form the fertilisation pore. Clearly, a sexual characteristic, the partial wall weakening, has become somewhat randomly expressed in vegetative cells (Pickett-Heaps, 1975b).

Fritsch (1902) mentions that germinating zoospores of *Oedogonium* often form an apical "tip" or hair-like extension before their first division. I have also often encountered this morphology in natural collections of *Oedogonium* and it looks suggestively like a miniature hair cell of *Bulbochaete*. This minor detail does suggest that *Oedogonium* has an innate capacity, not widely expressed, that could have evolved into the hair cell of *Bulbochaete*. Germinating zoospores of such species create this tip before the first division and thus closely resemble those of *Bulbochaete* (Chap. 3).

Chap. 3. Asexual Reproduction by Zoospores

The complexity of zoosporogenesis is revealed by ultrastructural investigation (Pickett-Heaps, 1971). Since zoospores often differentiate in temporal order from the apical end of a filament back, cells in a single filament will illustrate the progression of morphogenetic events in linear order. Thus, one can demonstrate with confidence that centrioles appear *de novo* from a small diffuse mass located at the nuclear envelope. The mature flagellar apparatus is extraordinarily complex structurally, consisting of the ring of basal bodies interconnected by a web of fibrous components (as in the sperm cell: Hoffman & Manton, 1962, 1963; Markowitz, 1978); alternating with the basal bodies, a set of rootlets MTs, each adjacent to a specific type of striated fiber (Hoffman, 1970), radiate out under the cell membrane of the zoospore.

The vesicle surrounding the zoospore is proteinaceous (Retallack & Butler, 1970), but also contains polysaccharide (Pickett-Heaps, 1971). It probably acts as a semipermeable membrane whose osmotic uptake of water assists in breaking the wall at the weakness (Pickett-Heaps, 1972a). On germination, the flagella are shed and then the whole flagellar apparatus is disassembled; broken segments of it are visible in the dome as the cell starts forming the holdfast (Pickett-Heaps, 1972b). Meanwhile, the contents of the dense vesicles are discharged through the membrane at the dome, presumably contributing to the adhesive nature of the rhizoidal outgrowths that are capable of penetrating into porous substrates such as Millipore filters. Even though *Oedocladium* zoospores do not form a holdfast, they still may secrete adhesive (Markowitz, 1978).

Chaps. 4.1-2 Macandrous Sexual Reproduction

Oedogonium offers a beautiful example of how asymmetric divisions can be used in cellular differentiation (Coss & Pickett-Heaps, 1973). For formation of the small antheridia, cell division is modified so that the wall ring is small and the mitosis strongly polarised **apically** (Chap. 4.1). Cell expansion after division is correspondingly limited and the antheridium is short and discoidal. For cell division in the oogonial initial cell, the wall ring is extra large and mitosis is strongly **basally** polarised (Chap. 4.2). As a result, the oogonial swells into a large rotund cell, while the initial basal location of the phycoplast ensures that virtually all the cytoplasmic contents of the original cell passes to the forming oogonium; the impoverished basal cell left behind is called the suffultory cell.

Spermatogenesis is preceded by a second division in the antheridium. The antheridial cell now uses cleavage for cytokinesis, instead of the cell plate; this change in mechanism is interpreted as a reversion to a more primitive situation, when cell elongation via wall rings and movement of the cell-plate, does not occur. Spermatogenesis has been described by Coss & Pickett-Heaps (1973, 1974a) while Hoffman (1971, 1973a) describes the oogonium prior to fertilisation.

The oogonium does not have a normal wall weakening; instead, it has a partial one situated toward the equator of the oogonium. The female cell has to break open the fertilisation pore by turgor. This is probably aided by pressure being specifically concentrated on the wall weakening by swelling of the mucilage secreted under it. Once the wall is broken, the oogonium is subject to osmotic uptake of water (just as the naked zoospore is) and it responds, as expected, by contractile vacuoles appearing all over its surface. Thus, the oogonial cell shrinks immediately after wall breakage. Older or unhealthy oogonia will sometimes bulge through the fertilisation pore, usually a sign of their imminent death by rupture.

After fertilisation, fusion of the male and female nucleus is initiated by contact of the nuclear envelopes, and soon the nuclei merge (Hoffman, 1974). Germination of the resultant oospore is

preceded by meiosis; the oospore splits open to release four vegetative zoospores that are briefly contained within a vesicle (Hoffman, 1965).

Chap. 4.3 Fertilisation

Fertilization was of interest to early observers (e.g., Spessard, 1930) and a more recent, beautifully detailed account of fertilisation is given by Hoffman (1973a) who also encountered rare cases of polyspermy (Hoffman, 1973b). The attraction of sperm to the oogonial pore is clearly via chemotaxis (Hoffman, 1973a; Rawitscher-Kunkel & Machlis, 1962). The approach of the sperm to the pore is aggressive and thrusting, and the mucilage plug blocking the pore is dissolved in seconds (Hoffman quotes 14" and 21" in two measured examples), presumably via enzymes released from granules in the dome of the sperm. The slight but rapid shape changes concurrently undergone by the elongated sperm just prior to fusion indicate that its cytoskeleton of rootlet MTs is very dynamic, eventually undergoing abrupt collapse as the sperm rounds up upon fusion with the female cell. Hoffman's and my observations support the notion that elongation is important for the sperm to be able to squeeze through the narrow fertilisation pore. Sperm have a limited life, becoming rotund and incapable of fertilization as they age; in one recorded case, a bloated sperm became stuck in the pore for 20 mins. Eventually these older sperm rupture, presumably because of failure of their contractile vacuole.

As in the germinating zoospore, a shivering motion accompanies shedding of the flagella upon plasmogamy.

Chaps. 5.1-2 Nannandrous Sexual Reproduction

The reason(s) that the complexities of nannandrous reproduction evolved in the Oedogoniales became clear from the work of Machlis (1961) and Rawitscher-Kunkel & Machlis (1962). Working with a heterothallic *Oedogonium* (possibly *O. borisianum*), they found that:

i) androspores are strongly attracted to the oogonial initial cells located at intervals along the filament, and they germinate on or as close to the base of these cells as they can. Whether initial androspore differentiation is similarly stimulated by a sexual hormone is unclear, but it seems likely.

ii) the oogonial initial cell does **not** divide until androspores attach to it. In the absence of androspores attaching, the dense female cell remains in an arrested, premitotic stage. The oogonium has a limited life expectancy once it has finally committed to sexual reproduction by opening its fertilisation pore: it becomes vulnerable to both external predators and eventual loss of contractile vacuole function (and subsequent death by rupture). By waiting for a signal from the androspore, the female ensures that sexual maturity will be achieved concurrently and that sperm will be available very soon after the pore is opened.

iii) the oogonium secretes a thick gelatinous sheath which traps the sperm upon their release; this innovation would be useful in flowing water when released sperm might be swept away. Even when in the sheath, sperm can move and they congregate around the unopened fertilisation pore. As soon as the pore opens, fertilisation follows.

iv) the direction of growth of the germinating dwarf males is towards the oogonial cell, in another apparent response to chemotaxis, and this also serves to ensure that released sperm are embedded in the sheath.

v) as a final refinement, androspores which cannot find a female, can germinate like zoospores to form a vegetative filament. Thus, they may not commit to dwarf male formation until attached to the female. This ability to switch between the asexual and sexual mode may be under chemical (hormonal) control (Hill et al., 1989)

The development of dwarf males and oogonia has been described by Retallack & Butler (1973), Pickett-Heaps (1975b) and Leonardi et al. (1998). The use of two asymmetric divisions in the oogonial initial to create a large oogonium in *Bulbochaete* (Cook, 1962) is, I believe, unique to this genus. The oospore wall is thick and composed of at least seven layers.

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