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REVIEW

WHAT DO WE KNOW ABOUT CHAROPHYTE (STREPTOPHYTA) LIFE CYCLES?[1]

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The charophyte algae are the closest living relatives of land plants. Their life cycles are usually characterized as haploid with zygotic meiosis. This conclusion, however, is based on a small number of observations and on theoretical assumptions about what kinds of life cycle are possible. Little is known about the life cycles of most charophytes, but unusual phenomena have been reported in comparatively well-studied taxa: *Spirogyra* and *Sirogonium* are reported to produce diploid gametes with synapsis of homologous chromosomes before fusion of gametic nuclei; *Closterium ehrenbergii* is reported to undergo chromosome reduction both before and after syngamy; and zygotes of *Coleochaete scutata* are reported to replicate their DNA to high levels before a series of reduction divisions. All of these phenomena require confirmation, as does the conventional account.

Key index words: **alternation of generations; *Chara*; charophyte; *Closterium*; *Coleochaete*; meiosis; *Spirogyra*; syngamy**

Abbreviations: **C, the amount of DNA in an unreplicated haploid genome; G, the amount of DNA in a gametic nucleus immediately prior to karyogamy**

Nineteenth-century botanists recognized an alternation of asexual and sexual generations. An asexual generation produced offspring that developed from a single cell (spore), whereas a sexual generation produced offspring that developed from the union of two cells (gametes). For land plants, the two kinds of generations had contrasting morphologies, but, among algae, sexual and asexual generations were sometimes indistinguishable apart from their reproductive structures. For example, vegetative thalli of *Coleochaete* sometimes reproduced by zoospores, in which case the thallus was an asexual generation, and sometimes by gametes, in which case the thallus was a sexual generation (Haig 2008).

Toward the end of the century, zoologists discovered that ova and sperm had half the number of chromosomes of somatic cells, and botanists determined that the sexual generation of land plants had half the number of chromosomes of the asexual generation (Farley 1982). Therefore, the life cycles of both plants and animals were seen to alternate between two nuclear phases with a 2-fold difference in chromosome number. The reduction in chromosome number was immediately followed by syngamy in animals. Therefore, all cells except gametes were diploid. However, in land plants, chromosome reduction and syngamy were both followed by a series of cell divisions such that the life cycle contained both multicellular haploid and diploid phases.

The recognition of an alternation of haploid and diploid phases changed the way the alternation of generations was conceptualized. The sexual (gametophyte) generation of land plants was haploid, and the asexual (sporophyte) generation was diploid, but this close correspondence did not apply to the sexual and asexual generations of algae. For example, zoospore-producing and gamete-producing thalli of *Coleochaete* both develop from zoospores and presumably have the same chromosome number. Before the discovery of an alternation of nuclear phases, these thalli were viewed as representing an alternation of asexual and sexual generations, but since the discovery, the two kinds of thalli have increasingly been conceptualized as a single kind of thallus, a haploid (gametophytic) generation with alternative reproductive modes (Haig 2008).

When botanists set out to understand how chromosome number changed during algal life cycles, most implicitly assumed that algae would exhibit a similar alternation between haploid and diploid nuclear phases (Renner 1916). Therefore, a life cycle would be defined by whether mitotic divisions followed the reduction division, creating a multicellular haploid phase, and whether mitotic divisions followed syngamy, creating a multicellular diploid phase. Algal life cycles were expected to follow ''rules'' established in land plants, and their descriptions were often shoe-horned into an ill-fitting terminology suited to land plants rather than described in their own terms.

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One of the principal reasons for studying algal life cycles was the hope that such studies would shed light on the origin of the sporophyte of land plants. Interpretation, however, was hampered by uncertainty about algal phylogeny. Molecular phylogenies now unequivocally establish that embryophytes were derived from within the charophyte algae (Karol et al. 2001, Qiu et al. 2007; I use ''charophyte'' in the broad sense of Lewis and McCourt 2004 and use ''stonewort'' to refer to the members of the Charales). Charophyte algae are generally believed to possess life cycles in which vegetative cells are haploid and zygotes are the only diploid cells. Therefore, such a life cycle has been inferred to have been present in the algal ancestors of embryophytes and to support the ''antithetic'' theory for the origin of sporophytes (Blackwell 2003, Donoghue 2005, Haig 2008, Becker and Marin 2009).

Common knowledge is sometimes collective misinformation, and it is worthwhile to occasionally subject what everybody knows to critical reappraisal. This paper reviews more than a century of studies of charophyte life cycles and finds few observations that have been replicated by multiple observers. I conclude that something like the standard interpretation may be true for some forms, although supporting evidence is flimsy, and that the diversity of charophyte algae is likely to encompass a corresponding diversity of life cycles, some of which will not fit neatly into conventional categories.

Changes in DNA content. The default assumption, since the discovery of an alternation of nuclear phases, has been that sexual life cycles operate at two ploidy levels. The amount of DNA in a nucleus doubles during the course of a conventional cell cycle and then is reduced by half at mitosis. Therefore, the alternation of haploid and diploid phases has been assumed to imply an alternation between 4C and 2C levels in diploids, and between 2C and 1C levels in haploids, where C is the amount of DNA in an unreplicated haploid genome. If meiosis immediately follows syngamy, then the zygote is the only diploid cell in the life cycle and all other cells are haploid (Fig. 1a). If meiosis and syngamy are both followed by mitosis, then the life cycle contains both vegetative haploid and vegetative diploid cells (Fig. 1b). If meiosis immediately precedes syngamy, then gametes are the only haploid cells and all other cells are diploid (Fig. 1c).

Haploid–diploid alternation requires mechanisms for doubling DNA content (DNA replication and syngamy) and mechanisms for halving DNA content (meiosis I, meiosis II, and mitosis) that are sufficient, in theory, to allow life cycles that encompass more than three levels of DNA content per nucleus. Indeed, 8-fold or greater reduction in chromatin content has been reported in nuclear cycles from pyrsonymphids (Hollande and Carruette-Valentin 1970), radiolaria (Lécher 1978), red algae (Goff and Coleman 1986), and brown algae (Garman et al. 1994, Garbary and Clarke 2002). Among charophyte algae, 8-fold or higher reduction has been reported in the zygospore of *Coleochaete* (Hopkins and McBride 1976) and in somatic cells of *Chara* (Shen 1967).

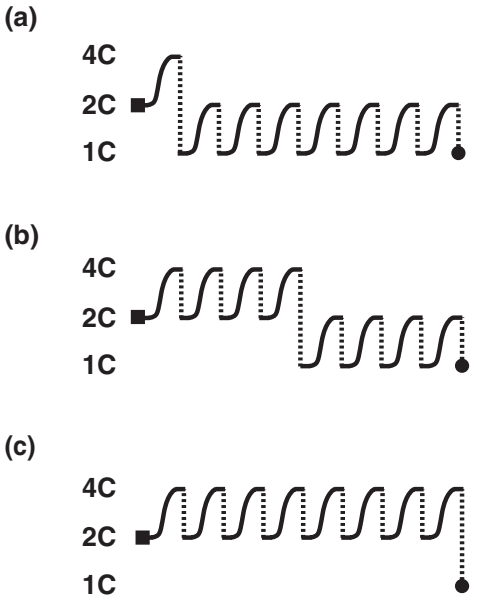

FIG. 1. Conventional interpretations of algal life cycles. Each life cycle is represented as proceeding from a zygotic nucleus (square) to a gametic nucleus (circle). Rising solid lines represent the increase in DNA content during a cell cycle. Dotted lines represent the decrease in DNA content per nucleus at cell division. Mitosis is associated with a halving of DNA content at a single division, whereas meiosis is associated with a reduction to one-quarter over the course of two divisions. (a) Life cycle with zygotic meiosis. DNA content is raised to the 4C level after syngamy. Meiosis reduces DNA content to the 1C level. Haploid nuclei alternate between the 1C and 2C level of DNA. (b) Life cycle with multicellular diploid and haploid phases. After syngamy, DNA content of diploid nuclei alternates between the 2C and 4C levels. Meiosis reduces DNA content to the 1C level. Haploid nuclei alternate between the 1C and 2C levels. (c) Life cycle with gametogenic meiosis. Diploid nuclei alternate between 2C and 4C levels. Meiosis produces 1C gametic nuclei.

As I do not wish to assume that charophyte life cycles are ''well-behaved,'' I will use 2G to refer to the amount of DNA in a zygotic nucleus immediately after karyogamy and 1G to refer to the amount of DNA in gametic nuclei immediately prior to karyogamy. The latter is not necessarily equal to 1C, the amount of DNA in an unreplicated haploid genome, because gametic DNA may have replicated prior to karyogamy, or gametes may contain more than one haploid genome. I will use ''meiosis'' to refer to a sequence of two (or more) divisions without intervening synthesis of DNA.

Charophyte life cycles. Little is known about the life cycles of most charophyte algae. Sexual reproduction has never been described in significant taxa such as *Mesostigma viridis* and *Chlorokybus atmophyticus*. Syngamy has been reported in *Chaetosphaeridium*

globosum (Thompson 1969) and *Klebsormidium flaccidum* (Wille 1912), but these descriptions provide no information about germination of zygospores or about chromosome numbers at different life-history stages. Below, I review evidence from a few select taxa where more-detailed studies exist.

Spirogyra *and* Sirogonium: Molecular phylogenies place *Spirogyra* and *Sirogonium* in a clade that is sister to the remainder of the conjugating green algae (Hall et al. 2008). Prior to syngamy, the protoplast of a ''male'' gamete is transferred via a conjugation tube into the cell wall of a ''female'' gamete. A zygospore is formed after fusion of the two protoplasts. The zygotic nucleus divides twice to produce four nuclei, each with the gametic chromosome number. Three of the four nuclei degenerate. Germination of the zygospore releases a single germling containing the surviving nucleus (Godward 1961).

The conventional interpretation of this life cycle is that it involves union between haploid gametes to produce a diploid zygote, followed by meiosis to restore haploidy (Fig. 1a). Harada and Yamagishi (1981, 1984) describe nuclear behavior in six strains of *Spirogyra* and *Sirogonium* that challenges this simple interpretation. Synapsis of homologs was observed before fusion of gametic nuclei, with karyogamy delayed until late prophase I. *Spirogyra crassa* will serve as an exemplar. Gametic nuclei contained 12 chromosomes. After syngamy, but before karyogamy, six bivalents were formed in each gametic nucleus. Only then did the gametic nuclei fuse so that the metaphase plate contained 12 bivalents each containing four chromatids. Twelve half-bivalents separated to opposite poles at the first division of the zygospore nucleus, which was immediately followed by separation of the chromatids of the half-bivalents at the second division. Three of the resulting nuclei aborted, leaving a single nucleus with 12 chromosomes.

The above sequence could be interpreted as the fusion of diploid gametes ($2n = 12$) to produce a tetraploid zygote ($4n = 24$) with subsequent reduction to diploidy. As a result, the diploid germling receives a haploid set of chromosomes ($n = 6$) from each parent. The diploid gametic genomes essentially undergo meiosis in parallel, because nowhere in the process is there pairing, followed by segregation, of homologous segments from the two gametes. Mendelian segregation would be limited to separation of ''grandparental'' alleles that came together in zygospores of the previous generation.

The amount of DNA per nucleus has not been measured at different stages of the life cycle, but I will present a hypothesis that is compatible with the cytological observations. The zygotic nucleus (2G by definition) undergoes two divisions, apparently without DNA replication, to produce four nuclei (0.5G), one of which survives. The simplest interpretation is that vegetative nuclei alternate between 0.5G (before DNA replication) and 1G (after DNA replication), with DNA synthesis occurring in 0.5G gametic nuclei to bring them up to 1G before karyogamy (Fig. 2a). Gametic nuclei contain bivalents, each of four chromatids, before karyogamy. Therefore, G is at least 4C, and the zygotic nucleus at least 8C.

The sequence could also be interpreted as fusion of tetraploid gametes ($4n = 12$) to produce an octoploid zygote ($8n = 24$) with reduction to tetraploidy in two divisions. Evidence that gametic nuclei of *Sp. crassa* might contain four haploid sets of three chromosomes comes from *Sp. crassa* X, a strain that resembles *Sp. crassa* except that cells are smaller and gametic nuclei contain six, rather than 12, chromosomes (Harada and Yamagishi 1984). In this strain, three bivalents are formed in each gametic nucleus before karyogamy. The meiotic divisions then produce a single germling with six chromosomes, three derived from each parent.

Many years previously, Tröndle (1911) had also reported synapsis in gametic nuclei of *Spirogyra neglecta*. After karyogamy, 12 bivalents (each of four chromatids) were present on the metaphase plate. Twelve half-bivalents moved to opposite poles at first anaphase, and then 12 chromatids moved to each

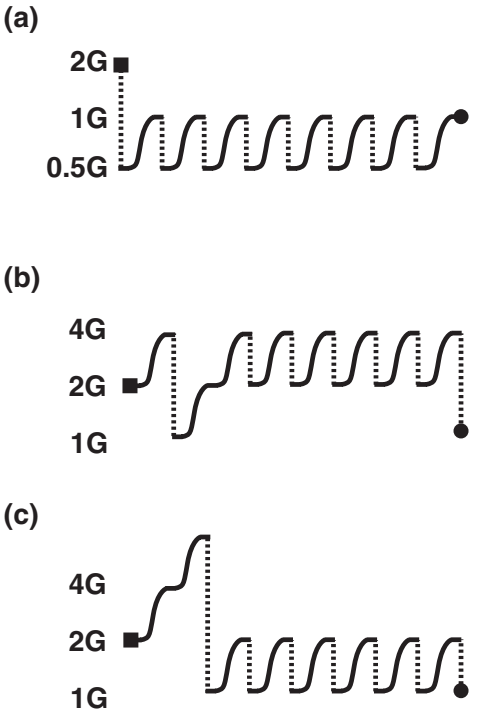

FIG. 2. Unusual life cycles reported in charophyte algae. (a) In *Spirogyra*, DNA replication and synapsis occur before fusion of gametic nuclei. Syngamy is directly followed by zygotic meiosis. (b) In *Closterium ehrenbergii*, DNA replicates after syngamy, followed by zygotic meiosis. Meiotic products quadruple their DNA content before the first vegetative division. Gametes are produced by a second round of ''meiosis.'' (c) In *Coleochaete scutata*, DNA content is increased 4-fold after syngamy, followed by a series of nuclear divisions without DNA replication.

pole at second anaphase. However, Tröndle described a different meiotic sequence in *Spirogyra calospora* (with similar observations in *Spirogyra longata*). In *Sp. calospora*, 18 chromatic bodies moved to each pole at the first division, but nine bodies moved to each pole at the second division. Moreover, bivalents were not evident at the first division. These observations seem to imply that pairing of homologs occurred after the first division. Unfortunately, Tröndle did not report observations of synapsis in this intriguing species. Karsten (1908) reported the ''conventional'' sequence of synapsis after karyogamy followed by reduction in chromosome number at the first division of the zygotic nucleus of *Spirogyra jugalis*.

Hoshaw et al. (1985) observed spontaneous decreases of ploidy in clonal cultures of *Spirogyra singularis*. Nuclei of filaments initially contained 24 chromosomes, but narrower filaments, with nuclei containing 12 chromosomes, spontaneously appeared in culture. These filaments keyed out as a different species, *Spirogyra communis*. Narrow and broad filaments were sexually compatible and produced zygospores that germinated to produce intermediate-width progeny with 18 chromosomes, suggesting the formation of 18 bivalents during meiosis. The latter implies a haploid number of six (possibly three) rather than 12, and that the original filaments were at least diploid, possibly tetraploid or even octoploid. Filaments of different ploidy were found in a subsequent field sample (Wang et al. 1986), and similar vegetative changes in ploidy were observed in clonal cultures of *Spirogyra maxima* (Hoshaw et al. 1987). These observations suggest that some *Spirogyra* filaments may possess diploid (or higher-ploid) nuclei.

Zygotic meiosis has been the principal reason for identifying *Spirogyra* filaments as haploid. As Tröndle (1911) argued, if zygotes are diploid and divide by meiosis, then all other cells must be haploid. Tröndle did not recognize that his observation of synapsis in gametic nuclei undermined his implicit assumption that gametes must be haploid. Godward (1954) noted that the vegetative karyotypes of *Spirogyra* species could be arranged into homologous pairs and flirted with a hypothesis of diploid gametes, but her subsequent failure to observe quadrivalents during meiosis caused her to abandon this idea (Godward 1961). Quadrivalents, however, are not expected if synapsis occurs in diploid nuclei before they fuse to form tetraploid zygotes. Thus, Godward's rejection of vegetative diploidy was premature. Much remains to be discovered about the life cycles of *Spirogyra* and *Sirogonium*, but the case for haploidy (occurring at any stage in the life cycle of some species!) is weak.

Cl. ehrenbergii*:* Desmids have also been claimed to possess a haploid life cycle with the zygote as the only diploid cell. However, in the best-studied taxon, *Cl. ehrenbergii* (a complex of reproductively isolated but difficult to distinguish forms), a reduction in chromosome number, analogous to meiosis, has been reported to occur both before and after the union of gametes!

Two cell divisions intervene between the induction of sexual reproduction and the formation of gametes in *Cl. ehrenbergii* (Hogetsu and Yokoyama 1979), with the second division following the first without replication of DNA (Hamada 1987). In the process, nuclei undergo a 4-fold reduction in DNA content. I will call this process ''gametogenic meiosis'': a gametocyte (4G) divides to produce two pregametes (2G) that divide to produce four gametes (1G). The latter division occurs after pairing of pregametes of opposite mating type and generates a local cluster of four gametes. Nonsister gametes unite to produce twin zygospores (2G). After germination, each zygospore replicates its DNA (4G) and then undergoes two divisions without DNA replication to produce four 1G nuclei. I will call this process ''zygotic meiosis.'' The four products of zygotic meiosis are packaged into two binucleate cells that are released from the zygospore. One nucleus in each cell degenerates, and the surviving nucleus (1G) undergoes two rounds of DNA replication without cell or nuclear division (4G). The first vegetative cell division produces two daughter cells (2G) that replicate their DNA to restore the 4G level in preparation for the next vegetative division (Hamada et al. 1982, Kasai and Ichimura 1983, Hamada 1987). Thus, vegetative nuclei alternate between the 4G and 2G level of DNA (Fig. 2b).

Gametogenic and zygotic meiosis both involve two divisions without DNA replication in which DNA content is reduced from 4G to 1G. If gametic nuclei are 1C, then alleles can segregate during zygotic meiosis, but not during gametogenic meiosis (because 4G gametocytes are directly descended from a 1C product of zygotic meiosis). If, however, gametic nuclei are 2C or higher, then the products of zygotic meiosis may retain heterozygosity, allowing alleles to segregate during gametogenic, as well as zygotic, meiosis. The genetic ''logic'' of two rounds of meiosis is obscure.

The two gones that are released from a zygospore produce clones of opposite mating type. This observation is most easily explained if zygospores are diploid and gametes are haploid (Hamada et al. 1982, Kasai and Ichimura 1990). Other observations, however, argue for above-haploid levels of DNA in gametes of *Cl. ehrenbergii*. Kasai and Ichimura (1987) crossed a ''haploid'' line with a ''diploid'' line that arose from spontaneous chromosome doubling. All chromosomes in the resulting ''triploid'' zygospores ($3 \approx 300$) formed bivalents. Therefore, for each chromosome to have found a pairing partner, the number of genomes in the zygospore must have had two as well as three as a prime factor. If this reasoning is correct, normal gametes must be at least 2C and vegetative cells at least 8C after DNA replication

(because of the reduction from 4G to 1G during gametogenic meiosis). At present, there is no simple way to reconcile the diploid-like inheritance of mating type with the formation of regular bivalents in ''triploids.'' The very large number of chromosomes and large quantities of DNA per nucleus in many desmids are, at least, compatible with vegetative cells having polyploid nuclei (Kapraun 2007).

Desmids are diverse. Zygotic meiosis has been reported in several species (Kauffmann 1914, Potthoff 1927, Starr 1959, Kasai and Ichimura 1983), whereas gametogenic meiosis is reported in a single paper on *Cl. ehrenbergii*. Hamada (1987), however, cites unpublished data that gametogenic meiosis also occurs in *Netrium digitum*. If so, gametogenic meiosis may have been present in the last common ancestor of all desmids because the clade that includes *N. digitum* and *Cl. ehrenbergii* encompasses most, if not all, desmids (Hall et al. 2008). Confidence in the existence of chromosome reduction before syngamy would be enhanced by independent replication of Hamada's (1987) observations, including in other species.

Co. scutata: The multicellular phase of the *Coleochaete* life cycle is initiated when a zoospore settles on a suitable substrate and develops into a multicellular thallus. In asexual reproduction, individual cells of a thallus can differentiate into zoospores that disperse to establish new thalli. In sexual reproduction, zygospores are formed when ova attached to female thalli are fertilized by sperm released by male thalli. After a period of dormancy, the zygospore undergoes a series of divisions to produce up to 32 cells, enclosed within the zygospore wall. All of these cells are released in the form of zoospores that disperse to initiate new thalli (Lee 1989).

Allen (1905) observed differences in the compaction of chromosomes between the first and second divisions of *Co. scutata* zygospores and, on this basis, identified these divisions as meiosis I and meiosis II (to use modern terms). He observed ~34 chromosomes before the first division but did not count chromosomes in gametes or vegetative cells. As he inferred that chromosome reduction occurred in the first two divisions, Allen interpreted subsequent divisions within the zygospore as occurring at the haploid level, but he did not describe these divisions. Hopkins and McBride (1976) undertook a photometric analysis of DNA content in *Co. scutata* that challenges Allen's interpretation. Vegetative nuclei contained either the 1G or 2G amount of DNA (by reference to the 1G amount of sperm); however, zygotic nuclei were recorded with the 2G to 8G amount. These data are compatible with a 2G zygote undergoing two (perhaps more) rounds of DNA replication without cell division, followed by reduction to 1G over the course of three (perhaps more) divisions without DNA replication (Fig. 2c).

Chara *and* Nitella*:* Stoneworts produce flagellated sperm in antheridia and sessile eggs in oogonia. After a period of dormancy, the fertilized oogonium germinates to produce a ''proembryo,'' which gives rise to new upright plants. Meiosis has been reported to take place at three stages in the life cycle (Guerlesquin and Noor 1982).

Oehlkers (1916) described nuclear events during germination of oogonia of *Chara foetida*. He reported that the zygotic nucleus underwent two divisions followed by degeneration of three of the resulting nuclei, with the new plant developing from the surviving nucleus. Although he was unable to make confident counts of chromosomes at the first division, Oehlkers believed that a reduction in chromosome number took place. He observed 16 chromosomes in nuclei at telophase I and II, the same number that was observed at all other divisions. His paper was accompanied by a single schematic diagram.

Tuttle (1926) studied an unidentified species, resembling *Nitella*. The primary oocyte of the oogonium divided twice to produce a large egg and three polar bodies, the latter corresponding to the Wendungszellen or sterile oogonial cells of earlier authors. Tuttle's paper is accompanied by detailed drawings, one of which shows simultaneous anaphases of a primary oocyte, with 16 chromosomes going to each pole, and a nodal cell, with 32 chromosomes going to each pole. In the antheridium, meiosis produced a group of four cells that produced the spermatogenic filaments. Nuclei of these filaments had the haploid number of chromosomes, whereas nuclei of other cells in the antheridium had the diploid number.

Gonçalves da Cunha (1936, 1942) described chromosome reduction as occurring after germination of zygotes of *Chara vulgaris* var. *longibracteata*, at the transition from the proembryo to an upright multicellular stem. His low-resolution figures show more chromosomes in a dividing nucleus of the proembryo than are present at subsequent divisions (Gonçalves da Cunha 1942). Homology between the proembryo of *Chara* and the sporogonium of mosses had been proposed previously by Vines (1878).

The standard interpretation of stonewort life cycles is of haploid multicellular plants with zygotic meiosis. This interpretation is based on the observations of Oehlkers's (1916) and a failure to observe changes in chromosome number at other stages of the life cycle (Guerlesquin and Noor 1982). Nuclear events within the zygotes of stoneworts are difficult to observe because of abundant food reserves and the tough coat, and Oehlkers' incomplete descriptions are the only published observations of these divisions. Similarly, Gonçalves da Cunha's report of the diploid chromosome number in the proembryo is the only chromosome count that I have found at this stage of the life cycle. These reports are not strictly contradictory, because neither author observed the stage reported by the other.

Tuttle's observations are the most detailed of the three reports of meiosis but have been generally disbelieved (Guerlesquin and Noor 1982). An analogy between sterile oogonial cells and polar bodies was not new (Warming 1895, p. 67) but had been rejected because chromosome reduction was not observed during production of the single sterile cell in oogonia of *Chara* (Debski 1898, Götz 1899) and because the sterile cells are produced before, rather than after, fertilization (Lotsy 1909, p. 55; an argument that presupposes meiosis occurs in the zygote). Numerous authors have reported that a reduction in chromosome number does not occur during the formation of antheridia, apparently contradicting Tuttle's observations (Debski 1897, Karling 1926, Lindenbein 1927, Walther 1929, Gonçalves da Cunha 1942, Mendes 1944, Shen 1967).

Tuttle appears to have died early in 1926 (Anonymous 1926) without publishing the longer work in which he proposed to erect a new genus and species for his alga and without defending his interpretation against its critics. The observations of several researchers, working with other species, contradict various parts of Tuttle's scheme. Was he a victim of self-deception and artistic license, or did reduction occur at a different stage in his species than in other stoneworts so far studied? The identity of Tuttle's specimens remains a mystery, although tetrascutate antheridia (a character emphasized by Tuttle) have been reported in only six species of stoneworts (Mann and Raju 2002). Wood (1954, p. 67) describes a herbarium specimen of Tuttle's alga as ''identical in all critical respects'' to the octoscutate [!] *Nitella microcarpa*.

Compilations of chromosome numbers for stoneworts frequently show polyploid series (e.g., $n = 6$, 12, 18 among *Nitella* spp.; Williams and Tindall 1975). However, taxa with a polyploid origin are usually assumed to behave genetically as haploids and to possess gene pools that are isolated from gene pools of related taxa of different ploidy. Vegetative cells of stoneworts exhibit considerable flexibility in changes of nuclear ploidy: nuclei can reach high ploidy via endoreduplication (Kwiatkowska et al. 1990, Maszewski 1991), and nuclei of high ploidy can produce nuclear descendants of low ploidy via a series of divisions without DNA replication (Shen 1967). If similar flexibility exists in reproductive divisions, stonewort life cycles need not be constrained to operate at only two ploidy levels.

Summary. Charophyte algae are commonly believed to be vegetatively haploid with zygotic meiosis. Evidence in favor of this interpretation is thin, despite its wide acceptance. The conventional story is probably correct in so far as chromosome reduction occurs in zygotes, but the further inference that vegetative cells are haploid is based on a number of implicit assumptions that are challenged by published observations: gametes have been assumed to be haploid, an assumption that is challenged by observations of synapsis in gametic nuclei of *Sp. neglecta* (Tröndle 1911); meiocytes have been assumed to be diploid with reduction from 4C to 1C in two nuclear divisions, an assumption that is challenged by 8G nuclei in zygospores of *Co. scutata* (Hopkins and McBride 1976); and meiosis has been assumed to occur at only one stage in the life cycle, an assumption that is challenged by reduction from 4G to 1G before, as well as after, syngamy in *Cl. ehrenbergii* (Hamada 1987).

The evidence for each of these oddities is based on a small number of observations, often unreplicated and weakly supported by evidence, and should not be accepted uncritically. Although there are several reports of phenomena that do not fit neatly within the conventional scheme, these reports do not cohere to give a unitary, alternative account of charophyte life cycles. Rather, each life cycle appears to have its own idiosyncrasies.

My review has focused on the charophyte algae, but ''unconventional'' behaviors are reported in several other algal groups, even though these life cycles continue to be described with terminology that was developed for land plants. For example, gametophytes and tetrasporophytes of the red alga *Polysiphonia* are isomorphic apart from their reproductive cells. Both generations are formed from highly polyploid apical cells by a process of sequential ploidy reduction (i.e., a series of nuclear divisions without DNA replication; Goff and Coleman 1986). In *Gracilaria* and some other red algae, not only are gametophytes and tetrasporophytes isomorphic, but tetrasporangia, carpogonia, and spermatia may occur on the same plant (van der Meer and Todd 1977). Is there any value in describing one of the ''generations'' as haploid and the other as diploid? Why should the final two divisions within a tetrasporangium be described as meiotic while earlier divisions that also reduce DNA content are ''mitotic''? Could the occurrence of mixed-phase plants be explained by somatic segregation of sex factors as a result of sequential ploidy reduction in vegetative divisions (Haig 1993)? If somatic segregation produces a genetically heterogenous soma, could this explain why planetic nuclei are donated to nonsister cells via secondary pit connections (Goff and Coleman 1986)?

Farley (1982) has argued cogently that cytological observations are inherently ambiguous and compatible with multiple interpretations. In his historical account, consensus about the details of ''conventional'' meiosis was not achieved by improved cytology, but from the advent of Mendelian genetics, which allowed phenotypic markers of chromosome segments to be followed through a series of crosses. I suspect that the same will be true for understanding charophyte life cycles. The good news is that modern molecular markers should facilitate a new Mendelian genetics for those taxa whose life cycles can be completed in culture.

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