COLEOCHAETE AND THE ORIGIN OF SPOROPHYTES[1]

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- *Premise of the study:* Zygotes of *Coleochaete* are provisioned by the maternal thallus before undergoing 3–5 rounds of division to produce 8–32 zoospores. An understanding of the selective forces favoring postzygotic divisions would be relevant not only to the interpretation of *Coleochaete* life history but also to the origin of a multicellular diploid phase in embryophytes.
- *Methods:* Simple optimization models are developed of the number of zygotes per maternal thallus and number of zoospores per zygote.
- *Key results:* Zygotic mitosis is favored once zygotic size exceeds a threshold, but natural selection usually promotes investment in additional zygotes before zygotes reach this threshold. Factors that favor production of fewer, larger zygotes include multiple paternity, low fecundity, and accessory costs of zygote production. Such factors can result in zygotes exceeding the size at which zygotic mitosis becomes profitable.
- *Conclusions:* *Coleochaete* may possess large zygotes that undergo multiple fission because of accessory costs associated with matrotrophy, including costs of cortical cells and unfertilized oogonia. The unpredictability of fertilization on land is proposed to have increased accessory costs from unfertilized ova and, as a consequence, to have favored the production of larger zygotes that underwent postzygotic division to produce diploid sporophytes.

Key words: alternation of generations; *Coleochaete*; matrotrophy; size vs. number; sporophyte.

Many nineteenth-century botanists considered the multicellular "fruits" (zygospores) of *Coleochaete* to be analogous, perhaps even homologous, to the sporophytes of land plants. Supporters of both the homologous and the antithetic theories of the origin of sporophytes used the "fruit" as a model but disagreed about how it should be interpreted, whether as a modified asexual generation or as a novel interpolated structure (Haig, 2008). *Coleochaete* fell from favor in these debates after Allen (1905, 1906) concluded that the first two divisions of its zygote were heterotypic and homotypic (in modern parlance, meiosis I and II). Since then, the "fruit" has generally been interpreted as a haploid rather than diploid structure.

Interest in *Coleochaete* has revived with recognition that it belongs among the closest algal relatives of embryophytes (Ruhfel et al., 2014). The absence of a multicellular diploid phase in streptophyte algae is now considered strong support for the antithetic theory because it weakens the case for an ancestral isomorphic alternation of generations as envisioned in modern versions of the homologous theory (Blackwell, 2003; McManus and Qiu, 2008). Clearly, contemporary arguments about homologous versus antithetic alternation of generations bear only a tenuous relation to the morphological questions at the heart of the nineteenth-century debate (Haig, 2008). Although the "fruit" has lost favor as an analogue of sporophytes, matrotrophy has gained prominence as a feature shared by *Coleochaete* and embryophytes. *Coleochaete* zygotes increase in size and accumulate reserves after syngamy, which suggests that the haploid maternal parent transfers resources to the diploid product of fertilization (Graham and Wilcox, 1983, 2000).

Although the occurrence of zygotic meiosis in *Coleochaete* is generally accepted, evidence in support of this "common knowledge" is thin. Allen's (1905) conclusion that meiosis occurred in the zygote was based on differences in chromosome compaction between the first two divisions of zygospores, but Hopkins and McBride (1976) detected nuclei with eight times the unreplicated haploid quantity of DNA (8C) within germinating zygotes. A division sequence that reduces DNA levels from 8C to 1C corresponds to neither meiosis nor mitosis as conventionally understood (Haig, 2010).

Here, I present simple life-history models of the transition from a single-celled zygote to a multicelled "fruit." These models are agnostic about the precise nature of *Coleochaete*'s postzygotic divisions, whether meiotic, mitotic, or something else. Zygotes are assumed to develop attached to a multicellular maternal thallus. Therefore, developmental mechanisms required for postzygotic multicellularity are assumed already to be present and expressed in prezygotic parents (for a discussion of the origin of these mechanisms, see Niklas, 2014). Although my focus is on the evolution of the multicellular "fruit" of *Coleochaete*, implications for early stages in the evolution of the multicellular sporophytes of land plants will also be considered.

Size-versus-number trade-offs—Haploid parents will be called "moms" and "dads" to distinguish them from diploid

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mothers and fathers (Haig, 2013). Two size-versus-number trade-offs will be considered. The first is faced by moms: whether to produce a few large or many small zygotes. The second is faced by zygotic offspring: how many zoospores to produce from a zygote's reserves. These interrelated questions can be conceptualized as asking how should a mom allocate an amount Z among n zygotes each of which produces m zoospores.

Coleochaete filaments produce oogonia one at a time, whereas the postzygotic divisions involve successive bipartitions of the zygote cytoplasm without an increase in zygote size (multiple fission or palintomy; Umen, 2014). Therefore, the number of zygotes will be assumed to change by integral increments (n, $n + 1$, $n + 2$, …) but the number of zoospores per zygote by successive doublings (m, $2m$, $4m$, …). My models address a specific question: Under what conditions does natural selection favor a change from producing m to $2m$ zoospores per zygote. The fitness contribution of each zoospore will be represented by a function, $f(x)$, where x is a measure of the zoospore's nutrient reserves. Following Smith and Fretwell (1974), $f(x)$ is assumed to increase with x, subject to diminishing marginal returns, $f''(x) < 0 < f'(x)$, with some minimum positive value of x below which $f(x) = 0$. Maternal fitness is $mnf(x)$. Thus, zoospores are assumed to make independent contributions to maternal fitness determined by zoospore "size" x.

Let maternal investment consist solely of zoospore reserves. A mom that invests a total amount Z in zygote production invests $X = xm$ in each of $n = Z/X$ zygotes. Z is optimally distributed when each zygote receives $\hat{X} = m\hat{x}$, where $\hat{x}$ is the investment per zoospore at which marginal returns on investment equal average returns:

$$f'(\hat{x}) = \frac{f(\hat{x})}{\hat{x}}$$

When n is large, moms are predicted to respond to variation in Z by varying the number rather than the size of zygotes (Smith and Fretwell, 1974; Lloyd, 1987).

Under the assumption that $f''(x) < 0 < f'(x)$, there will be a critical investment x^* for which $f(x^*) = 2f(x^*/2)$. For a zygote of size X, higher fitness would be obtained by dividing X among m zoospores for $X < mx^*$, but by dividing X among $2m$ zoospores for $X > mx^*$. However, the optimal size of zoospores is less than this critical size, $\hat{x} < x^*$ (Fig. 1). If moms always produced zygotes of size $\hat{X} = m\hat{x}$, then these zygotes would be smaller than the "size" at which an extra division becomes profitable.

Changes in Z and X are continuous, but changes in m and n occur by integral steps. At least one zoospore must receive more or less than $\hat{x}$ if Z is not a precise multiple of $\hat{X}$. Suppose that $n\hat{X} < Z < (n+1)\hat{X}$, where $Z = n\hat{X} + \Delta Z$. For ΔZ close to zero, Z is better distributed evenly among n zygotes, but for ΔZ above some critical value, Z is better distributed evenly among $n + 1$ zygotes. As ΔZ approaches this critical value, optimal zoospore size approaches x', then abruptly decreases to x'' as the mom switches from investing in n to $n + 1$ zygotes, where $nf(x') = (n + 1)f(x'')$. As n becomes large, x' and x'' converge on $\hat{x}$. Conversely, low fecundity (small n) favors greater variation in zygote size as Z fluctuates. The difference between x' and x'' is maximal for $n = 1$ when $x' = x^*$ and $x'' = x^*/2$. In the special case when $Z = X^* = mx^*$, three alternatives yield the maximum return on investment: (i) a single zygote that produces m zoospores of size x^*; (ii) two zygotes that each produce m zoospores of size $x^*/2$; or (iii) a single zygote that undergoes an extra division to produce $2m$ zoospores of size $x^*/2$.

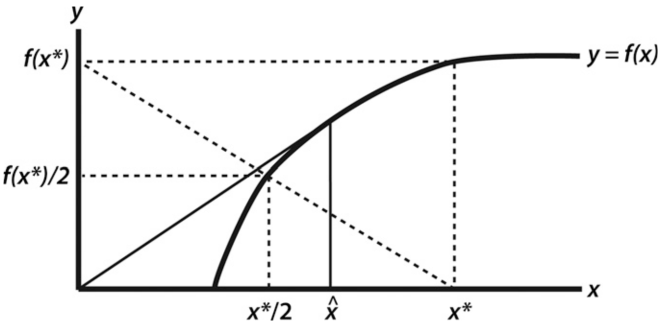

Fig. 1. Maternal resources are optimally allocated when each zoospore receives $\hat{x}$ which is less than x^*, the investment per zoospore at which $f(x^*) = 2f(x^*/2)$. Therefore, $\hat{x}$ is better left undivided because allocation of $\hat{x}$ to two zoospores each receiving $\hat{x}/2$ yields a lower return on investment than allocation of $\hat{x}$ to a single zoospore.

The above model predicts that adaptive adjustment of x will be achieved by changing n (number of zygotes) rather than m (number of zoospores per zygote) except when n is small. The addition of an extra postzygotic division involves an abrupt halving of zoospore size from x to $x/2$, whereas addition of an extra zygote involves a smaller decrease in zoospore size in the ratio $n + 1$ to n. Thus, for $n > 1$, zoospore number can be adjusted more smoothly by varying n rather than m. Control of m can be likened to adjusting the coarse focus on a microscope, and control of n to adjusting the fine focus. Under the assumption that zoospore size is already close to optimal, improvements are more likely to be made with the fine focus than with the coarse focus (Fisher, 1958:44).

Accessory costs—An accessory cost is a cost of offspring production that is paid independently of the provisioning cost. Accessory costs shift the optimal size-versus-number trade-off in the direction of fewer, larger offspring (Haig and Westoby, 1991). This is because increments in the provisioning cost per offspring are associated with smaller decrements in offspring number as the accessory cost per offspring increases. For example, materials invested in zygote walls and corticating cells would be considered accessory costs, as would costs of producing ova that remain unfertilized or zygotes that abort before being provisioned (Haig, 1990). In the context of the models of this paper, accessory costs may affect the probability of zygote survival before zoospores are released, but a zoospore's fitness once it is released is determined solely by the provisioning cost x.

Suppose that maternal fitness is proportional to $mnf(x)$ but that each zygote is associated with an accessory cost A such that the cost per zygote is $A + X$ and the cost per zoospore is $a + x$, where $m = A/a = X/x$. The model of the previous section corresponds to the special case where $A = 0$ and maternal investment consists solely of partible provisions X. In the more general model of this section, a mom invests $A + X$ in each of $n = Z/(A + X)$ zygotes, and the optimal zoospore size is

$$f'(\hat{x}) = \frac{f(\hat{x})}{a + \hat{x}}$$

An additional postzygotic division increases maternal fitness when $a > a^*$ where a^* is the accessory cost per zoospore at which $\hat{x} = x^*$ (Fig. 2). At a^*, a $2m$-zygote that produced $2m$ zoospores each of cost $(a^* + x^*)/2$ would yield the same return on investment as an m-zygote that produced m zoospores of cost $a^* + x^*$; but moms would increase their fitness by reallocating resources from m-zygotes to $2m$-zygotes because the latter provide a higher marginal rate of return, $f'(x^*/2) > f'(x^*)$. As a consequence, the optimal size of $2m$-zygotes is greater than the optimal size of m-zygotes. By contrast, the optimal size of zoospores from $2m$-zygotes ($\tilde{x}$) is smaller than the optimal size of zoospores from m-zygotes because

$$f'(\tilde{x}) = \frac{f(\tilde{x})}{a/2 + \tilde{x}}$$

(Fig. 2). Thus, a shift from m-zygotes to $2m$-zygotes is predicted to be associated with fewer, larger zygotes but with more numerous, smaller zoospores.

This model can be applied to each successive doubling of zoospores per zygote ($m = 4, 8, 16, \ldots$). For given Z, n (maternal fecundity) decreases as m (zygote fecundity) increases. An implication is that x (provisions per zoospore) becomes more variable for variable small Z. For given $f(x)$, each additional division requires twice the accessory cost and provisioning cost per zygote to favor the next division. Because the critical accessory cost per zygote that is necessary to favor another division doubles for each extra division, selection to minimize accessory costs may place an upper bound on the number of zoospores per zygote.

What about sex?—All zygotes inherit a mom's entire haploid genome (maternal relatedness $r_m = 1$). Therefore, optimal allocations are identical for moms and for maternal genomes of zygotes. Previous sections view the allocation of resources from this haploid maternal perspective, but intergenerational and intragenomic conflicts can arise because zygotes also have dads (Haig and Wilczek, 2006).

Paternal relatedness of a mom's zygotes, r_p, measures shared haploid paternity. Maternal and paternal genomes favor the same allocation of resources when all zygotes have the same dad ($r_m = r_p = 1$), but paternal genomes favor greater allocation to their own zygotes when zygotes have multiple dads ($r_p < 1$).

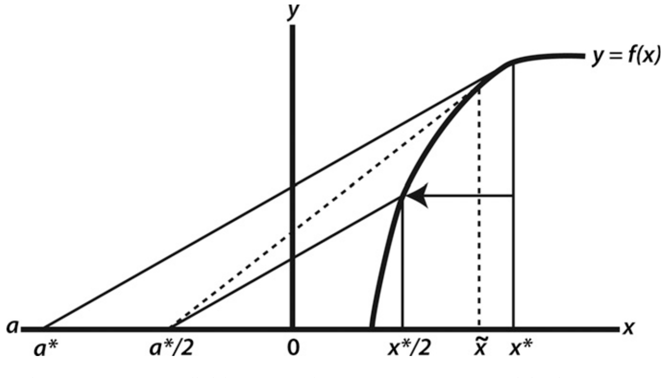

Fig. 2. A zygote divides to produce m zoospores. Provisioning costs per zoospore, x, are represented to the right of the origin and accessory costs per zoospore, a, to the left. The optimal value of x increases with a where a^* is the accessory cost per zygote at which $f(x^*) = 2f(x^*/2)$. At this critical size, equal fitness is obtained by dividing mx^* among m or $2m$ zoospores (leftward arrow). Accessory costs per zoospore are halved for $2m$ zoospores with the new optimal level of provisioning $\tilde{x}$.

Maternal investment in zygotes fathered by other dads can be conceptualized as an increased accessory cost per zygote from the perspective of each zygote's paternally derived genes (Haig, 1992). The less the value of r_p, the greater the optimal size of a zygote from this paternal perspective.

If imprinted or unimprinted paternal genes influence the acquisition of reserves by zygotes, then paternal genes will favor greater acquisition than maternal genes. In the limit, when $r_p = 0$, paternal genes favor commitment of all maternal investment to their zygote. Thus maternal and paternal genes of zygotes are predicted to favor different levels of resource acquisition from mom. Despite this conflict over zygote size, maternal and paternal genomes agree on an extra division of the zygote whenever $x > x^*$.

Sexual reproduction generates novel genotypes. Svedelius (1927) proposed that postzygotic divisions confer an evolutionary advantage because a delay of meiosis "secures to the plant the possibility of bringing about numerous reduction divisions and thereby numerous character combinations." This argument is dubious. Consider a comparison between (i) a mom that produces n zygotes that produce $4n$ zoospores by meiosis versus (ii) a mom that produces a single zygote that divides to produce n sporocytes that divide by meiosis to produce $4n$ zoospores. If a single dad produced the sperm that fertilized every zygote, then the two scenarios are genetically equivalent because all zygotes in either scenario have the same dad and mom ($r_m = r_p = 1$), and possess identical diploid genotypes. However, if $r_p < 1$, then (i) results in multiple diploid genotypes and greater genetic variation among zoospores than (ii). Although an extra division doubles the number of recombinant haploid genotypes generated from a single zygote, it reduces the diversity of offspring of a haploid parent if the alternative is production of an extra zygote.

Greater diversity of a mom's offspring is achieved by producing zygotes with multiple dads than with a single dad. But from each dad's perspective, increased diversity of a mom's haploid partners reduces the number of his offspring but does not increase their genetic variability. If every zygote had a different dad, $r_p = 0$, then each dad would clearly favor maximizing maternal investment in his zygote at the expense of his rivals' zygotes. From a paternal perspective, the major advantage of scenario (ii) compared with scenario (i) is that maternal investment is not "wasted" on offspring of other dads.

Understanding Coleochaete—A key question about the life cycle of *Coleochaete* has now been identified. Why should maternal thalli produce 32 zoospores from a single large zygote when greater genetic diversity of offspring could be achieved by producing 32 zoospores from eight smaller zygotes? The models identified three factors that favor larger zygotes. First, larger accessory costs favor greater maternal investment per zygote. Second, the paternal complement of zygotic genomes evolves to take more than the maternal optimum. Third, low fecundity causes zygote size to fluctuate with available resources so that zygotes occasionally approach the size that favors an extra division.

The origin of matrotrophy was probably associated with increased accessory costs of zygote production. Neighboring maternal filaments envelop *Coleochaete* zygotes after fertilization to form a cortex that probably has protective and nutritive functions. Cortical cells of some species develop elaborate wall ingrowths that are believed to deliver nutrients to the expanding zygote (Graham and Wilcox, 1983, 2000). The cortex may comprise a substantial part of the cost per zygote. For example, *Coleochaete areolata* Entwisle and Skinner zygotes of 75 μm diameter are enclosed in "spermocarps" of 125 μm diameter (Entwisle and Skinner, 2001).

Provisioning of zygotes after fertilization, rather than provisioning of oogonia before fertilization, means that maternal resources can be reallocated from unfertilized to fertilized oogonia and creates opportunities for moms to abort low-quality zygotes. From a maternal perspective, costs of unfertilized oogonia and unprovisioned zygotes are accessory costs of the production of provisioned zygotes (Haig, 1990). Matrotrophy also allows the paternal genomes of zygotes to influence maternal investment in favor of larger zygotes (Haig and Wilczek, 2006). Finally, *Coleochaete* is less fecund than larger multicellular algae because it produces diminutive thalli with relatively large zygotes. *Coleochaete* should therefore be subject to greater fluctuation in optimal zygote size.

Cell growth without division followed by rapid division without growth is a feature of the life cycle of many green algae, known as "multiple fission" or "palintomy" (Bišová and Zachleder, 2014). Temporal separation of growth and cell division may allow favorable conditions for growth to be fully exploited without pauses for division (Cavalier-Smith, 1980). *Chlamydomonas* cells, for example, grow during the day but undergo multiple fission at night (Craigie and Cavalier-Smith, 1982). *Coleochaete* zygotes similarly grow to full size before entering dormancy then undergo multiple divisions without growth after exit from dormancy. Zygotic palintomy may have evolved in *Coleochaete* because time-out for cell divisions would reduce competitiveness in the scramble for maternal investment among the zygotic progeny of a single mom.

Variation within Coleochaete—Molecular divergence between *Coleochaete scutata* Bréb. and *C. irregularis* Pringsh. is similar to that between ginkgo and angiosperms (Delwiche et al., 2002). The genus *Coleochaete* thus encompasses comparable phylogenetic depth to the clade that includes all living seed plants and probably contains rich variation in reproductive biology and evolutionary ecology. Life-history variation within *Coleochaete* has been little studied. Therefore, this section will pose questions for future study.

Coleochaete zygotes function as perennating structures. They remain uninucleate and dormant through winter until spring and then undergo multiple fission before all cells are released as motile zoospores (Pringsheim, 1860). The release of 8, 16, or 32 zoospores (Lee, 1989) suggests a progression of three, four, or five rounds of division, but the process is probably not that regular. Oltmanns (1898) reported a variable number of divisions in *C. pulvinata* depending on zygote size, with some zygotes containing 24 cells because four cells had divided at the eight-cell stage and four had remained undivided.

Given the great age of the genus, one can ask why *Coleochaete* zygotes never produce four zoospores (two postzygotic divisions) or 64 zoospores (six postzygotic divisions). A possible explanation is that the limited variation in zoospore numbers is a consequence of developmental constraints. With respect to the minimum of eight zoospores, 8C nuclei have been observed in zygotes of *C. scutata* (Hopkins and McBride, 1976), and the single zygotic chloroplast of *C. pulvinata* divides three times to produce eight chloroplasts before the zygote accumulates food reserves and enters winter dormancy, but the zygotic nucleus does not divide until the spring, at which time three nuclear divisions associate each chloroplast with a nucleus (Oltmanns, 1898). If 8C zygotic nuclei are a conserved feature of *Coleochaete*, then zygotes would need to undergo a minimum of three divisions to produce 1C zoospores.

One might speculate that the maximum of 32 zoospores per zygote is also set by a developmental constraint, in this case arising from the increased difficulty of dividing larger reserve-filled zygotes. Although palintomic green algae typically produce 8–32 daughter cells per mother cell, the number of daughter cells per mother cell can be considerably larger in some taxa (Bišová and Zachleder, 2014). Thus, there is no absolute constraint on higher orders of palintomy. Moreover, if mechanical difficulties preclude the production of 64 zoospores by successive bipartitions of a large zygote, one might ask why zygotes do not divide first and then accumulate reserves as occurs in bryophytes. Palintomic development has evolved into nonpalintomic development (cell growth between divisions) multiple times in multicellular *Volvox* (Herron et al., 2010).

The maximum of five postygotic divisions in *Coleochaete* may be determined by a selective rather than a developmental constraint. In this scenario, additional divisions of larger zygotes would be developmentally possible but, beyond a certain size, higher maternal fitness is obtained by producing extra zygotes rather than larger zygotes. In the model of a previous section, each additional round of cell division required a doubling of the accessory (nonprovisioning) cost per zygote. Other things being equal, natural selection will tend to minimize accessory costs because the more resources committed to accessory costs the less remain for provisioning zoospores. Thus, selective constraints on the magnitude of accessory costs may shift size-versus-number trade-offs toward smaller, more numerous zygotes.

Coleochaete zygotes are surrounded by a cortex of maternal cells. Cortication of zygotes varies, among species, from complete enclosure to sparse overgrowth by a few nearby filaments (Delwiche et al., 2002). Complete enclosure implies larger accessory costs and is therefore predicted to be associated with larger zygotes with more postzygotic divisions; but, to my knowledge, whether zoospore numbers differ between fully corticated and sparsely corticated species has never been investigated.

Costs of unfertilized ova and aborted zygotes, and of waiting for fertilization, are accessory costs of zygote production. *Coleochaete scutata* is dioicous and produces many oogonia that abort without producing mature zygotes (Pringsheim, 1860; Wesley, 1930). Fertilization is likely to be less reliable, and accessory costs of failed reproduction greater, in dioicous species than in monoicous species. Therefore, dioicous species might be expected to produce fewer, larger zygotes than otherwise comparable monoicous species. *Coleochaete scutata* produces dormant vegetative cells known as "akinetes" (Davis, 1965). Therefore, these asexual propagules may perform some of the perennating functions of sexual zygospores. Akinetes could be considered insurance against sexual failure, with dioicous species predicted to invest more in akinetes than monoicous species.

Origin of sporophytes—Previous sections address the evolution of postzyotic divisions in *Coleochaete*. This final section considers selective factors in the origin of the multicellular sporophytes of land plants (for other recent discussions, see Niklas and Kutschera, 2010; Brown and Lemmon, 2011; Qiu et al., 2012). Embryophytes will be assumed to have evolved from an ancestor with zygotic meiosis and to have initially possessed dependent sporophytes provisioned by maternal gametophytes, as occurs in extant bryophytes.

The models of this paper were crafted to conform to the developmental pattern of *Coleochaete* in which the number of cells produced from a zygote is constrained to increase by successive powers of 2 ($m = 4, 8, 16, \ldots$). The size of *Coleochaete* zygotes and the number of subsequent divisions are possibly also constrained by a form of matrotrophy in which provisioning is complete before the zygote divides. As a result, the initial division of a *Coleochaete* zygote probably becomes increasingly cumbersome with increasing size. Both constraints are relaxed in the development of sporophytes.

Mitotic divisions of embryophyte zygotes commence before (rather than after) matrotrophy is complete. Therefore, a highly multicellular sporophyte can be produced without the early postzygotic divisions having to occur in reserve-filled cells of enormous size. The models presented here make no assumption about the timing of cell division in relation to provisioning and, thus, also apply to division of zygotes with the embryophyte pattern of provisioning. A more important difference from *Coleochaete* is the absence, in sporophytes, of the palintomic constraint of successive cell doublings. Cell numbers can therefore be adjusted less coarsely than by powers of 2. Nonetheless, I believe that my models have some value for thinking about the initial transition from zygotic meiosis to a few-celled embryo. I do not address the subsequent elaboration of sporophytes here.

Sporophytes of all living bryophytes differ from the multicellular "fruits" of *Coleochaete* in several important respects. Zygotes of *Coleochaete* contain up to 32 cells, every one of which becomes a zoospore, whereas even the simplest sporophyte contains many thousands of cells, including "sterile" cells that do not undergo meiosis and do not differentiate as spores. Moreover, the flagellated zoospores of *Coleochaete* are replaced in embryophytes by wind-dispersed meiospores, and the zygospore is replaced as the perennating phase by meiospores with sporopollenin-containing cell walls (Brown and Lemmon, 2011). If sporophytes had palintomic development like *Coleochaete* zygotes, then an enormous zygote would accumulate maximum reserves before its cytoplasm underwent n rounds of division to produce 2^n cells (in a manner akin to the division of the giant cell of *Acetabularia*: Koop, 1979), but embryophyte moms provision actively dividing sporophytes with much more flexible patterns of cell division.

Svedelius (1927) proposed that postzygotic mitosis of land plants conferred a great evolutionary advantage because a multicellular sporophyte allowed many gene combinations to be generated from a single fertilization (a hypothesis recently revived by McManus and Qiu, 2008; Qiu et al., 2012). However, this hypothesis confounds genetic variability with number of spores because Svedelius did not consider the alternative of producing multiple zygotes (von Wettstein, 1943). Greater genetic diversity of spores is achieved by provisioning n zygotes that produce $4n$ spores by zygotic meiosis than by provisioning a single sporophyte that produces $4n$ spores, because multiple zygotes can sample the allelic variation of multiple dads. Reduced genetic diversity of offspring is a cost of producing a sporophyte rather than multiple zygotes.

A venerable hypothesis posits that sporophytes evolved as a response to the rarity of fertilization on land, allowing many spores to be produced from a single zygote (e.g., Bower, 1890:362; Campbell, 1905:567; Searles, 1980). However, if opportunities for fertilization are rare, the production of multiple zygotes remains an effective alternative for producing many spores if these opportunities are predictable in advance. Moreover, the rarity of fertilization can be overstated. Monoicous mosses produce abundant sporophytes (Gemmell, 1950), as do female gametophytes of many dioicous mosses when male gametophytes occur within the range of sperm movement (Longton and Greene, 1969).

The models of this paper suggest that it was the unpredictability, not the rarity, of fertilization that favored zygotic amplification in embryophytes. If opportunities for fertilization are unpredictable and brief, then moms must produce archegonia without guarantee they will be fertilized. Suppose that suitable conditions occur erratically once every few months and that archegonia have limited longevity. A mom that produced several archegonia per month would "waste" more resources on unfertilized archegonia than a mom that produced one archegonium per month. Although the number of unfertilized archegonia per zygote is the same for both kinds of mom, the cost of unfertilized archegonia per spore is lower for the mom that produces fewer archegonia but amplifies zygotic products. Higher accessory costs from unfertilized archegonia favor a shift in maternal investment toward fewer, larger zygotes. If these costs were sufficiently great, then optimal zygote size may have exceeded the size at which extra postzygotic divisions became profitable.

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