

# Organismal duplication, inclusive fitness theory, and altruism: Understanding the evolution of endosperm and the angiosperm reproductive syndrome

(double fertilization/Gnetales)

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**ABSTRACT** For almost a century, events relating to the evolutionary origin of endosperm, a unique embryo-nourishing tissue that is essential to the reproductive process in flowering plants, have remained a mystery. Integration of recent advances in phylogenetic reconstruction, comparative reproductive biology, and genetic theory can be used to elucidate the evolutionary events and forces associated with the establishment of endosperm. Endosperm is shown to be derived from one of two embryos formed during a rudimentary process of “double fertilization” that evolved in the ancestors of angiosperms. Acquisition of embryo-nourishing behavior (with accompanying loss of individual fitness) by this supernumerary fertilization product was dependent upon compensatory gains in the inclusive fitness of related embryos. The result of the loss of individual fitness by one of the two original products of double fertilization was the establishment of endosperm, a highly modified embryo/organism that reproduces cryptically through behavior that enhances the fitness of its associated embryo within a seed. Finally, although triploid endosperm remains a synapomorphy of angiosperms, inclusive fitness analysis demonstrates that the embryo-nourishing properties of endosperm *initially* evolved in a diploid condition.

Angiosperms possess a suite of unique and defining (apomorphic) features associated with the process of sexual reproduction (1–6). Prominent among these is the formation of an embryo-nourishing “tissue,” endosperm, during the process of double fertilization. Double fertilization in flowering plants, in which one sperm fertilizes an egg, while a second sperm fuses with two nuclei of the female gametophyte, leads to the establishment of a zygote and an associated heterozygous and typically triploid endosperm. Through its role in the acquisition of nutrients from the maternal sporophyte and the subsequent contribution of these reserves to the developing embryo, endosperm serves as an essential link in the life cycle of flowering plants. Ultimately, endosperm is consumed entirely by its companion embryo.

In contrast to angiosperms, almost all nonflowering seed plants (conifers, cycads, *Ginkgo*, *Ephedra*) rely on the formation (from a haploid megaspore) of a large homozygous female gametophyte to nourish the young embryo within a seed, and this general pattern of seed development is plesiomorphic (“primitive”) among seed plants. Unlike endosperm, growth and provisioning of the embryo-nourishing female gametophyte by the maternal sporophyte in nonflowering seed plants occurs partially (conifers and Gnetales) or entirely (cycads and *Ginkgo*) in advance of fertilization (1).

Although considerable research has been directed toward developmental, physiological, and ecological aspects of en-

dosperm, relatively little effort has been made to circumscribe the specific evolutionary forces that led to the establishment of this distinctive reproductive feature of angiosperms. Recent advances in phylogenetic reconstruction (2–4) and comparative reproductive biology suggest that endosperm evolved from a genetically redundant embryo formed during a rudimentary process of double fertilization in the ancestors of angiosperms (5, 6). This paper will examine how loss of individual fitness by one of the two original products of double fertilization resulted in the establishment of endosperm, a highly modified embryo/organism that reproduces cryptically through behavior that enhances the fitness of its associated embryo within a seed. Finally, while triploid endosperm remains a synapomorphy of angiosperms, inclusive fitness analysis will be employed to determine when the triploid nature of endosperm was established relative to the acquisition of embryo-nourishing properties by the second fertilization product.

**Previous Hypotheses for the Evolution of Endosperm.** Over the course of the last century, diverse arguments have been advanced to account for the establishment of a triploid sexually produced endosperm in flowering plants, along with the developmental reduction and loss of embryo-nourishing function by the female gametophyte. Various workers have suggested that the developmental benefits of hybridity, heterosis, and triploidy have been critical to the achievement of higher rates of growth by endosperm *compared* with the female gametophytes of nonflowering seed plants (7–11). Accordingly, the evolution of a heterozygous and polyploid endosperm has been viewed as a response to trends in the reduction of the female gametophyte, the shift from preferential fertilization to postfertilization development of the embryo-nourishing tissue (9, 12), and a general reduction in the overall time required for reproduction among angiosperms and their ancestors (11).

Recently, it has been proposed that the evolution of a heterozygous and polyploid endosperm can be viewed as the outcome of (i) conflict between male and female parents over the investment of nutrients in the embryo-nourishing tissues of seeds of a single maternal sporophyte (“intersexual conflict”) and/or (ii) conflict among sibling embryos for resources from the maternal sporophyte (“kin conflict” or “parent–offspring conflict”) (1, 12–21). Both intersexual conflict and kin conflict hypotheses assume that the resources available for the production of seeds by a maternal sporophyte are limiting, and, as a consequence, a subset of embryos/seeds on a given plant will abort. Central to these ideas is the supposition that the relative “aggressiveness” of an embryo-nourishing tissue to procure nutrients on behalf of its own embryo can be affected by relative changes in the relatedness of the embryo-nourishing tissue to its own embryo, the maternal and paternal sporophytes, and other embryos and embryo-nourishing tissues on a single maternal sporophyte (11, 13, 14). Both theories predict that the evolution of a heterozygous endosperm should result in an embryo-nourishing tissue that, *in comparison to a female*

*gametophyte*, will more aggressively acquire nutrients on behalf of its associated embryo (12–21).

It is unquestionably true that endosperm may derive developmental benefits from its heterozygous and polyploid nature and that endosperm is genetically more similar to its associated embryo than is a female gametophyte. However, two critical shortcomings of hypotheses concerning the origin of endosperm have become apparent. First, previous analyses of the evolution of endosperm have been undertaken without explicit knowledge of the key evolutionary/historical events associated with the origin of the angiosperm reproductive syndrome (11). Second, these theories suggest that endosperm exhibits developmental and/or genetic properties “superior” to those of the embryo-nourishing female gametophyte of nonflowering seed plants. By extension, these “adaptive” qualities have often been invoked to explain the underlying forces responsible for the origin of endosperm. Unfortunately, comparative analysis of the embryo-nourishing processes in flowering and nonflowering seed plants cannot address the fundamental question of how the product of a second fertilization event *initially* acquired the developmental characteristics now associated with endosperm (11).

To evaluate the underlying forces associated with the evolution of the angiosperm reproductive syndrome, it is first necessary to account for the specific character transformations that resulted in the establishment of a triploid, sexually produced endosperm (11). This analysis must take into account not only the characteristics of the end products of evolutionary transformation (i.e., the reproductive syndrome of angiosperms) but also, most importantly, the key transitional features of the ancestors of flowering plants, in which endosperm evolved. Until very recently, however, the series of evolutionary events associated with the establishment of endosperm were unknown (5, 6, 22–25).

**Historical Analysis of the Evolution of Double Fertilization and Endosperm.** During the last 5 years, significant progress has been made toward the construction of an explicit historical hypothesis for the origin of double fertilization and endosperm. These advances have been predicated on the documentation of a rudimentary process of double fertilization in *Ephedra* (5, 6, 22), a nonflowering seed plant that is a basal member of the Gnetales, the closest living relatives of angiosperms (2–4). As a consequence of the critical phylogenetic position of the Gnetales (Fig. 1), character traits shared by

*Ephedra* and angiosperms represent potential evolutionary homologues (synapomorphies) inherited from a common pre-angiosperm ancestor.

In *Ephedra*, double fertilization produces two diploid nuclei within an egg cell: a “normal” zygote nucleus and a “supernumerary” zygote nucleus (6). Both fertilization products proceed to initiate embryos and an embryo derived from either fertilization event may mature to fill the seed (26). As is the case with basal seed plants (cycads, conifers, and *Ginkgo*), the large multicellular female gametophyte functions to nourish the developing embryos (6). In addition, the female gametophyte of *Ephedra* always produces two or more genetically identical eggs (a plesiomorphy of seed plants) (23). Thus, if sufficient pollen is received, multiple double fertilization events may occur within a single ovule, a phenomenon that will be referred to as “complex simple polyembryony” (multiple single, but not double, fertilizations of two or more eggs within a seed are common among nonflowering seed plants and are referred to as “simple polyembryony”). However, regardless of the number of embryos initiated within a single seed of *Ephedra* (or any nonflowering seed plant), only one embryo will develop to maturity; the rest will eventually abort.

Double fertilization events in basal angiosperms and *Ephedra* display several critical points of similarity. In angiosperms with a plesiomorphic monosporic embryo sac (*Polygonum* type), the two female nuclei with which the second sperm fuses are genetically identical to the egg nucleus. In *Ephedra*, the single female nucleus involved in the second fertilization event is also genetically identical to the egg nucleus (5, 6). In both groups of seed plants, the sperm involved in double fertilization are derived from a single pollen tube and are genetically identical (5, 6). Thus, although endosperm in basal angiosperms and the supernumerary zygote in *Ephedra* differ with respect to ploidy and developmental fate, the second fertilization product in each of these groups of seed plants is identical (at the level of alleles) to the zygote resulting from the first fertilization event.

Expression of a regular process of double fertilization in *Ephedra* is congruent with a concept that a rudimentary type of double fertilization evolved in a common ancestor of Gnetales and angiosperms and, hence, predates the origin of flowering plants (22). Moreover, the discovery that the second fertilization product in *Ephedra* produces supernumerary embryos indicates that in its original manifestation, double fertilization produced two diploid embryos (5, 6). These findings strongly support the hypothesis that endosperm represents a highly modified evolutionary derivative of an embryo (6, 27) and can no longer be considered a “tissue” in the classical sense of the term. Rather, endosperm must be seen as an evolutionary homologue of an embryo or, in other words, as an *organism*, a view first espoused by Sargent (27) and Thomas (28) at the turn of the century.

**Reproductive Features of the Common Ancestors of Angiosperms and Gnetales.** Based upon comparative analysis of the plesiomorphic features of reproduction in basal angiosperms and *Ephedra*, the following characteristics of fertilization and embryogeny are likely to have defined the common ancestors of these two clades (Fig. 2): (i) *A rudimentary process of double fertilization that involved the fusion of sperm from a single pollen tube with the egg nucleus and its sister nucleus.* The product of this second fertilization event was diploid and expressed the developmental program of an embryo. It is assumed that the supernumerary embryo in the common ancestors of angiosperms and Gnetales had positive fitness and could potentially germinate (as is the case in *Ephedra*). (ii) *A single female gametophyte within each seed that was monosporic in origin, contained two or more genetically identical eggs, and attained sufficient size to function in the nourishment of embryos.* This pattern of development is plesiomorphic and fundamentally similar to what is found among extant basal seed plants

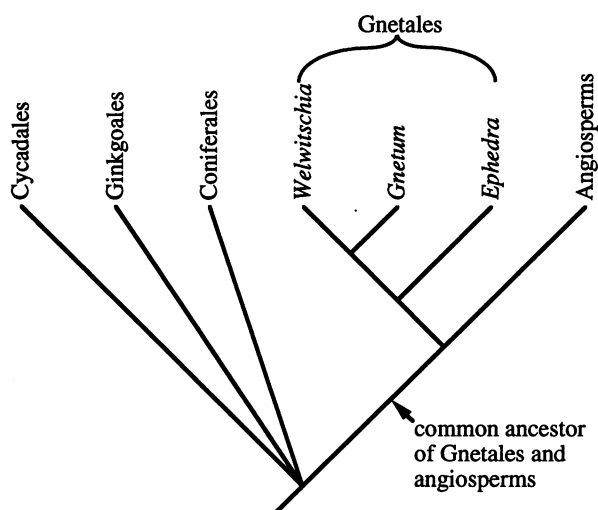


FIG. 1. Phylogeny of extant seed plants based upon recent molecular and morphological cladistic analyses (2–4). Gnetales is the most closely related taxon to angiosperms; cycads, conifers, and *Ginkgo* are less closely related and their interrelationships are currently unresolved.

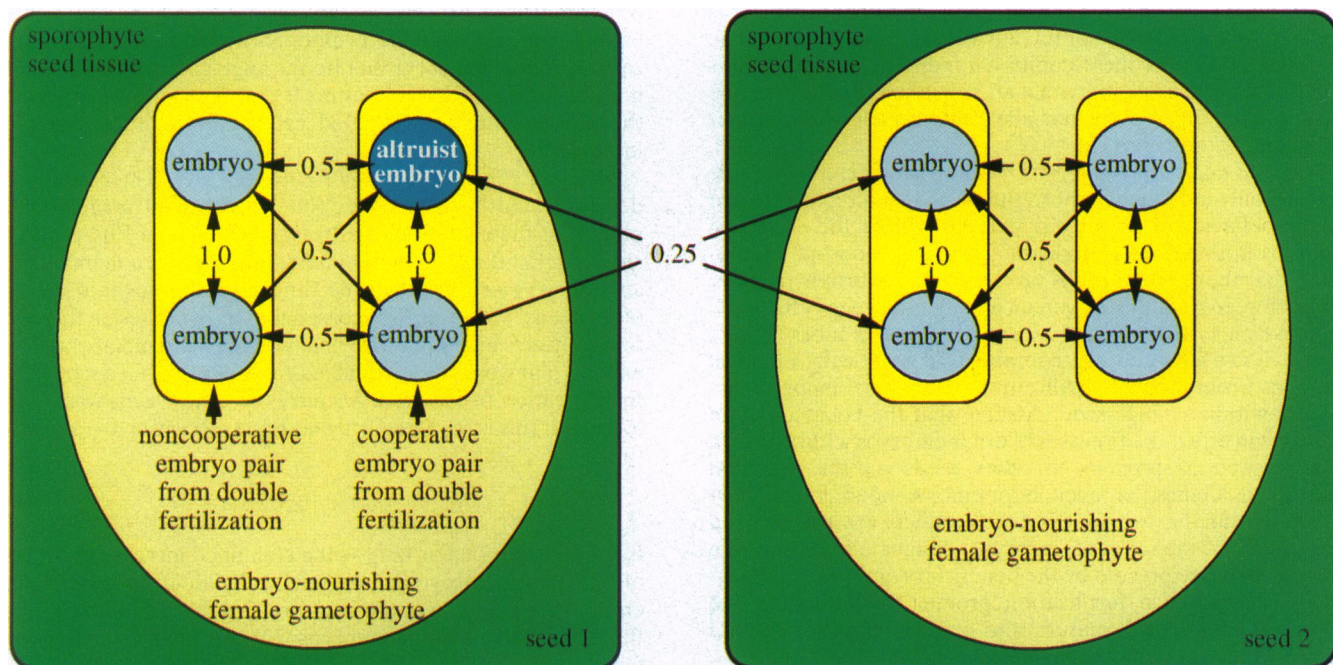


FIG. 2. Schematic of two seeds in the hypothesized ancestors of flowering plants in which a rudimentary process of double fertilization that yielded two genetically identical embryos ( $r = 1.0$ ) had been established. If more than one egg was double fertilized in a seed (complex simple polyembryony), embryos sired by different fathers shared half of their genes by descent. Embryos in different seeds on a maternal sporophyte shared only one-quarter (on average) of their genes by descent (assuming panmixis). Genes for altruistic behavior are present within the genomes of both members of a cooperative pair of embryos derived from a double fertilization event but are only expressed by one member of the embryo pair. The female gametophytes of these flowering plant ancestors participated in the nourishment of embryos and always produced two or more eggs. Only one embryo ultimately matured within each seed. Numbers in the figure refer to the coefficients of relatedness between embryos derived from double fertilization events on a single maternal sporophyte.

(cycads, conifers, *Ginkgo*) and *Ephedra*. (iii) *The potential for multiple double fertilization events within a single seed (complex simple polyembryony)*. Assuming sufficient pollen was received, each of the two or more eggs within a female gametophyte could have been (double) fertilized by different pollen tubes. (iv) *The developmental constraint that, although one or more pairs of embryos were initiated within a seed, only a single embryo fully matured in each seed*. The abortion of embryos in excess of one is a universal feature of seed development among nonflowering seed plants (flowering plants initiate only one embryo per seed). (v) *A unique set of genetic relationships among the progeny of a single maternal sporophyte*. Each member of a pair of embryos derived from a double fertilization event within a single egg cell was genetically identical (coefficient of relatedness,  $r = 1.0$ ). Assuming that pollen parents were unrelated, embryos formed in separate eggs within a single seed shared one-half of their genes by descent ( $r = 0.5$ ); embryos formed in different seeds on a single maternal sporophyte shared (on average) one-quarter of their genes by descent ( $r = 0.25$ ), since the female gametophyte of each seed is derived from a separate meiotic event.

The evolution of endosperm from an embryo (with an accompanying loss of individual fitness) mandates analysis within the constructs of inclusive fitness theory. In addition, the role of multiple double fertilization events within a single seed (complex simple polyembryony, a phenomenon not found among flowering plants) must be considered. Thus, the central question is under what conditions could potential development of an embryo (with subsequent production of progeny) have been sacrificed to a developmental program of altruism, determinate growth, and programed death, the three characteristics that ultimately define endosperm.

**Hypothesis for the Underlying Forces Responsible for the Evolution of Endosperm.** The evolutionary forces and events associated with the origin of endosperm can be characterized

as 3-fold and interrelated: (i) *organismal duplication*, in which the establishment of a rudimentary double fertilization process led to the regular formation of a supernumerary embryo that was genetically identical to (and redundant with) the normal embryo; (ii) *divergence of function*, in which aberrant development of one of the two fertilization products resulted in nourishing behavior to assist with the development of the normal embryo; (iii) *increased inclusive fitness through cooperative developmental behavior*, whereby genes that promoted nourishing behavior by one of the two fertilization products (with an associated loss of individual fitness) were selectively favored as a consequence of increases in the inclusive fitness of the altruist and beneficiary embryos.

In order for alleles for embryo-nourishing behavior to have been maintained within the gene pool, these genes had to have been carried by both of the products of double fertilization and, hence, inherited from genetically identical pairs of male or female gametes. However, expression of these genes must have been differential (as is currently the case with an embryo and its associated endosperm): while the supernumerary embryo displayed altruistic and aberrant patterns of development (along with a loss of individual fitness), development of the other embryo remained normal (Fig. 2).

General conclusions about the developmental and genetic forces associated with the evolution of endosperm can be developed most precisely within the constructs of inclusive fitness theory. This analysis depends on the basic principles first formulated by Hamilton (29), in which altruistic behavior (i.e., a loss of individual fitness associated with increased fitness of relatives) will be selectively favored when:

$$\Delta\omega_a + r_{a,b}\Delta\omega_b + \sum r_{a,i}\Delta\omega_i > 0, \quad [1]$$

where  $\Delta\omega_a$  is the change (loss) in fitness of the altruist,  $r_{a,b}$  is the coefficient of relatedness of the altruist to the beneficiary,  $\Delta\omega_b$  is the gain in fitness of the beneficiary,  $r_{a,i}$  is the relatedness

of the altruist to each additional individual whose fitness is affected by the behavior of the altruist, and  $\Delta\omega_i$  is the change in fitness of each of these additional individuals. Relatedness is defined as the probability that an individual (in this case, the altruist) contains a particular allele in common with another individual by descent (13).

*Interseed and intraseed effects model (general case).* Assume that the only individuals whose fitness can be directly affected by the behavior of an altruist embryo will be the cohort of embryos initiated on an individual maternal sporophyte. Assume that there are  $m$  seeds on a maternal sporophyte ( $m \geq 1$ ). Each seed contains  $e_m$  genetically identical egg cells ( $e_m \geq 2$ ), of which  $f_m$  are fertilized by unrelated pollen tubes ( $1 \leq f_m \leq e_m$ ). Each fertilized egg contains two genetically identical embryos from double fertilization. Only one embryo can mature within a single seed. Assume that the behavior of an altruist can affect the fitnesses of other embryos within its own seed as well as progeny in other seeds on the maternal sporophyte. Genes that encode for embryo-nourishing behavior by one of the two fertilization products are present and expressed by the altruist embryo (designated  $a$ ) and are present, but unexpressed by the beneficiary embryo (designated  $b$ ). Fitness of a fertilization product is defined as the probability that it will mature into a viable embryo within a seed.

Let  $\Delta\omega_a$  and  $\Delta\omega_b$  be the respective changes in fitness of an altruist and beneficiary embryo pair derived from double fertilization. Let  $\Sigma\Delta\omega_s$  equal the sum of the changes in fitness of all embryo pairs initiated in different eggs within the same seed as the altruist. Let  $\Sigma\Delta\omega_o$  equal the sum of the changes in fitness of all embryo pairs initiated within seeds other than that of the altruist. Coefficients of relatedness of an altruist embryo to embryos potentially affected by the behavior/development of the altruist are as follows: for the beneficiary embryo within the same egg  $r_{a,b} = 1.0$ , for embryos in different eggs within the same seed  $r_{a,s} = 0.5$ , and for embryos in other seeds on the maternal sporophyte  $r_{a,o} = 0.25$  (Fig. 2).

For loss of individual fitness (altruistic behavior) of an embryo to be selectively favored:

$$\Delta\omega_a + r_{a,b}\Delta\omega_b + \Sigma r_{a,s}\Delta\omega_s + \Sigma r_{a,o}\Delta\omega_o > 0. \quad [2]$$

$$(\Delta\omega_a + \Delta\omega_b) + (0.5)\Sigma\Delta\omega_s + (0.25)\Sigma\Delta\omega_o > 0. \quad [3]$$

Thus, the combined change in fitness of the genetically identical altruist and beneficiary embryos must exceed one-half of the total change in fitness of other embryos within the same seed ( $r_{a,s} = 0.5$ ) plus one-quarter of the total change in fitness of embryos within other seeds ( $r_{a,o} = 0.25$ ) on an individual maternal sporophyte. If these conditions are met, embryo altruism and cooperative behavior between products of double fertilization can evolve.

According to the constructs of this model, as alleles for altruism shift from rarity to a condition of fixation within a population, most embryo pairs (from double fertilization) will bear these genes and will no longer accrue selective advantage (i.e., fitness gains) relative to other embryo pairs on a maternal sporophyte. This, in turn, leads to a ratcheting effect: subsequent introduction (through random mutations) of new alleles for enhanced cooperative behavior between products of double fertilization, with eventual fixation within the population. Ultimately, continued selection for altruist/cooperative alleles is predicted to result in a second fertilization product with a fitness of zero.

Interestingly, Eq. 3 (as well as Eq. 4 below) clearly demonstrates that it cannot be determined which of the two original fertilization products (embryos) in the ancestors of flowering plants was subsequently modified into endosperm. It is entirely possible that the normal first fertilization product (that is homologous with the fertilization products and embryos of all

other nonflowering seed plants) was ultimately modified into endosperm; and that the evolutionarily novel second fertilization product has survived into the angiosperm lineage as the normal embryo. All that matters is that the inclusive fitness of the altruist and its associated genetically identical embryo increases.

*Intraseed effects only model (restricted case).* The conditions developed for the general case (interseed and intraseed effects model) of the evolution of altruistic behavior in Eqs. 3 and 4 are such that developmental interactions between members of an embryo pair can affect the fitness of embryos initiated in other seeds. However, it is reasonable to hypothesize that the fitness effects of cooperative behavior between members of an embryo pair were confined (at least initially) within a seed (i.e., the allocation of maternal resources to other seeds was unaffected). If this is so,  $\Sigma\Delta\omega_o = 0$  and Eq. 3 reduces to the simpler form:

$$(\Delta\omega_a + \Delta\omega_b) + (0.5)\Sigma\Delta\omega_s > 0. \quad [4]$$

Eq. 4 indicates that as long as the combined increase in fitness of the altruist embryo and its genetically identical beneficiary embryo is more than one-half as great as the combined loss in fitness of the remaining embryos within a seed, selection will favor the evolution of cooperative/altruistic behavior.

Under conditions in which cooperative behavior between members of an embryo pair is selectively favored, Eq. 4 clearly identifies a "protagonist." If alleles that encode for embryo altruism are present in the female gametophyte, all embryo pairs within a seed will inherit and express cooperative behavior, and intergenotype advantage between embryo pairs sired by unrelated paternal sporophytes does not obtain. In order for altruistic/cooperative genes to confer advantage, these genes *must* be borne by the male gametes from a pollen tube. Thus, "interpaternal competition," manifest through complex simple polyembryony, is revealed as a sufficient and potentially important force in the initial evolution of altruism and endosperm.

Finally, if cooperative behavior between products of double fertilization does not affect the fitness of embryos in other seeds (intraseed effects only model), embryo-nourishing behavior can evolve without modification of patterns of resource allocation by a maternal sporophyte to its constituent seeds (i.e., those that contain cooperative pairs of embryos vs. those that do not). Until now, altered resource allocation by the maternal sporophyte (in response to the establishment of a heterozygous embryo-nourishing tissue) has been viewed as a critical force behind the evolution of endosperm and is a central assumption of all previous kin selection models (11).

**Evolution of Triploidy.** For almost a century, the question of when triploidy evolved with respect to the second fertilization event and endosperm has remained a mystery (6, 14). However, one of the most profound consequences of the preceding integrated historical, developmental, and genetic analysis is the discovery that if endosperm evolved from an embryo with nonzero fitness (as postulated for the ancestors of angiosperms), embryo-nourishing behavior must have been established while the second fertilization product was still diploid.

A triploid fertilization product has (as a consequence of dysfunctional meiosis) an individual fitness of zero. Thus, the evolution of a triploid fertilization event (from a diploid condition) results in an immediate and total loss of fitness of this fertilization product that is equal to the original fitness of the diploid fertilization product:  $\Delta\omega_a = -\omega_a$ . Returning to Eq. 3 (interseed and intraseed effects model) and with substitution:

$$\Delta\omega_b + (0.5)\Sigma\Delta\omega_s + (0.25)\Sigma\Delta\omega_o > \omega_a. \quad [5]$$

If there are no effects of cooperative behavior on embryos in other seeds (intraseed effects only model),  $\Sigma\Delta\omega_o = 0$  and:

$$\Delta\omega_b + (0.5)\Sigma\Delta\omega_s > \omega_a. \quad [6]$$

Eqs. 5 and 6 clearly show that a nonreproductive triploid second fertilization product can only be selectively favored if the immediate and total loss of fitness by the second fertilization product is compensated for by equal or greater gains in the inclusive fitness of related embryos on an individual maternal sporophyte. This can only occur if the evolution of triploidy coincides *precisely* with the acquisition of embryo-nourishing (cooperative) behavior, an unlikely result, at best. Thus, triploidy can only evolve after the individual fitness of the second fertilization product approaches zero. In short, endosperm (in the physiological and behavioral sense) was initially diploid and the present triploid nature of endosperm (a synapomorphy of angiosperms) represents a later modification of the second fertilization event that is entirely unrelated to the initial acquisition of embryo-nourishing behavior.

**Evolutionary Reduction of the Female Gametophyte.** The evolution of a novel structure capable of assisting with the nourishment of its associated embryo is almost certain to have created an intermediate condition in which both a female gametophyte and a rudimentary endosperm participated in the nourishment of an embryo (6, 14). Although two embryo-nourishing systems may have functioned within individual seeds of the ancestors of flowering plants, developmental effects of polyploidy, heterozygosity, intersexual conflict, and kin conflict are likely to have resulted in enhanced embryo-nourishing properties for endosperm, in comparison with the female gametophyte. This, in turn, promoted the progressive and complete substitution of endosperm for the female gametophyte, with respect to provisioning of embryos.

It is critical to note, however, that hypotheses of purported endosperm "advantage," in comparison with a female gametophyte, can only account for the substitution of endosperm for the female gametophyte after the initial acquisition of embryo-nourishing (altruistic) behavior by the second fertilization product. They are not able to circumscribe the conditions under which embryo-nourishing behavior by a second fertilization product initially evolved (11, 13).

**Conclusions.** Integration of historical, developmental, and genetic data and theory clearly demonstrates that the origin of endosperm lies in the developmental modification of an embryo. This embryo was derived from a genetically redundant pattern of double fertilization (to produce two embryos) that evolved in the common ancestors of angiosperms and Gnetales. Acquisition of embryo-nourishing behavior (with accompanying loss of individual fitness) by one of the two fertilization products is shown to have been dependent upon gains in the inclusive fitness of this altruist embryo and its associated genetically identical beneficiary embryo. The end result of the loss of individual fitness by one of the two products of double fertilization was the establishment of endosperm, a highly modified embryo/organism that reproduces cryptically through behavior that enhances the fitness of its associated beneficiary embryo. Inclusive fitness analysis suggests that

either of the two embryos produced by a rudimentary process of double fertilization in the ancestors of angiosperms could have been modified into endosperm.

The question of the relative timing of the origin of triploid endosperm is also resolved: the embryo-nourishing properties of the second fertilization product initially evolved in a diploid condition. Addition of a second female nucleus to the second fertilization event, a synapomorphy of angiosperms, is unassociated with the initial acquisition of embryo-nourishing behavior by a rudimentary endosperm in the ancestors of flowering plants.

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