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Evolutionary Ecology of the Prezygotic Stage

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The life cycles of sexually reproducing animals and flowering plants begin with male and female gametes and their fusion to form a zygote. Selection at this earliest stage is crucial for offspring quality and raises similar evolutionary issues, yet zoology and botany use dissimilar approaches. There are striking parallels in the role of prezygotic competition for sexual selection on males, cryptic female choice, sexual conflict, and against selfish genetic elements and genetic incompatibility. In both groups, understanding the evolution of sex-specific and reproductive traits will require an appreciation of the effects of prezygotic competition on fitness.

Multicellular animals and flowering plants (angiosperms) spend most of their life cycle in the diploid state. This cycle, however, begins with a short haploid phase, which ends when male and female gametes form a zygote that develops into a new diploid individual (*1*). The brevity of the haploid phase contrasts with the huge number of "individuals" involved: sperm cells in animals and male gametophytes (pollen grains) in angiosperms. Large numbers of sperm and pollen increase the opportunity for selection on gametes [or gametophytes (*1*)] and for recombination of the segregated genetic contributions of the diploid parents. Selection at this stage, reinforced by adaptive-choice mechanisms and promiscuity of the parent generation, may increase offspring quality and contribute to the evolutionary success of both clades.

Competition between males for access to females and their ova has shaped the haploid phase in animals and angiosperms (table S1). First, the fate of sperm and pollen depends on competition between males to father as many offspring as possible (*2–4*). Second, sperm and pollen face female responses to male competitive strategies. These responses can allow females to influence paternity, so as to increase offspring number, genetic diversity, and quality (*5*). This includes mechanisms aimed at maintaining heterozygosity and at avoiding inbreeding, genetic incompatibility (*6*), and selfish genes (genetic elements that enhance their own transmission). Third, selection on males to increase fertilizing ability and on females to influence paternity may produce an evolutionary conflict leading to the evolution of manipulative and resistance traits of males and females. Fourth, sperm and pollen traits are affected by their mode of dispersal.

Despite the evolutionary importance of these processes in both plants and animals, botanists and zoologists do not share common theory nor collect directly comparable data. A unified approach (table S1) would yield better interpretations and speed progress toward a general understanding of the importance of the prezygotic phase for lifetime fitness. We synthesize recent findings from both groups, explore similarities and differences, and pose questions that can be transferred from animals to plants, and vice versa.

Male Competitive Ability

In animals and angiosperms, male-male competition selects for male traits that increase fertilization success. These traits can be expressed at the level of the male, its ejaculate, and its gametes or gametophytes [sperm or pollen (*1*)]. In angiosperms and internally fertilizing animals, after sperm transfer or pollen deposition, competition for fertilizations among males occurs among their sperm or pollen within the female reproductive tract (Figs. 1 and 2).

The use of genetic markers has shown that females of many animal species under natural conditions copulate with more than one male (*5*). This allows male-male competition to continue via sperm. In angiosperms, pollen competition occurs when pollen received by a pistil exceeds the number of egg cells (*3*, *4*). Pollen competition can occur at the level of flowers, even if at the whole-plant level there is pollen limitation (*7*). In outbreeding plants, genetic analyses have shown that seeds in a single fruit can result from pollination by several donors (*8*, *9*). Questions common to both clades are whether and how males can maximize their competitive ability by influencing the behavior of sperm or export of pollen, and to what extent male-male competition affects traits of male gametes.

Competition can occur between sperm from different males or among a single male's sperm (*10*). Although ejaculates are genetically heterogeneous as a result of meiosis, haploid gene expression in sperm, which may make some individual sperm cells more competitive than others, appears to be limited (*11*). In contrast, the haploid genotypes of pollen are expressed during growth toward the ovule, making pollen competition likely to occur both among different donor plants and among the pollen grains of a single donor. This leads to responses in both gametophytes and their diploid parents.

In animals, expression of sperm genes may be suppressed to favor competitive strategies at the level of the male, thereby granting the male control over sperm or ejaculate traits and avoiding expression of selfish genetic elements that may reduce the number of viable sperm transferred by a male. For instance, sperm carrying a meiotic drive allele increase their transmission rate by sabotaging gametes with alternative alleles. Therefore, fewer viable sperm are transferred in one ejaculate or spermatophore (*12*). This intragenomic conflict results in selection at the male level to suppress haploid gene expression in sperm because the number of viable sperm is important in competition against other males (*13*). Indeed, sperm development and growth occur mainly in the primary spermatocyte, that is, before meiosis and hence under diploid control (*11*). Nevertheless, in some cases sperm may "signal" their haplotype, thereby affecting their fertilization success (*14–16*).

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Haploid gene expression is common in plant gametophytes (*17*, *18*). For example, in *Arabidopsis thaliana*, on a chip of ~8200 genes, 1584 genes were expressed in pollen (*19*). In angiosperms, male-male competition may not have led to the evolution of suppression of haploid gene expression because transfer by wind or insects results in scattered, random distribution of pollen, and pollen loads are often mixtures from several donors (*12*). Also, haploid gene expression may be needed for pollen-tube growth through the style toward the ovules (*1*) (Fig. 2).

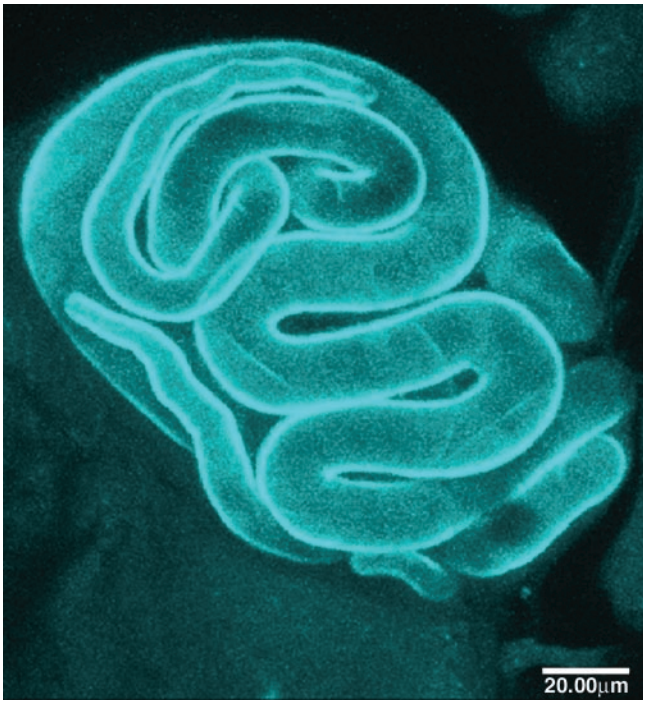

Fig. 1. Sperm storage organ in the red flour beetle *Tribolium castaneum* (micrograph: G. Bernasconi). Sperm storage before fertilization intensifies sperm competition.

If gametophytically expressed genes in plants affect the fitness of the offspring, as may be the case for genes affecting metabolic function, haploid expression may act as a quality advertisement, similar to ornamental traits of male animals. This results in selection acting on the gametophyte for traits also expressed in diploid offspring (*20*) or in sexual selection for gametophytic traits. In maize, specific alleles of ROP2 guanosine triphosphatase confer a competitive advantage to growing pollen tubes (*21*). However, pollen-tube growth rate can be influenced by both donor and pollen genes (*22*). Thus, in plants, selection can act at the level of both the diploid pollen donor and the haploid pollen grain.

The consequences of haploid gene expression in angiosperms are potentially far-reaching, especially for inbreeding. First, interactions of the haploid pollen with the diploid pistil regulate gametophytic self-incompatibility (*23*). Second, because of haploidy, even recessive deleterious mutations are purged from the gene pool when expressed in pollen. Mutation purging is intensified by pollen competition and by the very large pollen numbers (*24*–*27*). The extent to which pollen competition amplifies mutation purging could be tested experimentally by manipulating genetic composition (diversity, relatedness, presence of specific genes), genetic load, and size of pollen mixtures from different donors. Purging of mutations through haploid gene expression has also been suggested in haplodiploid insects (*28*).

In most animal and plant species, individuals produce only one type of sperm or pollen. However, both clades include heteromorphic species, where individuals produce more than one type of sperm or pollen. Heteromorphism was long considered a developmental abnormality until research on postmating, prefertilization male-male competition suggested that heteromorphism may increase the competitive ability of the ejaculate or pollen load (*29*, *30*).

In animals with sperm heteromorphism, sperm types differ in morphology and genetic content. As a rule, one type is fertile (eusperm) and the other sterile, not contributing genetically to fertilization (parasperm). Possible selective advantages include parasperm helping to transport eusperm, displacing rival sperm (*29*), or serving as a target for a female's immune response, thereby protecting the fertilizing sperm. These hypotheses interpret parasperm as an altruistic caste, which increases the chances of fertilization of one ejaculate against unrelated ejaculates (*31*). Parasperm could also signal male quality during cryptic female choice (see below). As we learn more about the interactions between ejaculate and the female reproductive tract, similar to pollen-pistil interactions known to occur in plants, we will be able to test these hypotheses.

In plants with pollen heteromorphism, pollen types differ in the number and position of apertures in the external wall through which pollen tubes germinate and grow toward the ovules. All pollen types are usually fertile. One exception is species with anther dimorphism [feeding versus pollinating anthers (*32*)], whereby sterile pollen of feeding anthers may be viewed as an altruistic pollen caste. More generally, pollen heteromorphism is related to within-male bet-hedging in response to unpredictable pollination conditions. In *Viola diversifolia*, pollen with few apertures has better survival rates, whereas pollen with more apertures germinates faster and is thus more competitive on young stigmas (*33*).

The functional differences of sperm and pollen heteromorphism are consistent with the differences in levels of selection identified above. Because gene expression is absent or limited in sperm, selection acts among males in animals. In angiosperms, selection on heteromorphism, on the optimal proportions of each type, and on their fertility acts both among and within pollen loads from different donor plants. It would be interesting to explore experimentally how the relative strengths of within- versus between-donor pollen competition affect the selective advantage of pollen heteromorphism (*30*).

Thus, selection for male ability to gain fertilizations acts not only on males but also on sperm and pollen traits. Pollen, unlike sperm, expresses many genes and may thus directly respond to selection for competitive ability.

Female Control of Paternity

Females may enhance offspring quality by promoting sperm or pollen competition (*2*–*5*, *34*). Costs arising from mating with multiple males or prolonged floral longevity (*35*) to favor multiple pollinations can be offset by the benefits of selecting among gametes and gametophytes. The elongated, morphologically and physiologically complex reproductive tract (Fig. 1) or pistil (Fig. 2) (*36*) thus provides an example of a selection arena (*37*) acting before fertilization. Selecting among gametes or gametophytes is likely to cause less costs to females than the elimination of zygotes or early embryos.

In many animals, females can influence the number and identity of their partners (*38*). In some species, the fate of sperm from rival males during and after copulation can depend on female behavior, complexity of female reproductive tract, or female genotype (*39*–*44*). The ability of females to control paternity after mating (cryptic female choice) (*5*) will, however, be opposed by male counteradaptations.

Plants have no direct control over the identity of their mates, but attractive floral displays, floral longevity, or rewards for pollinators can increase the chances to sample pollen from several donors (*3*, *4*, *27*). Pollen-tube growth rates and seed paternity can vary with identity of the recipient plant (*9*, *20*, *45*). In several species, the style actively provides nutrients for pollen-tube growth, thereby influencing pollen-tube development (*46*), and it is plausible that such maternal influence may be sensitive to the genotype of the male gamete (*20*, *21*, *47*). Finally, the female gametophyte may also affect the outcome of mating: In *A. thaliana*, female gametophyte genes control the release of sperm cells from the pollen tube (*48*, *49*).

Female cryptic choice can serve to avoid fertilizations from genetic relatives, including selfing in hermaphrodites. Many angiosperms possess mechanisms by which they avoid self-fertilization (*23*, *27*). The effectiveness of these mechanisms can depend on pollen competition: In some cases, incompatible self-pollen never fertilizes ovules in single-donor pollinations, but it achieves fertilization in mixtures containing compatible pollen (*9*, *50*). The elucidation of self-incompatibility systems is a long-standing concern of botanists. In contrast, attention has only recently focused on prezygotic incompatibility mechanisms in animals (*6*, *51*). Incompatibility, often postzygotic, can cause infertility and is generated by a variety of factors, including the immune system (*52*, *53*). Importantly, when incompatibility occurs, the effect of male genes on maternal fitness will vary with male and female genotypes (*5*). Multiple mating (polyandry) and cryptic choice may allow females to exploit postcopulatory mechanisms to reduce the cost of fertilization by incompatible sperm (*52*, *54*).

Polyandry may also defend against meiotic drive. Males that are heterozygous for a meiotic drive allele typically produce fewer functional sperm or pollen than do homozygous normal males. Thus, the transmission advantage is diminished when competition among the gametes or gametophytes of different males is intense (*12*, *55*). There are astonishing parallels between plants and animals with regard to polyandry as a defense against fertilization by drive allele–carrying sperm [e.g., (*56*)] and pollen (*55*). In these examples, XY meiotic drive occurs, and competition among sperm (pollen) reduces the success of the driving allele. From the female's perspective, selection should favor the avoidance of males carrying drive alleles, because drive-allele homozygosity often results in embryo death, sterility, or reduced fertility.

Pollen and sperm competition thus provide females with opportunities to be selective, thereby increasing offspring quality. This favors polyandry and the evolution of morphological and physiological mechanisms of cryptic female choice.

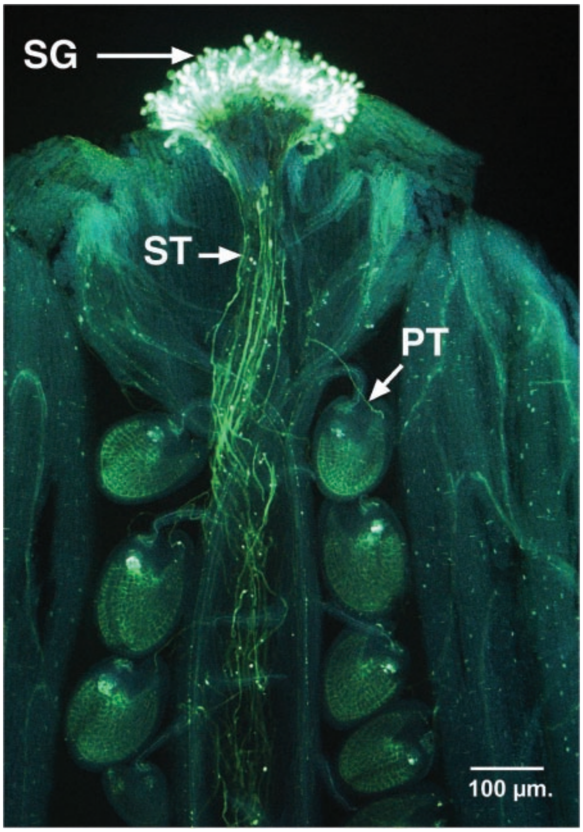

Fig. 2. Female reproductive tract in *A. thaliana* (micrograph: J. M. Escobar Restrepo). Pollen tubes (PT) germinate on the stigma (SG), grow through the style (ST), and deliver the sperm cells to the female gametophyte.

Evolutionary Conflict Between the Sexes

There is scope for conflict between levels of selection (diploid male versus haploid male gametes) and different players (male versus female). Diverging evolutionary optima between the sexes can arise under polyandry, when males and females maximize their fitness for different values of offspring paternity (the number of and skew among males fathering a seed-family or brood), rate of female remating, and postzygotic offspring provisioning. Sexual conflict over fertilization, for example, occurs when female fitness is maximized by producing progeny from different fathers as a form of bet-hedging, whereas each male is under selection to father all of the female's offspring. Conflicts between the sexes can lead to the evolution of manipulative and resistance traits. Manipulative traits are exemplified by seminal-fluid proteins in some internal fertilizers. For instance, seminal fluid products in *Drosophila* alter female reproductive physiology (increased egg laying) and behavior (reduced remating propensity) and thereby affect sperm competition success (*57*, *58*). These effects shorten female life-span, promoting antagonistic coevolution between the sexes (*59*). Consistent with sexual conflict, recent work has shown higher evolutionary rates for reproductive traits than for traits not directly associated with reproduction, and higher speciation rates in groups where females mate with many males than in related groups where females copulate with only one male (*60*). Accordingly, expression levels of genes that are male-specific vary more among populations than do levels of genes expressed in both sexes (*61*).

Sexual conflict, first proposed for animals (*59*, *62*), may also occur in plants, provided that gene expression can be sex-limited. Male and female gametophytes of angiosperms are sexually dimorphic. It is therefore possible that gametophytic traits with sex-limited gene expression convey antagonistic interactions either of pollen and embryo sac (*1*) or, especially in dioecious species, between pollen donor and recipient. Studies of sexual conflict in plants may thus provide a novel and general test of how, at reproduction, one sex is the environment for the other sex (*63*).

Mode of Gamete/Gametophyte Dispersal

Angiosperms and animals crucially differ in the relative strength of within- and between-male competition. This results from different modes of gamete dispersal. In both clades, however, there are groups with analogous gamete dispersal, that is, plants with animal-like mating and animals with plant-like mating (fig. S1). Mode of gamete dispersal, body architecture, and mating patterns of marine sessile forms dominating the fauna of hard surfaces (e.g., sponges, corals, bryozoans, and colonial ascidians) show stronger analogies with flowering plants than with most animals. First, the presence of multiple pistils per plant individual and modules per colony in sessile aquatic animals can lead to the accumulation of pollen (*8*, *9*) and passively disseminated, waterborne sperm (*64*) from different donors. High diversity of paternal genotypes may be beneficial when organisms cannot actively seek suitable environments or partners and gene flow only occurs via gametes and propagules (*27*). Second, as in plants, realized mating patterns of sessile animals are influenced by genetic-incompatibility systems (*23*, *51*, *65*). Third, in both groups there is the ability to trigger major female investment only after receipt of compatible pollen or sperm (*64*). Finally, plants and animals with plant-like mating are mostly obligatory hermaphrodites with flexible allocation of resources to gender, depending on mating history and environmental conditions (*64*, *66*). The accumulation of water-borne sperm during mating should relax the constraints on expression of the sperm haploid genome, and it is noteworthy that the best-characterized incompatibility mechanism in this group is apparently "gametophytic" (*65*).

In plants with animal-like mating (milkweed, most orchids), numerous pollen grains are transferred together in compound structures (pollinia). The opportunity for within-male competition to reduce between-male competitive ability is high within pollinia, similar to within-ejaculate competition in animals (*12*). For the same reason that haploid gene expression is limited in sperm, selection to maximize among-male competitive ability may favor suppression of pollen gene expression within pollinia (*12*). However, empirical tests are yet to be done.

These analogies suggest that reproductive traits evolve in concert with body architecture, mating system, and mode of gamete dispersal, rather than representing lineage effects peculiar to flowering plants and animals.

Conclusions

Prezygotic events in animals and flowering plants are subject to similar selective pressures, mediated mainly by sperm and pollen competition and cryptic female choice. These selective pressures are largely unaffected by organizational differences in the diploid phase, such as behavior in animals or modular growth in plants. Studies of plant and animal mating systems have traditionally focused on different mechanisms that produce nonrandom mating. In plants, attention has focused on incompatibility and inbreeding avoidance, whereas fewer studies have investigated differences in paternity achieved by compatible, unrelated donors (*8*, *9*, *27*). In contrast, zoology has focused on mechanisms of sperm competition (*5*, *10*, *34*). For most species, DNA profiling has established that females are promiscuous and that both sperm competition and cryptic female choice are important determinants of reproductive success. A general understanding of the benefits of female promiscuity in animals is, however, lacking (*2*, *5*).

Plant studies may move beyond the tradition of considering classes of mating (self/outcross) to investigate quantitative contributions of individuals via male and female function (*27*). Novel experimental designs may extend beyond the double-mating/pollination design, to include greater diversity of pollen donors (*67*). Questions that emerge include the influence of floral morphology and longevity, plant size, and clonal architecture on mating patterns and male success (*27*), and identifying functional analogs in animals. Since Darwin, floral traits have been known to represent adaptations both to attract pollinators and to promote outcrossing (*27*), yet we need to explore their role in promoting multiple paternity. In animals, postmating sexual selection has shaped male adaptations to obtain fertilizations (*2*, *34*) and female adaptations to bias paternity and resist male manipulations (*5*, *59*). In plants, genetic studies on seed paternity may better highlight the importance of postpollination selection on male and female traits (*8*, *9*). On the other hand, we need better understanding of the relevance of inbreeding avoidance, genetic incompatibility, and selfish genes to the evolution of polyandry in animals [e.g., (*68*)]. Bridging plant and animal studies would also benefit from extending mathematical models of prezygotic competition (*12*, *13*, *30*), cryptic female choice (*44*), and haploid gene expression across the two clades (*12*).

Applying the idea of sexual conflict to plants, in particular plant gametophytes with sex-specific gene expression, generates novel hypotheses. Genomics allows us to investigate changes induced in stigma and style by pollination, and in the female reproductive tract by mating, sperm, or seminal fluid. Some of these changes may unveil manipulative and resistance traits. For plants, we understand the mechanisms underlying male-female interactions that regulate self-incompatibility. Evidence for interactions between male and female genotype in determining paternity in compatible crosses in both clades calls for studying the physiological mechanisms involved (e.g., the nature of female receptors for seminal fluid proteins). Finally, the study of key groups of organisms within each clade indicates that the evolutionary consequences of gamete-dispersal systems on reproductive traits are not taxon-specific. A general synthesis of the evolutionary consequences of a short and prolific haploid phase and of the associated reproductive traits can emerge when we exploit the respective advantages of animals and plants to test theories that are of fundamental importance beyond taxonomic boundaries.

References and Notes

1. In both clades, the haploid generation starts with meiosis in the diploid parent. Animals: Gametes arising through meiosis do not divide further before fertilization. Only primordial germ cells that are set aside early during development undergo meiosis. Angiosperms: Stem cells produce leaves and shoots until they switch to reproduction. Meiosis is followed by mitotic divisions to yield male (pollen grain) and female (embryo sac) gametophytes. These produce the gametes. Both clades: The haploid sperm is transferred (usually directly in animals, via pollen in plants) from its diploid male parent to the haploid egg inside the female parent. Functional integration of paternal and maternal genomes in the offspring may continue after the zygote has been formed (e.g., imprinted genes controlling early embryonic growth, delayed expression of paternal genes).

2. T. R. Birkhead, A. P. Møller, Eds. *Sperm Competition and Sexual Selection* (Academic Press, San Diego, CA, 1998).
3. M. F. Willson, N. Burley, *Mate Choice in Plants: Tactics, Mechanisms, and Consequences* (Princeton Univ. Press, Princeton, NJ, 1983).
4. L. F. Delph, K. Havens, in *Sperm Competition and Sexual Selection*, T. R. Birkhead, A. P. Møller Eds. (Academic Press, San Diego, CA, 1998).
5. T. R. Birkhead, T. Pizzari, *Nature Rev. Genet.* **3**, 262 (2002).
6. J. A. Zeh, D. W. Zeh, *Proc. R. Soc. London Ser. B* **263**, 1711 (1996).
7. T.-L. Ashman *et al.*, in preparation.
8. A. A. Snow, P. O. Lewis, *Annu. Rev. Ecol. Syst.* **24**, 331 (1993).
9. G. Bernasconi, *Perspect. Plant Ecol. Evol. Syst.* **6**, 147 (2003).
10. G. A. Parker, *Biol. Rev. Cambridge Philos. Soc.* **45**, 525 (1970).
11. G. A. Parker, M. A. Begon, *Proc. R. Soc. London Ser. B* **253**, 255 (1993).
12. D. Haig, C. Bergström, *J. Evol. Biol.* **8**, 265 (1995).
13. G. A. Parker, *Proc. R. Soc. London Ser. B* **242**, 120 (1990).
14. D. Carré, C. Rouviere, C. Sardet, *Dev. Biol.* **147**, 381 (1991).
15. N. Schultz, F. K. Hamra, D. L. Garbers, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 12205 (2003).
16. C. Wedekind, *Philos. Trans. R. Soc. London Ser. B* **346**, 303 (1994).
17. D. R. Page, U. Grossniklaus, *Nature Rev. Genet.* **3**, 124 (2002).
18. D. Honys, D. Twell, *Plant Physiol.* **132**, 640 (2003).
19. J. D. Becker, L. C. Boavida, J. Carneiro, M. Haury, J. A. Feijó, *Plant Physiol.* **133**, 713 (2003).
20. I. Skogsmyr, Å. Lankinen, *Biol. Rev.* **77**, 537 (2002).
21. K. Arthur, Z. Vejlupkova, R. B. Meeley, J. E. Fowler, *Genetics* **165**, 2137 (2003).
22. A. G. Stephenson, S. E. Travers, J. I. Mena-Ali, J. A. Winsor, *Philos. Trans. R. Soc. London Ser. B* **358**, 1009 (2003).
23. J. B. Nasrallah, *Science* **296**, 305 (2002).
24. D. L. Mulcahy, *Science* **206**, 20 (1979).
25. J. P. Vielle-Calzada, R. Baskar, U. Grossniklaus, *Nature* **404**, 91 (2000).
26. V. Walbot, M. M. S. Evans, *Nature Rev. Genet.* **4**, 369 (2003).
27. S. C. H. Barrett, *Philos. Trans. R. Soc. London Ser. B* **358**, 991 (2003).
28. L. Keller, *Trends Ecol. Evol.* **10**, 355 (1995).
29. J. G. Swallow, G. S. Wilkinson, *Biol. Rev.* **77**, 153 (2002).
30. I. Till-Bottraud, D. L. Venable, I. Dajoz, P. H. Gouyon, *Am. Nat.* **144**, 395 (1994).
31. H. M. Moore, K. Dvorakova, N. Jenkins, W. Breed, *Nature* **418**, 174 (2002).
32. K. A. W. Bowers, *Am. J. Bot.* **62**, 633 (1975).
33. I. Dajoz, I. Till-Bottraud, P. H. Gouyon, *Science* **253**, 66 (1991).
34. G. A. Parker, in *Sperm Competition and Sexual Selection*, T. R. Birkhead, A. P. Møller, Eds. (Academic Press, San Diego, CA, 1998).
35. T.-L. Ashman, D. J. Schoen, *Nature* **371**, 788 (1994).
36. M. Herrero, J. I. Hormaza, *Sex. Plant Reprod.* **9**, 343 (1996).
37. S. C. Stearns, *The Evolution of Sex and Its Consequences* (Birkhäuser, Basel, 1987).
38. J. A. Zeh, S. D. Newcomer, D. W. Zeh, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 13732 (1998).
39. A. G. Clark, D. J. Begun, *Genetics* **149**, 1487 (1998).
40. N. Wilson, S. C. Tubman, P. E. Eady, G. W. Robertson, *Proc. R. Soc. London Ser. B* **264**, 1491 (1997).
41. M. Edvardsson, G. Arnqvist, *Proc. R. Soc. London Ser. B* **267**, 559 (2000).
42. B. Hellriegel, G. Bernasconi, *Anim. Behav.* **59**, 311 (2000).
43. P. I. Ward, *Evolution* **54**, 1680 (2000).
44. B. Hellriegel, P. I. Ward, *J. Theor. Biol.* **190**, 179 (1998).
45. D. L. Marshall, *Am. J. Bot.* **85**, 1389 (1998).
46. E. M. Lord, *J. Exp. Bot.* **54**, 47 (2003).
47. D. C. Queller, in *Sexual Selection: Testing the Alternatives*, J. W. Bradbury, M. Andersson Eds. (Wiley, Chichester, UK, 1987).
48. N. Huck, J. M. Moore, M. Federer, U. Grossniklaus, *Development* **130**, 2149 (2003).
49. N. Rotman *et al.*, *Curr. Biol.* **13**, 432 (2003).

50. R. I. Bertin, M. Sullivan, *Am. J. Bot.* **75**, 1140 (1988).
51. J. D. D. Bishop, *Proc. R. Soc. London Ser. B* **263**, 369 (1996).
52. T. Tregenza, N. Wedell, *Nature* **415**, 71 (2002).
53. J. A. Zeh, D. W. Zeh, *Anim. Behav.* **61**, 1051 (2001).
54. J. A. Zeh, D. W. Zeh, *Proc. R. Soc. London Ser. B* **264**, 69 (1997).
55. D. R. Taylor, M. Saur, E. Adams, *Evolution* **53**, 1028 (1999).
56. G. S. Wilkinson, C. L. Fry, *Proc. R. Soc. London Ser. B* **268**, 2559 (2001).
57. T. Chapman *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 9923 (2003).
58. H. Liu, E. Kubli, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 9929 (2003).
59. W. R. Rice, *Nature* **381**, 232 (1996).
60. G. Arnqvist, M. Edvardsson, U. Friberg, T. Nilsson *Proc. Natl. Acad. Sci. U.S.A.* **97**, 10460 (2000).
61. C. D. Meiklejohn, J. Parsch, J. M. Ranz, D. L. Hartl, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 9894 (2003).
62. T. Pizzari, R. R. Snook, *Evolution* **57**, 1223 (2003).
63. J. Wolf, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 4665 (2003).
64. R. N. Hughes, P. H. Manriquez, J. D. D. Bishop, *Proc. Natl. Acad. Sci. U.S.A.* **99**, 14884 (2002).
65. V. L. Scofield, J. M. Schlumpberger, L. A. West, I. L. Weissman, *Nature* **295**, 499 (1982).
66. R. N. Hughes, P. H. Manríquez, J. D. D. Bishop, M. T. Burrows, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 10326 (2003).
67. G. Bernasconi, M. Paschke, B. Schmid, *Oikos* **102**, 217 (2003).
68. K. Foerster, K. Delhey, A. Johnsen, J. T. Lifjeld, B. Kempenaers, *Nature* **425**, 714 (2003).

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Supporting Online Material

www.sciencemag.org/cgi/content/full/303/5660/971/DC1

Fig. S1

Table S1

Fig. S1 Plant-like mating in sessile aquatic animals, exemplified by a thecate hydroid in which the medusa stage is suppressed (broadly representing many sponges and corals, bryozoans and colonial ascidians). Passive external dissemination of sperm is followed by fertilization of retained eggs, brooding of embryos and dispersal of sexually produced propagules. *Italics*: equivalent stages in angiosperms.

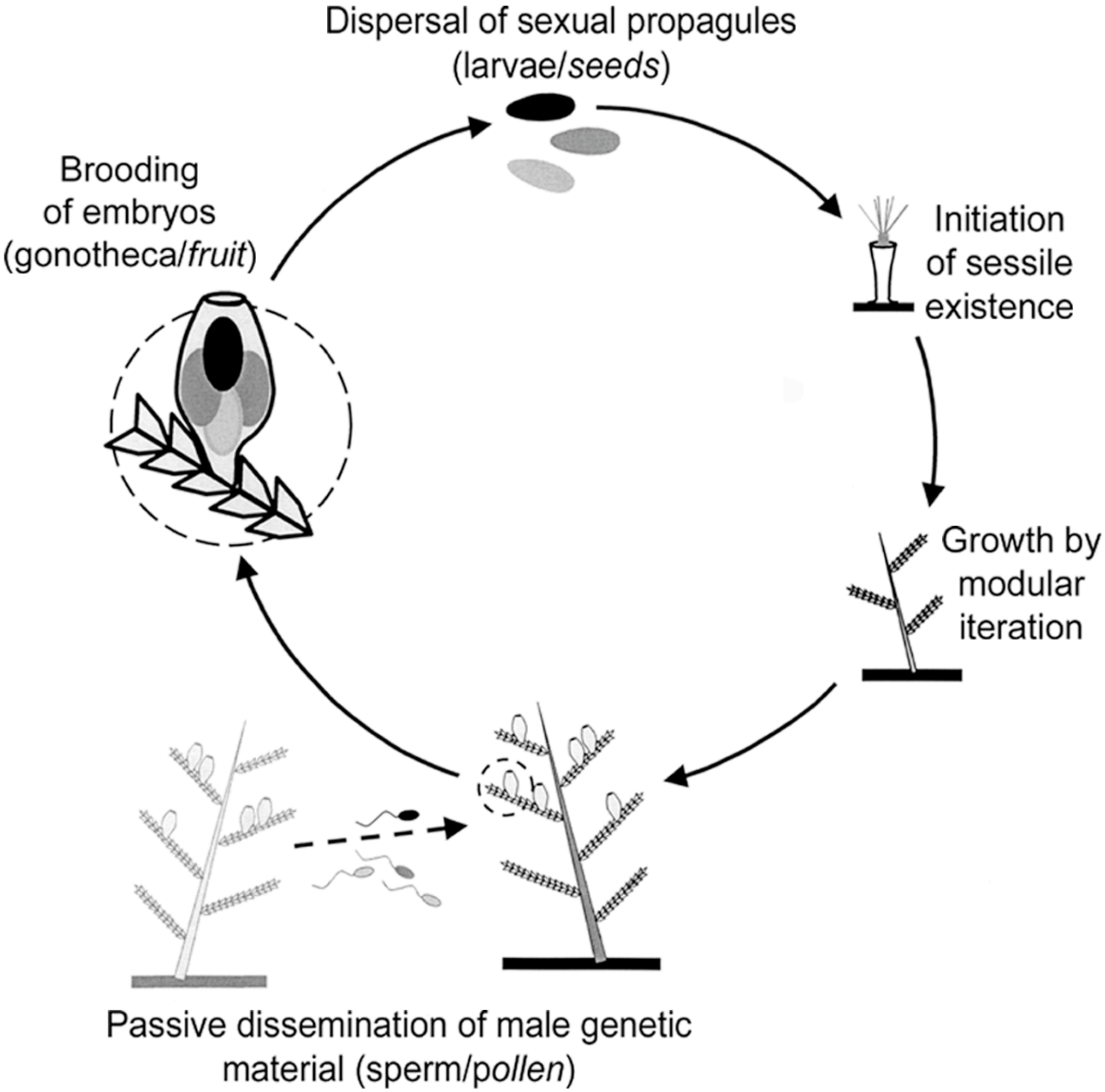
Dispersal of sexual propagules
(larvae/*seeds*)
Initiation
of sessile
existence
Growth by
modular
iteration
Passive dissemination of male genetic
material (sperm/p*ollen*)
Brooding
of embryos
(gonotheca/*fruit*)

Table S1. Significant processes of the pre-zygotic phase.

	Animals	Flowering plants	Fitness consequences	Evolutionary consequences
Male competitive ability	Sperm competition (SC): Selection acts on males, ejaculates and sperm. Haploid gene expression in sperm limited. Many data on paternity.	Pollen competition (PC): Selection acts on donor plants and pollen. Substantial haploid gene expression in pollen. PC intensifies mutation purging in the haploid phase. Few data on paternity.	Competition intensity affects male reproductive success, genetic diversity of progeny, and offspring quality if correlated with male competitive ability.	Evolution of SC mechanisms and traits enhancing male fertilization success.
Female control of paternity	Within female reproductive tracts differential sperm storage and use can result in female ability to bias paternity (cryptic female choice).	Mechanisms investigated for self-incompatible species. Few data on compatible crosses. Post-zygotic seed abortion important.	Choice mechanisms affect genetic diversity of progeny, enhance offspring quality, protect from inbreeding, selfish genes and genetic incompatibility.	Evolution of cryptic female choice and polyandry.
Sexual conflict	Polyandry can lead to different evolutionary optima of males and females for traits affecting paternity.	Conflict over paternity possible since gametophytes have separate sexes allowing for sex-specific trait expression	Manipulative male traits can evolve even if they lower female fitness.	Antagonistic coevolution between the sexes, with implications for speciation.

Mode of dispersal	Sperm usually transferred as ejaculates or in spermatophores (exception: sperm-casting aquatic animals). This creates the potential for within-male sperm competition.	Pollen grains are usually dispersed singly or in small groups (exception: pollinia). Thus, potential for within-male pollen competition to lower between-male competitive ability is lower than in animals.	Within-ejaculate competition could lower between-male competitive ability and this may explain why it is apparently suppressed in animals.	Equivalent modes of gamete dispersal favor similar traits.