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978-0-521-88095-4 - The Evolution of Anisogamy: A Fundamental Phenomenon
Underlying Sexual Selection

Edited by Tatsuya Togashi and Paul Alan Cox

Excerpt

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PAUL ALAN COX

Introduction: The evolutionary mystery of gamete dimorphism

We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements, instead of by a process of parthenogenesis.

Charles Darwin (1862)

The mystery which Darwin struggled with, the existence of sex in the plant and animal kingdoms, continues to fascinate biologists today. While many plant and animal species reproduce sexually, others continue to succeed with asexual reproduction.

Consider, for example, *Prorodon utahensis*, a small animal which flourishes in the hypersaline waters of the Great Salt Lake (Figure 0.1). There are few other forms of life that can tolerate these salinities, which have been measured at up to 27%. The quivering hair-like cilia of *Prorodon* provide its tiny body – scarcely the width of a human hair – with sufficient locomotion to zip about its otherwise lethal environment, consuming organic detritus, cyanobacteria and the salt-tolerant green alga *Dunaliella*. In the shallow waters of the Great Salt Lake, which are too salty for fish, these tiny *Prorodon* are the major hunters, the equivalent of sharks at the microscopic level. Reproduction in *Prorodon* is a simple matter – it simply splits in half. Without resorting to sexual recombination, *Prorodon* is able to lock in its genetic combination for survival and success in this most hostile of environments. Asexual reproduction also grants *Prorodon utahensis* a significant numerical advantage in progeny. A single individual splits, producing two, then four, then eight, then sixteen, then thirty-two genetically identical

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Figure 0.1 Differential interference contrast microphotograph of a drop of water from the Great Salt Lake containing the asexual ciliate *Prorodon utahensis* and the isogamous green alga *Dunaliella salina*.

offspring. This remorseless process of binary division can rapidly fill a small saline pond or even the Great Salt Lake with hundreds of millions of ciliates from a single immigrant. Were *Prorodon* to reproduce sexually, the number of offspring it produces would be halved, since in a population characterized by separate males and females, only half of the reproductive individuals can produce offspring. Biologically, in terms of population growth, males are of such little consequence that wildlife demographers sometimes simply ignore them. “Why do males exist?” is not a radical feminist slogan, but instead a valid and largely unanswered evolutionary mystery, a mystery which, at the level of female and male gametes, is the essence of this book.

The mystery of sexual dimorphism exists at a variety of modular levels (Cox, 1988), some of which are easily observable without a microscope. The fact that male date palms cannot produce dates, but contribute only pollen was of grave concern to ancient farmers. Stone images carved nearly 3000 years ago in the Assyrian city of Nimrud (about 30 kilometers southeast of present-day Mosul, Iraq) depict winged gods carrying pollen from the male trees of *Phoenix dactylifera* to the female trees. While the necessity of pollination for a successful crop was considered so important that deities were invoked as pollen vectors, the actual function of the pollen was poorly understood. In the third century BC, Theophrastus, a student of Plato, opined in *De Causis Plantarum* that female date palms require pollen as a needed dessicant, otherwise the developing fruit will mold and rot.

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A better understanding of the role of pollen in reproduction would require the invention of the microscope two millenia later.

The differential contributions of male and female date palms to one offspring are mirrored in the stunning difference in the number of gametes the two sexes produce. The large female gametes are produced by megaspores embedded in ovules in the carpels of the female flowers. After pollination, the female gametes develop into embryos, the ovules become seeds, and the carpel which surrounds them matures to become the fruit. Because date palms can survive harsh desert conditions, their fruits are regarded with reverence by the nomadic and pastoral people of the Middle East. In modern Oman, a cultivated female date palm annually produces about 4000 dates, with the total harvest from a single tree weighing a total of 40 kilograms. This seems to indicate a large number of female gametes – at least 4000 – to be produced by a single female tree. Yet a single male tree produces millions of pollen grains. Traditional wisdom holds that a “harem” of 50 female date trees – which would produce a total of 200 000 dates – can all be fertilized by the pollen from a single male tree. Since male to female sex ratios at inception in dates is 50:50, this means in traditional Omani orchards, 49 male trees can be culled or destroyed with no measurable loss of date production. We might safely assume that this disparity between male and female reproductive success was mirrored in natural *Phoenix dactylifera* populations prior to their cultivation by humans. The resultant variation in reproductive success is far greater among male trees than among female trees: given adequate pollination, nearly all female trees set fruit, but only a few males have a disproportionately high success in siring offspring. This essential difference in variability of male and female reproductive success drives sexual selection.

Although sexual selection does occur in plants (see Willson, 1994), the consequences of sexual selection in animals are perhaps more familiar. In Jackson Hole, Wyoming, where I write these words, the large elk herd which winters at the National Wildlife Refuge consists of thousands of adult females, but only several hundred reproductive adult males. During mating season, a few extremely large male elk, resplendent with large antlers, each defend a harem of 15 to 20 females with eerie whistle-like calls that pierce the crisp fall air. An alpha bull elk challenges any male aspirant to his harem leadership with snorting, aggressive displays and occasional violence. Head butting and locking of antlers are the major mode of combat. Lacerations, crippling injuries and sometimes death are outcomes of these battles. Usually

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the largest male with the largest rack of antlers is ascendent. As a result, although nearly all of the reproductive females in a population produce calves, only a few dominant males sire the next generation of the herd. The cost these male elk pay, for carrying about their large racks each fall, incurring risk of serious injury and even death from ongoing battles is large, yet sexual selection continues to maintain the production of massive displays of antlers.

These differences between male and female, so stunning in larger animals, also have a counterpart in the microscopic realm. Consider, for example, the different sizes of male and female gametes in higher plants and animals. In human beings, a typical sperm is 5 to 7 μm long, while the diameter of a receptive human ovum is 20 times greater. How did this vast difference in size arise?

In this book, the contributors focus on the phenomenon of different-sized male and female gametes, a condition known as anisogamy, which underlies all sexual selection. Why do nearly all animal and plant species have gametes of two different sizes, as opposed to producing gametes of a single size, a condition known as isogamy?

The evolution of anisogamy, one of the major evolutionary riddles to remain unsolved in the nineteenth and twentieth centuries, emerges into the twentieth-first century as potent a mystery as ever. The prevalence of anisogamy in the animal and plant kingdoms – with isogamy characterizing only a few algal species – is an astonishing testament of the evolutionary ascendancy of anisogamy as a robust evolutionary solution. Yet, I am reminded of Gertrude Stein's query to Alice B. Toklas as she was wheeled into surgery. "What is the answer?" Stein asked. Toklas responded, "In that case, what is the question?" To paraphrase, if anisogamy is the answer, what was the evolutionary question?

The earliest theories of gametes, emerging from the pre-Renaissance period, were focused on concatenation of future generations within an ovum, much like interlocking Russian matruska dolls. This pre-existence theory was articulated by Nicolas Malebranche in 1673:

We may with some sort of certainty affirm, that all trees lie in miniature in the cicatride of their seed . . . All the bodies of men and of beasts, which shall be born or produced till the end of the world, were possibly created from the beginning of it. (as quoted in Farley, 1982, p. 17)

This matruska-doll theory of the egg was later mirrored in a similar theory for sperm, which were discovered with the newly

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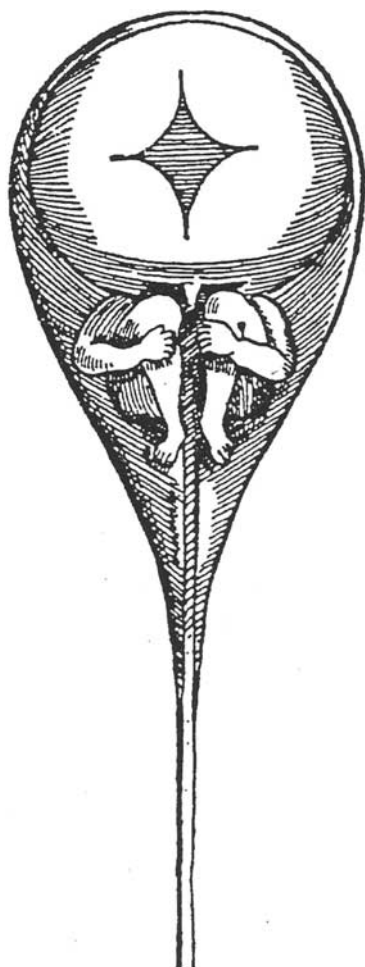
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Figure 0.2 1695 drawing of human homunculus in sperm

invented microscope by Antonie van Leeuwenhoek in 1679. Leeuwenhoek found that ejaculate of a male teems with countless “small animalcules.” Although some argued that these animalcules represented parasites within the male testes, it was not long until Nicolas Hartsoeker in 1694 and others argued that these “small animalcules” were in fact containers for entire preformed men (see Farley, 1982; Birkhead and Montgomerie, 2009). Referred “the homunculus” (Figure 0.2) this new theory suggested that each sperm enclosed a tiny human. These miniature human beings held within them homunculi for even smaller human beings, which in turn contained

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even smaller homunculi, generation after generation, until the very end of time.

While we may smile at the naiveté of the homunculus theory of gametes, surprisingly, the discovery of gamete fusion as the fundamental basis for sexual reproduction did not occur until the middle of the nineteenth century. In 1843, embryologist Martin Barry published his note entitled “On the penetration of spermatazoa into the interior of the ovum” based on his discovery of sperm inside the ova of rabbits. Barry’s finding triggered Geissen professor Theodor Ludwig Wilhelm von Bischoff in 1847 to propose a theory of sexual reproduction based on gamete fusion. In this theory, he bravely reversed his earlier 1842 claim that entry of sperm to an egg is “absolutely impossible.” “I do not hesitate however in declaring absolutely the opposite view, that only the dissolve part of the semen enter the egg” (as quoted in Farley, 1982, p. 56). The gamete contact theory of Barry and von Bischoff was highly controversial, resulting in a contentious scientific debate. It required 33 years for von Bischoff’s theory to gain traction, and it achieved acceptability only after the careful embryological studies of Oscar Hertwig, who discovered that fertilization of sea urchin eggs requires penetration of a sperm (Austin, 1961). Hertwig also was apparently the first investigator to propose that a division of labor between the sexes gives an advantage to gamete dimorphism:

In the first place, it is necessary for the nuclear substances of the two cells to become mixed, hence the cells must be able to find one another and unite. Secondly . . . it is equally important that there should be present, quite from the beginning, a sufficient quantity of developmental substance . . . In order to satisfy the first of these conditions, the cells must be motile, and hence active; in order to satisfy the second, they must collect these substances, and hence increase in size, and this of necessity interferes with their motility . . . Nature has solved the difficulty by dividing these properties – which cannot of necessity be united in one body, since they are opposed to one another . . . She has made one cell active and fertilizing, that is to say male, and the other passive and fertilizable, or female. (Hertwig, 1901, p. 278)

Botanists were a bit slower than zoologists to accept the theory of gamete contact as the basis for sexual reproduction. Like early Greek thinkers who believed that semen represented a type of seed, which when planted in a fertile field (e.g. a reproductive female) yielded offspring, mid-nineteenth century botanists such as Hermann Schacht

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argued that “the grain of pollen therefore is *not* the fecundating organ . . . *but the egg of the plant*” (Farley, 1982, p. 52). Even so great a botanical observer as Wilhelm Hofmeister claimed that entrance of the pollen tube into the egg is impossible. He instead subscribed to a type of catalytic theory suggesting that the egg is somehow stimulated into developing by the fluid from the pollen tube. Harvard botanist Asa Gray remained agnostic as to gamete contact as late as the sixth edition of his textbook: “Cross fertilization, or Allogamy [is] the action of the pollen of one flower on the pistil of some other flower of the same species” (Gray, 1879, p 216).

Soon, advances in phycology brought gametes, and particularly gamete dimorphism, to the attention of botanists throughout the world. Since algal species, unlike animals, show a variety of gamete types ranging from gametes of identical size (isogametes), to gametes of greatly different sizes (anisogamy), botanists were forced to recognize and explain these differences. The most influential botany textbook of the early twentieth century, that of Strasburger and his colleagues in Germany, suggested that these different forms of gametes represent a type of evolutionary progression:

Sexual reproduction is met within the vegetable kingdom in very different forms; the extremes are very distinct but are connected by many intermediate forms . . . In the lowest grade we find two completely similar motile cells (gametes); they are evidently to be phylogenetically derived from swarm-spores, but are distinguished from them by undergoing further development after fusion (certain Brown and Green Algae). At a slightly higher stage one of the two gametes is distinguished by its size and by losing the power of movement earlier than the other one; it is the female gamete, and when at rest is sought out and fertilized by the male gamete. At a further stage, this egg-cell has completely lost the power of movement. (Strasburger *et al.*, 1921)

With isogamy firmly relegated as an evolutionary relic, the rather vague botanical explanations for the evolution of gamete dimorphism focused on evolutionary progress and efficiency. This sense of isogamous algal species as atavisms which somehow evidence the progressive nature of evolutionary advance is exemplified by E. J. H. Corner in his discussion of seaweed reproduction:

The remarkable point about these slight differences in gamete behavior, however, is that there should still be plants of relative simplicity satisfied with what seem imperfect, as they are intermediate, steps in

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the evolution of reproduction by eggs, whereas most plants have long ago completed this lap of evolution's race. (Corner, 1964, p. 87)

Yet Corner, unlike other botanists, who were content to merely catalog the differences in gamete types, sought for some type of selective force to explain gamete dimorphism. He proposed what I have termed "the lost child in the woods model," a theory for the evolution of anisogamy based on what could be termed disruptive selection:

If two persons wish to find each other it is better for one to wait while the other searches. And if on meeting they must journey, it is better if she who waits should be provisioned while he that searches may travel light and fast. The principle of assignation was worked out long ago by gametes . . . Reproduction by eggs has arisen presumably through the selection and inheritance of variations that have helped both the mating of the gametes and the establishment of the zygote as a new plant. The variations have led to the breakdown of female mobility, but out of this has come better provision for the offspring. (Corner, 1964, p. 86)

This suggestion, that in Jack Sprat fashion, a division of labor between male and female gametes allows for efficient search and adequate provisioning of the zygote, is a theme that has been pursued by more recent authors. Lynn Margulis – inventor of the five kingdom system for classification of life – and her son Dorion Sagan argued, "As long as the equality of the parental nuclear contributions is maintained, division of labor leads to efficiency: one parent cell stores food and stays put and the other loses all its excess baggage and moves around" (Margulis and Sagan, 1986, p. 195).

More recent botany textbooks continue to extol this theme of efficiency gained by gamete dimorphism, via both increased fusions through enhanced male motility and increased fitness of the zygote which is largely provisioned by the female gamete.

With forms inhabiting moving water, isogamous reproduction must be extremely wasteful, and there are evident advantages if one gamete remains relatively stationary, especially if it secretes chemotactic pheromones causing the male gametes to accumulate around it. Moreover, a zygote which begins life with a copious food reserve has a better chance of survival than one with little. Increasing size, however, severely limits mobility, so again advantages can be envisaged in a situation in which one gamete, the male, remains small and motile, and the other, the female, loses motility and specializes in the laying down of food reserves. (Bell, 1992)

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This theme of efficiency of a division of labor between male gametes (motility) and female gametes (provisioning) captured the imagination of zoologists and theorists as well. In his elegantly argued book, Michael Ghiselin likened gamete production to a manufacturing enterprise:

Suppose that a manufacturer of heavy goods such as machine tools wanted to set up an effective program for both selling them and getting them to his customers. He might equip each salesman with a large truck piled high with machinery to be sold on the spot, and have them scout the countryside for customers. This arrangement would have certain advantages, such as immediate delivery, but at the same time a lot of energy would be wasted hauling the stock from place to place. It would be cheaper to use a heavy vehicle only for delivery, and to provide the salesmen with automobiles in which they could cover a far wider area on a given amount of fuel. Extending the analogy, we do not expect a manufacturer to mount his entire plant on wheels and produce goods on the road . . . So it is with sexual roles. Eggs differ from sperm because the female gametes specialize in providing the zygotes with energy and other resources. The male gametes are specialized for uniting the female ones. Any energy used by the females in moving about would necessarily be subtracted from that passed on to the zygotes. Hence the ideal female would be an absolutely passive organism. The male, on the other hand, should concentrate upon obtaining maximal dispersal from a given quantity of energy. (Ghiselin, 1974, pp. 101–102)

This general sense of isogamy as a primitive condition from which nearly all plants and animals have escaped driven by selection for division of labor between the sexes is appealing in a certain anthropomorphic sense. However, we might remember the anecdote attributed to the physicist Wolfgang Pauli, who when confronted with a laboriously written manuscript by a young physicist, exclaimed, “It is not even wrong” (Peierls, 1960).

Analysis of efficiencies gained due to gamete dimorphism are unlikely to yield a wrong answer, but this surely can’t be the whole story, otherwise isogamous species would have perished long ago. Given that small, stripped-down male gametes are indeed far more motile, and that zygotes can better be provisioned by large female gametes lacking flagella, we still must confront the continuing success of species of isogamous algae. Again, referring to Figure 0.1 of the ciliate *Prorodon utahensis* in the Great Salt Lake, which, at the beginning of this chapter, I argued benefits from asexuality, please note the small round organisms to the bottom right of the ciliate. These are the

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green algae *Dunaliella salina*, which can reproduce sexually and are isogamous in reproductive biology. *Dunaliella salina* is so prolific in the hypersaline northern arm of the Great Salt Lake that, together with the cyanobacterium *Aphanothece halophytica*, it turns the water red, a feature observable from outer space (Roney *et al.*, 2009). If asexuality is the correct answer to a hypersaline environment for *Prorodon*, it is hard to see why 10 to 20 billion or so *Dunaliella* continue to thrive in the Great Salt Lake using the wrong answer.

As a young botanist, I questioned the theories extolling the unparalleled advantages of anisogamy for the entire natural world, particularly since isogamous algae seem to proliferate in hypersaline environments, shallow ponds, and near-shore intertidal marine ecosystems. The interesting question, therefore, became in my mind not why anisogamy characterizes most higher plants and animals, but instead why do the relatively few isogamous species continue to thrive? Using simple numerical experiments, beginning with a programmable hand calculator I had with me during fieldwork in Samoa, and then moving to Harvard's mainframe computer (whose computing power today is doubtlessly eclipsed by an ordinary cell phone), I first tested Corner's "lost boy in the woods model" to see if immobility of one of the pair of gametes indeed increases gamete encounters and fusions. My simulations suggested that immobility of one partner does not increase frequency of encounter. Later exploring search theory, as developed for submarine warfare in World War II by Columbia University mathematician Bernard Koopman, I discovered that the probability of an encounter in three dimensions during a random search is not based solely on the velocity of the mobile gamete alone, but instead increases with the *sum of the velocities* of both gametes (Koopman, 1980).

Eliminating female immobility as an advantage for gamete encounter, I wondered if it is possible that a complex adaptive topography, of the type proposed by Sewall Wright (1977), might come into play. Is it possible that anisogamy represents a high-fitness Everest, while extant isogamous species are stranded on smaller fitness foothills, which they cannot reach without first descending through a fitness trough? Together with U.C. Berkeley mathematician James Sethian, I made numerical experiments on a supercomputer of random gamete encounters in three dimensions; Sethian then confirmed the results of these experiments with analytical solutions (Cox and Sethian, 1984; 1985).

Accepting the fact that small male gametes not only can move faster than large female gametes, but also that in the low Reynolds