
REVIEW

No universal differences between female and male eukaryotes: anisogamy and asymmetrical female meiosis

ROOT GORELICK^{1,2*}, JESSICA CARPINONE¹ and LINDSAY JACKSON DERRAUGH¹

¹*Department of Biology, Carleton University, 1125 Raven Road, Ottawa, Ontario, K1S 5B6, Canada*

²*School of Mathematics & Statistics and Institute of Interdisciplinary Studies, Carleton University, 1125 Raven Road, Ottawa, Ontario, K1S 5B6, Canada*

Received 14 May 2016; revised 30 June 2016; accepted for publication 1 July 2016

We previously showed that, across eukaryotes, universal differences do not exist between diploid females and males; hence, in the present study, we examine haploid stages. Unlike animal sperm, flowering plant sperm have nuclear pores, and so cannot be used to distinguish haploid females from males. Female and male gametes are not complementary: eggs and can fertilize eggs, whereas sperm can fertilize sperm, in some taxa. One sex of gametes is not universally parasitic on the other. Commonly held differences between eggs and sperm (e.g. only eggs, and not sperm, are large, long-lived, and immobile) do not apply to many eukaryotes. Many or all angiosperms have small eggs, sperm without flagella, and long-lived pollen. In many plants, we supposedly can distinguish females from males, although they have similar sized gametes. Theories of anisogamy are based on less energy being required to produce small sperm than large eggs. However any selective advantage of smaller sperm is nullified by sequestering most cytoplasmic biomass as residual bodies following meiosis in metazoa. Moreover, zoidogamous gymnosperms have numerous huge sperm. In both animals and plants, sperm are not the immediate products of meiosis but, instead, develop afterwards via haploid cell divisions. Consequently, we examined whether the most promising universal sexual difference in animals applies to plants and stramenopiles, namely asymmetrical female meiosis vs. symmetrical male meiosis. A few angiosperms (and some animals) have asymmetrical male meiosis, whereas many plants have symmetrical female meiosis. All bryophytes and stramenopiles with UV chromosomes do not have asymmetrical female meiosis insofar as meiosis produces two female and two male gametophytes. Homosporous monilophytes, lycophytes, and anthocerotophytes lack female vs. male meiosis, although they have distinct eggs and sperm. Therefore, currently, there are no universal criteria for distinguishing females from males across all animals, across all plants or across all stramenopiles, let alone across all eukaryotes. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2017, **120**, 1–21.

KEYWORDS: anisogamy – gender – meiosis – meiotic – polar bodies – polar nuclei – residual body – sex.

INTRODUCTION

Separate diploid sexes are not well-defined entities because of hermaphroditism and intersex. Diploid sexes are generally assumed to have evolved multiple times from hermaphroditic ancestors (Gorelick, 2003). Inexplicably, there has been a general assumption that diploid sex (i.e. femaleness vs. maleness) is determined at a single genetic locus (Wachtel

& Tiersch, 1994; Mittwoch, 2000). Several biologists have, however, asserted that there is no systematic way to distinguish female from male diploid metazoans (Fausto-Sterling, 2000; Jordan-Young, 2010; Gorelick, Carpinone & Derraugh, 2013). Previously, we addressed this lack of diploid differences between female and male eukaryotes (Gorelick *et al.*, 2013), as summarized below. Even if present, it is often difficult to discern whether external sex organs are female vs. male. As Reinier de Graaf effectively recognized in 1672, in humans, the clitoris is

*Corresponding author: E-mail: root.gorelick@carleton.ca

homologous to penis, both with the same sensory function (de Graaf, 1672; Cobb, 2006). Heteromorphic sex chromosomes are largely restricted to birds and mammals and hence often cannot be used to distinguish the sexes (Solari, 1994; Gorelick, 2003, 2005; Charlesworth, Charlesworth & Marais, 2005), admitting that heteromorphic sex chromosomes appear in a few species of several disparate taxa. In a large number of diverse plant and animal taxa, organelles are inherited paternally and biparentally (Corriveau & Coleman, 1988; Mogensen, 1996; Jannotti-Passos *et al.*, 2001; Barr, Neiman & Taylor, 2005), including in molluscs with doubly uniparental inheritance (Zouros *et al.*, 1992; Garrido-Ramos *et al.*, 1998), and hence cannot be used to distinguish the sexes. The production of eggs vs. sperm is often cited as a way of distinguishing between the sexes (Parker, Smith & Baker, 1972; Parker, 1982). However, a single multicellular diploid individual can often produce both eggs and sperm, either simultaneously or sequentially (e.g. gobionid fishes; Nakashima, Kuwamura & Yogo, 1996). Thus, all obvious differences between diploid females and males appear to be inapplicable in many eukaryotes.

Because there are no universal differences between the two diploid sexes, any universal differences between the two sexes will be between haploid individuals (*sensu* Gorelick, 2012b). Very few studies have been concerned with differences between sexes of haploid nuclei, haploid cells, haploid organisms or gametes. This may be a result of the putatively ephemeral and single-celled nature of gametes in animals. Because hermaphrodites exist in multicellular haploid individuals (e.g. gametophytes of homosporous ferns that produce both eggs and sperm; Bell & Hemsley, 2000), assigning sexes to multicellular haploids is not universally feasible either, at least not amongst all eukaryotes. It can often be difficult to distinguish haploids from diploids because most metazoan eggs require fertilization to complete egg meiosis (Austin, 1965; Sagata, 1996), meaning that most metazoan egg cells are diploid, or at least 2C, at the time of fertilization, and haploid females are therefore ephemeral, if not absent completely. For example, in humans, an egg nucleus only becomes haploid after the egg cell has been fertilized by a sperm cell (i.e. after plasmogamy but before karyogamy) (note that a glossary is provided in the Appendix). Although there is no definition of female and male that can be applied universally to multicellular diploids or haploids, there could be universal differences between *gametic nuclei* (egg and sperm nuclei, regardless of whether eggs are haploid) that allow us to systematically assign a sex as either female or male. Although many metazoan gamete nuclei can be unambiguously assigned to either a

female or male sex, it would be interesting to determine whether these differences apply to all eukaryotes.

The present review is about sex, not gender, two terms whose meanings have shifted over the centuries, with modern uses only beginning to stabilize in the 1950s (Fausto-Sterling, 2000; Hird, 2004). Sex is usually conceptualized as a biological binary with only two instantiations, female and male; whereas gender is usually conceptualized as a cultural continuum. So, for example, Lloyd's (1980) famed continuous measure was of gender of plants, not of sex.

POSSIBLE DIFFERENCES BETWEEN GAMETIC FEMALES AND MALES?

What makes an egg 'female' and a sperm 'male'? Most people suspect that there are fundamental differences between eggs and sperm, although such putative differences, and also whether they hold universally amongst eukaryotes, remain to be clarified. We present eight possible differences for distinguishing females from males. At least amongst metazoans, seemingly obvious (but not necessarily true) differences between haploid females and males include:

| | | |
|----|--|---|
| 1. | Eggs are immobile and lack flagella | Sperm are mobile via flagella |
| 2. | Eggs are large (anisogamy) | Sperm are small (anisogamy) |
| 3. | Eggs can only be fertilized by sperm | Sperm can only fertilize eggs |
| 4. | Eggs are hosts | Sperm are parasites |
| 5. | Eggs are long-lived | Sperm are short-lived |
| 6. | Eggs need fertilization to complete meiosis | Sperm complete meiosis without fertilization |
| 7. | Eggs have nuclear pores and do not form pronuclei | Sperm lack nuclear pores and form true pronuclei |
| 8. | Haploid females are produced by asymmetrical meiosis | Haploid males are produced by symmetrical meiosis |

EGGS ARE IMMOBILE AND LACK FLAGELLA; SPERM ARE MOBILE VIA FLAGELLA

Eggs are often immobile and lack flagella, although so are many sperm. At least eight animal phyla include species in which sperm lack flagella, and instead move via pseudopodia or are not independently mobile (Morrow, 2004). These include at least

one chordate family, freshwater elephant fish of the Gymnarchidae (Mattei, 1991; Morrow, 2004). Furthermore, metazoan eggs can be mobile. Rabbit eggs travel close to 20 cm from the ovary down the fallopian tubes to the uterus, at times as fast as 1 cm h^{-1} (Harper *et al.*, 1960). By contrast, rabbit sperm travel a relatively short distance following ejaculation. This is probably true amongst most mammals and birds, where eggs travel farther and faster than sperm that have been deposited in the female reproductive tract. Similarly, angiosperm and conifer sperm are completely non-motile, lacking flagella and pseudopodia, and are only transported in pollen grains and by (phallic) elongating pollen tubes (Chamberlain, 1935; Mauseth, 2009).

Welwitschia mirabilis (Gnetales) provides a curious case of the similarities between haploid females and males. Haploid *Welwitschia* males are conventional siphonogamous seed plants with an elongating pollen tube that carries two sperm cells towards the female gametophyte. Haploid females are striking in that they also grow a prothallial tube, which has the appearance of a pollen tube and grows through the nucellus to come in contact with the male's pollen tube (Friedman, 2015). The prothallial and pollen tubes then fuse with one another and one sperm nucleus fuses with one egg nucleus to form a zygote.

EGGS ARE LARGE; SPERM ARE SMALL (ANISOGAMY)

With polyploidy and endoploidy, the size of the cell body is proportional to size of the nucleus and quantity of DNA in the nucleus (Masterson, 1994; Conlon & Raff, 1999; Knight & Beaulieu, 2008; Lomax *et al.*, 2009; Gorelick, 2014; Maciak & Michalak, 2015); hence, haploid nuclei and their cells should be relatively small compared to diploid cells of the same species. Buntrock *et al.* (2012) provided a particularly compelling case in which organ growth in a moth is not a function of cellular or nuclear division but, instead, a function of the single nucleus in a single cell increasing in size proportionally via repeated endoploidy, to over 16 000-ploid also see (Lee, Davidson & Duronio, 2009). As shown below, the lack of nuclear pores in male gametic nuclei of animals renders their sperm nuclear genome inactive such that neither replication nor translation can occur. Animal sperm chromosomes can therefore be retained in a condensed state. As a result of having condensed chromosomes, the size of most animal sperm nuclei should be smaller than egg nuclei with their decondensed chromosomes, which are needed for transcription (Ausió, González-Romero & Woodcock, 2014). The key word here is 'most', given that there

are instances of very large sperm (e.g. *Drosophila hydei*, *Drosophila bifurca*), although these generally have extremely long flagella and not necessarily large cell bodies nor large nuclei (Pitnick & Markow, 1994; Pitnick, Spicer & Markow, 1995). This is why we restrict attention to the size of the cell body to ignore large cellular appendages, such as flagella of sperm cells or axons of nerve cells (Polilov, 2012). The only metazoans we know of whose sperm have large cell bodies are taxa with amoeboid sperm, such as nematodes, and these also happen to lack nuclear membranes and lack condensed chromosomes (Yushin & Malakhov, 2014). Anisogamy therefore appears to be a reasonable way of distinguishing females from males in most metazoans (Weismann, 1886 [1889]), at least for those animals that have not secondarily lost their sperm nuclear membranes.

Egg cells are usually large, presumably to provision developing embryos, such as the huge eggs of birds and cycads. Indeed, after fertilization, the zygotic nucleus repeatedly divides mitotically (at least after the cleavage division), although the size of the diploid embryo for a long time is no larger than the size of the egg cell from which it arose (Romanes, 1910). However, there are certainly exceptions to eggs being large, such as the minute eggs and correspondingly minute seeds of orchids. Mature egg cells of the orchid *Cypripedium cordigerum* are only approximately 0.015 mm (15 μm) in diameter (Sood & Rao, 1988). In accordance with the perspective of Bjork & Pitnick (2006) suggesting that isogamy means almost equal investments in eggs and sperm, orchids would be considered isogamous, even though the shapes of their eggs and sperm are typical of those of other angiosperms. Instead of a female parent investing in eggs and seeds, such investment in orchids comes from mycorrhizal fungi parasitized by a germinated orchid seed (Rasmussen & Rasmussen, 2009). Typical egg cells in other flowering plants are not particularly large, being much smaller than the central cells that form endosperm (flowering plant embryos are also nourished by diploid perisperm derived from the nucellus). On the male side, zooidogamous plants have sperm cells that are primarily composed of a massive cell body and relatively small flagella (Stewart, 1951; Norstog, 1993; Poort, Visscher & Dilcher, 1996; Friedman & Gillford, 1997). Anisogamy is not a great way of distinguishing females from males in plants. Near the end of the present review, we provide a possible reason why plants seem less anisogamous (more isogamous, to avoid the double negative) than animals.

All theories on evolution of anisogamy appear to presume that sperm size is inversely proportional to sperm number (Parker *et al.*, 1972; Parker, 1982). The presumption is that, by making sperm smaller,

a larger number of sperm can be produced without being a resource drain on the parent. What these theories appear to ignore is how sperm develop. In metazoans, the primordial germ cells that eventually undergo meiosis to produce sperm are normal-sized or larger than normal-sized spherical diploid cells. Meiosis produces four spherical haploid cells, each of which is approximately one-quarter the volume of the cell that underwent meiosis (i.e. approximately 80% the diameter of the diploid cell). All four products of male metazoan meiosis are fairly standardized or large cells. Only later in sperm development is cytoplasm siphoned off from metazoan sperm in the form of a residual body. Animal sperm cell sizes shrink dramatically by undergoing a cell division without nuclear division, with the nucleus partitioned to a very small sperm cell and most of the cytoplasm partitioned to a cell called the residual body that lacks a nucleus (Grier, 1975, 1976), although this asymmetrical cell division only occurs after meiosis in metazoans. If individual selection based on resource limitation were really driving evolution of small sperm, with the number of gametes produced being inversely proportional to their size (Bell, 1978, 1982; Maynard, 1978; Parker, 1982; Cox & Sethian, 1984), then residual bodies would be maladaptive. Instead, it appears that animal sperm have no way of jettisoning extra cytoplasm other than by the maladaptive process of creating residual bodies, admitting that residual bodies are later phagocytized (i.e. recycled). In an oddly complementary and possibly not coincidental fashion, egg development also has an apparently maladaptive process of jettisoning nutrient-rich material but, with eggs, it is the jettisoning of nuclei and chromosomes (not cytoplasm) in the form of polar bodies, whose nucleic acids may also be recycled. In some taxa, there are only polar nuclei, not polar bodies, in which meiotic karyogenesis (nuclear division) occurs without meiotic cytokinesis (cell division). Another problem with existing theories of evolution of anisogamy is the implication that anisogamy should only arise in multicellular eukaryotes. Yet, polar nuclei clearly exist in the unicellular stramenopile genus *Paramecium* (Hiwatashi *et al.*, 1985) and in most ciliates (Margulis *et al.*, 1990), and anisogamy arises in small volvocine green algal colonies, with as few as 16 cells per colony (Knowlton, 1974). Anisogamy even exists in some ciliates, such as *Epistylis umbellaria*, where the smaller haploid nuclei move between cells during conjugation and the larger haploid nuclei remain in the cell from which the micronuclei arose via meiosis (Calkins, 1901). Below, after rejecting notions of symmetry of meiosis as being a useful way of distinguishing females from males because of organisms with UV chromosomes, we provide further reasons

for rejecting anisogamy as a way of distinguishing the sexes. Data on gamete development indicate that we need to reject a large body of literature on evolution of anisogamy.

Geoff Parker (1982: 282) explicitly based his theories about evolution of anisogamy on the idea that 'There is a fixed energy budget per parent, so that if an adult produces gametes of size m , the relative number of gametes produced is proportional to m^{-1} .' This appears to be true for *Drosophila* insofar as their sperm have cell bodies approximately the same size of other metazoan sperm cell bodies, although the giant sperm that occur in some *Drosophila* species all have extremely long flagella and are produced in extremely small number. By contrast, we have not seen data showing this inverse relationship between sperm number and size for large sperm that are large as a result of being amoeboid. Given the way that metazoan sperm develop, by jettisoning cytoplasm via residual bodies, it is difficult to imagine this often presupposed inverse relationship between sperm size and number applying to any taxa with large sperm cell bodies (i.e. applying to any animal taxa other than drosophilids with their long sperm flagella).

What do the data show regarding negative correlation between sperm size and number? This negative correlation appears to be unequivocal in the Drosophilidae (Pitnick, 1996; Schärer, Da Lage & Joly, 2008; Markow, Beall & Castrezana, 2012). The negative correlation between sperm size and number is far less certain in other taxa. Gomendio & Roldan (1991) showed a positive correlation between sperm size and number of ejaculates in mammals, with number of ejaculates being a proxy for the number of sperm. However, the length of sperm varied by only a factor of two in that study. In mammals, Ramm & Stockley (2010) found a negative correlation between sperm length and rate of spermatogenesis, which is a proxy for the number of sperm produced, although we cannot discern the range of mammalian sperm sizes in their study. Immler *et al.* (2011) compared sperm size with number in both passerine birds and drosophilids and, with data for those two taxa combined, found a negative correlation. However, almost all of the variation in sperm size was in the flies, with a more than 1000-fold difference in sperm length between the shortest and longest fly sperm, whereas there was only a six-fold difference (Immler *et al.*, 2011: table S1) or less than a two-fold difference (Immler *et al.*, 2011: figure 2a) in sperm length between the shortest and longest bird sperm. Consequently, the flies, not the birds, almost exclusively drove their result of a negative correlation between sperm size and number. 'Caution is needed when seeking evidence for a sperm size-number trade off (Parker *et al.*, 2010: 1003).

The best places to look for correlations between sperm size and number are with clades that have atypically large sperm. This explains the extensive work on drosophilids. However, there are huge gaps in our knowledge about anisogamy because such correlational studies have not been conducted, as far as we know, with any of the taxa that have amoeboid sperm, which all appear to have sperm with large cell bodies, and not just long flagella. Amoeboid sperm occur in at least a dozen metazoan phyla: Acanthocephala, Annelida, Arthropoda, Chordata, Dicyemida, Gastrotricha, Gnatostomulida, Kinorhyncha, Nematomorpha, Pentastomida, Platyhelminthes, and Rotifera (Rohde & Faubel, 1998; Czaker, 2001; Morrow, 2004; Reunov, 2005; Pitnick, Hosken & Birkhead, 2009; White-Cooper & Bausek, 2010; Trovato *et al.*, 2011; Piper, 2013; Yushin & Malakhov, 2014). There is also extensive variation in sperm size in at least two arthropod lineages, ostracods and hemipterans, both of which contain taxa with giant sperm (Tandler & Moriber, 1974; Matzke-Karasch, 2005).

The huge emphasis on drosophilids, although very productive, has also distorted basic evolutionary nomenclature. The prefix 'iso-' in most parlances means equal or alike, with an antonym of 'aniso-'. Traditionally, if two entities differed in any ways, the prefix 'iso-' does not apply. Thus anisogamy refers to a condition with any noticeable difference between eggs and sperm. This difference could be in size or shape. In that sense, eggs and sperm are clearly distinguishable, even in *D. bifurca* and *Drosophila hydei*, in which eggs are spherical aflagellate cells with a huge cell body, whereas their sperm are elongated cells with a tiny cell body but a huge flagellum. However, studies investigating how resource constraints have caused a putative negative correlation between sperm size and number have instead defined isogamy as a condition in which 'investment per gamete by males approaches that by females' (Bjork & Pitnick, 2006: 742). It is not obvious how that investment would be measured other than by strictly looking at either gamete number or size, which presupposes the result of a negative correlation between sperm size and number.

A cursory look at seed plants shows that an inverse relationship between sperm cell size and number does not hold. Sperm of zoidogamous gymnosperms are much larger than sperm of siphonogamous taxa, yet sperm numbers are approximately the same for zoidogamous and siphonogamous taxa because both groups of plants produce approximately the same amounts of pollen and always produce the same number (two) sperm per pollen tube (Poort *et al.*, 1996; Friedman & Gillford, 1997; Gorelick, 2001), except for up to a dozen sperm per pollen tube

in *Microcycas calocoma* (Norstog, 1993). Sperm are larger in zoidogamous taxa only because their pollen tubes are more highly parasitic on the nucellus (Chamberlain, 1919, 1935). Sperm size in seed plants is almost all a result of cell body size, with the only exception being the wings (also known as bladders, vesicles, sacca) on pine pollen, in which the pollen is siphonogamous and relatively small, even with the wings.

Perhaps anisogamy arguments should not be based on differences in size but, instead, on differences in functionality. A common reaction is that haploid females, usually eggs, provide the biochemical machinery for the developing embryo, whereas the haploid males, usually sperm, only provide the genetic code that directs development of that embryo. This is a very old idea, dating back at least to Aristotle, an idea that persists despite the aforementioned evidence. Quoting Cobb (2006: 15), 'In Aristotle's view the female provided the matter that would constitute the foetus, while the male's semen contributed the form, shaping and sculpting the embryo (Mayhew, 2004).' Mendelian inheritance debunks this erstwhile Aristotelian notion insofar as both eggs and sperm provide almost equal amounts of nuclear DNA coding for the developing diploid embryo. We also now know that sperm not only contribute more than chromosomes to the next generation, but also contribute nuclear envelopes and epigenetic elements to the zygote.

If anisogamy had a single origin amongst early eukaryotes, then it would provide a fine universal way of distinguishing females from males. However, anisogamy is usually considered to have arisen independently many times during eukaryote evolution (Bell, 1978; Billiard *et al.*, 2011; Lehtonen, Parker & Schärer, 2016). Amongst other mechanisms, anisogamy may have evolved independently multiple times because of sperm competition and sperm limitation (Lessells, Snook & Hosken, 2009; Immler *et al.*, 2011). It appears nonsensical to have different criteria to distinguish females from males, with one criterion for each independent origin of anisogamy. This would not be an essential difference between the sexes. Further confounding matters, there is a genuine continuum between isogamy and anisogamy, which is especially evident in green algae and fungi (Billiard *et al.*, 2011; Togashi & Bartlett, 2011). How much smaller does a sperm cell body need to be than an egg cell of the same species before we consider this a *bona fide* case of anisogamy?

We have just provided extensive theoretical and empirical reasons for why anisogamy fails to provide a universal difference between haploid females and males. We are, however, perplexed as to why these many independent arguments appear to be lacking

from the literature. Even the preponderance of work on model organisms cannot explain this gap because, although much research on anisogamy has relied on small fruit flies, family *Drosophilidae*, the fascinating large amoeboid sperm in nematodes, some of which are also model organisms, has been effectively ignored, at least in discussions of evolution of anisogamy.

EGGS CAN ONLY BE FERTILIZED BY SPERM; SPERM CAN ONLY FERTILIZE EGGS

If eggs can only be fertilized by sperm and sperm can only fertilize eggs, this would show that there are two separate haploid sexes, even if this does not distinguish which haploids are female and which are male. Such a criterion could be referred to as polarity of gametes, a notion that parallels discussions of (non-existent) diploid sex complementarity and dualism between females and males (Scheibinger, 1993; Hird, 2004). However, in taxa with central fusion and terminal fusion, which are known from many eukaryotes, eggs or egg nuclei fuse with other eggs or egg nuclei (Stenberg & Saura, 2009; Booth *et al.*, 2014). Although much rarer, two sperm pronuclei fuse to form a zygote, for example in the androgenetic stick insect *Bacillus grandii* (Tinti & Scali, 1992). Although we do not know whether it is possible in such species for all eggs to fuse with all other eggs or all sperm to fuse with all other sperm, at least some eggs can fuse with one another and some sperm can fuse with one another. Therefore sexes do not always correspond with mating types. There is no universal complementarity between female and male gametes.

EGGS ARE HOSTS; SPERM ARE PARASITES

Aristotle's idea that females provide nutrition and biochemical machinery, whereas males provide the genetic code an organism is debunked by Mendelian inheritance, although it does find some limited support in androgenetic taxa, such as *B. grandii*, *Corbicula leana*, and *Cupressus duprezina*, where all egg nuclei are ejected like polar bodies, leaving only sperm chromosomes (Tinti & Scali, 1992; Komaru, Kawagishi & Konishi, 1998; Pichot *et al.*, 2001). The opposite is true in gynogenetic and hybridogenetic taxa, in which eggs use sperm to initiate diploid or triploid development and possibly to unpause suspended female meiosis, in which case eggs are effectively parasitizing sperm (Schultz, 1967; Mantovani & Scali, 1992; Tinti & Scali, 1992; Alves, Coelho &

Collares-Pereira, 1998; Schatten & Chakrabarti, 2000; Schlupp, 2005; Bogart *et al.*, 2007).

EGGS ARE LONG-LIVED; SPERM ARE SHORT-LIVED

Although examination of humans appears to imply that eggs have much greater longevity than sperm, the opposite may be true for their haploid nuclei. Human oocytes may survive for three or four decades but in a state of suspended meiosis, that is not yet haploid. Note that we object to the phrase 'arrested meiosis' because it implies that only females can be arrested, and not males (Gorelick, 2012a); hence, we substitute for it the less pejorative phrase 'suspended meiosis'. In most metazoans, egg meiosis is suspended either at the 4C or 2C stage, that is just before the first or second reduction division (Austin, 1965). Egg meiosis does not resume until one or more sperm nuclei enter the egg cell, soon after which the newly formed haploid egg nucleus undergoes karyogamy with a haploid sperm nucleus (Sagata, 1996). By contrast, consider the longevity of egg and sperm nuclei in many attine ants. The queen mates with a handful of drones on a nuptial flight, after which she chews off her wings and starts a colony (Hölldobler & Wilson, 1990). The queen then undergoes meiosis to produce millions of eggs over the course of her decade or two of life, ostensibly inseminating them with sperm that she stored from her single nuptial flight. This scenario admittedly assumes that the queen does not mate incestuously with her own male offspring prior to those young males leaving the colony, as suggested by Sue Bertram (Gorelick *et al.*, 2013). Another eusocial hymenopteran, the honeybee, *Apis mellifera*, does something similar, where females embark on a single nuptial flight and store sperm for up to 8 years to produce up to 1.7 million fertilized eggs, although only using an average of two sperm to fertilize each egg (Baer *et al.*, 2016). Similarly, in seed plants, pollen can be preserved in a viable state for many years (admitting that we often do not know whether a pollen grain can remain viable after the two haploid mitotic divisions to form the pair of sperm cells). Sperm nuclei often are long-lived, especially compared to haploid egg nuclei. Metazoan sperm nuclei should be especially long-lived with no activity of chromosomes as a result of being encased in a membrane lacking nuclear pores (as is explained below), especially with no DNA replication. Lack of translated mRNA should not be a problem if sperm are in a quiescent state. Many cells survive long periods without nuclei, such as for months in human red blood cells and decades to centuries in palm phloem

sieve cells (Tomlinson & Huggett, 2012), and so extraordinary longevity should be possible for sperm. We are not implying that fully developed sperm cells can use flagella to swim for months or years at a time, only that a sperm nucleus lacking pores can exist for a long time. By contrast, haploid egg nuclei should be and usually prove to be quite short-lived. Although not exactly the prototypical organism (Ottolini *et al.*, 2015; Zanders & Malik, 2015), human egg haploid nuclei only exist for a matter of minutes or hours. Although human oocytes may survive in a quiescent state for decades, this is in a state of suspended meiosis, that is not yet with haploid nuclei. By contrast, in those few metazoans that complete female meiosis before fertilization, female gametic nuclei live significantly longer (i.e. cnidarians and sea urchins) simply because they become haploid earlier. In general, haploid gametic males have the ability to be extremely long-lived compared to haploid gametic females.

Sperm cells in several plants survive for more than 1 year, although, as we will see below, these sperm are not in a quiescent state but have nuclear pores and undergo transcription and translation. The duration between pollination and fertilization is more than 1 year in several species of *Quercus* (oak; a flowering plant), *Agathis* (a conifer), and several Cycadales (Chamberlain, 1919; Williams, 2008). In *Taxus* (a conifer), female gametophyte development largely does not begin until pollen tubes arrive at the egg cell (Chamberlain, 1935). In each of these instances, however, the generative cell (also known as spermatogenous cell or body cell) does not divide to form two sperm cells until after pollination. The sperm and rest of the male gametophyte often need many months to fully develop.

EGGS NEED FERTILIZATION TO COMPLETE MEIOSIS; SPERM COMPLETE MEIOSIS WITHOUT FERTILIZATION

Eggs need sperm to complete meiosis in all amphimictic metazoans, except cnidarians and sea urchins, which complete female meiosis without plasmogamy (Austin, 1965; Gorelick, 2012a). Furthermore, automictic parthenogenesis (e.g. central or terminal fusion) is widespread across metazoans, including in chordates (e.g. fish, reptiles, birds), as well as in almost all other phyla, including arthropods, nematodes, rotifers, platyhelminthes, molluscs, and annelids (Bell, 1982). These automictic eggs clearly do not require fertilization by sperm to complete meiosis.

Plants (Archaeplastida) and other heterosporic organisms, such as some stramenopiles (e.g.

Laminaria), with multicellular female haploid stages must have female meiosis occur independent of sperm; otherwise, the female haploid stage (megagametophyte) could not be multicellular.

EGG NUCLEI HAVE NUCLEAR PORES; SPERM NUCLEI LACK NUCLEAR PORES

Nuclear pores are complex structures built around specific trans-membrane proteins that control the passage of substances, such as nucleotides, mRNA, and proteins, in and out of a nucleus. We previously defined haploid male nuclei as the only nuclei that completely lack nuclear pores (Gorelick *et al.*, 2013), keeping in mind that all somatic cells have nuclear pores. Our cursory survey of metazoans indicates that not all sperm lack nuclear pores. More specifically, sperm nuclei are the only nuclei that have absent or *localized* nuclear pores. Examples of localized nuclear pores in sperm exist in many animal phyla, including some chordates and insects (Cloney & Abbott, 1980). During spermatogenesis in many of these taxa, nuclear pores are redistributed and localized in the so-called 'redundant nuclear envelope' in the posterior (flagellar) end of the sperm (Ho, 2010). The redundant nuclear envelope probably serves as excess nuclear envelope that is saved and packaged near the tail of the sperm during nuclear condensation and does not enclose chromosomes. The function of the redundant nuclear envelope is unknown, although Fawcett & Ito (1965) suggested that, in bats (*Myotis lucifugus* and *Eptesicus fuscus*), the redundant nuclear envelope is reincorporated into the nuclear membrane during pro-nuclear formation when the sperm nucleus greatly increases in volume. Nematodes with amoeboid sperm vacuously lack nuclear pores insofar because they lack nuclear envelopes (Yushin & Malakhov, 2014). We suspect that other animals with amoeboid sperm also lack nuclear envelopes, although we have not found data either for or against this notion. In animals, we can thus define females as possessing porous nuclear membranes so long as we restrict our definition to include only gametic nuclei because all somatic cell nuclei contain pores. We can define haploid male animals as lacking nuclear pores, if we assert that *only* males lack or have localized nuclear pores. In animals, localized or absent nuclear pores equates to male, although the presence of nuclear pores does not necessarily equate to female because all somatic cells contain nuclear pores. In animals, only male gametes lack nuclear pores in the nuclear envelope surrounding their chromosomes. This definition of males turns conventional wisdom on its head insofar

as females are the archetypal sex and males are distinguished by lacking something, that is nuclear pores.

There may be something like a redundant nuclear envelope in ostracods with giant sperm. Unlike Drosophilidae, these ostracods have large but very narrow cell bodies, with nuclei that are extremely narrow for eukaryotes (Matzke-Karasz, 2005; Gorelick, 2014). The reason that we suspect the existence of a redundant nuclear envelope is that chromosomes are localized to only a very small portion of the nucleus in these ostracods, at least in *Mytilocypris praenuncia* (Matzke-Karasz, 2005).

Unlike animals, flowering plants have nuclear pores in their sperm cells, at least in the few taxa where people have looked. Taylor *et al.* (1991) and Southworth, Strout & Russell (1997) showed the presence of nuclear pores in the sperm cells of the eudicots *Brassica* and *Plumbago*, respectively, and their nuclear pores do not appear to be localized. Several studies have shown that monocot sperm cells in *Oryza*, *Zea*, and *Lilium* undergo both transcription and translation, which is consistent with possessing nuclear pores (Zhang, Gifford & Cass, 1993; Blomstedt, Knox & Singh, 1996; Abiko *et al.*, 2013; Zhao, Yang & Wang, 2013).

The monilophyte *Marsilea* uses stored mRNA transcripts for protein synthesis during sperm (spermatozoid) development (Hart & Wolniak, 1998, 1999), which is circumstantially indicative of a lack of nuclear pores. In terms of nuclear pores, *Marsilea* gametes therefore look metazoan. We are unaware of the existence of data either for or against the presence of sperm nuclear pores in any other plants.

Without nuclear pores or with localized nuclear pores, mRNA cannot be transported to ribosomes; hence, no transcription can occur in a mature sperm cell. Without nuclear pores, nucleotides cannot be transported from cytoplasm to nucleus; hence, chromosomes cannot be replicated and mitosis is thereby inhibited. At least in metazoans, and possibly in all eukaryotes, egg and sperm nuclei duplicate all their chromosomes between plasmogamy and karyogamy, in which endomitosis occurs immediately after pronuclear association (Gorelick & Carpinone, 2009) [apparently also noted in Romanes (1910), citing Édouard von Beneden]. Therefore, prior to karyogamy, sperm must replace their nuclear membrane that lacks pores with a nuclear membrane largely derived from the egg's endoplasmic reticulum and, if it exists, from the sperm's redundant nuclear envelope. Sperm must thus also replace their poreless nuclear membranes in androgenetic species, regardless of whether two sperm nuclei fuse to effect karyogamy (e.g. *Bacillus grandii*) or a single sperm nucleus restores diploidy via endomitosis (e.g. *Corbicula leana*) with gametic doubling (Tinti &

Scali, 1992; Komaru *et al.*, 1998; McKone & Halpern, 2003). Egg nuclei and all somatic nuclei never replace their nuclear membrane without an intervening chromosomal duplication or reduction division; hence, they never have true pronuclei, as do metazoan sperm following plasmogamy.

Given that sperm of flowering plants contain nuclear pores, there is no reason for them to replace this nuclear membrane following plasmogamy. On the other hand, *Marsilea*, which we expect to have sperm that lack nuclear pores, probably does undergo metazoan-like replacement of their nuclear envelope following plasmogamy so that the male nucleus can replicate its chromosomes prior to karyogamy (Gorelick & Carpinone, 2009). The bottom line is that the presence/absence of true pronuclear formation is simply a corollary of whether nuclear pores need to be added to sperm nuclei prior to karyogamy.

It is likely that metazoan sperm nuclei contain unique nuclear proteins and lack other proteins that are otherwise ubiquitous across all other nuclear membranes. Evidence exists that some lamin B proteins (Collas & Poccia, 1998) and some genes (e.g. *BOULE*; Shah *et al.*, 2010) are unique to metazoan sperm nuclei. Proteins unique to animal sperm cells are also responsible for the highly condensed state of sperm chromosomes (Eirin-Lopez & Ausió, 2009). However, we caution that relatively few sperm nuclear membranes have been analyzed for their protein content. Sperm-specific nuclear proteins may exist in taxa whose sperm lack nuclear pores (e.g. metazoans) but not exist in taxa whose sperm have nuclear pores (e.g. flowering plants). Indeed, there appears to be a link between sperm nuclear condensation and uniqueness of sperm produced proteins (Dacks & Kasinsky, 1999).

HAPLOID FEMALES ARE PRODUCED BY ASYMMETRICAL MEIOSIS; HAPLOID MALES ARE PRODUCED BY SYMMETRICAL MEIOSIS

Here, we define female (male) meiosis to be any meiotic division in which female (male) haploid nuclei are ultimately produced. That is, female meiosis is defined by the resulting gametophyte(s) producing eggs, and male meiosis is defined by the resulting gametophytes producing sperm. We previously hypothesized that, in all metazoans, female meiosis is asymmetrical with only one (or two with central or terminal fusion) of the nascent haploid nuclei transmitted to the next generation (Gorelick *et al.*, 2013). Supposedly, eggs need more nutritional provisions than sperm to enhance fitness of the resulting embryo (Schuh & Ellenberg, 2008). We also

previously hypothesized that, in all metazoans, male meiosis is symmetrical, with all four resulting gametic nuclei harbouring the ability to be transmitted to the next generation. However, we will also show that these terms ‘female meiosis’ and ‘male meiosis’ are not well-defined entities, thereby providing further evidence for no universal differences between females and males.

In all animals, meiosis that produces females appears to be asymmetrical. Several products of female meiosis are smaller than others and these smaller cells and smaller nuclei are evolutionarily discarded as polar bodies and polar nuclei. In amphimictic metazoa, only one of four haploid products of female meiosis appears to be transmitted to the next generation, and can only do so if fertilized by another gamete. Similarly, only the largest haploid female nucleus survives until the next generation in those taxa with pre-meiotic doubling and gamete doubling. The only instance in which more than one of the four haploid egg nuclei is transmitted to the next generation is with central or terminal fusion, in which two of the four haploid products of the same meiotic division fuse with one another to restore diploidy. The other two haploid products of meiosis in central or terminal fusion are ejected or digested as polar bodies/polar nuclei. By contrast, in all animals, except sciarid flies, male meiosis is symmetrical. All four male haploid cells and nuclei are of the same shape and size and have the ability to contribute DNA to subsequent generations, except in sciarid flies. We have not found any other exceptions to this rule in metazoans, except that, in some animals with amoeboid sperm, there appear to be five cells produced by meiosis but only four of these contain nuclei (Smith, 2006). The fifth cell lacks a nucleus and is a single residual body shared between the four nucleated sperm cells. Residual bodies are ubiquitous in metazoan sperm, albeit usually with one residual body per sperm cell, (Yushin & Malakhov, 2014).

Meiosis in male sciarid flies produces one functional spermatozoid and three aborted meiotic products (Haig, 1993). Sciarids also have peculiar genetic and epigenetic systems for imprinting and eliminating chromosomes of the paternal parent (Crouse, 1960; Goday & Esteban, 2001), which may be relevant to their peculiar asymmetrical male meiosis.

Exceptions to the general rule of asymmetry in female meiosis and symmetry in male meiosis exist amongst plants, with there being symmetrical female meiosis in several taxa and asymmetrical male meiosis in a few taxa. In the two extant genera of heterosporous lycophytes, *Isoetes* and *Selaginella*, meiosis forms a tetrad of four equal-sized and equally functional megaspores (Eames, 1936; Morbelli, Rowley &

El-Ghazaly, 2003; Blackmore *et al.*, 2012). These four products of female meiosis are slightly unusual, being much larger than the diploid cell from which they arose (Blackmore *et al.*, 2012), a trait also possessed by the products of male meiosis in lycophytes and zoidogamous seed plants (Stewart, 1951; Norstog, 1993; Poort *et al.*, 1996; Friedman & Gillford, 1997; Blackmore *et al.*, 2012). In extant heterosporous lycophytes, the mature megagametophyte is the same size as the mature megaspore. As an important aside, there is no contention about what constitutes female or male gametophytes in heterosporous lycophytes. Male lycophyte gametophytes produce numerous small sperm that swim with flagella to egg cells. Female lycophyte gametophytes have large sessile egg cells attached to them and, after fertilization, the embryo parasitizes the female gametophyte. Female lycophyte gametophytes are larger than male gametophytes (i.e. classical anisogamy), although both sexes have symmetrical meiosis.

At least two flowering plant lineages, one monocot and one eudicot, have secondarily evolved asymmetrical male meiosis. Instead of male meiosis producing four equal-sized and equally functional pollen grains, in some species in the sedge family Cyperaceae and the heather family Ericaceae subfamily Stypelioideae, male meiosis is asymmetric, producing so-called ‘pseudomonad’ pollen in which three of the four products of male meiosis degenerate much as polar bodies (Kirpes, Clark & Lersten, 1996; Brown & Lemmon, 2000; Furness, 2009; Furness & Rudall, 2011; San Martin *et al.*, 2013). The pseudomonad pollen grain is the largest of the four products of male meiosis; the other three haploid cells receive less cytoplasm. Pseudomonad pollen formation is assumed to occur because of unequal segregation of chromosomes during meiosis, possibly as a result of these taxa having holocentric chromosomes (i.e. with diffuse centromeres) (Hipp, 2007; Furness & Rudall, 2011). However, we do not fully understand why rampant aneuploidy usually results in one viable and three degenerate pollen grains, nor why aneuploid cells should receive less cytoplasm at meiotic divisions. Nonetheless, the one pseudomonad pollen grain per meiotic division typically develops into a perfectly normal angiosperm pollen tube, with a pair of sperm cells. In these few angiosperms with asymmetrical male meiosis, female meiosis is that of typical angiosperms, that is asymmetrical.

Asymmetries in angiosperm female meiosis can be either obvious or subtle (Hoekstra, 2011). The fate of nuclei can be immediate or delayed. Angiosperms with tetrasporic development of female gametophytes do not have any polar bodies/polar nuclei, although they still evolutionarily discard three of four products of meiosis, that is the mitotic products of these

three nuclei are not passed to the next generation. One haploid nucleus, the so-called ‘germinal spore’ (Haig, 1986), becomes the egg cell that, after fertilization, becomes the zygote. A second haploid nucleus divides mitotically to ultimately form the two polar nuclei of the central cell that, after double fertilization, becomes triploid endosperm. [Note that standard nomenclature results in problems here, with the term ‘polar nucleus’ being used in two completely different ways. Previously, we used the term ‘polar nucleus’ to refer to the two or three smaller products of asymmetrical *meiotic* karyogenesis. However, here, the term ‘polar nucleus’ refers to the two products of haploid *mitotic* karyogenesis that form the central cell in a megagametophyte. This is the only time in the present review that we use the term ‘polar nuclei’ to refer to anything but products of meiosis. Also note that, purely for simplicity, we assumed that angiosperm female gametophytes only have two polar nuclei and have triploid endosperm. Indeed, there is much variation between taxa in angiosperm female gametophytes, which can have from one to eight polar nuclei and from diploid to nonaploid endosperm (Klekowski, 1988; Williams & Friedman, 2002; Yadegari & Drews, 2004).] Endosperm genomes are not passed on to the next generation. The remaining two haploid products of meiosis are also incorporated into the female gametophyte but not to the egg or central cell. In tetrasporic angiosperms, more than one product of female meiosis survives to divide mitotically, although the cell fate is specified for all four haploid nuclei, and only one nucleus passes on its genome to the next generation (Yadegari & Drews, 2004).

In many gymnosperm taxa, more than one egg per megagametophyte can be fertilized by sperm, thereby forming multiple viable diploid embryos in a single ovule, which is known as ‘simple polyembryony’ (Singh, 1978; Smoot & Taylor, 1986; Becwar *et al.*, 1991). However, it appears that these multiple fertilized eggs are monospermic, that is originating from only the chalazal product of female meiosis in all gymnosperms except Gnetales (Friedman, 1990, 2015; Carmichael & Friedman, 1995). Although *Gnetum* and *Ephedra* (Gnetales) undergo a form of double fertilization to form a supernumerary zygote, this second megaspore does not form a viable diploid embryo that transmits genes to subsequent generations; only the chalazal megaspore nucleus does that. Thus, these aberrant cases in gymnosperms are still examples of asymmetrical female meiosis.

Several stramenopile lineages with separate female and male gametophytes appear to have symmetrical female meiosis, noting that symmetry of female meiosis is widely variable in the Fucales (Nagasato, Motomura & Ichimura, 2001). As with

land plants, in the brown algae Fucales, meiotic and mitotic nuclear division (karyogenesis) is not necessarily accompanied by cell division (cytogenesis), for example it is possible to have between one and eight haploid nuclei per egg cell. In Fucales, female meiosis is immediately followed by a single mitotic division of each of the four resulting haploid nuclei, thereby forming anywhere from one to eight eggs, depending on how many degrade as polar nuclei. The type genus *Fucus* has eight functional egg cells, each with one haploid nucleus, which is considered to be the ancestral condition in this order (Brawley, Quatrano & Wetherbee, 1977; Clayton, 1984; Nagasato *et al.*, 2001). There appears to be no doubt about what is female and what is male in heterosporous stramenopiles: females produce sessile eggs that are attached to female gametophytes, whereas males produce sperm with flagella that swim with flagella from their male gametophyte of origin to an egg cell, with eggs cells larger and less numerous than sperm cells. What is striking here is that symmetrical female meiosis exists in a kingdom other than plants, and may be ancestral in the SAR supergroup [Stramenopiles (Heterokonta) Alveolata and Rhizaria].

Most kelps are problematic for defining females as the sex with asymmetric meiosis because most kelps have meiosis in which two of the meiotic products produce female gametophytes and the other two meiotic products produce male gametophytes. Female gametophytes undergo haploid mitosis and eventually produce sessile aflagellate egg cells in which sporophytes remain attached to female gametophytes, whereas male gametophytes eventually produce and release flagellate motile sperm. Yet there is only one form of meiosis in most kelp, a meiotic division that produces 50% female spores and 50% male spores, even though these kelp are heterosporous. In other words, it is nonsensical to refer to female meiosis or male meiosis in most kelp.

For identical reasons, it is nonsensical to refer to female meiosis or male meiosis in bryophytes and stramenopiles that have UV sex chromosomes. Those bryophytes include both mosses and liverworts that have heteromorphic sex chromosomes (Allen, 1917; Khanna, 1971; Bischler, 1986). The diploid stage always has one U and one V chromosome, whereas meiosis produces two haploid spores, each with a U chromosome, and two haploid spores, each with a V chromosome, that is two haploid females and two haploid males (Allen, 1945; Khanna, 1971; Gorelick, 2005; Bachtrog *et al.*, 2011; Ahmed *et al.*, 2014).

There are only a few examples of fossilized chromosomes (Bomfleur, McLoughlin & Vajda, 2014) and no known examples of fossilized UV chromosomes in either plants or stramenopiles. Fossil gametes are

often detached from their gametophytes and from their sporophytes, making it difficult to infer lifecycles. Anisogamy is difficult to infer in fossils, let alone to observe whether a single meiotic division produced both female and male spores in fossil taxa. What we do know, however, from the fossil record is that there was sexual dimorphism in spores, also known as heterospory, sometimes with intrasporangial heterospory, that is female and male spores were produced within the same sporangium, although not necessarily produced from the same meiotic division (Cichan, Taylor & Brauer, 1984). Although heterospory provides only circumstantial evidence for anisogamy, we know that heterospory evolved independently many times (Bateman & DiMichele, 1994), providing tantalizing hints that anisogamy may have also evolved independently many times. If true, then there is no reason to think that there will be any essential differences between females and males based on anisogamy insofar as anisogamy had multiple origins.

Extant homosporous plants and stramenopiles also lack distinct female meiosis and male meiosis insofar as meiosis in homosporous taxa creates gametophytes that each produce both eggs and sperm. Most monilophytes are homosporous, as are some lycophytes and all extant anthocerotophytes (Bell & Hemsley, 2000).

We began by defining female (male) meiosis to be any meiotic division in which female (male) haploid nuclei are ultimately produced. We have thus constructed a *reductio ad absurdum* argument because organisms in which a meiotic division can produce both female and male haploid stages do not fit neatly into a sexual dichotomy. Meiosis that produces two female and two male haploid spores does not, as far as we can determine, ever produce polar bodies. We have thus shown that there is no sensible thing as ‘female meiosis’ or ‘male meiosis’ and hence these two terms cannot help us in distinguishing females from males across all eukaryotes.

NO UNIVERSAL DIFFERENCES BETWEEN FEMALE AND MALE EUKARYOTES

Several researchers have convincingly demonstrated that there are no universal differences between diploid females and males (Fausto-Sterling, 1985), a finding utterly consistent with intersex, trans-sex, and environmental sex determination in many eukaryotes. Therefore, the focus here has been on haploid and gametic differences between females and males. We showed that females cannot be distinguished from males on the basis of requiring plasmogamy to complete meiosis because this only

appears to apply to metazoans and ciliates (Austin, 1965; Raikov, 1982 [1978]), and not plants and stramenopiles. In an earlier paper (Gorelick *et al.*, 2013), we asserted that differences between females and males cannot be completely distinguished on the basis of eggs and sperm, which are themselves distinguished by eggs being long-lived, sessile aflagellate cells whereas sperm are short-lived, mobile flagellate cells. Males are not complementary to females, not even in gametes, that is eggs can sometimes fertilize eggs and sperm can sometimes fertilize sperm. In general, male gametes are no more parasitic than female gametes. Here, we summarize how three remaining putative characters for distinguishing females from males – only sperm lack nuclear pores, anisogamy, and asymmetry of female meiosis – do not appear to work either.

All male metazoans appear to have sperm cells that lack nuclear pores or at least lack nuclear pores surrounding their chromosomes. This renders it impossible for mRNA transcripts to be transported to the ribosomes for translation (unless the sperm lacks a nuclear envelope). Given how complex eukaryotic membrane pores are, it is not too surprising that such nuclei without pores would have unique proteins. Between the events of plasmogamy and karyogamy, both egg and sperm nuclei duplicate their chromosomes, which means that the sperm nucleus has to exchange its nuclear membrane lacking pores for one that has pores, almost certainly built from the egg’s endoplasmic reticulum (Gorelick & Carpinone, 2009) and possibly in part from the sperm’s redundant nuclear envelope, if it had one. The new nuclear envelope with pores is called a pronucleus. The egg does not need to shed its nuclear membrane because it already contains nuclear pores. Up to this point, this appears to apply to all metazoans and a few plants such as the monilophyte *Marsilea* (Hart & Wolniak, 1998, 1999) but not to angiosperms. There is definitive evidence that eudicot sperm nuclei have relatively evenly distributed nuclear pores (Taylor *et al.*, 1991; Southworth *et al.*, 1997) and that monocot sperm undergo transcription and translation (Zhang *et al.*, 1993; Blomstedt *et al.*, 1996; Abiko *et al.*, 2013; Zhao *et al.*, 2013), thereby indicating the presence of nuclear pores in angiosperm sperm.

Surprisingly, anisogamy proves to be a poor means of distinguishing haploid females from males, both for empirical and theoretical reasons. Many angiosperms have tiny eggs, which is most poignant in orchids. Metazoans with amoeboid sperm have very large sperm cells. There exist many plant and stramenopile taxa with approximately equal-sized eggs and sperm, yet in which it is otherwise apparently obvious which sex is female and which is male.

Almost all theories on origins of anisogamy via individual selective advantages have problems in assuming, because of resource constraints, that the number of sperm is inversely proportional to the size of sperm. This inverse correlation cannot be the case in most metazoans, which have primordial germ cells that are of typical cell size or unusually large for that individual. Animals sperm cells only become unusually small after an asymmetrical cell division to form two cells: a tiny sperm cell with a nucleus and a comparatively huge residual body without a nucleus. It appears to be maladaptive to discard cytoplasm-rich residual bodies in males and nucleic acid-rich polar nuclei in females. But that is the patched together suboptimal design that all metazoans and possibly many other eukaryotes have inherited. This is François Jacob's (1977) notion of evolution as a tinkerer, rather than an engineer. Another problem is that, if anisogamy evolved independently multiple times, then anisogamy cannot provide a good universal way of distinguishing females from males. Although sperm size and number are negatively correlated in the fruit fly family *Drosophilidae*, it is not obvious whether this negative correlation holds for mammals, birds or the dozen or more metazoan phyla in which there are amoeboid sperm. Although there is not much size variation in sperm amongst birds and mammals, amoeboid sperm tend to be huge, especially compared to sister taxa that lack amoeboid sperm. More poignantly, there appears to be absolutely no (zero) correlation between sperm size and number in seed plants, where siphonogamous taxa have small sperm and zoidogamous taxa have large sperm. The paradigmatic theory of evolution of anisogamy therefore appears to be entirely inapplicable to plants and may be inapplicable to all animals other than small fruit flies.

Views on what constitutes females and males can be biased by evolutionary biologists' zoological focus, especially a focus on the small fruit fly family *Drosophilidae*. Most animal sperm have flagella but, given the preponderance of angiosperms, most land plants do not. Most animals require plasmogamy by a sperm cell for female meiosis to be completed; something that is unknown in other ophisthokonts, and unknown in all plants and stramenopiles. Anisogamy is exaggerated in animals because most animal sperm lack nuclear pores and have highly condensed chromosomes, whereas sperm in flowering plants contain nuclear pores and have transcriptionally-active decondensed chromosomes. A lack of nuclear pores plus perpetually condensed chromosomes in animal sperm results in smaller cell nuclei and hence smaller sperm cell bodies. Here, the exception of large amoeboid metazoan sperm, which lack nuclear envelopes and lack condensed

chromosomes, proves the rule. We strongly disagree with Roughgarden & Iyer's (2011: 97) claim that 'egg and sperm cannot both be tiny and still produce zygotes big enough to survive'. Although eggs must be large in animals, plants and stramenopiles can and sometimes do have tiny egg cells that are supported by large multicellular female gametophytes. In angiosperms, small eggs are fertilized by equally small sperm lacking flagella, and the resulting embryos are largely nourished by endosperm and perisperm. Or, in the case of orchids, which have utterly miniscule eggs and seeds that have very little endosperm or perisperm, the newly germinated seed simply parasitizes a mycorrhizal fungus for its nourishment. It should not be too surprising that parasitism can result in miniaturization, something that can be taken to extreme, such as in parasitic wasps so small that the neurons in their adult stage lack cell bodies (Polilov, 2012). However, regarding seed plants, we concede that angiosperms, which are siphonogamous, evolved from gymnosperms, and ancestral gymnosperms were almost certainly zoidogamous (i.e. evolved from ancestors whose sperm were quite large and had to swim to an egg using flagella).

That leaves just one possible universal difference between females and male across all eukaryotes, namely that females have asymmetrical meiosis and males have symmetrical meiosis (Gorelick, 2012a). By asymmetrical meiosis, we mean that only one of the four meiotic products (megaspores in plants; and possibly only three, not four, meiotic products if one polar body or polar nucleus is diploid) makes it into subsequent generations. The other two or three immediate products of meiosis may degenerate as polar nuclei or be ejected as polar bodies, the latter of which, in metazoans, are often with almost no cytoplasm between the cell and nuclear membranes. Alternatively, the other two or three immediate products of meiosis may undergo one or several haploid mitotic divisions, as seen in many plants. However, the question remains. Do these contribute to subsequent generations or are they ontogenetic dead-ends, as with flowering plant endosperm? Seed plants show this latter pattern, with only one of the four megaspores surviving to form a diploid plant that will eventually undergo meiosis to form the next generation. Our primary contribution has been to cite examples from lycophytes and stramenopiles in which females have symmetric meiosis, as well as a few angiosperms and dipterans in which males have asymmetrical meiosis. In this sense, females have evolved more innovations than males insofar as females have independently evolved to have symmetrical meiosis far more often than males have evolved to have asymmetrical meiosis.

Although obvious to phycologists (Scagel *et al.*, 1966), we have highlighted that female meiosis does not exist in most kelp (Laminariales). Even though most kelp are heterosporous, each meiotic division produces two female and two male spores. Something similar occurs in those bryophytes and stramenopiles with UV chromosomes, with two products of meiosis being haploid females and two being haploid males. Furthermore, most monilophytes, many lycophytes, and all extant anthocerotophytes are homosporous, and hence do not have distinct female meiosis vs. male meiosis, even though they have very distinct eggs vs. sperm. This renders symmetry of meiosis as another failed criterion for distinguishing females from males.

Asymmetrical female meiosis is by far the most reliable way of distinguishing the sexes when looking across all eukaryotes. However, exceptions to this criterion have arisen independently in many plants and most large multicellular stramenopiles. Unlike in physics, in the evolution of sex, the important exceptions are not a breaking of symmetry but, instead, the establishment of unexpected symmetry, here in the guise of symmetrical female meiosis. Only in sciarid flies, sedges, and a few flowering plants related to heaths, with apparently no other exceptions amongst eukaryotes, is male meiosis asymmetric. By contrast, female meiosis has become symmetric in many lycophytes and phaeophytes, comprising two very unrelated taxa. Thus, although females are ancestral to males amongst all eukaryotes (all-female lineages exist but all-male lineages cannot exist), females in two very distinct lineages appear to have converged on a symmetrical condition, rendering impossible the concept of a universal character to distinguish females from males across all eukaryotes. Compounding this problem, metazoan sperm ontogeny is asymmetrical, albeit not at the stage of meiosis but soon thereafter when large portions of the cytoplasm are parsed off as a residual body without a nucleus. Maybe the apparent symmetry in metazoan male meiosis is a heterochronic shift from that of female meiosis, in which asymmetries in males have been deferred to a later stage of development (i.e. after meiosis II). Even more problematic for using symmetry to distinguish the sexes, separate haploid females and males (megagametophytes and microgameophytes) appear to exist in many bryophytes and stramenopiles, although without there being separate female and male forms of meiosis and without the existence of polar bodies or polar nuclei.

'The origins of asymmetric female meiosis in animals and seed plants were ancient events' (Haig, 2010: 409). But did this asymmetry in female

meiosis precede the deep evolutionary split in eukaryotes between unikonts and bikonts? Most evolutionary biologists consider that this asymmetry in female meiosis arose in conjunction with or as a result of the transition from isogamy to anisogamy in eukaryotes. Yet the huge number of exceptions to asymmetrical female meiosis, especially in bikonts, such as plants and stramenopiles, provides evidence that asymmetrical female meiosis may not be ancient, and may have arisen independently within and between different eukaryotic supergroups. Independent evolutionary origins of asymmetrical female meiosis and anisogamy mean that any delineation of female vs. male based on these characters is artificial, that is analogy rather than homology.

The more organisms that we examine, the more we are convinced of the arbitrariness of how humans have classified and designated the two sexes, female and male, with exceptional cases in all three eukaryotic supergroups that contain massively multicellular individuals: Ophisthokonta, Archaeplastida, and the SAR clade (which includes stramenopiles) *sensu* Simpson & Roger (2004), notwithstanding the classification critiques of Kim & Graham (2008). Also note that asymmetrical meiosis occurs in some unicellular eukaryotes, such as the stramenopile *Paramecium* (Hiwatashi *et al.*, 1985). Hood-Williams (1996) argued that the distinction between sex and gender may be crumbling and that universal differences between the sexes is illusory. The lack of consistent differences between the sexes can be translated into there being no essential differences between females and males, invoking feminist notions of essentialism. As anti-essentialist feminist evolutionary biologists, we are tickled by this conclusion. Colker (1994) argued in *Pregnant Men* that the consideration of biological differences between the sexes can ultimately be anti-essentialist. In an evolutionary context, Gowaty and Hubbell provided an anti-essentialist perspective for differences between females and males, including providing an alternative theory to evolution of anisogamy by 'mak[ing] no assumptions about underlying sex differences' (Gowaty & Hubbell, 2009: 10021).

Although we typically think of females and males as being well-defined categories across all three eukaryotic supergroups that contain massively multicellular taxa, namely animals, plants, and brown algae (Ophisthokonta, Archaeplastida, and Heterokonta), all of the above criteria for differences between females vs. males are illusory and/or inconsistent. Amongst eukaryotes, there is no essential/universal difference between females and males.

ACKNOWLEDGEMENTS

Joe Williams, Scott Russell, Gary Saunders, Edie Taylor, Karl Niklas, and two anonymous reviewers provided extremely helpful feedback. The Natural Sciences and Engineering Council of Canada (NSERC) provided a Discovery Grant (#341399) to RG that funded this work.

REFERENCES

- Abiko M, Furuta K, Yamauchi Y, Fujita C, Taoka M, Isobe T, Okamoto T. 2013.** Identification of proteins enriched in rice egg or sperm cells by single-cell proteomics. *PLoS ONE* **8**: e69578.
- Ahmed S, Cock JM, Pessia E, Luthringer R, Cormier A, Robuchon M, Sterck L, Peters AF, Dittami SM, Corre E, Valero M, Aury J-M, Roze D, Van de Peer Y, Bothwell J, Marais GAB, Coelho SM. 2014.** A haploid system of sex determination in the brown alga *Ectocarpus* sp. *Current Biology* **24**: 1945–1957.
- Allen CE. 1917.** A chromosome difference correlated with sex differences in *Sphaerocarpos*. *Science* **46**: 466.
- Allen CE. 1945.** The genetics of bryophytes. *II. Botanical Review* **11**: 260–287.
- Alves MJ, Coelho MM, Collares-Pereira MJ. 1998.** Diversity in the reproductive modes of females of the *Rutilus alburnoides* complex (Teleostei, Cyprinidae): a way to avoid the genetic constraints of uniparentalism. *Molecular Biology and Evolution* **15**: 1233–1242.
- Ausió J, González-Romero R, Woodcock CL. 2014.** Comparative structure of vertebrate sperm chromatin. *Journal of Structural Biology* **188**: 142–155.
- Austin CR. 1965.** *Fertilization*. Edgewood Cliffs, NJ: Prentice-Hall.
- Bachtrog D, Kirkpatrick M, Mank JE, McDaniel SF, Pires JC, Rice WR, Valenzuela N. 2011.** Are all sex chromosomes created equal? *Trends in Genetics* **27**: 350–357.
- Baer B, Collins J, Maalaps K, den Boer SPA. 2016.** Sperm use economy of honeybee (*Apis mellifera*) queens. *Ecology and Evolution* **6**: 2877–2885.
- Barr CM, Neiman M, Taylor DR. 2005.** Inheritance and recombination of mitochondrial genomes in plants, fungi and animals. *New Phytologist* **168**: 39–50.
- Bateman RM, DiMichele WA. 1994.** Heterospory: the most interactive key innovation in the evolutionary history of the plant kingdom. *Biological Reviews of the Cambridge Philosophical Society* **69**: 345–417.
- Becwar MR, Blush TD, Brown DW, Chesick EE. 1991.** Multiple paternal genotypes in embryogenic tissue derived from individual immature loblolly pine seeds. *Plant Cell Tissue and Organ Culture* **26**: 37–44.
- Bell G. 1978.** Evolution of anisogamy. *Journal of Theoretical Biology* **73**: 247–270.
- Bell G. 1982.** *The masterpiece of nature: the evolution and genetics of sexuality*. Berkeley, CA: University of California Press.
- Bell PR, Hemsley AR. 2000.** *Green plants: their origin and diversity, 2nd edn*. Cambridge: Cambridge University Press.
- Billiard S, López-Villavicencio M, Devier B, Hood ME, Fairhead C, Giraud T. 2011.** Having sex, yes, but with whom? Inferences from fungi on the evolution of anisogamy and mating types. *Biological Reviews* **86**: 421–442.
- Bischler H. 1986.** *Marchantia polymorpha* L. s. lat. karyotype analysis. *Journal of the Hattori Botanical Laboratory* **60**: 105–107.
- Bjork A, Pitnick S. 2006.** Intensity of sexual selection along the anisogamy-isogamy continuum. *Nature* **441**: 742–745.
- Blackmore S, Takahashi M, Uehara K, Wortley AH. 2012.** Development of megaspores and microspores in *Isoetes japonica* A. Br. (Lycopodiophyta: Isoetaceae). *Grana* **51**: 84–96.
- Blomstedt CK, Knox RB, Singh MB. 1996.** Generative cells of *Lilium longiflorum* possess translatable mRNA and functional protein synthesis machinery. *Plant Molecular Biology* **31**: 1083–1086.
- Bogart JP, Bi K, Fu JZ, Noble DWA, Niedzwiecki J. 2007.** Unisexual salamanders (genus *Ambystoma*) present a new reproductive mode for eukaryotes. *Genome* **50**: 119–136.
- Bomfleur B, McLoughlin S, Vajda V. 2014.** Fossilized nuclei and chromosomes reveal 180 million years of genomic stasis in royal ferns. *Science* **343**: 1376–1377.
- Booth W, Schuett GW, Ridgway A, Buxton DW, Castoe TA, Bastone G, Bennett C, McMahan W. 2014.** New insights on facultative parthenogenesis in pythons. *Biological Journal of the Linnean Society* **112**: 461–468.
- Brawley SH, Quatrano RS, Wetherbee R. 1977.** Fine-structural studies of gametes and embryo of *Fucus vesiculosus* L. (Phaeophyta). 3. Cytokinesis and multicellular embryo. *Journal of Cell Science* **24**: 275–294.
- Brown RC, Lemmon BE. 2000.** The cytoskeleton and polarization during pollen development in *Carex blanda* (Cyperaceae). *American Journal of Botany* **87**: 1–11.
- Buntrock L, Marec F, Krueger S, Traut W. 2012.** Organ growth without cell division: somatic polyploidy in a moth, *Ephestia kuehniella*. *Genome* **55**: 755–763.
- Calkins GN. 1901.** *The protozoa*. New York, NY: Columbia University Press.
- Carmichael JS, Friedman WE. 1995.** Double fertilization in *Gnetum gnemon*: the relationship between the cell cycle and sexual reproduction. *Plant Cell* **7**: 1975–1988.
- Chamberlain CJ. 1919.** *The living cycads*. Chicago, IL: University of Chicago Press.
- Chamberlain CJ. 1935.** *Gymnosperms: structure and evolution*. Chicago, IL: University of Chicago Press.
- Charlesworth D, Charlesworth B, Marais G. 2005.** Steps in the evolution of heteromorphic sex chromosomes. *Heredity* **95**: 118–128.
- Cichan MA, Taylor TN, Brauer DF. 1984.** Ultrastructural studies of *in situ* Devonian spores: *Protobarinophyton pennsylvanicum* Brauer. *Review of Palaeobotany and Palynology* **41**: 167–175.
- Clayton MN. 1984.** Evolution of the Phaeophyta with particular reference to the Fucales. *Progress in Phycological Research* **3**: 11–46.

- Cloney RA, Abbott LC. 1980.** Spermatozoa of ascidians: acrosome and nuclear envelope. *Cell and Tissue Research* **206**: 261–270.
- Cobb M. 2006.** *The egg & sperm race: the seventeenth-century scientists who unravelled the secrets of sex, life and growth*. London: Pocket Books.
- Colker R. 1994.** *Pregnant men*. Bloomington, IN: Indiana University Press.
- Collas P, Poccia D. 1998.** Remodeling the sperm nucleus into a male pronucleus at fertilization. *Theriogenology* **49**: 67–81.
- Conlon I, Raff M. 1999.** Size control in animal development. *Cell* **96**: 235–244.
- Corriveau JL, Coleman AW. 1988.** Rapid screening method to detect potential biparental inheritance of plastid DNA and results for over 200 angiosperm species. *American Journal of Botany* **75**: 1443–1458.
- Cox PA, Sethian JA. 1984.** Search, encounter rates, and the evolution of anisogamy. *Proceedings of the National Academy of Sciences of the United States of America* **81**: 6078–6079.
- Crouse HV. 1960.** The controlling element in sex chromosome behavior in *Sciara*. *Genetics* **45**: 1429–1443.
- Czaker R. 2001.** Newly identified ‘wanderer’ cells in the dicyemid mesozoan *Kantharella antarctica*: a new mode of reproduction? *Journal of Submicroscopic Cytology and Pathology* **33**: 323–328.
- Dacks JB, Kasinsky HE. 1999.** Nuclear condensation in protozoan gametes and the evolution of anisogamy. *Comparative Biochemistry and Physiology. A. Molecular & Integrative Physiology* **124**: 287–295.
- Eames AJ. 1936.** *The morphology of vascular plants, lower groups (Psilophytales to Filicales)*. New York, NY: McGraw-Hill.
- Eirin-Lopez JM, Ausió J. 2009.** Origin and evolution of chromosomal sperm proteins. *BioEssays* **31**: 1062–1070.
- Fausto-Sterling A. 1985.** *Myths of gender: biological theories about women and men*. New York, NY: Basic Books.
- Fausto-Sterling A. 2000.** *Sexing the body: gender politics and the construction of sexuality*. New York, NY: Basic Books.
- Fawcett DW, Ito S. 1965.** The fine structure of bat spermatozoa. *American Journal of Anatomy* **116**: 567–609.
- Friedman WE. 1990.** Sexual reproduction in *Ephedra nevadensis* (Ephedraceae): further evidence of double fertilization in a nonflowering seed plant. *American Journal of Botany* **77**: 1582–1598.
- Friedman WE. 2015.** Development and evolution of the female gametophyte and fertilization process in *Welwitschia mirabilis* (Welwitschiaceae). *American Journal of Botany* **102**: 312–324.
- Friedman WE, Gillford EM. 1997.** Development of the male gametophyte of *Ginkgo biloba*: a window into the reproductive biology of early seed plants. In: Hori T, Ridge RW, Tulecke W, Del Tredici P, Trémouillaux-Guillen J, Tobe H, eds. *Ginkgo biloba, a global treasure: from biology to medicine*. Tokyo: Springer-Verlag, 29–49.
- Furness CA. 2009.** Pollen evolution and development in Ericaceae, with particular reference to pseudomonads and variable pollen sterility in Styphelioideae. *International Journal of Plant Sciences* **170**: 476–495.
- Furness CA, Rudall PJ. 2011.** Selective microspore abortion correlated with aneuploidy: an indication of meiotic drive. *Sexual Plant Reproduction* **24**: 1–8.
- Garrido-Ramos MA, Stewart DT, Sutherland BW, Zouros E. 1998.** The distribution of male-transmitted and female-transmitted mitochondrial DNA types in somatic tissues of blue mussels: implications for the operation of doubly uniparental inheritance of mitochondrial DNA. *Genome* **41**: 818–824.
- Goday C, Esteban MR. 2001.** Chromosome elimination in sciarid flies. *BioEssays* **23**: 242–250.
- Gomendio M, Roldan ERS. 1991.** Sperm competition influences sperm size in mammals. *Proceedings of the Royal Society B-Biological Sciences* **243**: 181–185.
- Gorelick R. 2001.** Cycad prepollen: description and possible evolutionary consequences of zooidogamy. *Cycad Newsletter* **24**: 12–14.
- Gorelick R. 2003.** Evolution of dioecy and sex chromosomes via methylation driving Muller’s ratchet. *Biological Journal of the Linnean Society* **80**: 353–368.
- Gorelick R. 2005.** Theory for why dioecious plants have equal length sex chromosomes. *American Journal of Botany* **92**: 979–984.
- Gorelick R. 2012a.** Meiosis is not gender neutral. *BioScience* **62**: 623–624.
- Gorelick R. 2012b.** Mitosis circumscribes individuals; sex creates new individuals. *Biology & Philosophy* **27**: 871–890.
- Gorelick R. 2014.** Do Micrognathozoa have micro-genomes? *Biological Journal of the Linnean Society* **112**: 640–644.
- Gorelick R, Carpinone J. 2009.** Origin and maintenance of sex: the evolutionary joys of self sex. *Biological Journal of the Linnean Society* **98**: 707–728.
- Gorelick R, Carpinone J, Derraugh LJ. 2013.** Fundamental differences between females and males? In: Ah-King M, ed. *Challenging popular myths of sex, gender, and biology*. Heidelberg: Springer, 9–22.
- Gowaty PA, Hubbell SP. 2009.** Reproductive decisions under ecological constraints: it’s about time. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 10017–10024.
- deGraaf R 1672.** *De mulierum organis generationi inservientibus tractatus novus [New treatise concerning the generative organs of women]*. Hack: Leiden.
- Grier HJ. 1975.** Aspects of germinal cyst and sperm development in *Poecilia latipinna* (Teleostei: Poeciliidae). *Journal of Morphology* **146**: 229–250.
- Grier HJ. 1976.** Sperm development in teleost *Oryzias latipes*. *Cell and Tissue Research* **168**: 419–431.
- Haig D. 1986.** Conflicts among megaspores. *Journal of Theoretical Biology* **123**: 471–480.
- Haig D. 1993.** The evolution of unusual chromosomal systems in sciarid flies: intragenomic conflict and the sex ratio. *Journal of Evolutionary Biology* **6**: 249–261.

- Haig D.** 2010. Games in tetrads: segregation, recombination, and meiotic drive. *American Naturalist* **176**: 404–413.
- Harper MJK, Bennett JP, Bournnell JC, Rowson LEA.** 1960. An autoradiographic method for the study of egg transport in the rabbit fallopian tube. *Reproduction* **1**: 249–267.
- Hart PE, Wolniak SM.** 1998. Spermiogenesis in *Marsilea vestita*: a temporal correlation between centrin expression and blepharoplast differentiation. *Cell Motility and the Cytoskeleton* **41**: 39–48.
- Hart PE, Wolniak SM.** 1999. Molecular cloning of a centrin homolog from *Marsilea vestita* and evidence for its translational control during spermiogenesis. *Biochemistry and Cell Biology – Biochimie et Biologie Cellulaire* **77**: 101–108.
- Hipp AL.** 2007. Non-uniform processes of chromosome evolution in sedges (*Carex*: Cyperaceae). *Evolution* **61**: 2175–2194.
- Hird MJ.** 2004. *Sex, gender, and science*. Basingstoke: Palgrave Macmillan.
- Hiwatashi K, Kitamura A** 1985. Fertilization in *Paramecium*. In: Metz CB, Monroy A, eds. *Biology of fertilization, Vol. 1. Model organisms and oogenesis*. Orlando, FL: Academic Press, 57–85.
- Ho H-C.** 2010. Redistribution of nuclear pores during formation of the redundant nuclear envelope in mouse spermatids. *Journal of Anatomy* **216**: 525–532.
- Hoekstra RF.** 2011. Nucleo-cytoplasmic conflict and the evolution of gamete dimorphism. In: Togashi T, Cox PA, eds. *The evolution of anisogamy: a fundamental phenomenon in sexual selection*. Cambridge: Cambridge University Press, 111–130.
- Hölldobler B, Wilson EO.** 1990. *The ants*. Cambridge: Harvard University Press.
- Hood-Williams J.** 1996. Goodbye to sex and gender. *Sociological Review* **44**: 1–16.
- Immler S, Pitnick S, Parker GA, Durrant KL, Lüpold S, Calhim S, Birkhead TR.** 2011. Resolving variation in the reproductive tradeoff between sperm size and number. *Proceedings of the National Academy of Sciences of the United States of America* **108**: 5325–5330.
- Jacob F.** 1977. Evolution and tinkering. *Science* **196**: 1161–1166.
- Jannotti-Passos LK, Souza CP, Parra JC, Simpson AJG.** 2001. Biparental mitochondrial DNA inheritance in the parasitic trematode *Schistosoma mansoni*. *Journal of Parasitology* **87**: 79–82.
- Jordan-Young RM.** 2010. *Brainstorm: the flaws in the science of sex differences*. Cambridge, MA: Harvard University Press.
- Khanna KR.** 1971. Sex chromosomes in bryophytes. *Nucleus* **14**: 14–23.
- Kim E, Graham LE.** 2008. EEF2 analysis challenges the monophyly of Archaeplastida and Chromalveolata. *PLoS ONE* **3**: e0002621.
- Kirpes CC, Clark LG, Lersten NR.** 1996. Systematic significance of pollen arrangement in microsporangia of Poaceae and Cyperaceae: review and observations on representative taxa. *American Journal of Botany* **83**: 1609–1622.
- Klekowski EJ.** 1988. *Mutation, developmental selection, and plant evolution*. New York, NY: Columbia University Press.
- Knight CA, Beaulieu JM.** 2008. Genome size scaling through phenotype space. *Annals of Botany* **101**: 759–766.
- Knowlton N.** 1974. Evolution of gamete dimorphism. *Journal of Theoretical Biology* **46**: 283–285.
- Komaru A, Kawagishi T, Konishi K.** 1998. Cytological evidence of spontaneous androgenesis in the freshwater clam *Corbicula leana* Prime. *Development Genes and Evolution* **208**: 46–50.
- Lee HO, Davidson JM, Duronio RJ.** 2009. Endoreplication: polyploidy with purpose. *Genes & Development* **23**: 2461–2477.
- Lehtonen J, Parker GA, Schärer L.** 2016. Why anisogamy drives ancestral sex roles. *Evolution* **70**: 1129–1135.
- Lessells CM, Snook RR, Hosken DJ.** 2009. The evolutionary origin and maintenance of sperm: selection for a small, motile gamete mating type. In: Birkhead TR, Hosken DJ, Pitnick S, eds. *Sperm biology: an evolutionary perspective*. Burlington, ON: Academic Press, 43–67.
- Lloyd DG.** 1980. Sexual strategies in plants. III. A quantitative method for describing the gender of plants. *New Zealand Journal of Botany* **18**: 103–108.
- Lomax BH, Woodward FI, Leitch IJ, Knight CA, Lake JA.** 2009. Genome size as a predictor of guard cell length in *Arabidopsis thaliana* is independent of environmental conditions. *New Phytologist* **181**: 311–314.
- Maciak S, Michalak P.** 2015. Cell size and cancer: a new solution to Peto's paradox? *Evolutionary Applications* **8**: 2–8.
- Mantovani B, Scali V.** 1992. Hybridogenesis and androgenesis in the stick-insect *Bacillus rossius-grandii benazzii* (Insecta, Phasmoda). *Evolution* **46**: 783–796.
- Margulis L, Corliss JO, Melkonian M, Chapman DJ, eds.** 1990. *Handbook of Protozoists: The structure, cultivation, habitats and life histories of the eukaryotic microorganisms and their descendants exclusive of animals, plants and fungi: a guide to the algae, ciliates, foraminifera, sporezoa, water molds, slime molds and other protozoists*. Boston, MA: Jones and Bartlett.
- Markow TA, Beall S, Castrezana S.** 2012. The wild side of life *Drosophila* reproduction in nature. *Fly* **6**: 98–101.
- Masterson J.** 1994. Stomatal size in fossil plants: evidence for polyploidy in majority of angiosperms. *Science* **264**: 421–424.
- Mattei X.** 1991. Spermatozoon ultrastructure and its systematic implications in fishes. *Canadian Journal of Zoology - Revue Canadienne de Zoologie* **69**: 3038–3055.
- Matzke-Karasch R.** 2005. Giant spermatozoon coiled in small egg: fertilization mechanisms and their implications for evolutionary studies on Ostracoda (Crustacea). *Journal of Experimental Zoology Part B-Molecular and Developmental Evolution* **304B**: 129–149.
- Mauseth JD** 2009. *Botany: an introduction to plant biology (4th edition)*. Sudbury, MA: Jones & Bartlett.

- Mayhew R. 2004.** *The female in Aristotle's biology: reason or rationalization*. Chicago, IL: University of Chicago Press.
- Maynard Smith J. 1978.** *The evolution of sex*. Cambridge: Cambridge University Press.
- McKone MJ, Halpern SL. 2003.** The evolution of androgenesis. *American Naturalist* **161**: 641–656.
- Mittwoch U. 2000.** Three thousand years of questioning sex determination. *Cytogenetics and Cell Genetics* **91**: 186–191.
- Mogensen HL. 1996.** The hows and whys of cytoplasmic inheritance in seed plants. *American Journal of Botany* **83**: 383–404.
- Morbelli MA, Rowley JR, El-Ghazaly G. 2003.** Stages in development of *Selaginella diffusa* megaspores. *Journal of Plant Research* **116**: 57–64.
- Morrow EH. 2004.** How the sperm lost its tail: the evolution of aflagellate sperm. *Biological Reviews* **79**: 795–814.
- Nagasato C, Motomura T, Ichimura T. 2001.** Degeneration and extrusion of nuclei during oogenesis in *Silvetia babingtonii*, *Cystoseira hakodatensis* and *Sargassum confusum* (Fucales, Phaeophyceae). *Phycologia* **40**: 411–420.
- Nakashima Y, Kuwamura T, Yogo Y. 1996.** Both-ways sex change in monogamous coral gobies, *Gobiodon* spp. *Environmental Biology of Fishes* **46**: 281–288.
- Norstog KJ. 1993.** Spermatogenesis in *Microcycas*: evolutionary significance of male gametes of seed plants. In: Stevenson DW, Norstog KJ, eds. *The biology, structure, and systematics of the Cycadales*. Milton, QLD : Palm & Cycad Societies of Australia, 270–278.
- Ottolini CS, Newnham LJ, Capalbo A, Natesan SA, Joshi HA, Cimadomo D, Griffin DK, Sage K, Summers MC, Thornhill AR, Housworth E, Herbert AD, Rienzi L, Ubaldi FM, Handyside AH, Hoffmann ER. 2015.** Genome-wide maps of recombination and chromosome segregation in human oocytes and embryos show selection for maternal recombination rates. *Nature Genetics* **47**: 727–735.
- Parker GA. 1982.** Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *Journal of Theoretical Biology* **96**: 281–294.
- Parker GA, Smith VGF, Baker RR. 1972.** Origin and evolution of gamete dimorphism and the male-female phenomenon. *Journal of Theoretical Biology* **36**: 529–553.
- Parker GA, Immler S, Pitnick S, Birkhead TR. 2010.** Sperm competition games: sperm size (mass) and number under raffle and displacement, and the evolution of *P₂*. *Journal of Theoretical Biology* **264**: 1003–1023.
- Pichot C, Maataoui M, Raddi S, Raddi P. 2001.** Surrogate mother for endangered *Cupressus*. *Nature* **412**: 39.
- Piper R. 2013.** *Animal Earth: the amazing diversity of living animals*. New York, NY: Thomas & Hudson.
- Pitnick S. 1996.** Investment in testes and the cost of making long sperm in *Drosophila*. *American Naturalist* **148**: 57–80.
- Pitnick S, Markow TA. 1994.** Large-male advantages associated with costs of sperm production in *Drosophila hydei*, a species with giant sperm. *Proceedings of the National Academy of Sciences of the United States of America* **91**: 9277–9281.
- Pitnick S, Spicer GS, Markow TA. 1995.** How long is a giant sperm? *Nature* **375**: 109.
- Pitnick S, Hosken DJ, Birkhead TR. 2009.** Sperm morphological diversity. In: Birkhead TR, Hosken DJ, Pitnick S, eds. *Sperm biology, an evolutionary perspective*. Burlington, ON: Academic Press, 69–149.
- Polilov AA. 2012.** The smallest insects evolve anucleate neurons. *Arthropod Structure & Development* **41**: 29–34.
- Poort RJ, Visscher H, Dilcher DL. 1996.** Zoidogamy in fossil gymnosperms: the centenary of a concept, with special reference to prepollen of late Paleozoic conifers. *Proceedings of the National Academy of Sciences of the United States of America* **93**: 11713–11717.
- Raikov IB. 1982 [1978].** *The protozoan nucleus: morphology and evolution*. Vienna : Springer-Verlag.
- Ramm SA, Stockley P. 2010.** Sperm competition and sperm length influence the rate of mammalian spermatogenesis. *Biology Letters* **6**: 219–221.
- Rasmussen HN, Rasmussen FN. 2009.** Orchid mycorrhiza: implications of a mycophagous life style. *Oikos* **118**: 334–345.
- Reunov AA. 2005.** Problem of terminology in the characteristics of spermatozoa of multicellular animals. *Ontogenesis* **36**: 403–421.
- Rohde K, Faubel A. 1998.** Spermatogenesis of *Haplopharynx rostratus* (Platyhelminthes, Haplopharyngida). *Belgian Journal of Zoology* **128**: 177–188.
- Romanes GJ. 1910.** *Darwin and after Darwin: an exposition of the Darwinian theory and a discussion of post-Darwinian questions, 4th edn*. Chicago, IL : Open Court Publishing Company.
- Roughgarden J, Iyer P. 2011.** Contact, not conflict, causes the evolution of anisogamy. In: Togashi T, Cox PA, eds. *The evolution of anisogamy: a fundamental phenomenon in sexual selection*. Cambridge: Cambridge University Press, 96–110.
- Sagata N. 1996.** Meiotic metaphase arrest in animal oocytes: its mechanisms and biological significance. *Trends in Cell Biology* **6**: 22–28.
- San Martin JAB, Andrade CGT, Mastroberti AA, Mariath JED, Vanzela ALL. 2013.** Asymmetric cytokinesis guide the development of pseudomonads in *Rhynchospora pubera* (Cyperaceae). *Cell Biology International* **37**: 203–212.
- Scagel RF, Bandoni Robert J, Rouse GE, Schofield WB, Stein JR, Taylor TMC. 1966.** *An evolutionary survey of the plant kingdom*. Belmont, MA: Wadsworth Publishing.
- Schärer L, Da Lage J-L, Joly D. 2008.** Evolution of testicular architecture in the Drosophilidae: a role for sperm length. *BMC Evolutionary Biology* **8**: 143.
- Schatten H, Chakrabarti A. 2000.** Fertilization in invertebrates. In: Tarín JJ, Cano A, eds. *Fertilization in protozoa and metazoan animals: cellular and molecular aspects*. Berlin: Springer-Verlag, 27–87.
- Scheibinger L. 1993.** *Nature's body*. London: Pandora.
- Schlupp I. 2005.** The evolutionary ecology of gynogenesis. *Annual Review of Ecology Evolution and Systematics* **36**: 399–417.
- Schuh M, Ellenberg J. 2008.** A new model for asymmetric spindle positioning in mouse oocytes. *Current Biology* **18**: 1986–1992.

- Schultz RJ. 1967.** Gynogenesis and triploid in the viviparous fish *Poeciliopsis*. *Science* **157**: 1564–1567.
- Shah C, VanGompel MJW, Naeem V, Chen Y, Lee T, Angeloni N, Wang Y, Xu EY. 2010.** Widespread presence of human *BOULE* homologs among animals and conservation of their ancient reproductive function. *PLoS Genetics* **6**: e1001022.
- Simpson AGB, Roger AJ. 2004.** The real ‘kingdoms’ of eukaryotes. *Current Biology* **14**: R693–R696.
- Singh H. 1978.** *Embryology of gymnosperms*. Berlin: Gerbrüder Borntraeger.
- Smith H. 2006.** Sperm motility and MSP In: Moerman DG, Kramer JM, eds. *WormBook*. http://www.wormbook.org/chapters/www_spermmotilityMSP/spermmotilityMSP.pdf. DOI: 10.1895/wormbook.1.68.1.
- Smoot EL, Taylor TN. 1986.** Evidence of simple polyembryony in Permian seeds from Antarctica. *American Journal of Botany* **73**: 1079–1081.
- Solari AJ. 1994.** *Sex chromosomes and sex determination in vertebrates*. Boca Raton, FL: CRC Press.
- Sood SK, Rao PRM. 1988.** Studies in the embryology of the diandrous orchid *Cypripedium cordigerum* (Cypripediaceae, Orchidaceae). *Plant Systematics and Evolution* **160**: 159–168.
- Southworth D, Strout G, Russell SD. 1997.** Freeze-fracture of sperm of *Plumbago zeylanica* L. in pollen and in vitro. *Sexual Plant Reproduction* **10**: 217–226.
- Stenberg P, Saura A. 2009.** Cytology of asexual animals. In: Schön I, Martens K, van Dijk P, eds. *Lost sex: the evolutionary biology of parthenogenesis*. Heidelberg: Springer, 63–74.
- Stewart WN. 1951.** A new *Pachyteta* from the Berryville locality of southeastern Illinois. *American Midland Naturalist* **46**: 717–742.
- Tandler B, Moriber LG. 1974.** Ultrastructure of pseudochromosomes and calottes in spermatogenic cells of the backswimmer, *Notonecta undulata* (Say). *Tissue and Cell* **6**: 557–572.
- Taylor PE, Kenrick J, Blomstedt CK, Knox RB. 1991.** Sperm cells of the pollen tubes of *Brassica*: ultrastructure and isolation. *Sexual Plant Reproduction* **4**: 226–234.
- Tinti F, Scali V. 1992.** Genome exclusion and gametic DAPI-DNA content in the hybridogenetic *Bacillus rossius-grandii benazzi* complex (Insecta Phasmatodea). *Molecular Reproduction and Development* **33**: 235–242.
- Togashi T, Bartlett JL. 2011.** Evolution of anisogamy and related phenomena in marine green algae. In: Togashi T, Cox PA, eds. *The evolution of anisogamy: a fundamental phenomenon in sexual selection*. Cambridge: Cambridge University Press, 194–242.
- Tomlinson PB, Huggett BA. 2012.** Cell longevity and sustained primary growth in palm stems. *American Journal of Botany* **99**: 1891–1902.
- Trovato M, Mazzei V, Sinatra F, Longo G. 2011.** Presence of F-actin in sperm head of *Armadillidium peraccae* (Isopoda, Oniscidea). *Tissue and Cell* **43**: 304–310.
- Wachtel SS, Tiersch TR. 1994.** The search for the male-determining gene. In: Wachtel SS, ed. *Molecular genetics of sex determination*. San Diego, CA: Academic Press, 1–22.
- Weismann A. 1886 [1889].** The significance of sexual reproduction on the theory of natural selection [translator: S. Schöland]. In: *Essays upon heredity and kindered biological problems - Volume 1*. Oxford: Clarendon Press. 251–332.
- White-Cooper H, Bausek N. 2010.** Evolution and spermatogenesis. *Philosophical Transactions of the Royal Society Series B, Biological Sciences* **365**: 1465–1480.
- Williams JH. 2008.** Novelty of the flowering plant pollen tube underlie diversification of a key life history stage. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 11259–11263.
- Williams JH, Friedman WE. 2002.** Identification of diploid endosperm in an early angiosperm lineage. *Nature* **415**: 522–526.
- Yadegari R, Drews GN. 2004.** Female gametophyte development. *Plant Cell* **16**: S133–S141.
- Yushin VV, Malakhov VV. 2014.** The origin of nematode sperm: progenesis at the cellular level. *Russian Journal of Marine Biology* **40**: 71–81.
- Zanders SE, Malik HS. 2015.** Chromosome segregation: human female meiosis breaks all the rules. *Current Biology* **25**: R654–R656.
- Zhang G, Gifford DJ, Cass DD. 1993.** RNA and protein synthesis in sperm cells isolated from *Zea mays* L. pollen. *Sexual Plant Reproduction* **6**: 239–243.
- Zhao X, Yang N, Wang T. 2013.** Comparative proteomic analysis of generative and sperm cells reveals molecular characteristics associated with sperm development and function specialization. *Journal of Proteome Research* **12**: 5058–5071.
- Zouros E, Freeman KR, Ball AO, Pogson GH. 1992.** Direct evidence for extensive paternal mitochondrial DNA inheritance in the marine mussel *Mytilus*. *Nature* **359**: 412–414.

APPENDIX

GLOSSARY

| | |
|-------------------------------|---|
| Amphimictic | Obligately outcrossing. Almost antonyms: Automictic and Autogamic |
| Androgenetic | One or more sperm fertilize an egg but the egg nucleus then becomes degraded or ejected, much as a polar nucleus, and only the one or two sperm nuclei (not the egg) contribute their chromosomes to the next diploid generation |
| Anisogamous | Obvious phenotypic difference between eggs and sperm of a given species. These differences are often in size and shape. Antonym: Isogamous. See also 'Isogamous' for a slightly different definition |
| Automictic | The next diploid generation is formed from the products of a single meiotic division. Automixis could be as a result of terminal fusion, central fusion, premeiotic doubling, or gamete doubling |
| Central cell | The largest cell in most angiosperm female haploid stages (megagametophytes). In angiosperms, double fertilization of the central cell produces endosperm. In many angiosperms, the central cell contains a pair of haploid nuclei, although the number of haploid nuclei varies across taxa |
| Chalazal | Spatial end of the haploid female stage in seed plants that is farthest from where the pollen tube arrives with two sperm cells |
| Cytogenesis | Division of cells, which may be mitotic or meiotic. Cytogenesis can be without karyogenesis, resulting in one cell with a nucleus and one without, as in production of sperm cells and residual bodies in metazoans (amitotic) and companion cells and sieve cell in angiosperms (mitotic) |
| Endomitosis | Duplication of all chromosomes without nuclear division. See Endoploid |
| Endoploid | Tissues that have undergone one or more rounds of endomitosis, that is one or more rounds of chromosomal duplication without nuclear division. See Endomitosis |
| Endosperm | Tissue resulting from double fertilization in angiosperms of the central cell that provides nourishment for the developing embryo. Endosperm is triploid in many taxa |
| Gamete doubling | Duplication of all chromosomes (endomitosis) immediately <u>after</u> meiosis but without an intervening nuclear division. Gamete doubling is a heterochronic variation on premeiotic doubling, but in premeiotic doubling all chromosomes are duplicated immediately <u>before</u> the start of meiosis |
| Gametophyte | Haploid stage of life cycle. Antonym: Sporophyte. Meiosis and karyogamy form transitions between gametophyte and sporophyte generations. Given the prevalence of coenocytic cells, haploid refers here to nuclei, not cells. Given the prevalence of endoploidy in different tissues, gametophyte refers to having haploid nuclei in those tissues that undergo mitosis to form eggs and/or sperm |
| Gynogenetic | One or more sperm fertilize an egg, although all sperm then become degraded or ejected, much as a polar nucleus, and only the one or two egg nuclei (not the sperm) contribute their chromosomes to the next diploid generation |
| Heteromorphic sex Chromosomes | Sex chromosomes (XY, ZW, or UV) that are of different length in females vs. males. Antonym: Homomorphic sex chromosomes |
| Heterosporous | Meiosis that produces four morphologically and/or functionally different cells (called spores). See Intrasporangial heterospory. Antonym: Homosporous |
| Holocentric chromosome | Chromosome possessing a diffuse centromere |
| Homosporous | Meiosis that produces four morphologically and functionally indistinguishable cells, called spores. Each homosporous spore develops into a gametophyte that produces both eggs and sperm. Antonym: Heterosporous |
| Hybridogenetic | Life cycle with normal karyogamy but in which all paternal chromosomes are eliminated during egg gametogenesis |
| Intrasporangial heterospory | A single diploid organ (a sporangium) in which the cells undergo meiosis to produce multiple types of spores. The different types of spores are usually female spores and male spores. Intrasporangial heterospory can be a result of separate diploid cells undergoing female vs. male meiosis or a single meiotic cell producing both female and male spores |

Appendix. *Continued*

| | |
|----------------------------|---|
| Isogamous | No obvious phenotypic difference between eggs and sperm of a given species. Antonym: Anisogamous. A few authors define isogamous as eggs and sperm being of the same size, even if they are morphologically different, or define Isogamous as ‘investment per gamete by males approaches that by females’ (Bjork & Pitnick, 2006: 742) |
| Karyogamy | Amalgamation of two haploid nuclei to form a zygote. The two haploid nuclei do not so much fuse as have their nuclear membranes dissolved and then replaced by a single nuclear membrane. Gorelick & Carpinone (2009) showed that, immediately following pronuclear association, the two haploid nuclei duplicate their chromosomes; hence, the zygote has four copies of each homologous chromosome. Compare with Plasmogamy |
| Karyogenesis | Division of cell nuclei, which can be in either mitosis or meiosis. Karyogenesis can be without cytogenesis, resulting in coenocytic cells |
| Megagametophyte | Haploid stage that eventually produces eggs, but not sperm. See Gametophyte and compare with Microgametophyte |
| Megaspore | One of the four immediate products of meiosis that can produce a functional female haploid stage, that is produce a megagametophyte |
| Microgametophyte | Haploid stage that eventually produces sperm, but not eggs. See Gametophyte and compare with Megagametophyte |
| Monosporic | Only one of the four products of meiosis develops to form the haploid stage. Compare with Tetrasporic |
| Nucellus | Diploid tissue immediately surrounding female haploid tissue (surrounding megagametophyte) in seed plants |
| Plasmogamy | Sperm cell enters an egg cell but, at least ephemerally, egg and sperm nuclei remain physically separate in egg cytoplasm. Compare with Karyogamy |
| Polar body | Degenerate products of meiosis in females (see Pseudomonad pollen for males). Polar bodies may be haploid or diploid (technically, 2C), depending on whether they are formed in meiosis II or meiosis I. Polar bodies are composed of a nucleus and cell membrane but almost no cytoplasm. Sometimes only polar nuclei are formed if there is meiotic karyogenesis without meiotic cytogenesis |
| Primordial germ cell | Diploid cell whose fate is specified and will undergo meiosis after a few diploid mitotic divisions |
| Pronuclear association | Egg and sperm nuclei within an egg cell that are coming in proximity or touching after plasmogamy and immediately before karyogamy. Given our definition of pronuclei, pronuclear association can be between a pronucleus and a nucleus |
| Pronucleus | Nucleus in which the nuclear membrane (nuclear envelope) has been replaced, albeit without an intervening nuclear division. We think this only happens in males of some taxa, where a nuclear membrane lacking nuclear pores needs to be replaced with a nuclear membrane that contains nuclear pores |
| Pseudomonad pollen | Degeneration of three of the four products of meiosis in pollen formation. Pseudomonad pollen only occurs in very few taxa and is akin to a rare instance of males forming polar bodies |
| Redundant nuclear envelope | Part of the sperm nuclear envelope where all nuclear pores become localized. Redundant nuclear envelopes only occur in some taxa and are always found closest to the flagellum |
| Residual body | An anucleate cell formed in metazoan sperm development. After meiosis to form four immature spermatozoid cells, each haploid cell undergoes an asymmetrical cell division to form a sperm cell with a nucleus and very little cytoplasm and a residual body that lacks a nucleus and contains most of the cytoplasm |
| Siphonogamous | Plants with pollen that germinates into a mostly unbranched pollen tube that does not grow very much, but can become longer as a result of older parts of the pollen tube being emptied of cytoplasm and sealed off. Siphonogamous pollen tubes contain tiny sperm cells that are sessile other than being carried by the pollen tube. Antonym: Zoidogamous |
| Sporophyte | Diploid stage of life cycle. Antonym: Gametophyte. Meiosis and karyogamy form transitions between gametophyte and sporophyte generations. Given the prevalence of coenocytic cells, diploid here refers to nuclei, not cells. Given the prevalence of endoploidy in different tissues, gametophyte refers to having diploid nuclei in those tissues that undergo meiosis |
| Suspended meiosis | A kinder term for what is usually called ‘arrested meiosis’ |

Appendix. *Continued*

| | |
|----------------|---|
| Tetrasporic | All four products of meiosis develop to form the haploid stage. Together, these often form a 'tetrad'. However, as described in the main text, in females, all four products of tetrasporic meiosis are not passed on to the next generation. Compare Tetrasporic with Monosporic |
| UV chromosomes | Sex chromosomes of different length (heteromorphic) when the predominant stage of the life cycle is haploid, as in many mosses, liverworts, and stramenopiles. Cells in the physically small diploid stage contain both U and V chromosomes. Meiosis produces two female haploid spores with U chromosomes and two male haploid spores with V chromosomes |
| Zoidogamous | Plants with pollen (more accurately, pre-pollen) that germinates into a highly branched and highly parasitic male gametophyte that feeds on the female reproductive tissue (nucellus) on which it lands. Zoidogamous pollen tubes and their sperm typically grow orders of magnitude larger than the pollen/pre-pollen cell that they originally grew from. The name zoidogamous is derived from their giant sperm cells that swim to neck cells and then to the egg cell via the sperm's many flagella. Antonym: Siphonogamous |
