

Chapter 2

Fundamental Differences Between Females and Males?

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Hence, in regard to that most difficult question, what are the natural differences between the two sexes—a subject on which it is impossible in the present state of society to obtain complete and correct knowledge—while almost everybody dogmatizes upon it, almost all neglect and make light of the only means by which any partial insight can be obtained by it.

John Stuart Mill [1] (p. 22)

2.1 Introduction

John Stuart Mill's quote from *The Subjugation of Women* is as timely today as it was one and a half centuries ago. He approached differences between females and males from a purely human perspective, focusing on political science and psychology. From a modern perspective, Mill conflated sex and gender and, possibly for that reason, favored the role of nurture in the nature-nurture debates. By contrast,

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Charles Darwin, who was conservative with respect to sex (but very liberal with respect to race), especially in his epic *The Descent of Man, and Selection in Relation to Sex* [2], favored nature in the nature-nurture debates. Our purpose is not to rekindle the false nature-nurture dichotomy, which is an unfortunate historical artifact – nature and nurture interact far too much for a meaningful dichotomy. Instead we show that an evolutionary biological perspective can highlight problems with the customary differences between females and males and possibly illuminate previously unsuspected differences.

A definition of females and males should transcend as many species as possible. The act of sex (meiosis), vis-à-vis production of gametes (eggs and sperm) that have half the usual complement of chromosomes, is an ancient phenomenon that evolved before the diversification of life into animals, fungi, plants, and protists (single-celled organisms that have nuclei and other internal cell membranes). All animals and plants (by which we mean land plants, such as mosses, ferns, conifers, and flowers) have distinct eggs and sperm. Therefore, biological definitions of female and male should transcend all or most animals and plants.

Standard definitions of female and male when applied to humans are problematic, as anybody studying transsexuality and transgender can attest. There is simply too much fluidity, plasticity, and variation in human genitalia. We need look no further than the continuum of human phallic lengths to see that clitoris and penis are really the same (homologous) organs [3]. The location of the urinary opening is also variable, not always at the tip of the phallus in otherwise unambiguous males and not always near the base of the phallus in otherwise unambiguous females. For humans, Anne Fausto-Sterling [3] unmasked the false female-male dichotomy, at least for our diploid stage in which every cell nucleus has two copies of each chromosome. After extending her argument to all animals and plants, we then ask whether there is a female-male dichotomy for individuals with only one copy of each chromosome per nucleus (haploid), which for animals means eggs and sperm.

An overarching theme in women's and gender studies is elimination of essentialism, which is the notion that any entity, such as "female" or "male," has a fixed list of properties that it must possess. In tautological terms, essentialism means that there is some fixed essence of femaleness (or maleness) that all females (or males) possess.

Universal differences between the sexes are only expected if the evolution of two sexes from one sex only happened once (or, much less likely, via multiple origins of two sexes, followed by extinction of all species except those derived from one of the origination events). Multiple independent evolutionary origins of two sexes from a single sex would imply that differences between females and males should vary between organisms. With multiple independent origins, is it fair to use the same labels – female and male – for the resulting two sexes? In such instances, terminology would conflate and confound evolutionarily distinct events. Multiple evolutionary origins of sexes correspond with anti-essentialism, while single evolutionary origins correspond with essentialism.

2.2 Definitions

Our ideas will be easier to understand with the introduction of four technical biological terms describing a lifecycle (see glossary). All sexual organisms other than bacteria (which we do not consider sexual [4]) undergo the same cyclical process, known as alternation of generations. We begin by considering humans. Each cell nucleus in the zygote (in which egg and sperm nuclei have already fused in one cell), embryo, fetus, child, and adult has 46 chromosomes that come in 23 pairs – two copies of chromosome 1, two copies of chromosome 2, etc. – one copy inherited from each parent. Such organisms are known as *diploid*, where the prefix “di-” indicates that chromosomes come in twos. The diploid organism develops from the single-celled zygote all the way up to an adult by having each nucleus contain 46 chromosomes (a pair of each of 23 chromosomes), duplicating all 46 chromosomes, and then parsing those identical copies equally amongst two new nuclei. This copying process, preserving the number of chromosomes per nucleus, is called *mitosis*.

The diploid state alternates with the *haploid* state, in which each nucleus contains one copy of each chromosome (Fig. 2.1). The prefix “haplo-” means one. In humans and most other animals, haploid nuclei only exist in eggs and sperm

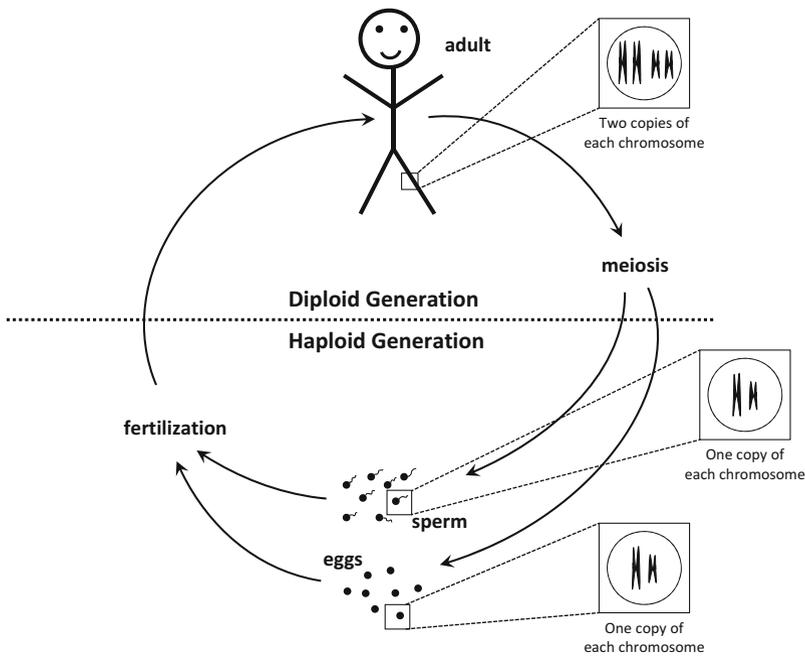


Fig. 2.1 Alternation of generations in animals

(human eggs and sperm contain one copy of each of the 23 chromosomes). Not all haploids are single celled. In haplodiploid animals, one sex (usually female) is diploid, but the other sex is haploid, with both sexes appearing morphologically similar, except for their genitalia. Haplodiploidy occurs frequently in insects and mites. Some plant stems and leaves can be composed of millions of cells with haploid nuclei, for example, the meter-long moss *Dawsonia superba*. These moss stems later produce haploid eggs and sperm via mitosis. The process by which an organism goes from diploid to haploid nuclei – that is, halving the number of copies of chromosomes per nucleus – is called *meiosis*.

There are two ways that an organism goes from a haploid back to a diploid state. The most common way is fertilization, where an egg and a sperm nucleus fuse, thereby restoring two copies of each chromosome. While much rarer and nonexistent in mammals, the diploid state can be restored by a haploid nucleus spontaneously duplicating all of its chromosomes at the start of meiosis, thereby producing diploid “gametes,” which can start the next generation without fertilization, for example, whiptail lizards (*Aspidoscelis* spp.) [5]. In many ways it is surprising that this does not happen more often insofar as many cells in so-called diploid individuals have duplicated their chromosomes via the same mechanism and have four, eight, or more copies of each chromosome, such as cells in your liver and muscles, especially heart muscles. Organisms always use meiosis to go from diploid to haploid but can use either fertilization or simple chromosomal duplication to go from haploid to diploid states.

The purpose of this chapter is to determine whether there are fundamental (“essential”) differences between females and males, differences that transcend as many different species as possible, such as all species but bacteria. We therefore take an evolutionary perspective to both debunk putative differences between the sexes and to construct possible unexplored differences.

2.3 Deconstruction: Debunking Accepted Differences Between Females and Males

We first examine traditional characterizations of female-male dimorphism, showing how these differences between the sexes break down in many instances. For a similar exposition applied to humans, see Fausto-Sterling [3]. We first look at macroscopic and microscopic differences between diploid parts of the lifecycle. The macroscopic differences encompass genitalia and secondary sexual characteristics, whereas microscopic differences encompass sex chromosomes (such as XY) and inheritance of portions of cells that are enveloped by internal membranes, such as mitochondria and chloroplasts. None of these circumscriptions of female and male work for defining sex based on fundamental differences; many of these even fail in mammals.

Alternatively, assuming that eggs and sperm are well-defined entities, we could try defining females as individuals that only produce eggs and males as individuals that only produce sperm. However, as Myra Hird [6] has elegantly detailed, there is

way too much transsex – such as temperature-dependent sex determination and sequential hermaphroditism – to make these viable definitions, something brought home beautifully by Isabella Rossellini’s video vignettes under the umbrella *Green Porno* (www.sundancechannel.com/greenporno).

Instead of looking at diploid individuals, maybe we would be better off looking at haploid individuals. For animals, this relegates us to the world of eggs and sperm, while plants have huge multicellular haploid parts. Nonetheless, conventional female-male dichotomies fail here too. The notions of eggs as large, rare, immobile, passive, long-lived entities and sperm as small, ubiquitous, mobile (with flagella), short-lived entities is incorrect in too many instances. What follows are details about female-male false dichotomies in both the diploid and haploid stage.

2.3.1 *Sexual Differences in Diploid Individuals*

A penis or lack thereof does not distinguish males from females. In mammals, clitoris and penis are essentially the same organs. Anne Fausto-Sterling has done an extraordinary job detailing the false dichotomy between the sexes in humans, especially in light of the huge number (1 in 60) of intersexuals [3]. While the typical human clitoris is shorter than the typical penis, some women have a clitoris that is sufficiently long to be used as an intromittent organ that can be inserted into female genitalia. It is more difficult to distinguish human females from males than it is in most other mammals because human males lack a penis bone, aka baculum. But not all male vertebrates have an intromittent organ. Male birds (except ducks) and amphibians lack any organ resembling a penis. Then there are some species in which males have a penis, but it is detachable: cephalopod (squid, octopus, etc.) hectocotyli, Malabar ricefish spermatophores, and banana slugs in which one copulating partner gnaws off the other’s penis. Seed plants have pollen, which is a detachable “penis” (an expandable, intromittent organ) that grows through female tissues to deposit sperm near an egg. External genitalia are not a consistent difference between females and males across plants and animals. We will therefore have to look for more microscopic differences.

Female mammals (except for platypus and echidnas) have a pair of X chromosomes, while males have one X and one Y chromosome, with Y being shorter than X. This is in diploid individuals. By contrast, mature mammalian eggs only have one X chromosome, and sperm have either an X or Y chromosome. In birds, females are the sex with unequal length sex chromosomes, with W shorter than Z. Male birds have two Z chromosomes. Different length sex chromosomes in either females or males is, however, very unusual, only occurring in mammals, birds, a few reptiles, several fishes, a few insects, and a few plants. Almost all diploid animals and plants have both sex chromosomes of equal length, when they have sex chromosomes at all, rendering this an unacceptable way to distinguish females from males. Many species of animals have environmental sex determination and therefore no sex chromosomes, let alone sex chromosomes of different length [7].

Mitochondria – the metabolic power plants inside cells – are often said to be exclusively inherited from females, providing a way to distinguish female from male parents. While this is a more consistent criterion than any of the ones we have thus far discussed, there are still lots of exceptions. Many plants inherit mitochondria from both parents, many from just their female parent, many others just from their male parent. Mitochondrial inheritance patterns are largely maternal in animals, with the primary exceptions seen in mollusks with doubly uniparental inheritance, known as DUI [8]. Female DUI mollusks inherit all their mitochondria from their female parent. Male DUI mollusks have most tissues in which mitochondria are from their female parent, as is typical, but their gonads have mitochondria from their male parent. Looking at diploid individuals will not allow for unambiguous differentiation of females and males. Plus, as we will see below with ribosomes, determining sex by asking about inheritance of subcellular parts is not very practical because this would require examination of individuals in two successive generations and would require being certain about paternity of each offspring.

Maybe we would have better luck by simply defining females as individuals that produce eggs and males as individuals that produce sperm [9]. While a seemingly simple solution, this also has major problems. What sex is a hermaphrodite, who either simultaneously or sequentially produces both eggs and sperm? What sex are fish, such as members of the genus *Gobiodon*, which includes the coral gobies, that can change from producing sperm to producing eggs and back to producing sperm based on environmental cues, such as number of nearby individuals of the species producing eggs or sperm [10]? What sex should we call the many animals with environmental sex determination, such as turtles and crocodiles, who produce ovaries and eggs if as juveniles they are raised at one temperature, but who produce testes and sperm if raised at a different temperature?

There is no consistent way to define the sexes based on fundamental differences for diploid plant and animal individuals. We therefore shift gears and ask whether there is such a thing as female and male haploids, including sperm and mature eggs. Our motivation for examining haploid stages – and, in fact, our motivation for looking for fundamental differences between haploid females and males – arises from the realization that humans are exceptional in having such a dominant, long-lived, free-living diploid stage, with a haploid stage that is short-lived and highly dependent on the diploid individual. While the haploid stages may superficially appear relatively insignificant in any species, including humans, they are vital because the next generation cannot be created without them [4]. Compounding the relative importance of haploids, the haploid stage is large, long-lived, and free-living in almost all fungi and algae, in most single-celled species, many plants, and even some animals. Being that sex evolved before animals existed – in the progenitors of all plants, animals, fungi, protists, etc. – we should be able to garner insight about sex from these other organisms. Furthermore, we can think of no decent philosophical reason why haploid individuals, including single-celled human eggs and sperm, should not be considered individuals on equal footing with our large diploid selves, reiterating that we are taking a broad evolutionary perspective. Thus, it is irrelevant to us that diploid humans have a brain and a phallus, while haploid humans clearly can have neither.

2.3.2 *Sexual Differences in Haploid Individuals*

Conventional wisdom holds that all eggs and sperm are haploid, and that eggs and sperm can be readily distinguished. However, this is wrong. While most sperm are haploid, with very few exceptions, many eggs have additional copies of each chromosome (and so maybe should not be called gametes). In almost all animals, egg nuclei start out with two copies of each chromosome, double that to four copies, and then later halve this to two copies, and finally halve this again to become haploid (meiosis: $2n \rightarrow 4n \rightarrow 2n \rightarrow 1n$, where n represents the base number of chromosomes, e.g., $n=23$ in humans). This fluctuation in number of copies is a normal part of the process – meiosis – that transitions organisms from diploid to haploid. In almost all animals except sea urchins and jellyfish (and their relatives), this process is arrested in eggs at some point in the process, before there is one copy per nucleus, and the process is only restarted and completed once an egg is fertilized by a sperm [11]. Thus, except in sea urchins and jellyfish, animal egg nuclei have either two or four copies of each chromosome when fertilized by a sperm whose nucleus has only one copy of each chromosome.

Even excepting sea urchins and jellyfish, requiring fertilization to halve their number of chromosomes is not a defining trait of females because there are many parthenogenetic (virgin birth) animals whose eggs complete meiosis without fertilization by sperm. In many animal groups, there exist a few species whose females manage to reduce their number of chromosomes down to one copy without fertilization. These individuals then take two of the four products of egg meiosis – namely, an egg cell and a polar body – and fuse these together to form a diploid zygote.

In all plants, eggs and sperm are haploid at the time of fertilization, but this is largely because the process of halving chromosomes (meiosis) occurs long before production of eggs and sperm. Plants produce a large multicellular stage in which every nucleus is haploid. It is from this stage that egg and sperm are later produced via mitosis. Sometimes a given haploid plant will produce only eggs, sometimes only sperm, and sometimes both. As with diploid animals, haploid plants can thus be female, male, or hermaphrodite. Consequently, instead of asking whether haploid individuals are female or male, we ask whether there are any fundamental and universal differences between eggs and sperm.

Before leaving the topic of sex differences between haploid individuals, we would be remiss to not presage that this tack does lead to one universal sexual difference: asymmetry of female meiosis versus symmetry of male meiosis. We defer discussion of this topic to the section on criteria that may work universally for distinguishing females from males.

2.3.3 *Sex Differences Between Eggs and Sperm*

Eggs are usually conceived of as large, passive, immobile, uncommon, and long-lived and sperm as small, active, mobile (propelled by flagella), common, and short-lived.

Unfortunately, none of these generalities are universally true. Below, we devote a short paragraph to each of these false dichotomies.

Humans are typical in that eggs are few, large, and very long-lived, while sperm are many, motile, and short-lived. Most eggs are produced prior to birth in humans, that is, they live for roughly a quarter to half a century – whereas sperm live for no more than one week. But sperm movement is not as efficient as many believe, largely moving from side to side (not forward) via their flagella [12]. Eggs also travel substantial distance, through fallopian tubes.

In some species, sperm are giant [13]. Some insects and cone-bearing seed plants produce enormous sperm with flagella. In these cone-bearing plants, sperm have thousands of flagella and grow to many times larger than the pollen grain that carried them to the female cone. In some small fruit flies (*Drosophila*), sperm are twelve times longer than the adult animals [14]. In the cases of insects with giant sperm, they usually produce very few sperm.

In some insects, males produce about the same number of sperm cells as females produce egg cells. Some species of ants produce colonies of several million individuals. A newly emerged (virgin) queen goes on a single mating flight during her lifetime, in which she mates with several males. She then lands on the ground, chews off her wings, and starts digging an underground colony from which she will never emerge and certainly never go on another mating flight. Over the next decade or two, she will form millions of eggs and fertilize them with the sperm that she stored from her one mating flight. Unlike in humans, these queen ants seem to undergo meiosis throughout their lives; hence their eggs may be shorter-lived than are the sperm the queens are storing. (Sue Bertram suggested that ant sperm may not be long-lived, but instead the queen ant may cryptically mate with her own sons while underground before her sons depart on their mating flight – but this has never been documented.)

Many animal and plant species have sperm that lack flagella. Flowering plants and conifers have sperm that lack flagella and are not independently motile. Their sperm are carried to the egg cell by the growing pollen tube, the erect detachable “penis” that grows through hollows in the female’s tissues. Many groups of animals have amoeboid sperm, lacking flagella [15], including species of segmented worms, round worms, flat worms, crustaceans, spiders, insects, and even one group of fish, the freshwater elephant fish. While amoeboid sperm are somewhat mobile, they are very different looking from sperm with flagella.

While sperm may seem more active than eggs, their nuclei are not. After fertilization, sperm nuclei are passive, but egg nuclei are not. Sperm nuclei – of which there may be many per egg cell in many species – are relatively sedentary once inside an egg cell. By contrast, egg nuclei of at least one species of comb jelly (*Beroe ovata*) move about their own cytoplasm, querying other nuclei about suitability for fusing [16]. The path of the egg nucleus is very directed.

Thus far we have briefly debunked all the common female-male dichotomies or at least showed that these dichotomies are only applicable to small subsets of species, certainly not all animals and plants. It turns out that there may be universal ways to distinguish females from males, but these other dichotomies, if they exist, will be highly nuanced, taking a highly magnified and well-trained eye to possibly differentiate females from males.

2.4 Reconstruction: Possible Differences Between Females and Males

We hypothesize four fundamental differences between females and males, all four of which only work for haploid individuals and which derive from an evolutionary perspective. First, only females contribute the subcellular machinery (ribosomes) responsible for translating DNA into proteins. Unfortunately this requires us to keep track of inheritance between subsequent generations, which is not a convenient way to distinguish the sexes. Second, during the process of meiosis, both females and males go from one diploid nucleus to four haploid nuclei. However, in females, this cell division is always asymmetrical; in males it is always symmetrical. Third, only sperm have nuclei without any pores. All other cell nuclei have pores. Sperm nuclei also have some unique proteins and genes. Fourth, only sperm replace their nuclear membrane (without pores) without any chromosomal replication, replacing it with a membrane that has pores. Below, we devote a paragraph or two to each of these four hypothesized ways of distinguishing females from males. However, note that there is still a paucity of corroborative evidence for each hypothesis.

In most species, eggs are large and sperm are small. When there are exceptions, it turns out that sperm are relatively large, while eggs are still the relatively large cells that exist in all related species. This implies that there may be a reason for eggs being large. The difference in size is probably not due to mitochondria or chloroplasts because inheritance of these organelles is not strictly maternal, and when these organelles are inherited paternally, eggs are still relatively large and sperm relatively small. The egg supplies the next generation with lots of cytoplasm, including all the biochemical machinery needed to carry out most metabolic functions. This includes internal membranes (endoplasmic reticulum) and ribosomes on many of those membranes. Ribosomes are huge globs of protein and RNA that translate the genetic code into proteins. Tinker with cellular machinery other than nuclei and mitochondria, such as ribosomes, and you can get a radically different organism. We hypothesize that ribosomes are strictly inherited from the maternal parent (egg), although new ribosomes are later made under control of the zygote's or embryo's DNA and hence may then have paternal contributions. This will confound using these cellular components as a defining characteristic of females versus males. A more operational way of defining the sexes would be helpful.

We hypothesize that in males, meiosis is always symmetrical; in females, meiosis is always asymmetrical. In males, a nucleus with two of each chromosome undergoes a replication of each chromosome (four copies of each chromosome) followed by two successive partitions of those copies into four separate nuclei in separate cells. We hypothesize that the four male cells and four male nuclei are completely symmetrical and all completely functional. Females also undergo meiotic divisions; however, the four nuclei may be in one, two, or four cells; the cells may be of different sizes from one another; and only one of the nuclei will go on to form the next generation. Occasionally two nuclei go on to the next generation in which case it is always because these two fuse with one another rather than with a sperm nucleus.

We briefly discuss one apparent exception to the previous paragraph, which on closer inspection turns out not to be an exception. Some plants with so-called tetrasporic meiosis seem to have somewhat more symmetrical meiosis, but even here meiosis is fundamentally asymmetrical. Tetrasporic meiosis results in one cell containing four haploid nuclei [17]. However, one of these nuclei migrates to one side of the cell and will eventually give rise to an egg cell. Another nucleus moves toward the center of the cell and will eventually give rise to nutritional tissue (endosperm, product of double fertilization) that will not be inherited by the next generation. The remaining two nuclei move to the opposite end of the cell from the first cell and are effectively unused after fertilization, and thus they are not passed along to the next generation. The asymmetry in female meiosis is still evident with tetrasporic species, but is more subtle.

We hypothesize that sperm are the only cells lacking nuclear pores [18, 19]. Most nuclei, including egg nuclei, have pores to allow messenger RNA out of the nucleus. This allows the information of the DNA code held in the chromosomes to be shuttled to the ribosomes, thereby providing a template for protein production. Various signals that turn on and off genes also need to travel in the opposite direction through these nuclear pores, as does DNA itself. When a nucleus replicates, the DNA comes from outside the nucleus. Nuclear pores are not only holes (where passage of substances are highly controlled by protein in the pores) but also the place where the nuclear envelope is contiguous with the internal cell membranes of the rest of the cell. Sperm nuclei are utterly atypical in lacking pores and being quite compact. Messenger RNA cannot leave a sperm nucleus, and chromosomes cannot be replicated in sperm. We do not know of any exceptions. However, the place to look for exceptions may be in sperm of ants in which the female stores mature sperm for a decade or two. Another place to look may be flowering plants whose pollen can stay viable for many decades, especially if the sperm cells have already differentiated in the pollen grain (so-called trisporic, and not bisporic, pollen). Sperm nuclei also contain proteins that only seem to be found in sperm, such as the protein lamin B [20] and expression of the gene *BOULE* [21]. This may be correlated with sperm lacking nuclear pores.

Lack of nuclear pores in sperm poses a quandary after fertilization. In all species that people have looked at, egg and sperm nuclei replicate all their chromosomes before their nuclei fuse with one another to form a zygote nucleus (sand dollars, rabbits, mice, frogs, and humans [22]). We therefore suspect that pore-less sperm nuclei have to break open inside the egg cell and have all or a portion of their nuclear envelope replaced with a pore-laden nuclear envelope formed from the egg cell's internal membranes, aka the egg's endoplasmic reticulum. Once this occurs, the sperm nucleus is called a pronucleus. Only then can and does the sperm replicate its chromosomes. This is also an event that is unique to sperm. During all other cell divisions, including meiosis and mitosis, nuclear membranes are only replaced after a replication of all chromosomes [23]. With sperm pronuclear formation, membranes are replaced without any intervening chromosomal replication, which only occurs immediately after the new membrane is in place [24].

There does not yet exist a corpus of evidence for any of the above hypotheses for female-male differences between haploid individuals. But we also do not know of any evidence to debunk any of these hypotheses.

2.5 Concluding Remarks

How often have two sexes evolved from species with only one sex? For diploids, the standard answer is many times, where hermaphrodites evolved multiple times into separate diploid females and males [7]. This is completely consistent with an utter lack of *universal* differences between female and male diploid individuals. Remember, multiple evolutionary origins correspond with anti-essentialism.

How often did two sexes evolve at the haploid level? Isogamous and anisogamous literally mean equal gametes and unequal gametes, respectively. Humans are anisogamous because eggs and sperm are different from one another. There are, however, many algae and fungi in which fertilization occurs between gametes that appear to be identical, which is termed isogamous. The first sentence of this paragraph then translates as: How often did anisogamy evolve? The standard answer is many times [9, 25]. However, if any of our four hypothesized universal differences between haploid females and males is supported, then anisogamy probably only evolved once. This is both a biologically radical notion and also one that makes us haploid essentialists.

John Stuart Mill, Anne Fausto-Sterling, and Rebecca Jordan-Young [1, 3, 26] were right: It is not easy telling the two sexes apart. Even though sex change is more difficult in mammals than in many other animals, sexual ambiguity is still prevalent, even in humans. One of our goals is to emphasize that this sexual ambiguity is real. From an evolutionary perspective, any reasonable way of distinguishing females from males via fundamental differences fails unless we look at individuals whose cell nuclei are haploid. Thus, we cannot distinguish females from males in adult animals, newborn animals, nor fetuses but can only distinguish females from males in animal gametes. Even if an adult (i.e., diploid) individual is naked, their sex is indeterminate. If evolutionary biology provides a cogent way of distinguishing the sexes – and it is not obvious yet if it can – then this will require careful examination of haploid cells and their nuclei.

One reason for the ambiguity in distinguishing the sexes is that we insisted that definitions should apply as universally as possible. This forces us to look at some peculiar species, but that is the price that must be paid to come up with a universal and operational definition of the sexes. “Darwin admonished us not to ignore the ‘oddities and peculiarities’ of life as we see it today. It is by the analysis of such oddities that evolutionary history can be reconstructed” [27] (p. 26). It is also the price that must be paid because separate diploid sexes independently evolved multiple times from hermaphrodites. It is remotely possible that haploid female and male gametes (anisogamy) evolved independently multiple times from species with only one type of gamete (isogamy), although the evidence we presented here strongly implies that anisogamy only evolved once.

We hypothesize that there exists a female-male dichotomy only when examining haploid individuals. For animals, this means that eggs and sperm are conceptualized as individuals, albeit single-celled haploid individuals that may be dependent upon diploid individuals. For diploid individuals, there is no female-male dichotomy. We are thus diploid anti-essentialists, but reluctantly hypothesize an essentialist view of haploids. There is very little biological evidence in support of and none in opposition to our four hypothesized differences between haploid females and males (nuclear pores, nuclear proteins, symmetry of meiosis, inheritance of ribosomes). Further evidence could readily debunk any or all of these hypotheses. But existing biological evidence leaves us in the uncomfortable position of suspecting that there may be subtle but fundamental differences between haploid female and male individuals.

There are some curious societal implications to being diploid anti-essentialists but haploid essentialists, none of which we have the space to explore here. For instance, in law, there should be absolutely no basis for different treatment of diploid females and males. However, one could envision a biologically based unequal legal treatment of human haploid individuals, that is, eggs and sperm. While we certainly do not advocate basing normative (moral) legal decisions regarding storage of human gametes or contraceptive technologies on this science, others may try.

2.6 Summary

All well-known putative differences between females and males are ambiguous or with many exceptions. There is no female-male dichotomy when looking at individuals who have two or more copies of each chromosome per nucleus (diploid) because there are many hermaphroditic species, intersex individuals, and species with environmental sex determination. Not all males have an intromittent organ, such as a penis. We are diploid anti-essentialists. Even standard female-male differences are illusory when looking at individuals with only one copy of each chromosome per nucleus (haploid), such as animal eggs and sperm. Not all sperm are mobile with flagella, short-lived, small, nor have a Y chromosome. Not all mitochondria, nor other membrane-bound organelles, are inherited from eggs. However, here we hypothesize two essential differences between haploid females and males. (1) Sperm are the only cells whose nuclei lack pores in their nuclear membranes. Sperm nuclei uniquely contain certain proteins in their nuclear membranes, but this is probably due to lack of pores. Furthermore, due to lack of pores, sperm nuclear envelopes must be replaced prior to chromosomal replication. (2) Reduction from two to one copy of each chromosome per nucleus (meiosis) is always symmetrical in males, but never in females. If applicable, the terms female and male fundamentally apply only to haploid cells and their nuclei, not to diploid cells and their nuclei. Neither of our two hypotheses has been well tested, hence we are reluctant haploid essentialists.

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Glossary

Haploid A nucleus containing only one copy of each chromosome. A nucleus containing two copies of each chromosome (usually one from the mother and one from the father).

Mitosis A cell division that results in the production of two identical sets of chromosomes partitioned into two identical daughter cells. Both new cells have the exact same chromosomal content as the cell that produced them. Mitosis is akin to photocopying.

Meiosis A cell division that reduces the number of chromosomes by half (e.g., a diploid cell produces haploid cells). Each newly produced nucleus contains one copy of each chromosome (either maternal or paternal copy), although crossing over and recombination can also produce chimeric chromosomes that are part maternal and part paternal. Meiosis is akin to shuffling cards.

Mitochondria Small completely symbiotic bacterial cells within every eukaryotic cell that are used for converting sugars to chemical energy.

Ribosomes Compact pieces of RNA and protein that translate messenger RNA (which itself was transcribed from DNA) into amino acids and proteins.

Endoplasmic Reticulum Internal cell membranes that form throughout the cell's cytoplasm and are used to construct the membrane of the cell nucleus. Presence of endoplasmic reticulum distinguishes eukaryotes from bacteria. Ribosomes are attached to a subset of the endoplasmic reticulum and the outer cell membrane.

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