The role of meiotic drive in chromosome number disparity between heterosporous and homosporous plants

Sylvia P. Kinosian[1*] and Michael S. Barker[1]

[1]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721
USA

Corresponding author: [*]Sylvia P. Kinosian, skinosian@arizona.edu

Abstract

In vascular plants, heterosporous lineages typically have fewer chromosomes than homosporous lineages. The underlying mechanism causing this disparity has been debated for over half a century. Although reproductive mode has been identified as critical to these patterns, the symmetry of meiosis during sporogenesis has been overlooked as a potential cause of the difference in chromosome numbers. In most heterosporous plants, meiosis during megasporogenesis is asymmetric, meaning one of the four meiotic products survives to become the egg. Comparatively, meiosis is symmetric in homosporous megasporogenesis and all meiotic products survive. The symmetry of meiosis is important because asymmetric meiosis enables meiotic drive and associated genomic changes, while symmetric meiosis cannot lead to meiotic drive. Meiotic drive is a deviation from Mendelian inheritance where genetic elements are preferentially inherited by the surviving egg cell, and can profoundly impact chromosome (and genome) size, structure, and number. Here we review how meiotic drive impacts chromosome number evolution in heterosporous plants, how the lack of meiotic drive in homosporous plants impacts their genomes, and explore future approaches to understand the role of meiotic drive on chromosome number across land plants.

Introduction

Across vascular land plant lineages, there is great diversity and disparity of genome size and chromosome number (Table 1). Specifically, flowering plants have smaller average nuclear genomes and lower chromosome numbers than most pteridophytes (ferns and lycophytes; Fig. 1), a pattern that is correlated with a difference in reproductive mode (Wagner and Wagner 1979; Klekowski and Baker 1966; Leitch and Leitch 2013; Nakazato et al. 2008). Seed plants (including flowering plants) reproduce via separate megaspores and microspores that develop into female and male gametophytes, respectively (Fig. 2A). In these heterosporous systems, female meiosis is typically asymmetric, and male meiosis is symmetric (Fig. 3A, B). Although some pteridophytes (Salviniales, Isoeteales, and Selaginellales) share this heterosporous system of gamete production (Bell 1981; Pettitt 1977), most pteridophytes and all bryophytes have a homosporous system (Fig. 2B) where symmetric meiosis leads to the production of only one type of spore that germinates into a gametophyte that is capable of producing eggs, sperm, or both. Homospory is the ancestral character state of land plants and heterospory has evolved independently a minimum of 11 times throughout the history of tracheophytes (Bateman and DiMichele 1994), including three extant lineages. These transitions from homospory to heterospory are often accompanied by distinct changes in genome structure, including a decrease in chromosome number and genome size (Clark et al. 2016; Carta, Bedini, and Peruzzi 2020). One exception to this pattern is gymnosperms, which are heterosporous with small chromosome numbers but unusually large genome sizes due to the accumulation of repetitive elements (e.g., (Nystedt et al. 2013) and few potential ancient WGD events (Li et al. 2015; One Thousand Plant Transcriptomes Initiative 2019; Stull et al. 2021; Wan et al. 2018; Liu et al. 2022; Wan et al. 2022).

Several mechanisms have been proposed to explain the differences in genome organization between homosporous and heterosporous plants (Barker and Wolf 2010; Kinosian, Rowe, and Wolf 2022; Haufler and Soltis 1986; Haufler 1987; Wagner and Wagner 1979; Klekowski and Baker 1966; Leitch and Leitch 2013). The most well-studied have been differences in whole genome duplications (WGDs) and diploidization (Haufler 1987; Wagner and Wagner 1979; Barker 2013; Klekowski and Baker 1966). Recent work has shown homosporous and heterosporous lineages have roughly the same number of WGDs, but likely different mechanisms or at least different rates of diploidization and fractionation (One Thousand Plant Transcriptomes Initiative 2019; McKibben, Finch, and Barker 2024; Li et al. 2021, 2024). In flowering plants, diploidization and fractionation can proceed rapidly via a reduction in chromosome number (descending dysploidy) and extensive gene deletions by ectopic recombination (Li et al. 2021; Wendel 2015). Diploidization in homosporous pteridophytes appears to involve limited chromosome loss accompanied by gene silencing rather than deletion, leading to their high chromosome numbers (Haufler 1987; Barker 2013; Barker and Wolf 2010; Li et al. 2024; Gastony 1991) and striking intra- and intergenomic collinearity (Li et al. 2024; Huang et al. 2022). Heterosporous pteridophytes, however, have chromosome numbers akin to heterosporous angiosperms (Klekowski and Baker 1966). The transition to heterospory might lead to smaller chromosome numbers and genomes through the dynamics of post-WGD diploidization, perhaps through fundamental changes in the symmetry of female meiosis associated with heterospory.

Female meiosis in heterosporous plants is asymmetric in terms of cell fate: of the four meiotic products, only one survives to become the egg cell and the three polar bodies do not enter the germline (Figs. 1A, 3A; Schmerler and Wessel 2011; Burt and Trivers 2009; Haig 2020). This asymmetry allows for a deviation in Medelian inheritance called meiotic drive (also referred to here as *female meiotic drive* or *true meiotic drive*), where genetic elements are preferentially transmitted to the germline specifically during asymmetric female meiosis (Sandler and Novitski 1957; Pardo-Manuel de Villena and Sapienza 2001b). Meiotic drive is a type of transmission ratio distortion (TRD) or non-random inheritance caused by different processes through an organism's life cycle, including meiosis, gametogenesis, fertilization, and development (Fishman and McIntosh 2019).

Female meiotic drive can have profound impacts on genome structure. In heterozygotes, a driving allele can rapidly rise to fixation within a handful of generations by taking advantage of a functionally asymmetric meiotic spindle pole and be preferentially transmitted into the surviving egg cell (Pardo-Manuel de Villena and Sapienza 2001b; Fishman and Willis 2005; Finseth 2023; Akera et al. 2017). The mechanisms of drive often act on entire chromosomes: meiotic drive can favor the inheritance of certain chromosomal rearrangements and morphologies, altering a species' karyotype and chromosome number (Burt and Trivers 2009; Fishman et al. 2014; Boman et al. 2024; Blackmon et al. 2019; Baack et al. 2015; Lindholm et al. 2016; Pardo-Manuel de Villena and Sapienza 2001a). In addition, female meiotic drive can lead to changes in centromere and chromosome size (Zedek and Bureš 2016; Finseth, Nelson, and Fishman 2021; Malik and Bayes 2006; Henikoff, Ahmad, and Malik 2001; Plačková et al. 2022). Drive has been proposed as a mechanism of karyotype evolution in mammals (Pardo-Manuel de Villena and Sapienza 2001a; Blackmon et al. 2019), as well as examined in the context of symmetric and asymmetric meiosis (Zedek and Bureš 2016; Plačková et al. 2024) and heterosporous and homosporous reproductive modes (Kinosian, Rowe, and Wolf 2022) in plants.

We propose that female meiotic drive may be an important force behind differences in chromosome number evolution across land plants. In heterosporous angiosperms, chromosome number decreases by descending dysploidy following WGD (Li et al. 2024, 2021). Descending dysploidy occurs at a slower rate in homosporous pteridophytes, about half that of angiosperms (Li et al. 2024). As discussed by (Kinosian, Rowe, and Wolf 2022) and (Plačková et al. 2024), this disparity could be explained by the presence of meiotic drive in heterosporous lineages and its absence in homosporous lineages. Meiotic drive is a known mechanism for chromosomal rearrangements to overcome a heterozygote disadvantage, and rearrangements involving the centromere would be preferentially inherited (Searle and de Villena 2022; Searle 1993; White 1968). Specifically, rearrangements like Robertsonian translocations can be favored by drive and reduce overall chromosome number and could be part of how dysploidy occurs during the diploidization process (Searle and de Villena 2022; Escudero et al. 2014). Homosporous plants may go through slower post-WGD dysploid changes because they have strictly symmetric meiosis, eliminating the possibility of genome restructuring by true meiotic drive. Other types of TRD can occur in lineages with symmetric meiosis, although these processes typically occur before or after meiosis and often act on specific genotypes (Lindholm et al. 2016). Here we review how female meiotic drive impacts genome evolution and chromosome number across vascular land plants with asymmetric meiosis (focusing on angiosperms), what genome characteristics and types of TRD we would expect to see in a lineage with symmetric meiosis (focusing on pteridophytes), how homosporous genomes may evolve in the absence of meiotic drive, and conclude with future directions for incorporating meiotic drive into the growing body of work on post-WGD genome evolution in plants.

The influence of meiotic drive on heterosporous genome structure

Changes in genome structure as a consequence of female meiotic drive have been described across eukaryotes (e.g., Blackmon et al. 2019; Chmátal et al. 2014; Pardo-Manuel de Villena and Sapienza 2001a; Fishman et al. 2014). Female meiotic drive can happen via different mechanisms during meiosis I or II, depending on which aspects of cell division are available to create preferential inheritance (Clark and Akera 2021). The most well-studied drive mechanism is centromere drive, which has direct effects on chromosome number, shape, and size (Mayrose and Lysak 2021; Dudka and Lampson 2022; Plačková et al. 2024; Blackmon et al. 2019). In centromere drive, cell signaling during meiosis I differentiates the egg (surviving, enters the germ line) and cortical (polar body, does not enter the germline) sides of the spindle (Figs. 2A, 3A; Akera et al. 2017; Silva and Akera 2023). Larger centromeres have a stronger kinetochore-spindle connection, resulting in the larger homologous centromere (and attached homolog) being preferentially attached to the more stable microtubules on the egg side of the spindle (Fig. 4B; Dudka and Lampson 2022; Akera et al. 2017; Peris et al. 2009). In drive systems that favor larger centromeres, chromosome fusions can be preferentially inherited, reducing overall chromosome number (Pardo-Manuel de Villena and Sapienza 2001a; Lindholm et al. 2016). For example, Robertsonian translocations are a type of chromosome fusion where two acro- or telocentric chromosomes fuse to form a new metacentric chromosome; these fused centromeres create stronger bond to the spindle fiber (Chmátal et al. 2014). Therefore, Robertsonian translocations are preferentially transmitted in human female meiosis despite deleterious effects (Talbert and Henikoff 2022; Poot and Hochstenbach 2021; Daniel 2002; de Lima et al. 2024); similar fused chromosomes are also preferentially transmitted in *Drosophila* (Stewart et al. 2019). Chromosome number evolution mediated by chromosomal rearrangements has been documented across heterosporous plants, including Brassicaceae (Mandáková and Lysak 2008; Lysak et al. 2006), Orchidaceae (Moscone et al. 2007), and Podocarpaceae (Hair and Beuzenberg 1958; Jones 1979), with fusions being noted as a potential mechanism of genomic downsizing and chromosome number reduction following polyploidy (Jones 1998; Mayrose and Lysak 2021; Mandáková and Lysak 2018). Chromosome fusions favored by meiotic drive could be an important part of how heterosporous plants cytologically downsize (i.e., descending dysploidy) following WGD; the absence of meiotic drive in homosporous plants would eliminate this process as a mechanism for genome downsizing.

In addition to chromosome number, meiotic drive can cause different morphologies (meta-, acro-, or telocentric chromosomes) to be favorably inherited depending on the system, although it is unclear exactly in what stage of meiosis this occurs (Burt and Trivers 2009; Dudka and Lampson 2022). Chromosome morphology changes caused by meiotic drive are known to occur in mammals and fishes, where a change in the polarity of meiotic drive (i.e., which meiotic product survives, Fig. 4A) favors a specific chromosome morphology, causing rapid rearrangement of chromosome structure and number (Blackmon et al. 2019; Molina et al. 2014).

For example, in mammals, some species have a karyotype comprising mostly metacentric chromosomes, some have mostly acro- or telocentric chromosomes, and others have a mix of both chromosome morphologies (Burt and Trivers 2009; Pardo-Manuel de Villena and Sapienza 2001b). Rates of chromosomal evolution are slower in species with one chromosome morphology and higher in species with a mix of morphologies (Blackmon et al. 2019). Meiotic drive is thought to stabilize chromosome morphology within a species, and drive can cause rapid karyotype change if the polarity of drive changes (Blackmon et al. 2019; Pardo-Manuel de Villena and Sapienza 2001a). Interestingly, most angiosperms species have only metacentric chromosomes (Weiss-Schneeweiss and Schneeweiss 2013; Stebbins and Others 1971), perhaps because the polarity of meiosis is weaker compared to animals (Huang and Russell 1992). However, within some lineages like monocots, for example, karyotypes can be much more variable (Hamouche et al. 2010; Choi et al. 2008; Stedje 1989; McKain et al. 2012; Plačková et al. 2022). Research in the Brassicaceae suggests that a karyotype comprising multiple chromosome morphologies is perhaps a transition state (Mandáková and Lysak 2008; Lysak et al. 2009; Weiss-Schneeweiss and Schneeweiss 2013) that could be created by drive if the polarity of meiosis recently changed, perhaps following one of the many WGD in evolutionary history of the family (e.g., McKibben, Finch, and Barker 2024; Lysak et al. 2009; Mabry et al. 2020; Mandáková et al. 2017; Mabry et al. 2024).

Other types of meiotic drive can occur via mechanisms in meiosis II, although the exact mechanisms by which this happens are unclear because the egg and polar sides of the spindle are not established through the same signalling mechanisms as is meiosis I (Clark and Akera 2021). A neocentromere on chromosome Ab10 in maize acts during meiosis II, where the driving neocentromeres are transmitted to the outer cells of the tetrad, one of which survives to become the egg (Dawe et al. 2018). In addition, cytokinesis in female meiosis is asymmetrical, with a majority of the cytoplasm remaining in the egg cell. Certain chromosomes can lag during cytokinesis of meiosis II and remain in the egg cytoplasm, similar to biased transmission of B chromosomes (Wu et al. 2019; Chen, Birchler, and Houben 2022).

As mentioned previously, the mechanisms and effects of female meiotic drive are incredibly variable. One aspect of this variability is the polarity of meiotic drive, where either large or small centromeres are favored depending on which meiotic product survives to become the egg (Blackmon et al. 2019; Plačková et al. 2024). It has been hypothesized that centromere size may mediate chromosome size, with larger centromeres associated with larger chromosomes, and vice versa (Plačková et al. 2022, 2024). Indeed, centromere size has been observed to scale with chromosome size in Agavoideae (Plačková et al. 2022) and grasses (Zhang and Dawe 2012; Bennett et al. 1981). This could extend to meiotic drive favoring different chromosome traits, depending on the polarity of drive. For example, there is evidence that centromere drive can favor chromosome fusions in one species of butterfly, but conserve chromosome structure by selecting against chromosome fusions in another (Boman et al. 2024). In addition, in *Mimulus* it is thought that chromosome fissions supported by meiotic drive are responsible for chromosome number doubling, not polyploidy (Fishman et al., 2014). Considering that drive is variable across systems (e.g., Lindholm et al. 2016), additional work is needed to understand the mechanisms at play.

It is important to note that there are many ways in which angiosperm megasporogenesis happens (Huang and Russell 1992; Kaur, Kathpalia, and Koul 2024), with different types of cells developing into the megaspore resulting in variable mechanisms of meiotic drive (Fig. 3D, 4A). Indeed, a correlation between the type of sporogenesis and nuclear genome size has been made in angiosperms species that undergo disporic or tetrasporic megasporogenesis have larger genomes than those with monosporic sporogenesis (Bharathan 1996). In monosporic megasporogenesis, following meiosis one of the four resulting one-nucleate cells survived to become the egg cell; in disporic megasporogenesis, one of the two resulting two-nucleate cells survives; and in tetrasporic megasporogenesis, a single four-nucleate cell survives (e.g., Drews and Koltunow 2011; Haig 1990, 2020). Meiotic drive would be the strongest in a monosporic system, and present but less strong in a disporic system. In tetrasporic megasporogenesis, the egg cell develops much later, and within an embryo derived from one genetic background (Yadegari and Drews 2004). As a result, drive would act differently and potentially be weaker than in the other two types of megasporogenesis.

Megasporogenesis in heterosporous ferns has similar variability in the degree of asymmetry as angiosperm megasporogenesis. In the heterosporous fern *Marsila*, 1 out of 32 megaspores are ultimately viable. Megasporogenesis in *Marsilea* produces eight tetrads of megaspores (and in each tetrad just one megaspore survives), but only one of the eight survives to maturity (Bell 1981). The final surviving megaspore typically comes from the tetrad closest to the attachment point of the sporangium to its stalk (Sheffield and Bell 1987). Comparatively, in the heterosporous lycophyte *Selaginella* one or two meiotic products survive megasporogenesis (John M. Pettitt 1971), and micosporogenesis can also be asymmetric (Pettitt 1977). Finally, all meiotic products in the heterosporous lycophyte *Isoetes englemanii* survive (Pettitt 1976), eliminating the possibility of meiotic drive in this lineage. More research on the dynamics of meiosis in heterosporous ferns and lycophytes is needed to better understand the asymmetries and types of drive in these lineages.

It is important to note that microsporogenesis can be asymmetric in the case of angiosperms with pseudomonad pollen, which presents an opportunity for meiotic drive (Furness and Rudall 2011). At maturity, pollen often comprises solitary grains (monads), but can be in groups of four (tetrads). It is hypothesized that pseudomonad pollen evolved from tetrad pollen where three of the four cells produced by meiosis do not mature (Walker and Doyle 1975). Pseudomonad pollen has evolved independently multiple times in angiosperms, including in the monocot family Cyperaceae (sedges) and the eudicot subfamily Styphelioideae (Ericaeae, heathers), with the developmental mechanisms being slightly different in each lineage (Brown and Lemmon 2000; Furness 2009). Several authors have speculated that meiotic drive is present in lineages with pseudomonad pollen, perhaps causing the large variation in chromosome number observed in these groups (Furness and Rudall 2011; Hipp 2007). Cyperaceae and Styphelioideae have a high frequency of aneuploidy, with the most extreme example being the large genus *Carex* (Cyperaceae) varying from *n*=6-68 (Davies 1956). Interestingly, Cyperaceae frequently have holocentric chromosomes (diffuse centromeres) while Styphelioideae do not, presenting a unique comparative system to look at how holocentric chromosomes and meiotic drive interact (e.g., (Krátká et al. 2021). These examples of asymmetric male meiosis in heterosporous plants offer a different way to look at the role of meiotic drive in chromosome number and genome structure evolution, as the asymmetry of microsporogeneis could have similar consequences as asymmetric megasporogenesis, despite different mechanisms. In addition, it will be important to consider the possibility of asymmetrical meiosis in homosporous plants and the different ways drive may impact those systems.

In summary, meiotic drive can influence genome structure by the non-Mendelian inheritance of chromosomes with larger centromeres, and chromosome number by inheritance of chromosomal rearrangements involving and strengthening centromeres. The potential for meiotic drive may be part of the reason why heterosporous plants, in particular angiosperms, have a large diversity and relatively rapid evolution of genome structure and organization. Competition among centromeres and chromosomes in plant lineages with meiotic drive may lead to lower chromosome numbers especially if fusions or larger centromeres and chromosomes are favored in their drive systems. In contrast, the absence of meiotic drive in homosporous plants may explain the comparative lack of diversity and slower evolution in their genome structure and organization such as largely stable and high chromosome numbers over time.

Meiotic drive and symmetric meiosis

In contrast to the genomes of the heterosporous angiosperms, the genomes of plants with symmetric meiosis—namely homosporous pteridophytes and bryophytes—cannot be influenced by female meiotic drive. Homosporous pteridophytes have a unique kind of symmetric meiosis, different from that of male meiosis in heterosporous plants. In leptosporangiate ferns, spores are produced via four rounds of mitosis and one round of meiosis (Fig. 3C). In eusporangiate ferns, hundreds of spores are produced in tetrads via one round of meiosis, akin to male meiosis in heterosporous plants (Brown and Lemmon 2001). Sporogenesis in bryophytes is also symmetric; however, unlike pteridophytes, some bryophytes have sex chromosomes, which could lead to other mechanisms of TRD (e.g., Presgraves, Severance, and Wilkinson 1997; Fedyk, Bajkowska, and Chętnicki 2005; Úbeda, Patten, and Wild 2015). In these plants without true meiotic drive, we expect to see slower chromosomal change, limited selection pressure on chromosome size and morphology, and larger genomes. Through empirical work on homosporous pteridophytes, we observe high chromosome numbers (Klekowski and Baker 1966) and large genomes (Pellicer and Leitch 2020; Kinosian, Rowe, and Wolf 2022), slow rates of dysploidy (Li et al. 2024) and genome size change (Clark et al. 2016), as well as limited gene order (collinearity) change across hundreds of millions of years (Huang et al. 2022; Li et al. 2024). These observations are consistent with the hypothesis that diploidization in plants with symmetric meiosis is fundamentally different than in plants with asymmetric meiosis, potentially due to the absence of meiotic drive.

Previous work has shown that centromere drive is absent in lineages with symmetric meiosis (Zedek and Bureš 2016; Plačková et al. 2024). Evidence for this comes from molecular evolutionary analyses of histones, in particular CenH3, which is often rapidly evolving with signals of positive selection in lineages with asymmetric meiosis, but evolutionarily constrained and under purifying selection in organisms with symmetric meiosis (Zedek and Bureš 2016; F. R. Finseth, Nelson, and Fishman 2021; Plačková et al. 2024). Centromere histones are thought to be rapidly evolving to counteract the changes caused by centromere drive. Thus, rapid histone evolution is not expected or observed in lineages with symmetric meiosis because centromeres are conserved in the absence of meiotic drive (Zedek and Bureš 2016; Plačková et al. 2024). In previous work, all pteridophytes have been categorized as having symmetric meiosis, so investigating the evolution of CenH3 in heterosporous pteridophytes would reveal if this pattern held across all lineages with asymmetric meiosis.

The absence of meiotic drive in homosporous plants means no possibility for the preferential inheritance of certain karyotypes, chromosome morphologies, or rearrangements (Burt and Trivers 2009), and could be part of the reason why homosporous pteridophytes have relatively stable chromosome structures (Clark et al. 2016; Wagner and Wagner 1979; Bomfleur, McLoughlin, and Vajda 2014), uniform chromosome sizes (Clark et al. 2016; Wagner and Wagner 1979; Manton 1950; Nakazato et al. 2008), and relatively slow rates of chromosome number evolution (Li et al. 2024). The size range variation in homosporous fern chromosomes is only 31-fold, compared to 1300-fold in heterosporous angiosperms (Clark et al. 2016). It has been hypothesized that this stability and uniformity is due to a limit on the amount of genetic material in each chromosome (Liu et al. 2019), but also may come from the lack of meiotic drive influencing chromosome morphological change (Plačková et al. 2024). Despite the extensive research on pteridophyte cytology (e.g., Manton 1950; Klekowski and Baker 1966), limited information has been published on their chromosome morphology. We surveyed the literature for pteridophytes chromosome morphology data, finding only ten studies describing eleven taxa and a broad range of chromosome morphologies (Table 2). Further studies on homosporous and heterosporous pteridophyte chromosome morphology and karyotype structure, ideally in a phylogenetic context, are needed to understand what processes are influencing these traits.

Transmission ratio distortion can operate in organisms with symmetric meiosis, but these types of TRD occur post-meiotically, and so are different from true meiotic drive (Fishman and Willis 2005; Sandler and Novitski 1957; Pardo-Manuel de Villena and Sapienza 2001b). One example of post-meiotic drive is spore drive, which results from competition between spores containing different haplotypes, often called killer and alternative haplotypes (Lindholm et al. 2016;

Grognet et al. 2014; Harvey et al. 2014; Raju 1994). Spore drive is best characterized in ascomycete fungi, where the spores are packaged together in an ascus. The proximity of spores in an ascus allows for a “killer” haplotype to kill or disable neighboring spores with an alternate or “target” haplotype. Similar spore production occurs in pteridophytes and bryophytes with spores packaged in a sporangium. Spore drive has not been tested in ferns, but reductions in spore numbers within a sporangium has been observed across populations of homosporous ferns (Barker and James Hickey 2006; A. L. Grusz, Pers. Ob.) which suggests it could occur. In addition, dispersal can also influence spore drive, with drive being more prevalent if spores do not travel far from one another (Lindholm et al. 2016). The majority of fern spores disperse only a few meters from the parent plant (Rose and Dassler 2017; Conant 1978), but because ferns produce vast numbers of spores, some do travel great distances (e.g., Tryon 1970). The greater distance that spores disperse from one another, the smaller the potential effect from spore drive (Lindholm et al. 2016).

Another example of post-meiotic drive is male drive, which occurs when a drive locus kills sperm with a target locus (e.g., Presgraves, Severance, and Wilkinson 1997; Taylor 1994). Similar to spore drive, one genotype will kill an alternate genotype regardless of the fitness consequences (Lindholm et al. 2016; Rice 2013). There is limited research on fern sperm competition, but observational studies have described competition in the archegonium before sperm meet the egg (Lopez-Smith and Renzaglia 2008). Further work is needed to understand competition and potential male drive among sperm of homosporous plants, as well as in other flagellate plants.

Because of fundamental differences in meiosis, meiotic drive cannot happen in homosporous pteridophytes in the same way as in heterosporous plants. TRD can still influence the genomes of homosporous plants by removing certain genotypes but likely does not shape the genome in the same ways as true meiotic drive. Several homosporous pteridophyte genome assemblies are now published (Marchant et al. 2022; Li et al. 2024; Yu et al. 2023; Fang et al. 2021; Huang et al. 2022), giving us insight into plant genome structure in the absence of female meiotic drive. Perhaps most striking is that these species have highly conserved intra- and intergenomic synteny over millions of years (Huang et al. 2022; Li et al. 2024); the same is true for hornworts (Schafran et al. 2025). An exception is *Ceratopteris richardii*, which has a rate of fractionation rivaling many angiosperm species (Marchant et al. 2022; Nakazato et al. 2006), but the mechanisms causing this rapid diploidization are unclear. Broad patterns in homosporous pteridophytes suggest that, while genic diploidization and fractionation occur, in the apparent absence of meiotic drive there are limited mechanisms or forces causing cytological restructuring of the genome following WGD.

Conclusions and future work

Here we describe how meiotic drive may be a potential mechanism behind the disparity in genome architecture among land plants, specifically influencing chromosome number and structure of heterosporous plants. Other types of TRD or drive can occur in homosporous lineages, but not true meiotic drive, as sporogenesis is symmetric. Although the symmetry of meiosis has not been explicitly explored in the context of homosporous plants, other authors have noted that genome evolution is likely dependent on the mechanics of meiosis (e.g., Burt and Trivers 2009; Kinosian, Rowe, and Wolf 2022; Finseth 2023; Lindholm et al. 2016). Pteridophytes are an ideal system to study the effects of drive on genome structure, as there are sister lineages with asymmetric and symmetric meiosis in both ferns and lycophytes. Here we discuss a few ways to investigate how drive or other types of transmission ratio distortion might affect homosporous vascular land plant genomes.

Finding natural examples of meiotic drive can be challenging, as a driving locus is often rapidly fixed in a population, and therefore undetectable. However, these can re-emerge following a hybridization event, or even be part of hybrid sterility (Lindholm et al. 2016). An example of this is in yellow monkeyflowers, where hybrids between *Mimulus guttatus* and *M. nasutus* exhibit strong female meiotic drive and the driving locus is nearly fixed in only a handful of generations (Fishman and Willis 2005; Fishman et al. 2001; Finseth, Nelson, and Fishman 2021). Testing for such cryptic drive systems could be a potential avenue of research in pteridophytes, specifically in those with known hybrid sterility. Pteridology has a rich history of work on hybrid species, including studies on the model system *Ceratopteris* (e.g., Hickok and Klekowski 1974; Hickok 1973). Genomic resources available for *Ceratopteris* (Marchant et al. 2022; Nakazato et al. 2006) would make testing for drive in a hybrid mapping population feasible (e.g., Fishman and Willis 2005). Even without genomic resources, detecting TRD in pteridophytes is possible by genotyping gametophyte progeny arrays to determine meiotic product ratios (described in Kinosian et al. 2022). An important step for understanding meiotic drive and TRD in pteridophytes will be to sequence and assemble centromere diversity, ideally among closely related species. Cytology suggests that ferns have distinct monocentric chromosomes, rather than dispersed holocentric chromosomes (e.g., Manton, 1950); however, no published fern genomes have assembled centromeres. Interestingly, bryophyte taxa typically have monocentric chromosomes, but have small units of euchromatic and heterochromatin dispersed along a chromosome (Schafran et al. 2025; Hisanaga et al. 2023), rather than the large regions of heterochromatin which characterize centromeres in monocentric angiosperms (Guerra 2000). Considering that fern genes are more or less evenly distributed along chromosomes (Marchant et al. 2022; Rabinowicz et al. 2005; Wolf et al. 2015), their chromatin landscapes may look more similar to bryophytes than to angiosperms.

Consistent with the absence of meiotic drive, past studies have shown that homosporous ferns have strong Mendelian inheritance (Andersson-Kottö 1927; Dedera and Werth 1987). Ferns have relatively low gene densities compared to flowering plants (Rabinowicz et al. 2005; Wolf et al. 2015), perhaps because of a lack of meiotic drive selecting for genome downsizing or, alternatively, pseudogenization caused by transposons in ferns (Lisch 2013). Long terminal repeat retrotransposon (LTR-RT) have a high birth but low death rate in homosporous ferns, with the inverse occurring in heterosporous lycophytes (Yu et al. 2023; Wang et al. 2021). Older LTR-RTs are associated with larger haploid nuclear genome size in pteridophytes (Baniaga and Barker 2019). The exact role of transposons in unclear in pteridophytes, but more research is warranted, especially because transposons are known to be associated with meiotic drive (Eickbush, Young, and Zanders 2019; Vogan et al. 2021). In addition, the expansion of different gene families as well as the rate of meiosis gene evolution is greater in heterosporous angiosperms than in homosporous pteridophytes (Li et al. 2024; Dhakal, Harkess, and Wolf 2025), suggesting that different selection pressures, perhaps one of those being meiotic drive, are acting on meiosis in heterosporous lineages. It will also be important to look at TRD and sex chromosome drive in bryophytes. In particular, mosses have dynamic genomes (Fujiwara et al. 2025; Patel, Budke, and Bainard 2025) that may be affected by sex chromosome drive (e.g., (Úbeda, Patten, and Wild 2015). Segregation distortion of loci and biased sex ratios have been detected in the moss *Ceratodon* (McDaniel, Willis, and Shaw 2007). While our understanding of bryophyte genome evolution is improving (Schafran et al. 2025; Fujiwara et al. 2025; Patel, Budke, and Bainard 2025), TRD has not been explored in hornworts and liverworts.

A post-meiotic TRD mechanism that could occur in homosporous plants is spore drive. In fungi, spores are affected by drive when a certain genotype kills an alternative genotype. Considering the large number of spores produced within a sporangium by both eusporangiate and leptosporangiate lineages, the ingredients for spore drive are present. DNA expression studies have identified spore drive systems, revealing that the driving element can lethally target specific genes (Urquhart and Gardiner 2023). A consistent reduction in spore number per sporangium in leptosporangiate ferns has been observed (Barker and James Hickey 2006; A. L. Grusz, Pers. Ob.), suggesting something may be happening during sporogenesis to reduce spore number. Additional work counting spores could better characterize this pattern. If more concrete patterns of spore reduction are observed and connected to a spore drive system, the model fern *Ceratopteris* could help understand the genetic mechanisms for homosporous spore drive.

Other processes outside of meiotic and related drive systems could affect chromosome number and genome size. Population size can be a greater force on chromosome number than meiotic drive in Carnivora: smaller populations had greater variation in chromosome number than large populations (Jonika et al. 2024). Ferns appear to have generally high gene flow among populations (Pelosi and Sessa 2021), which could partially explain their consistently high stable chromosome numbers. Another hypothesis for the evolution of chromosome number is the minimum interaction theory, which postulates smaller chromosomes are selected to reduce reciprocal translocation; consequently, chromosome number will increase as more chromosomes are needed to contain the genome (Imai et al. 1986). Ferns are the only lineage with a positive correlation between genome size and chromosome number (Nakazato et al. 2008; Bainard et al. 2011; Clark et al. 2016; Fujiwara et al. 2021; Kinosian, Rowe, and Wolf 2022). It has been suggested that fern chromosome size is limited by the amount of genetic material per chromosome (Liu et al. 2019), however, the minimum interaction theory could explain the mechanism behind this limitation.

Exploring ecology and natural history in homosporous plants could be another avenue to understand their distinct genome organization outside of meiotic drive. It is well-established that the rate of molecular evolution is higher and genome size is smaller in plants with shorter life cycles, compared to those with longer life cycles (Cavalier-Smith 2005; Smith and Donoghue 2008). There is also a correlation between vascular structure (i.e., the presence or absence of tracheids) and genome size (Cavalier-Smith 2005). Heterosporous ferns (Salviniales) and *Selaginella* have tracheids and small genome sizes, but gymnosperms and the heterosporous lycophyte *Isoëtes* lack tracheids and have large genomes (Leitch et al. 2005; Cavalier-Smith 1978). Comparing life history and genome traits in a phylogenetic context could help tease apart complex interactions between these variables (Soltis and Soltis 1990; Pelosi and Sessa 2021).

The proliferation of a selfish element is key in female meiotic drive and TRD systems, yet the mechanisms by which this occurs are incredibly varied (Saupe and Johannesson 2022; Lindholm et al. 2016; Burt and Trivers 2009). Female meiotic drive is potentially a mechanism behind the rapid diploidization and downsizing following WGD in heterosporous plants. TRD in pteridophytes and bryophytes is probably distinct from true meiotic drive in angiosperms, fungi, or animals. The absence of meiotic drive would help explain large and stable genomes, uniform chromosome sizes, relatively static chromosome numbers following WGDs, as well as the current challenges with assembling centromeres in homosporous fern and lycophyte genomes. Although almost certainly only one piece of the puzzle, researching meiotic drive in homosporous plants is important to broaden our understanding of the unique genomes of this lineage.

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Table 1. Genome traits and potential types of meiotic drive for land plants.

Group	**Average Genome size (1C)**	**Average Haploid Chromosome Number (n)**	**Average Inferred rounds of WGD**	**Asymmetric meiosis**	**Potential types of drive**	**Citations**
Angiosperm	4.4	15.99	3.5	Yes	Centromere, chromosome, female meiotic drive	(Pellicer and Leitch 2020; Klekowski and Baker 1966; McKibben, Finch, and Barker 2024; One Thousand Plant Transcriptomes Initiative 2019; Z. Li et al. 2024)
Gymnosperm	15.51	11.69	1.63	Yes	Centromere, chromosome, female meiotic drive	(One Thousand Plant Transcriptomes Initiative 2019; Pellicer and Leitch 2020; A. Rice et al. 2015; Z. Li et al. 2024)
Heterosporous pteridophyte (Salviniales, Isoetales, Selaginellales)	1.01	13.62	2.4	Yes	Centromere, chromosome, female meiotic drive	(Pellicer and Leitch 2020; Z. Li et al. 2024; Klekowski and Baker 1966)
Homosporous pteridophyte	15.13	57.5	2.82	No	Spore drive, other non-meiotic TRD	(Pellicer and Leitch 2020; Z. Li et al. 2024; Klekowski and Baker 1966)
Bryophytes	0.72	10.23	2.28	No	Spore drive, other non-meiotic TRD, sex chromosome drive	(Pellicer and Leitch 2020; Z. Li et al. 2024; Klekowski and Baker 1966) N. Patel, et al. 2025)

Table 2. Published descriptions of chromosome morphology for homosporous and heterosporous pteridophytes.

Taxon	**Reproductive mode**	**Chromosome morphology**	**Citation**
Claytosmunda claytoniana	homosporous	acrocentric, very few metacentric	(Seizi Tatuno and Yoshida 1967)
Osmundastrum cinnamomeum	homosporous	acrocentric, very few metacentric	(Seizi Tatuno and Yoshida 1967)
Plenasium banksiaefolium	homosporous	acrocentric, very few metacentric	(Seizi Tatuno and Yoshida 1967)
Hymenophyllum barbatum	homosporous	acrocentric, some metacentric	(Seizi Tatuno and Takei 1969)
Asplenium incisum	homosporous	acrocentric, very few metacentric	(S. Tatuno and Kawakami 1969)
Pteris	homosporous	acrocentric	(Kawakami 1971)
Regnellidium diphyllum (Salviniales)	heterosporous	Submetacentric and subtelocentric	(Kuriachan 1994)
Selaginella (Selaginellales)	heterosporous	Metacentric, telocentric	(Adriana Buarque Marcon, Barros, and Guerra 2005; Takamiya 1993)
Danaea	homosporous	submetacentric	(Benko-Iseppon, Rodrigues, and da Fonsêca 2000)
Acrostichum	homosporous	subtelocentric	(Adriana B. Marcon, Barros, and Guerra 2003)
Doryopteris triphylla	homosporous	telocentric	(Neira et al. 2017)

Figures

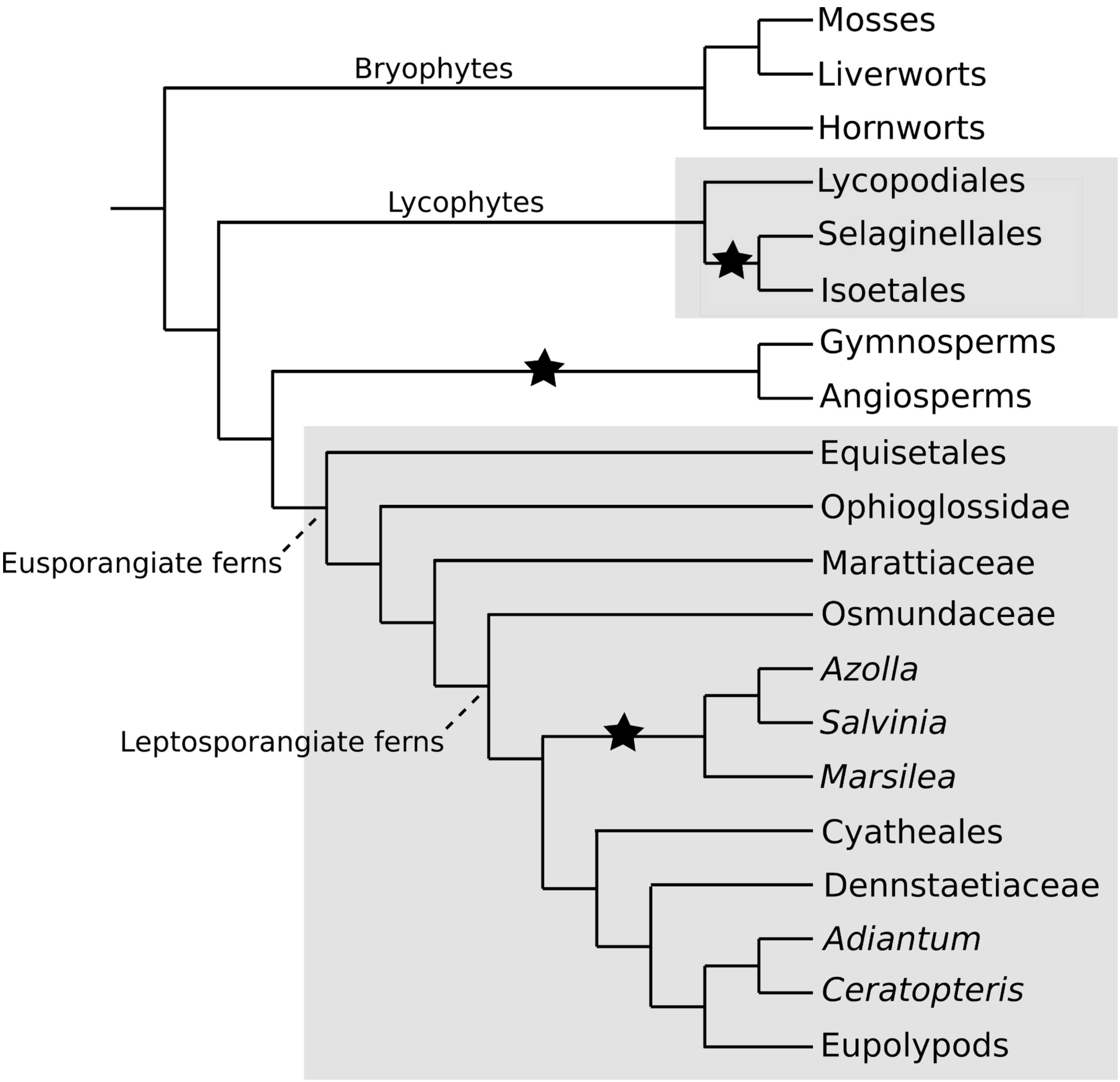

Figure 1. Cartoon phylogeny of land plants, including notable groups discussed in this paper but not all major lineages. Grey boxes distinguish pteridophytes, a paraphyletic group comprising lycophytes (above) and ferns (below). Black stars distinguish the three extant heterosporous plant clades. Modified from (PPG I 2016) and (Patel, Budke, and Bainard 2025).

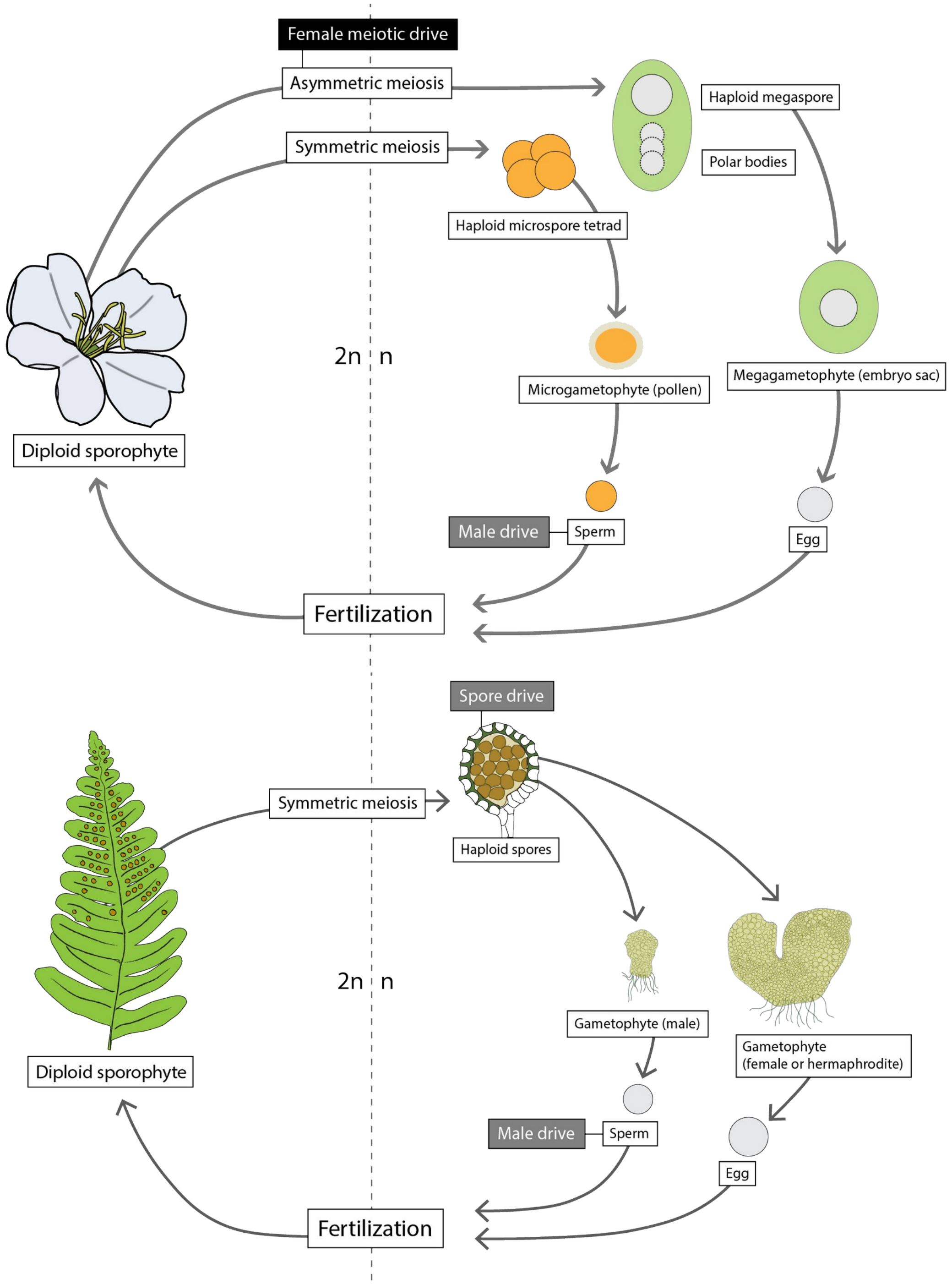

Figure 2. Life cycles of heterosporous (top) and homosporous (bottom) land plants. Locations of female meiotic drive and other types of transmission ratio distortion are denoted in black and gray boxes, respectively.

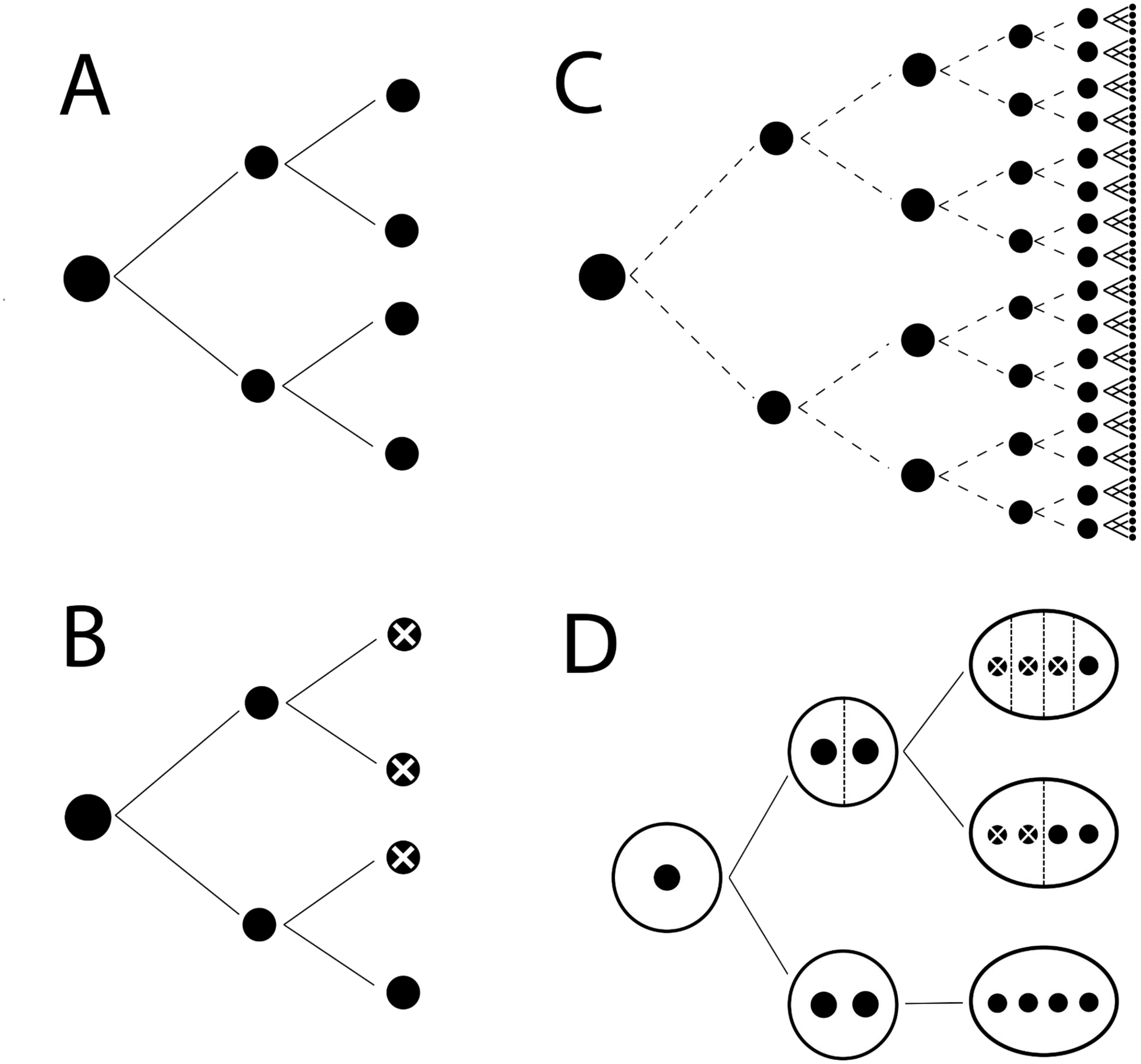

Figure 3. Examples of different types of meiosis. In each panel, the far left circle depicts the sporocyte, and succeeding divisions proceeding to the right. Solid lines indicate meiosis and dotted lines indicate mitosis. A) Heterosporous female meiosis, where only one meiotic product survives and the remaining three polar bodies die (can be either top or bottom, resulting from the cell on the chalazal or micropylar end surviving, see Fig. 4A). B) Heterosporous male meiosis, where all meiotic products survive. C) Leptosporagiate sporogenesis where 64 spores are generated through four rounds of mitosis and one round of meiosis; all spore survive. D) Types of angiosperm megasporogenesis: monosporoic (top), bisporic (middle), and tetrasporic (bottom), modified from (Haig 1990, 2020); meiosis proceeds similarly to (A), but differing numbers of nuclei survive due to variable cytokinesis in meiosis II.

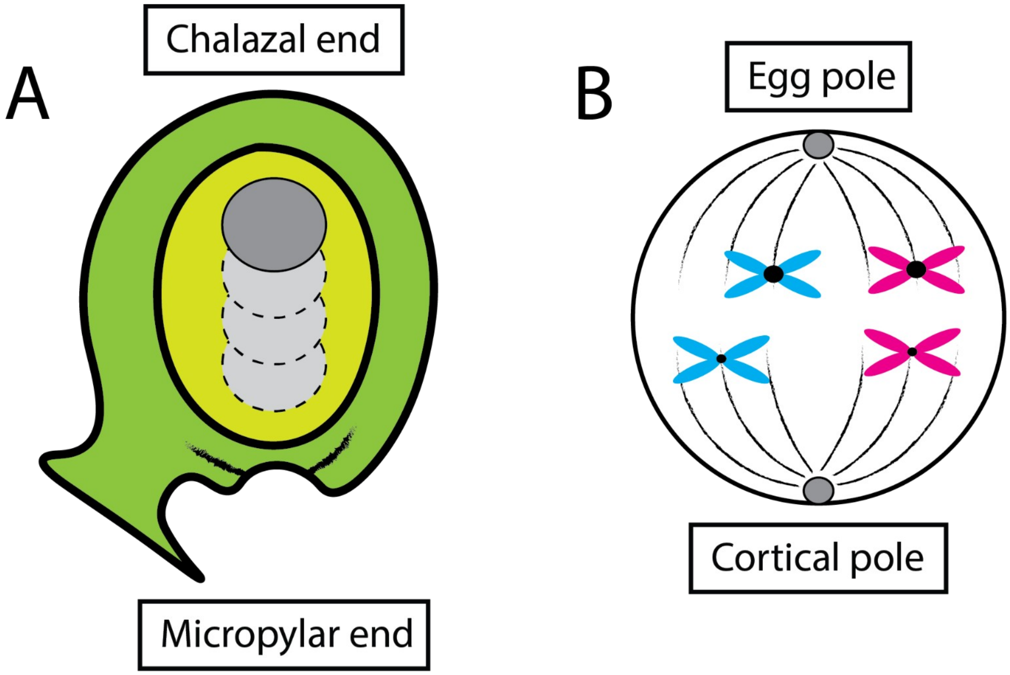

Figure 4. A) Organization of megasporogenesis in a heterosporous ovule, the cell on the chalazal end often survives, but alternatively the cell on the micropylar end can become the egg. B) Centromere drive, where larger centromeres are preferentially transmitted to the egg pole in meiosis I (anaphase I is depicted); the egg pole is often associated with the chalazal end of the ovule (see panel A), and the cortical side the micropylar end.

Glossary

Transmission ratio distortion - non-random inheritance of parental alleles in the offspring population, occuring before, during, or after meiosis.

Meiotic drive - non-random inheritance of alleles, chromosomes, or other genome structures specifically during asymmetrical meiosis.

Spore drive - observed in ascomycete fungi where spores are packages together in an ascus, a spore with the "killer" haplotype will kill spores with the alternative haplotype, particularly in when spores are in close proximity.

Male drive - biased transmission that occurs during or after male meiosis; typically involves an allele that kills certain sperm cells.

Sporogenesis - the generation of a spore cell by meiosis (in heterosporous plants) or mitosis (in homosporous plants)

Megasporogenesis - creation of spores that will develop into a female gametophyte (megagametophyte)

Microsporogenesis - creation of spores that will develop into a male gametophyte (megagametophyte)

Homosporous - an organism that produces one type of spore. This spore develops into a gametophyte which can produce male and/or female gametes.

Heterosporous - an organism that produces two types of spores. These are the mega- and microspores, which develop into gametophytes capable of producing eggs or sperm, respectively.

Pteridophyte - a plant classified as a fern or lycophyte. This group is paraphyletic but is functionally important because all taxa are seedless vascular plants.

Leptosporangiate fern - ferns that produce sporangia with a long stalk that arise from a single epidermal cell. Their spore production proceeds from a single spore mother cell through four rounds of mitosis and one round of meiosis to form 64 spores.

Eusporangiate fern - ferns that produce sporangia with a short or no stalk that arise from several epidermal cells. Hundreds to thousands of spores are produced in each sporangium via meiosis.

Metacentric - a chromosome with the centromere positioned in the middle, with both arms being the same length.

Acrocentric - a chromosome with the centromere close to one end, with one arm being much longer than the other.

Telocentric - a chromosome where the centromere is at one end, causing there to be effectively only one arm rather than two.

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