Archives of Current Research International

Volume 25, Issue 5, Page 404-418, 2025; Article no.ACRI.135465
ISSN: 2454-7077

Molecular Regulation of the Transition from Vegetative Growth to Meiosis in Plants and Model Organisms

Ammireddy Suguna [a*] and Gibence H. Rose Winnie [a]

[a] Centre for Plant Biotechnology and Molecular Biology, Kerala Agricultural University, Vellanikkara, Thrissur, 680656, India.

Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

Article Information

DOI: https://doi.org/10.9734/acri/2025/v25i51220

Open Peer Review History:
This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: https://pr.sdiarticle5.com/review-history/135465

Review Article

Received: 05/03/2025
Accepted: 09/05/2025
Published: 10/05/2025

ABSTRACT

This review examines the molecular mechanisms regulating the transition from vegetative growth to meiosis across plants and other eukaryotic models. It highlights key genetic pathways controlling floral meristem identity, ovule development, and meiotic entry, emphasizing conserved genes and regulatory networks in species like Arabidopsis, rice, yeast, and mice. The roles of hormonal signals, environmental cues, and nutrient sensing in meiosis initiation are discussed, along with mechanisms governing chromosome pairing, recombination, and segregation. Understanding these conserved processes offers insights into reproductive development and provides avenues for crop improvement and fertility management.

Keywords: Chromosomes; molecular processes; meiotic regulation; vegetative development.

**Corresponding author: Email: ammireddysuguna1136@gmail.com;*

Cite as: *Suguna, Ammireddy, and Gibence H. Rose Winnie. 2025. "Molecular Regulation of the Transition from Vegetative Growth to Meiosis in Plants and Model Organisms". Archives of Current Research International 25 (5):404-18. https://doi.org/10.9734/acri/2025/v25i51220.*

1. INTRODUCTION

The transition from vegetative to reproductive development is critical for ensuring the species' ability to reproduce and sustain itself. This process, known as flowering, is tightly controlled by a complex interaction of genetic programming and environmental inputs. In many plant species, including the well-studied model organism Arabidopsis thaliana and staple crops such as rice, wheat, and barley, the transition to the reproductive phase is managed by integrating stimuli like as light, temperature, and plant hormones (Cheng et al., 2014). The activation of genes involved in defining floral meristem identity, which initiates flowering and gives rise to reproductive organs, is an important step in this transformation (Dreni et al., 2007). These same signals also prompt meiosis, a unique cellular division that reduces the chromosome number and promotes genetic variability in gametes (Kleckner, 1996).

Plants, like other eukaryotes, go through a highly coordinated and complex meiotic process that includes prophase I, metaphase I, anaphase I, and telophase I, followed by a secondary meiotic division (Terasawa et al., 1995). During these stages, homologous chromosomes couple, recombine, and segregate, ending in the formation of haploid gametes. Model systems such as Arabidopsis, mice, Drosophila melanogaster, Caenorhabditis elegans, and Saccharomyces cerevisiae have identified a wide range of essential genes that govern meiotic events such as chromosomal alignment, recombination, and division—examples include MSH4 in yeast, Rec8 in mice, and Dmc1 in Arabidopsis. Crops such as rice, barley, and wheat also contain unique meiotic genes that are essential for reproductive efficiency (Muralla et al., 2011).

Unravelling the genetic frameworks that control flowering and meiosis is not only important for understanding plant biology, but it also has substantial agronomic implications. By modifying these pathways, we can improve crop output, resistance, and adaptability (Zickler & Kleckner, 1999). This review discusses the molecular pathways that govern the vegetative-to-reproductive transition and meiotic control in plants and other model organisms. It focuses on the conserved genes required for each meiotic phase, stressing their significance in evolutionary continuity and reproductive optimization in species such as Arabidopsis, rice, wheat, yeast, and mice.

2. GENETIC KEYS THAT DRIVE THE TRANSITION FROM VEGETATIVE GROWTH TO THE FLOWERING PHASE

Flowering plants go through a series of developmental steps as they move from vegetative to reproductive growth. Okada & Shimura, (1994) identify five major steps: establishment of the inflorescence meristem, specification of the floral meristem, determination of floral organ number and placement, identification of organ kinds, and final development of floral organs. Genetic study in Arabidopsis mutants has revealed the presence of numerous regulatory genes involved in these stages. Ovule formation is an important element of the reproductive process, with distinct physical distinctions between species. Arabidopsis (a dicot) and rice (a monocot) produce anatropous, unitegmic ovules, whereas maize, wheat, barley, and tomato produce bitegmic ovules (Drews & Yadegari, 2004; Wang & Ren 2008; Shi & Yang 2011). The placenta produces ovule primordia, and their development is affected by hormone interactions, particularly auxin and cytokinin, as well as transcription factors such as PIN1, ANT, and the CUC gene family (Balasubramanian & Schneitz, 2000; Elliott *et al*., 1996; Ceccato *et al*., 2013). *INO, ATS*, and *WUSCHEL* govern the asymmetric development of the outer and inner integuments (Baker *et al*., 1997; Balasubramanian & Schneitz, 2002; Gross-Hardt *et al*., 2002). In cereals such as rice, wheat, and barley, orthologs such as *OsMADS13, OsINO*, and *OsWOX9 B* play conserved roles that are frequently influenced by auxin gradients. These regulatory components work together to guide precise ovule patterning and megagametophyte growth in both monocot and dicot plants.

3. MEIOSIS

In higher plants, meiotic processes are similar to those found in other eukaryotes, with conserved mechanisms for homologous pairing and recombination. However, the molecular signals that begin the shift from the diploid sporophyte to the haploid gametophyte phase are still poorly understood. This generational shift usually happens in the late stages of cell differentiation, but it may also be intentionally induced in undifferentiated tissues, emphasizing the stark distinction between sporophyte and gametophyte development.

Meiosis, a specialized division crucial for all sexually reproducing eukaryotes, consists of a

single DNA replication event followed by two consecutive nuclear divisions. Meiosis I separates homologous chromosomes, whereas meiosis II divides sister chromatids in a manner comparable to mitosis (Gerton & Hawley 2005). The proper production of gametes is dependent on precise regulation during prophase I, which includes homolog recognition, pairing, recombination, and ultimately segregation.

4. ENTRY INTO MEIOSIS I FROM MITOTIC CELL DIVISION IN ANGIOSPERMS

In flowering plants, meiosis begins in ovules and anthers with the transition of subepidermal cells into archesporial cells, which grow directly into megaspore mother cells (MMCs) without going through mitosis (Maheshwari, 1950; Reiser & Fischer, 1993). Normally, a single MMC is present per ovule, although species such as *Paeonia calijkica* can develop 30-40 MMCs (Walters, 1962). Casuarinaceae, Amentiferae, Ranales, and several basic dicots all contain multiple MMCs (Eames, 1961; Maheshwari, 1950).

In Arabidopsis, for sporocyte identity to be established, interactions between the tapetum and meiocytes are essential. Male sterility results from mutations lacking *EMS1/EXS1* or *TPD1*, which overproduce sporocytes and fail to generate tapetal cells (Canales *et al*., 2002; Zhao *et al*., 2002). Genes like *AMS, MS1*, and *AtMYB103* are activated by the receptor kinase EMS1/EXS and are necessary for the differentiation of microspores and tapetums (Yang *et al*., 2003; Wilson *et al*., 2001; Sorensen *et al*., 2003; Higginson *et al*., 2003). *MSP1* builds the anther wall and limits sporocyte development in rice. Excess sporocytes and deformed anthers are produced by mutants that lack this function (Nonomura *et al*., 2003). One hypodermal cell in maize serves as the MMC in pseudocrassinucellate ovules, becoming more deeply embedded as the ovule grows (Randolph, 1936; Cooper, 1937).

5. NUTRITIONAL CUES AND REGULATORY PATHWAYS FOR MEIOSIS INITIATION IN YEAST AND OTHER MODEL ORGANISMS

The start of meiosis in *Saccharomyces cerevisiae* is directly related to the availability of nutrients. Carbon and nitrogen deprivation decrease the activity of important metabolic regulators such as Target of Rapamycin Complex I (TORC1) and protein kinase A (PKA). This activates the transcription factor IME1, which in turn triggers the induction of more than 300 genes required for meiosis (Weidberg *et al*., 2016; Chu *et al*., 1998; Primig *et al*., 2000). By phosphorylating and targeting Sic1, a cyclin-dependent kinase inhibitor, for degradation, another kinase, IME2, promotes entry into meiosis (Dirick *et al*., 1998; Benjamin *et al*., 2003). Meiosis is also disrupted by disruptions in tRNA genes like *SUP3*, which affect DNA replication and spore formation by causing incorrect translation termination (Liebman *et al*., 1976; Rothstein *et al*., 1977). According to Dirick *et al*., (1998), Stuart & Wittenberg (1998), and Smith *et al*. (2001), B-type cyclins CLB5 and CLB6 are necessary for premeiotic DNA replication and may also control recombination and the creation of synaptonemal complexes.

Meiosis in *Schizosaccharomyces pombe* is regulated via a unique mechanism. In budding yeast, the transcription factor Ste11 performs a similar role to *IME1* (Yamamoto, 1996; Honigberg & Purnapatre, 2003). *Pat1*, a kinase that maintains *Mei2* phosphorylated throughout mitosis, ordinarily represses the RNA-binding protein *Mei2,* which mediates entry into meiosis. Mei2 can go to the nucleus and start meiosis when Pat1 is deactivated due to hunger (Yamamoto, 1996; Marston & Amon, 2004). Phosphorylation-based control governs *Mei2*'s interactions with *Mip1p* (Yamashita *et al*., 1998; Sato *et al*., 2001; Shinozaki-Yabana *et al*., 2000; Shimada *et al*., 2003). Despite continuing mitotic cycles, mutations in *Mei1, Mei2*, or *Mei3* stop meiosis at the mononucleate stage (Egel, 1973), while *Mei4* mutants do not advance following DNA replication (Bresch *et al*., 1968; Egel, 1973; Egel & Egel-Mitani, 1974).

Repetitive routes involving *gld-1* and *gld-2*, which can independently induce meiosis, regulate meiotic entry in Caenorhabditis worms (Kadyk & Kimble, 1998). Likewise, in Drosophila, meiotic development in both sexes depends on the Cdc25 homolog Twine. Due to reduced meiotic division, sterility resulted from mutations that disrupt twine, such as *mat(2)synHB5* (Courtot *et al*., 1992; White Cooper *et al*., 1993). According to Zhang *et al*. (2025), MTR4, a critical cofactor of the nuclear RNA exosome, is essential for sperm production as well as embryonic development. Male infertility results from targeted ablation of *Mtr4* in germ cells, mainly because animals exhibit a marked impairment in the onset of meiosis.

6. Sexual Dimorphism in Meiosis Initiation in Mammals: A Complex, Sex-Specific Regulation

Males undergo a cyclical pattern of meiosis after birth, while females undergo it throughout embryogenesis (Juliano & Wessel, 2010; Lehmann, 2012). Gametes are produced by primordial germ cells (PGCs); females generate oocytes before birth, while males produce sperm after puberty. Both sexes undergo meiosis when exposed to retinoic acid (RA) from the mesonephros (Bowles *et al*., 2006; Koubova *et al*., 2006). However, Cyp26b1 degrades RA in the embryonic testes, preventing meiosis, whereas in the ovaries, its absence permits meiosis to proceed (Bowles *et al*., 2010). Meiotic initiation requires the transcription factor Stra8, which is activated by RA. To guarantee exact timing, Cyp26b1 activity regulates Stra8 expression (Koubova *et al*., 2006). Signalling molecules such as FGF9 and Cyp26b1 inhibit meiosis in the testes to preserve germ cell pluripotency, while RA activates Stra8 in the ovaries and postnatal testes, starting meiotic entry and premeiotic DNA synthesis. For both sexes, MEIOSIN, a partner of Stra8, further guarantees proper meiotic development (Anderson *et al*., 2008; Ishiguro *et al*., 2020).

7. KEY PLAYERS AND MECHANISMS IN PROPHASE AND ITS SUBPHASES IN MEIOSIS

The extended prophase I stage of meiosis includes leptotene, zygotene, pachytene, and diplotene subphases, and involves numerous gene-mediated steps for chromosomal pairing and synapsis. In maize, the *ameiotic1 (am1)* gene is indispensable for meiotic initiation; its mutants halt at interphase, similar to defects seen in *Stra8*-mutant mice (Pawlowski *et al*., 2009). The rice homolog *OsAM1* facilitates the leptotene-to-zygotene transition, and mutants lacking *OsAM1* arrest at leptotene, displaying disrupted recruitment of proteins like PAIR2, ZEP1, and OsMER3 (Che *et al*., 2011).

One important occurrence in early meiosis is telomere migration. Telomere attachment to the nuclear envelope in maize is made possible by proteins such as Ku and Nup145 (Strambio-de-Castillia *et al*., 1999). Areas of the envelope where the synaptonemal complex anchors are indicated by Lamin C2 (Alsheimer *et al*., 1999). *Ndj1p* and *Taz1p* are essential for bouquet formation and effective chromosomal pairing in budding and fission yeasts, and their mutations cause meiosis to be delayed (Conrad *et al*., 1997; Trelles-Sticken *et al*., 2000). Through the recruitment of SETDB1 to sex chromosomes and autosomal regions, the germline-specific protein ATF7IP2 (MCAF2) controls heterochromatin organization during male meiosis. Meiotic development is disrupted when it is absent (Alavattam *et al*., 2024).

8. MEIOTIC CHROMOSOMAL PAIRING AND SYNAPSIS: KEY GENES AND THEIR ROLES ACROSS SPECIES

A key component of chromatid cohesion is the cohesin complex. Yeast's *Rec8p* and other meiosis-specific components provide appropriate cohesion (Molnar *et al*., 1995). When *Smc1β* is mutated in mice, the synaptonemal complex structure is impaired, resulting in meiotic arrest and sterility (Revenkova *et al*., 2004). Like those without zip1, yeast *msh4* mutants show fewer crossovers (Novak *et al*., 2001).

Multiple conserved genes work together to form the synaptonemal complex (SC), which is necessary for homologous chromosome synapsis and crossover during meiosis. According to Siddiqi *et al*. (2000), mutations in the gene *DYAD* cause univalent formation and interrupted progression, as it is essential for female meiotic synapsis in Arabidopsis thaliana. For sister chromatid cohesion and bivalent formation, the yeast Rec8 homolog *SYN1/DIF1* gene is essential (Bai *et al*., 1999; Bhatt *et al*., 1999). Crossover formation is supported during meiosis by RCK, the plant homolog of yeast *MER3* (Chen *et al*., 2005). The heterodimer of the genes *AtSPO11-1* and *AtSPO11-2* is necessary for recombination and the creation of double-strand breaks (DSBs); as their mutants are unable to establish bivalent bonds or synapses (Grelon *et al*., 2001; Stacey *et al*., 2006). Chromosome fragmentation is a symptom of loss-of-function mutants of *MRE11*, *RAD50*, and *COM1,* proteins involved in DSB processing and repair (Puizina *et al*., 2004; Uanschou *et al*., 2007).

The HORMA-domain protein *PAIR2* plays a crucial role in the establishment of SC and chromosomal architecture in rice, as evidenced by its association with chromosome axes during early prophase I and persistence at centromeres until diakinesis (Nonomura *et al*., 2006). *PAIR3* is also essential for homolog synapses, and when it is disrupted, bivalent formation fails, leading to

sterility (Yuan *et al*., 2009). The deletion of *ZEP1,* which forms the transverse filament of the SC and is comparable to *ZYP1* in Arabidopsis, causes chromosomes to align but not synapses (Wang *et al*., 2010). Recombination and SC integrity depend on *OsRAD51C,* a homolog of human *RAD51C;* mutations show chromosomal breakage and sterility (Tang *et al*., 2014). *ZEP1* collaborates with the plant-specific protein *CRC1,* which is similar to *TRIP13* in mice and *Pch2* in yeast, to enhance meiotic growth and construct the SC core (Miao *et al*., 2013). Homologous pairing and bivalent formation depend on *OsDMC1*, and meiotic abnormalities result from its downregulation (Deng & Wang, 2007). The rice ortholog of *SPO11, OsSPO11-1*, controls the development of DSBs and crossovers; its mutants create telomere bouquets but are unable to construct SC and crossover (Yu *et al*., 2010; Wu *et al*., 2015). *OsSDS, PRD1, PRD2, AtPRD3/OsPAIR1*, and *DFO* are other DSB-associated genes in rice that show functional conservation with animal meiosis and yeast (Nonomura *et al*., 2004; De Muyt *et al*., 2007, 2009; Zhang *et al*., 2012).

According to Pawlowski *et al*. (2004), phs1 is essential for homolog detection and recombination in maize. Mutants that lack *RAD51* foci and exhibit nonhomologous pairing demonstrate a breakdown in recombination initiation. *DMC1*'s conserved function in meiotic processes is further supported by the fact that it is essential for appropriate DSB repair and chromosomal segregation in barley (Szurman-Zubrzycka *et al*., 2019).

In mammals, *SYCP3* is a structural element of the SC that is necessary for cohesion and synapsis; females show decreased fertility and aneuploidy, whereas males that have been knocked out are sterile because of meiotic arrest (Yuan *et al*., 2000; Kouznetsova *et al*., 2005). Synapsis and spermatogenesis are disrupted by the mei1 mutant; male fertility can be partially restored by cisplatin treatment (Libby *et al*., 2002, 2003). Male infertility results from meiotic disruption caused by loss-of-function in genes such as Dmc1, Msh4/5, and Rec8 (Pittman *et al*., 1998; Yoshida *et al*., 1998; Edelmann *et al*., 1999). DSB repair during meiosis is regulated by Cyclin A1, CDK2, and Ku70 (Muller-Tidow *et al*., 2004; Fuchimoto *et al*., 2001). Male mice lacking *Miwi* are infertile, whereas female mice are still fertile, and male mice lacking *Mili* are sterile compared to female mice that are fertile (Kuramochi-Miyagawa *et al*., 2004; Deng & Lin, 2002). DSB induction requires *SPO11,* which is preserved. Males with prophase arrest are infertile, although cisplatin can partially rescue them (Romanienko & Camerini-Otero, 2000). Both Romanienko and Camerini-Otero (2000) and Baudat *et al*. (2000) have reported that female *Spo11−/−* mice lose their oocytes after birth.

9. HOMOLOGOUS RECOMBINATION: KEY MECHANISMS AND INSIGHTS

The precise segregation of chromosomes and genetic diversity is guaranteed by homologous recombination. In plants such as *Lilium longiflorum*, where *Rad51* and *LIM15* (*DMC1*) localize to recombination sites in early prophase, *Rad51* and *DMC1* play a crucial role in recombination (Roeder, 1995). *LIM15* expression is limited to early meiosis, in contrast to other *LIM* genes with pre-meiotic expression. The existence of similar proteins in yeast (*ISC2/Isc10*) and *Antirrhinum majus* (*fil1*) supports evolutionary conservation (Kobayashi *et al*., 1994).

According to Meuwissen *et al*. (1992), *SCP1* is necessary for SC formation and pairing in mice. Female oocytes halt postnatally when Cdk2 is deleted; male meiosis is unaffected (Ortega *et al*., 2003). *Mei-2* and *asc*(DL243) mutations in Neurospora damage pairing, decrease recombination, and result in chromosome missegregation (Smith, 1975; DeLange & Griffiths, 1980).

Recombination and sister chromatid cohesion in Arabidopsis depend on *SWI1* (Mercier *et al*., 2001, 2003). *OsSUN1* and *OsSUN2* in rice encourage homologous pairing and telomere clustering; double mutants show impaired meiotic chromosomal organization (Zhang *et al*., 2020). The coordination of recombination and DNA repair is highlighted by mutants such as *Osatm* and *Osdmc1*, where *OsATM* functions downstream of *OsSPO11-1* and interacts with *OsDMC1* to preserve chromosomal integrity (Zhang *et al*., 2020).

The pachytene-to-diplotene transition in mice requires Cyclin A1, and mutants of *Mlh1* and *Mlh3* halt during meiosis, resulting in delayed meiosis in females and sterility in males because of more stringent checkpoints (Liu *et al*., 1998; Lipkin *et al*., 2002; Eaker *et al*., 2002; Edelmann *et al*., 1996). While females are unharmed, men with Fkbp6 deficiency are sterile because of early

prophase I failure (Crackower *et al*., 2003). Through the activation of mid-meiotic genes, *Ndt80* guides the advancement of S. cerevisiae beyond early meiosis; its activation is checkpoint-dependent to guarantee recombination completion (Xu *et al*., 1995). Meiotic and sporulation abnormalities are revealed at different stages by different *spo* mutants (Esposito and al., 1970; Moens *et al*., 1974).

10. MEIOTIC METAPHASE AND THE ROLE OF KEY GENES IN CHROMOSOME DYNAMICS

Chromosome alignment and segregation preparation occur during the critical meiotic phase known as metaphase I. By facilitating the passage from prophase I to metaphase I, the protein SKP1 is essential to male meiosis. It stops chromosomal pairing structures from disassembling too soon and localizes to the synaptonemal complex (Guan *et al*., 2020).

Organisms like Caenorhabditis elegans and Arabidopsis contain several Skp1-related genes, but species like yeast, mice, and humans only have one *Skp1* gene (Nayak *et al*., 2002; Zhao *et al*., 2003). By controlling proteins that uphold homologous connections, *ASK1* helps Arabidopsis separate homologs before anaphase I (Yang *et al*., 1999). In Arabidopsis, appropriate spindle assembly is controlled by the *ATK1* gene. Spindle structure is disturbed in *atk1-1* mutants, resulting in aberrant multi-axial arrays that cause improper chromosomal segregation during metaphase I (Chen *et al*., 2002).

In maize, the *afd1* gene interacts genetically with *dv1, dsy1,* and *as1*, which are likewise important for chromosomal mobility and synapsis, and is necessary for centromere cohesion and spindle orientation (Golubovskaya *et al*., 1993).

During metaphase I, *OsMTOPVIB* in rice transforms multipolar spindles into bipolar ones; if this function is lost, spindle development is flawed (Xue *et al*., 2019). It is hypothesized that *PRD1* influences sister kinetochores' alignment to promote the development of a bipolar spindle during rice meiosis (Shi *et al*., 2021). During meiosis I, proteasomal activity is essential in rat oocytes. Protease inhibition slows MPF (maturation-promoting factor) deactivation and prevents polar body extrusion, indicating that the proteasome aids in exiting metaphase I (Josefsberg *et al*., 2000). Additionally, rice *OsMRE11* contributes to chromosome integrity; mutants show chromosome breakage and entanglements during metaphase and anaphase I, indicating its significance in structural maintenance and homologous recombination (Ji *et al*., 2013).

11. KEY PLAYERS IN THE TRANSITION FROM METAPHASE I TO ANAPHASE I

In meiosis, precisely regulated regulatory proteins and kinases are involved in the transition from metaphase I to anaphase I. For this transition, the CDC28 kinase's regulatory component CKS2 is necessary. Male mice deficient in CKS2 have anaphase I arrest, which results in sterility (Spruck *et al*., 2003). Spindle stability and oocyte maturation in mice during this phase are guaranteed by ERK3, another crucial regulator (Li *et al*., 2010). The anaphase-promoting complex/cyclosome (APC/C) in C. elegans is home to the gene EMB-30, which is similar to APC4/Lid1 and regulates the onset of anaphase by ubiquitin-mediated degradation (Furuta *et al*., 2000).

According to Choi *et al*. (2019), Spindlin1 controls the expression of the spindle checkpoint protein *BUB3*, which is necessary for precise metaphase-anaphase progression in swine during meiosis I. Furthermore, through its interactions with APC/C and increased phosphorylation of APC3, Cyclin B3 (CycB3) facilitates the start of anaphase and increases its affiliation with coactivators such as Cdc20 during meiosis and mitosis (Garrido *et al*., 2020). The expression of *AMA1*, a member of the Cdc20 family, is dependent on the splicing factor MER1 and specifically regulates APC/C activity during meiosis in yeast (Cooper *et al*., 2000).

12. TRANSITION FROM MEIOSIS I TO MEIOSIS II: KEY REGULATORS AND MECHANISMS

Meiosis I to II progression is strictly controlled and varies from organism to organism. The transcription factor SAP is essential for female meiosis in Arabidopsis. *Sap* mutants exhibit severe reproductive abnormalities and are unable to initiate meiosis II (Byzova *et al*., 1999). APC/C targets securin for degradation, which is necessary for this transition, and so activates separase in mouse oocytes. Both S. cerevisiae and C. elegans share this mechanism (Terret *et*

al., 2003). According to Grandin & Reed (1993), B-type cyclins CLB1 and CLB4 are essential for meiosis II in yeast but not for meiosis I.

In vertebrates like starfish, the proto-oncogene *Mos* controls the progression to meiosis II, preventing oocytes from prematurely reentering the mitotic cycle (Tachibana *et al*., 2000). To fine-tune APC/C activity and enable oocytes to escape meiosis I and avoid S phase before entering meiosis II, Emi2 proteins in Xenopus induce partial degradation of cyclin B (Tang *et al*., 2008). *Mes1* controls the interphase between meiotic divisions in fission yeast by modifying APC/C coactivators such as *Fzr1/Mfr1* and *Slp1* (Kimata *et al*., 2011).

In Drosophila, cyclin A levels during the G2 phase are controlled by roughex (rux), which controls entry into meiosis II during spermatogenesis. Mutations in rux throw off this timing and stop progression (Gonczy *et al*., 1994). According to Bulankova *et al*. (2010), CDKA;1 activity in plants peaks during metaphase I and II, propelling meiotic progression. According to Marston & Amon (2005), precise exit from meiosis I and entry into meiosis II depend on the proper regulation of cyclin-CDK complexes and APC/C activity during interkinesis.

Although the meiosis regulatory phase is supported by the cyclin-CDK-APC/C network in all species, its molecular actors differ. Mes1 controls the transition in S. pombe, while *OSD1* operates in plants, and *Emi2* does the same in vertebrates (Izawa *et al*., 2005; Kimata *et al*., 2008; Madgwick *et al*., 2006). To guarantee meiotic exit in Arabidopsis, genes like *TAM* (a cyclin A), *OSD1* (an APC/C inhibitor), *SMG7* (associated with RNA degradation), and *TDM* work together. TDM mutants go through a third aberrant division, whereas *TAM* or *OSD1* mutants stop after meiosis I. Anaphase II advancement depends on *SMG7*, which also shows a link between meiotic regulation and RNA metabolism (Bulankova *et al*., 2010; Cromer *et al*., 2012). The RNA-processing domain found in AtPS1 facilitates this regulatory network as well (d'Erfurth *et al*., 2008). Lastly, the *STUD* gene is required for Arabidopsis cytokinesis during telophase II to promote the generation of viable male gametes (Hülskamp *et al*., 1997). Spindle reassembly was hampered and abnormal post-meiotic divisions were curbed in *smg7-6* plants due to a CENH3 mutation that increased meiotic exit by lowering CENH3 levels (Capitao *et al*., 2021).

13. CONCLUSION

Meiosis is controlled by a mix of species-specific regulatory networks and conserved mechanisms that work together to guarantee faithful chromosomal segregation and meiotic cycle completion. The orderly transition from metaphase to anaphase is maintained by essential elements such as *SKP1,* spindle assembly regulators, and the APC/C complex. Tightly regulated cyclin-CDK and APC/C activity support the transition from meiosis I to II, and various species use distinct regulatory proteins such as *Mos, TAM, OSD1,* and *SMG7* to ensure meiosis integrity.

A delicate balance between shared genetic modules and organism-specific adaptations is highlighted by the evolutionarily conserved core pathways that govern meiotic progression, although regulatory techniques vary among animals. A better comprehension of these mechanisms contributes to our understanding of genetic integrity and reproductive development and offers prospective paths toward increasing fertility and refining crop breeding techniques.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

Alavattam, K. G., Esparza, J. M., Hu, M., Shimada, R., Kohrs, A. R., Abe, H., Munakata, Y., Otsuka, K., et al. (2024). ATF7IP2/MCAF2 directs H3K9 methylation and meiotic gene regulation in the male germline. *Genes & Development*, *38*(3-4), 115–130.

Alsheimer, M., von Glasenapp, E., Hock, R., & Benavente, R. (1999). Architecture of the nuclear periphery of rat pachytene spermatocytes: Distribution of nuclear

envelope proteins in relation to synaptonemal complex attachment sites. *Molecular Biology of the Cell*, *10*, 1235–1245.

Anderson, E. L., Baltus, A. E., Roepers-Gajadien, H. L., Hassold, T. J., de Rooij, D. G., van Pelt, A. M., & Page, D. C. (2008). Stra8 and its inducer, retinoic acid, regulate meiotic initiation in both spermatogenesis and oogenesis in mice. *Proceedings of the National Academy of Sciences*, *105*(39), 14976–14980.

Bai, X., Peirson, B. N., Dong, F., Cai, X., & Makaroff, C. A. (1999). Isolation and characterization of *SYN1*, a *RAD21*-like gene essential for meiosis in *Arabidopsis*. *The Plant Cell*, *11*, 417–430.

Baker, S. C., Robinson-Beers, K., Villanueva, J. M., Gaiser, J. C., & Gasser, C. S. (1997). Interactions among genes regulating ovule development in *Arabidopsis thaliana*. *Genetics*, *145*(4), 1109–1124.

Balasubramanian, S., & Schneitz, K. (2000). NOZZLE regulates proximal-distal pattern formation, cell proliferation and early sporogenesis during ovule development in *Arabidopsis thaliana*. *Development*, *127*(19), 4227–4238.

Balasubramanian, S., & Schneitz, K. (2002). NOZZLE links proximal-distal and adaxial-abaxial pattern formation during ovule development in *Arabidopsis thaliana*.

Baudat, F., Manova, K., Yuen, J. P., Jasin, M., & Keeney, S. (2000). Chromosome synapsis defects and sexually dimorphic meiotic progression in mice lacking *Spo11*. *Molecular Cell*, *6*(5), 989–998.

Benjamin, K. R., Zhang, C., Shokat, K. M., & Herskowitz, I. (2003). Control of landmark events in meiosis by the CDK Cdc28 and the meiosis-specific kinase Ime2. *Genes & Development*, *17*(12), 1524–1539.

Bhatt, A. M., Lister, C., Page, T., Fransz, P., Findlay, K., Jones, G. H., Dickinson, H. G., & Dean, C. (1999). The *DIF1* gene of *Arabidopsis* is required for meiotic chromosome segregation and belongs to the *REC8/RAD21* cohesin gene family. *The Plant Journal*, *19*(4), 463–472.

Bowles, J., Feng, C. W., Spiller, C., Davidson, T. L., Jackson, A., & Koopman, P. (2010). FGF9 suppresses meiosis and promotes male germ cell fate in mice. *Developmental Cell*, *19*(3), 440–449.

Bowles, J., Knight, D., Smith, C., Wilhelm, D., Richman, J., Mamiya, S., Yashiro, K., Chawengsaksophak, K., Wilson, M. J., Rossant, J., & Hamada, H. (2006). Retinoid signaling determines germ cell fate in mice. *Science*, *312*(5773), 596–600.

Bresch, C., Müller, G., & Egel, R. (1968). Genes involved in meiosis and sporulation of a yeast. *Molecular and General Genetics*, *102*(4), 301–306.

Bulankova, P., Riehs-Kearnan, N., Nowack, M. K., Schnittger, A., & Riha, K. (2010). Meiotic progression in *Arabidopsis* is governed by complex regulatory interactions between *SMG7*, *TDM1*, and the meiosis I–specific cyclin *TAM*. *The Plant Cell*, *22*(11), 3791–3803.

Byzova, M. V., Franken, J., Aarts, M. G., de Almeida-Engler, J., Engler, G., Mariani, C., Campagne, M. M. V. L., & Angenent, G. C. (1999). *Arabidopsis STERILE APETALA*, a multifunctional gene regulating inflorescence, flower, and ovule development. *Genes & Development*, *13*(8), 1002–1014.

Canales, C., Bhatt, A. M., Scott, R., & Dickinson, H. (2002). *EXS*, a putative LRR receptor kinase, regulates male germline cell number and tapetal identity and promotes seed development in *Arabidopsis*. *Current Biology*, *12*, 1718–1727.

Capitao, C., Tanasa, S., Fulnecek, J., Raxwal, V. K., Akimcheva, S., Bulankova, P., Mikulkova, P., Crhak Khaitova, L., et al. (2021). A *CENH3* mutation promotes meiotic exit and restores fertility in *SMG7*-deficient *Arabidopsis*. *PLoS Genetics*, *17*(9), e1009779.

Ceccato, L., Masiero, S., Sinha Roy, D., Bencivenga, S., Roig-Villanova, I., Ditengou, F. A., Palme, K., Simon, R., & Colombo, L. (2013). Maternal control of *PIN1* is required for female gametophyte development in *Arabidopsis*. *PLoS ONE*, *8*(6), e66148.

Che, L., Tang, D., Wang, K., Wang, M., Zhu, K., Yu, H., Gu, M., & Cheng, Z. (2011). *OsAM1* is required for leptotene-zygotene transition in rice. *Cell Research*, *21*(4), 654–665.

Chen, C., Marcus, A., Li, W., Hu, Y., Calzada, J. P. V., Grossniklaus, U., Cyr, R. J., & Ma, H. (2002). The *Arabidopsis ATK1* gene is required for spindle morphogenesis in male meiosis. *Development*, *129*(10), 2401–2409.

Chen, C., Zhang, W., Timofejeva, L., Gerardin, Y., & Ma, H. (2005). The *Arabidopsis ROCK-N-ROLLERS* gene encodes a homolog of the yeast ATP-dependent DNA

helicase *MER3* and is required for normal meiotic crossover formation. *The Plant Journal*, *43*(3), 321–334.

Cheng, S., Huang, Y., Zhu, N., & Zhao, Y. (2014). The rice *WUSCHEL*-related homeobox genes are involved in reproductive organ development, hormone signaling and abiotic stress response. *Gene*, *547*(1), 197–207.

Choi, J. W., Zhou, W., Nie, Z. W., Niu, Y. J., Shin, K. T., & Cui, X. S. (2019). Spindlin1 alters the metaphase to anaphase transition in meiosis I through regulation of *BUB3* expression in porcine oocytes. *Journal of Cellular Physiology*, *234*(6), 8963–8974.

Chu, S., DeRisi, J., Eisen, M., Mulholland, J., Botstein, D., Brown, P. O., & Herskowitz, I. (1998). The transcriptional program of sporulation in budding yeast. *Science*, *282*(5389), 699–705.

Conrad, M. N., Dominguez, A. M., & Dresser, M. E. (1997). *Ndj1p*, a meiotic telomere protein required for normal chromosome synapsis and segregation in yeast. *Science*, *276*(5316), 1252–1255.

Cooper, D. C. (1937). Macrosporogenesis and embryo-sac development in *Euchlaena mexicana* and *Zea mays*. *Journal of Agricultural Research*, *55*(5), 5394–5551.

Cooper, K. F., Mallory, M. J., Egeland, D. B., Jarnik, M., & Strich, R. (2000). Ama1p is a meiosis-specific regulator of the anaphase promoting complex/cyclosome in yeast. *Proceedings of the National Academy of Sciences*, *97*(26), 14548–14553.

Courtot, C., Fankhauser, C., Simanis, V., & Lehner, C. F. (1992). The *Drosophila cdc25* homolog *twine* is required for meiosis. *Development*, *116*(2), 405–416.

Crackower, M. A., Kolas, N. K., Noguchi, J., Sarao, R., Kikuchi, K., Kaneko, H., Kobayashi, E., Kawai, Y., et al. (2003). Essential role of *Fkbp6* in male fertility and homologous chromosome pairing in meiosis. *Science*, *300*(5623), 1291–1295.

Cromer, L., Heyman, J., Touati, S., Harashima, H., Araou, E., Girard, C., Horlow, C., Wassmann, K., Schnittger, A., De Veylder, L., & Mercier, R. (2012). OSD1 promotes meiotic progression via APC/C inhibition and forms a regulatory network with TDM and CYCA1;2/TAM. *PLoS Genetics*, *8*(7), e1002865.

d'Erfurth, I., Jolivet, S., Froger, N., Catrice, O., Novatchkova, M., Simon, M., Jenczewski, E., & Mercier, R. (2008). Mutations in *AtPS1* (*Arabidopsis thaliana* parallel spindle 1) lead to the production of diploid pollen grains. *PLoS Genetics*, *4*(11), e1000274.

De Muyt, A., Pereira, L., Vezon, D., Chelysheva, L., Gendrot, G., Chambon, A., ... & Grelon, M. (2009). A high throughput genetic screen identifies new early meiotic recombination functions in Arabidopsis thaliana. *PLoS genetics*, *5*(9), e1000654.

De Muyt, A., Vezon, D., Gendrot, G., Gallois, J. L., Stevens, R., & Grelon, M. (2007). *AtPRD1* is required for meiotic double strand break formation in *Arabidopsis thaliana*. *The EMBO Journal*, *26*(18), 4126–4137.

DeLange, A. M., & Griffiths, A. J. F. (1980). Meiosis in *Neurospora crassa*. II. Genetic and cytological characterization of three meiotic mutants. *Genetics*, *96*(2), 379–398.

Deng, W., & Lin, H. (2002). *Miwi*, a murine homolog of *piwi*, encodes a cytoplasmic protein essential for spermatogenesis. *Developmental Cell*, *2*(6), 819–830.

Deng, Z. Y., & Wang, T. (2007). *OsDMC1* is required for homologous pairing in *Oryza sativa*. *Plant Molecular Biology*, *65*, 31–42.

Dirick, L., Goetsch, L., Ammerer, G., & Byers, B. (1998). Regulation of meiotic S phase by *Ime2* and a *Clb5,6*-associated kinase in *Saccharomyces cerevisiae*. *Science*, *281*(5384), 1854–1857.

Dreni, L., Jacchia, S., Fornara, F., Fornari, M., Ouwerkerk, P. B., An, G., Colombo, L., & Kater, M. M. (2007). The D-lineage MADS-box gene *OsMADS13* controls ovule identity in rice. *The Plant Journal*, *52*(4), 690–699.

Drews, G. N., & Yadegari, R. (2002). Development and function of the angiosperm female gametophyte. *Annual Review of Genetics*, *36*(1), 99–124.

Eaker, S., Cobb, J., Pyle, A., & Handel, M. A. (2002). Meiotic prophase abnormalities and metaphase cell death in *MLH1*-deficient mouse spermatocytes: Insights into regulation of spermatogenic progress. *Developmental Biology*, *249*(1), 85–95.

Eames, A. J. (1961). *Morphology of the angiosperms* (1st ed.).

Edelmann, W., Cohen, P. E., Kane, M., Lau, K., Morrow, B., Bennett, S., Umar, A., Kunkel, T., Cattoretti, G., Chaganti, R., & Pollard, J. W. (1996). Meiotic pachytene arrest in *MLH1*-deficient mice. *Cell*, *85*(7), 1125–1134.

Edelmann, W., Cohen, P. E., Kneitz, B., Winand, N., Lia, M., Heyer, J., Kolodner, R., Pollard, J. W., & Kucherlapati, R. (1999). Mammalian *MutS* homologue 5 is required for chromosome pairing in meiosis. *Nature Genetics*, *21*(1), 123–127.

Egel, R. (1973). Commitment to meiosis in fission yeast. *Molecular and General Genetics*, *121*(3), 277–284.

Egel, R., & Egel-Mitani, M. (1974). Premeiotic DNA synthesis in fission yeast. *Experimental Cell Research*, *88*(1), 127–134.

Elliott, R. C., Betzner, A. S., Huttner, E., Oakes, M. P., Tucker, W. Q., Gerentes, D., Perez, P., & Smyth, D. R. (1996). *AINTEGUMENTA*, an *APETALA2*-like gene of *Arabidopsis* with pleiotropic roles in ovule development and floral organ growth. *The Plant Cell*, *8*(2), 155–168.

Esposito, M. S., Esposito, R. E., Arnaud, M., & Halvorson, H. O. (1970). Conditional mutants of meiosis in yeast. *Journal of Bacteriology*, *104*(1), 202–210.

Fuchimoto, D. I., Mizukoshi, A., Schultz, R. M., Sakai, S., & Aoki, F. (2001). Posttranscriptional regulation of cyclin A1 and cyclin A2 during mouse oocyte meiotic maturation and preimplantation development. *Biology of Reproduction*, *65*(4), 986–993.

Furuta, T., Tuck, S., Kirchner, J., Koch, B., Auty, R., Kitagawa, R., Rose, A. M., & Greenstein, D. (2000). *EMB-30*: an *APC4* homologue required for metaphase-to-anaphase transitions during meiosis and mitosis in *Caenorhabditis elegans*. *Molecular Biology of the Cell*, *11*(4), 1401–1419.

Garrido, D., Bourouh, M., Bonneil, É., Thibault, P., Swan, A., & Archambault, V. (2020). Cyclin B3 activates the anaphase-promoting complex/cyclosome in meiosis and mitosis. *PLoS Genetics*, *16*(11), e1009184.

Gerton, J. L., & Hawley, R. S. (2005). Homologous chromosome interactions in meiosis: Diversity amidst conservation. *Nature Reviews Genetics*, *6*(6), 477–487.

Golubovskaya, I., Grebennikova, Z. K., Avalkina, N. A., & Sheridan, W. F. (1993). The role of the *ameiotic1* gene in the initiation of meiosis and in subsequent meiotic events in maize. *Genetics, 135*(4), 1151–1166.

Gönczy, P., Thomas, B. J., & DiNardo, S. (1994). *roughex* is a dose-dependent regulator of the second meiotic division during *Drosophila* spermatogenesis. *Cell, 77*(7), 1015–1025.

Grandin, N., & Reed, S. I. (1993). Differential function and expression of *Saccharomyces cerevisiae* B-type cyclins in mitosis and meiosis. *Molecular and Cellular Biology, 13*(4), 2113–2125.

Grelon, M., Vezon, D., Gendrot, G., & Pelletier, G. (2001). *AtSPO11-1* is necessary for efficient meiotic recombination in plants. *The EMBO Journal, 20*(3), 589–600.

Groß-Hardt, R., Lenhard, M., & Laux, T. (2002). *WUSCHEL* signaling functions in interregional communication during *Arabidopsis* ovule development. *Genes & Development, 16*(9), 1129–1138.

Guan, Y., Leu, N. A., Ma, J., Chmátal, L., Ruthel, G., Bloom, J. C., Lampson, M. A., Schimenti, J. C., Luo, M., & Wang, P. J. (2020). SKP1 drives the prophase I to metaphase I transition during male meiosis. *Science Advances, 6*(13), eaaz2129. https://doi.org/10.1126/sciadv.aaz2129

Higginson, T., Li, S. F., & Parish, R. W. (2003). *AtMYB103* regulates tapetum and trichome development in *Arabidopsis thaliana*. *The Plant Journal, 35*(2), 177–192.

Honigberg, S. M., & Purnapatre, K. (2003). Signal pathway integration in the switch from the mitotic cell cycle to meiosis in yeast. *Journal of Cell Science, 116*(11), 2137–2147.

Hülskamp, M., Parekh, N. S., Grini, P., Schneitz, K., Zimmermann, I., Lolle, S. J., & Pruitt, R. E. (1997). The *STUD* gene is required for male-specific cytokinesis after telophase II of meiosis in *Arabidopsis thaliana*. *Developmental Biology, 187*(1), 114–124.

Ishiguro, K. I., Matsuura, K., Tani, N., Takeda, N., Usuki, S., Yamane, M., Sugimoto, M., Fujimura, S., Hosokawa, M., Chuma, S., & Ko, M. S. (2020). MEIOSIN directs the switch from mitosis to meiosis in mammalian germ cells. *Developmental Cell, 52*(4), 429–445.

Izawa, D., Goto, M., Yamashita, A., Yamano, H., & Yamamoto, M. (2005). Fission yeast Mes1p ensures the onset of meiosis II by blocking degradation of cyclin Cdc13p. *Nature, 434*(7032), 529–533. https://doi.org/10.1038/nature03401

Ji, J., Tang, D., Wang, M., Li, Y., Zhang, L., Wang, K., Li, M., & Cheng, Z. (2013). *MRE11* is required for homologous

synapsis and DSB processing in rice meiosis. *Chromosoma, 122*, 363–376.

Josefsberg, L. B. Y., Galiani, D., Dantes, A., Amsterdam, A., & Dekel, N. (2000). The proteasome is involved in the first metaphase-to-anaphase transition of meiosis in rat oocytes. *Biology of Reproduction, 62*(5), 1270–1277.

Juliano, C., & Wessel, G. (2010). Versatile germline genes. *Science, 329*(5992), 640–641.

Kadyk, L. C., & Kimble, J. (1998). Genetic regulation of entry into meiosis in *Caenorhabditis elegans*. *Development, 125*(10), 1803–1813.

Kimata, Y., Trickey, M., Izawa, D., Gannon, J., Yamamoto, M., & Yamano, H. (2008). A mutual inhibition between APC/C and its substrate Mes1 required for meiotic progression in fission yeast. *Developmental Cell, 14*(3), 446–454.

Kleckner, N. (1996). Meiosis: How could it work? *Proceedings of the National Academy of Sciences, 93*(16), 8167–8174.

Kobayashi, T., Kobayashi, E., Sato, S., Hotta, Y., Miyajima, N., Tanaka, A., & Tabata, S. (1994). Characterization of cDNAs induced in meiotic prophase in lily microsporocytes. *DNA Research, 1*(1), 15–26.

Koubova, J., Menke, D. B., Zhou, Q., Capel, B., Griswold, M. D., & Page, D. C. (2006). Retinoic acid regulates sex-specific timing of meiotic initiation in mice. *Proceedings of the National Academy of Sciences, 103*(8), 2474–2479.

Kouznetsova, A., Novak, I., Jessberger, R., & Höög, C. (2005). SYCP2 and SYCP3 are required for cohesin core integrity at diplotene but not for centromere cohesion at the first meiotic division. *Journal of Cell Science, 118*(10), 2271–2278.

Kuramochi-Miyagawa, S., Kimura, T., Ijiri, T. W., Isobe, T., Asada, N., Fujita, Y., Ikawa, M., Iwai, N., Okabe, M., Deng, W., & Lin, H. (2004). *Mili*, a mammalian member of piwi family gene, is essential for spermatogenesis. *Development, 131*(4), 839–849.

Lehmann, R. (2012). Germline stem cells: Origin and destiny. *Cell Stem Cell, 10*(6), 729–739.

Li, S., Ou, X. H., Wang, Z. B., Xiong, B., Tong, J. S., Wei, L., Li, M., Yuan, J., Ouyang, Y. C., Hou, Y., & Schatten, H. (2010). ERK3 is required for metaphase-anaphase transition in mouse oocyte meiosis. *PLoS One, 5*(9), e13074. https://doi.org/10.1371/journal.pone.0013074

Libby, B. J., De La Fuente, R., O'Brien, M. J., Wigglesworth, K., Cobb, J., Inselman, A., Eaker, S., Handel, M. A., Eppig, J. J., & Schimenti, J. C. (2002). The mouse meiotic mutation *mei1* disrupts chromosome synapsis with sexually dimorphic consequences for meiotic progression. *Developmental Biology, 242*(2), 174–187.

Libby, B. J., Reinholdt, L. G., & Schimenti, J. C. (2003). Positional cloning and characterization of *Mei1*, a vertebrate-specific gene required for normal meiotic chromosome synapsis in mice. *Proceedings of the National Academy of Sciences, 100*(26), 15706–15711.

Liebman, S. W., Sherman, F., & Stewart, J. W. (1976). Isolation and characterization of amber suppressors in yeast. *Genetics, 82*(2), 251–272.

Lipkin, S. M., Moens, P. B., Wang, V., Lenzi, M., Shanmugarajah, D., Gilgeous, A., Thomas, J., Cheng, J., Touchman, J. W., Green, E. D., & Schwartzberg, P. (2002). Meiotic arrest and aneuploidy in *MLH3*-deficient mice. *Nature Genetics, 31*(4), 385–390.

Liu, D., Matzuk, M. M., Sung, W. K., Guo, Q., & Wang, P. (1998). Cyclin A1 is required for meiosis in the male mouse. *Nature Genetics, 20*(4), 377–380.

Madgwick, S., Hansen, D. V., Levasseur, M., Jackson, P. K., & Jones, K. T. (2006). Mouse Emi2 is required to enter meiosis II by reestablishing cyclin B1 during interkinesis. *Journal of Cell Biology, 174*(6), 791–801.

Maheshwari, P. (1950). *An introduction to the embryology of angiosperms*. (No publisher or place provided).

Marston, A. L., & Amon, A. (2005). Erratum: Meiosis: Cell-cycle controls shuffle and deal. *Nature Reviews Molecular Cell Biology, 6*(10), 818.

Mercier, R., Armstrong, S. J., Horlow, C., Jackson, N. P., Makaroff, C. A., Vezon, D., Pelletier, G., Jones, G. H., & Franklin, F. C. H. (2003). The meiotic protein SWI1 is required for axial element formation and recombination initiation in *Arabidopsis*. *Development, 130*(14), 3309–3318.

Mercier, R., Vezon, D., Bullier, E., Motamayor, J. C., Sellier, A., Lefèvre, F., Pelletier, G., & Horlow, C. (2001). SWITCH1 (SWI1): A novel protein required for the

establishment of sister chromatid cohesion and for bivalent formation at meiosis. *Genes & Development, 15*(14), 1859–1871.

Meuwissen, R. L., Offenberg, H. H., Dietrich, A. J., Riesewijk, A., van Iersel, M., & Heyting, C. (1992). A coiled-coil related protein specific for synapsed regions of meiotic prophase chromosomes. *The EMBO Journal, 11*(13), 5091–5100.

Miao, C., Tang, D., Zhang, H., Wang, M., Li, Y., Tang, S., Yu, H., Gu, M., & Cheng, Z. (2013). Central region component1, a novel synaptonemal complex component, is essential for meiotic recombination initiation in rice. *The Plant Cell, 25*(8), 2998–3009.

Moens, P. B., Esposito, R. E., & Esposito, M. S. (1974). Aberrant nuclear behavior at meiosis and anucleate spore formation by sporulation-deficient (SPO) mutants of *Saccharomyces cerevisiae*. *Experimental Cell Research, 83*(1), 166–174.

Molnar, M., Bähler, J., Sipiczki, M., & Kohli, J. (1995). The *rec8* gene of *Schizosaccharomyces pombe* is involved in linear element formation, chromosome pairing, and sister-chromatid cohesion during meiosis. *Genetics, 141*(1), 61–73.

Müller-Tidow, C., Ji, P., Diederichs, S., Potratz, J., Bäumer, N., Köhler, G., Cauvet, T., Choudary, C., Van Der Meer, T., Chan, W. Y. I., & Nieduszynski, C. (2004). The cyclin A1-CDK2 complex regulates DNA double-strand break repair. *Molecular and Cellular Biology, 24*(20), 8917–8928.

Muralla, R., Lloyd, J., & Meinke, D. (2011). Molecular foundations of reproductive lethality in *Arabidopsis thaliana*. *PLoS ONE, 6*(12), e28398.

Nayak, S., Santiago, F. E., Jin, H., Lin, D., Schedl, T., & Kipreos, E. T. (2002). The *Caenorhabditis elegans* Skp1-related gene family: Diverse functions in cell proliferation, morphogenesis, and meiosis. *Current Biology, 12*(4), 277–287.

Nonomura, K. I., Miyoshi, K., Eiguchi, M., Suzuki, T., Miyao, A., Hirochika, H., & Kurata, N. (2003). The *MSP1* gene is necessary to restrict the number of cells entering into male and female sporogenesis and to initiate anther wall formation in rice. *The Plant Cell, 15*(8), 1728–1739.

Nonomura, K. I., Nakano, M., Eiguchi, M., Suzuki, T., & Kurata, N. (2006). *PAIR2* is essential for homologous chromosome synapsis in rice meiosis I. *Journal of Cell Science, 119*(2), 217–225.

Nonomura, K. I., Nakano, M., Fukuda, T., Eiguchi, M., Miyao, A., Hirochika, H., & Kurata, N. (2004). The novel gene *Homologous Pairing Aberration In Rice Meiosis1* of rice encodes a putative coiled-coil protein required for homologous chromosome pairing in meiosis. *The Plant Cell, 16*(4), 1008–1020.

Novak, J. E., Ross-Macdonald, P. B., & Roeder, G. S. (2001). The budding yeast *Msh4* protein functions in chromosome synapsis and the regulation of crossover distribution. *Genetics, 158*(3), 1013–1025.

Okada, K., & Shimura, Y. (1994). Genetic analyses of signalling in flower development using *Arabidopsis*. *Plant Molecular Biology, 26*, 1357–1377.

Ortega, S., Prieto, I., Odajima, J., Martín, A., Dubus, P., Sotillo, R., Barbero, J. L., Malumbres, M., & Barbacid, M. (2003). Cyclin-dependent kinase 2 is essential for meiosis but not for mitotic cell division in mice. *Nature Genetics, 35*(1), 25–31.

Pawlowski, W. P., Golubovskaya, I. N., Timofejeva, L., Meeley, R. B., Sheridan, W. F., & Cande, W. Z. (2004). Coordination of meiotic recombination, pairing, and synapsis by *PHS1*. *Science, 303*(5654), 89–92.

Pawlowski, W. P., Wang, C. J. R., Golubovskaya, I. N., Szymaniak, J. M., Shi, L., Hamant, O., Zhu, T., Harper, L., Sheridan, W. F., & Cande, W. Z. (2009). Maize *AMEIOTIC1* is essential for multiple early meiotic processes and likely required for the initiation of meiosis. *Proceedings of the National Academy of Sciences, 106*(9), 3603–3608.

Pittman, D. L., Cobb, J., Schimenti, K. J., Wilson, L. A., Cooper, D. M., Brignull, E., Handel, M. A., & Schimenti, J. C. (1998). Meiotic prophase arrest with failure of chromosome synapsis in mice deficient for *Dmc1*, a germline-specific *RecA* homolog. *Molecular Cell, 1*(5), 697–705.

Primig, M., Williams, R. M., Winzeler, E. A., Tevzadze, G. G., Conway, A. R., Hwang, S. Y., Davis, R. W., & Esposito, R. E. (2000). The core meiotic transcriptome in budding yeasts. *Nature Genetics, 26*(4), 415–423.

Puizina, J., Siroky, J., Mokros, P., Schweizer, D., & Riha, K. (2004). Mre11 deficiency in *Arabidopsis* is associated with chromosomal instability in somatic cells

and Spo11-dependent genome fragmentation during meiosis. *The Plant Cell, 16*(8), 1968–1978.

Randolph, L. F. (1936). Developmental morphology of the caryopsis in maize.

Reiser, L., & Fischer, R. L. (1993). The ovule and the embryo sac. *The Plant Cell, 5*(10), 1291.

Revenkova, E., Eijpe, M., Heyting, C., Hodges, C. A., Hunt, P. A., Liebe, B., Scherthan, H., & Jessberger, R. (2004). Cohesin SMC1β is required for meiotic chromosome dynamics, sister chromatid cohesion and DNA recombination. *Nature Cell Biology, 6*(6), 555–562.

Roeder, G. S. (1995). Sex and the single cell: Meiosis in yeast. *Proceedings of the National Academy of Sciences, 92*(23), 10450–10456.

Romanienko, P. J., & Camerini-Otero, R. D. (2000). The mouse *Spo11* gene is required for meiotic chromosome synapsis. *Molecular Cell, 6*(5), 975–987.

Rothstein, R. J., Esposito, R. E., & Esposito, M. S. (1977). The effect of ochre suppression on meiosis and ascospore formation in *Saccharomyces*. *Genetics, 85*(1), 35–54.

Sato, M., Shinozaki-Yabana, S., Yamashita, A., Watanabe, Y., & Yamamoto, M. (2001). The fission yeast meiotic regulator Mei2p undergoes nucleocytoplasmic shuttling. *FEBS Letters, 499*(3), 251–255.

Shi, D. Q., & Yang, W. C. (2011). Ovule development in *Arabidopsis*: Progress and challenge. *Current Opinion in Plant Biology, 14*(1), 74–80.

Shi, W., Ji, J., Xue, Z., Zhang, F., Miao, Y., Yang, H., Tang, D., Du, G., Li, Y., Shen, Y., & Cheng, Z. (2021). *PRD1*, a homologous recombination initiation factor, is involved in spindle assembly in rice meiosis. *New Phytologist, 230*(2), 585–600.

Shimada, T., Yamashita, A., & Yamamoto, M. (2003). The fission yeast meiotic regulator Mei2p forms a dot structure in the horse-tail nucleus in association with the sme2 locus on chromosome II. *Molecular Biology of the Cell, 14*(6), 2461–2469.

Shinozaki-Yabana, S., Watanabe, Y., & Yamamoto, M. (2000). Novel WD-repeat protein Mip1p facilitates function of the meiotic regulator Mei2p in fission yeast. *Molecular and Cellular Biology, 20*(4), 1234–1242.

Siddiqi, I., Ganesh, G., Grossniklaus, U., & Subbiah, V. (2000). The *dyad* gene is required for progression through female meiosis in *Arabidopsis*. *Development, 127*(1), 197–207.

Smith, D. A. (1975). A mutant affecting meiosis in *Neurospora*. *Genetics, 80*(1), 125–133.

Smith, K. N., Penkner, A., Ohta, K., Klein, F., & Nicolas, A. (2001). B-type cyclins CLB5 and CLB6 control the initiation of recombination and synaptonemal complex formation in yeast meiosis. *Current Biology, 11*(2), 88–97.

Sorensen, A. M., Kröber, S., Unte, U. S., Huijser, P., Dekker, K., & Saedler, H. (2003). The *Arabidopsis Aborted Microspores (AMS)* gene encodes a MYC class transcription factor. *The Plant Journal, 33*(2), 413–423.

Spruck, C. H., de Miguel, M. P., Smith, A. P., Ryan, A., Stein, P., Schultz, R. M., Lincoln, A. J., Donovan, P. J., & Reed, S. I. (2003). Requirement of *Cks2* for the first metaphase/anaphase transition of mammalian meiosis. *Science, 300*(5619), 647–650.

Stacey, N. J., Kuromori, T., Azumi, Y., Roberts, G., Breuer, C., Wada, T., Maxwell, A., Roberts, K., & Sugimoto-Shirasu, K. (2006). *Arabidopsis SPO11-2* functions with *SPO11-1* in meiotic recombination. *The Plant Journal, 48*(2), 206–216.

Strambio-de-Castillia, C., Blobel, G., & Rout, M. P. (1999). Proteins connecting the nuclear pore complex with the nuclear interior. *Journal of Cell Biology, 144*(5), 839–855.

Stuart, D., & Wittenberg, C. (1998). *CLB5* and *CLB6* are required for premeiotic DNA replication and activation of the meiotic S/M checkpoint. *Genes & Development, 12*(17), 2698–2710.

Szurman-Zubrzycka, M., Baran, B., Stolarek-Januszkiewicz, M., Kwaśniewska, J., Szarejko, I., & Gruszka, D. (2019). The *dmc1* mutant allows an insight into the DNA double-strand break repair during meiosis in barley (*Hordeum vulgare* L.). *Frontiers in Plant Science, 10*, 761.

Tachibana, K., Tanaka, D., Isobe, T., & Kishimoto, T. (2000). *c-Mos* forces the mitotic cell cycle to undergo meiosis II to produce haploid gametes. *Proceedings of the National Academy of Sciences, 97*(26), 14301–14306.

Tang, D., Miao, C., Li, Y., Wang, H., Liu, X., Yu, H., & Cheng, Z. (2014). *OsRAD51C* is essential for double-strand break repair in rice meiosis. *Frontiers in Plant Science, 5*, 167.

Tang, W., Wu, J. Q., Guo, Y., Hansen, D. V., Perry, J. A., Freel, C. D., Nutt, L., Jackson, P. K., & Kornbluth, S. (2008). Cdc2 and Mos regulate *Emi2* stability to promote the meiosis I–meiosis II transition. *Molecular Biology of the Cell, 19*(8), 3536–3543.

Terasawa, M., Shinohara, A., Hotta, Y., Ogawa, H., & Ogawa, T. (1995). Localization of RecA-like recombination proteins on chromosomes of the lily at various meiotic stages. *Genes & Development, 9*, 925–938.

Terret, M. E., Wassmann, K., Waizenegger, I., Maro, B., Peters, J. M., & Verlhac, M. H. (2003). The meiosis I-to-meiosis II transition in mouse oocytes requires separase activity. *Current Biology, 13*(20), 1797–1802.

Trelles-Sticken, E., Dresser, M. E., & Scherthan, H. (2000). Meiotic telomere protein Ndj1p is required for meiosis-specific telomere distribution, bouquet formation and efficient homologue pairing. *Journal of Cell Biology, 151*(1), 95–106.

Uanschou, C., Siwiec, T., Pedrosa-Harand, A., Kerzendorfer, C., Sanchez-Moran, E., Novatchkova, M., Akimcheva, S., Woglar, A., Klein, F., & Schlögelhofer, P. (2007). A novel plant gene essential for meiosis is related to the human CtIP and the yeast COM1/SAE2 gene. *The EMBO Journal, 26*(24), 5061–5070.

Walters, J. L. (1962). Megasporogenesis and gametophyte selection in *Paeonia californica*. *American Journal of Botany, 49*(7), 787–794.

Wang, M., Wang, K., Tang, D., Wei, C., Li, M., Shen, Y., Chi, Z., Gu, M., & Cheng, Z. (2010). The central element protein ZEP1 of the synaptonemal complex regulates the number of crossovers during meiosis in rice. *The Plant Cell, 22*(2), 417–430.

Wang, Z.-F., & Ren, Y. (2008). Ovule morphogenesis in Ranunculaceae and its systematic significance. *Annals of Botany, 101*(3), 447–462.

Weidberg, H., Moretto, F., Spedale, G., Amon, A., & van Werven, F. J. (2016). Nutrient control of yeast gametogenesis is mediated by TORC1, PKA and energy availability. *PLoS Genetics, 12*(6), e1006075.

White-Cooper, H., Alphey, L., & Glover, D. M. (1993). The cdc25 homologue twine is required for only some aspects of the entry into meiosis in *Drosophila*. *Journal of Cell Science, 106*(4), 1035–1044.

Wilson, Z. A., Morroll, S. M., Dawson, J., Swarup, R., & Tighe, P. J. (2001). The *Arabidopsis* MALE STERILITY1 (*MS1*) gene is a transcriptional regulator of male gametogenesis, with homology to the PHD-finger family of transcription factors. *The Plant Journal, 28*(1), 27–39.

Wu, Z., Ji, J., Tang, D., Wang, H., Shen, Y., Shi, W., Li, Y., Tan, X., Cheng, Z., & Luo, Q. (2015). *OsSDS* is essential for DSB formation in rice meiosis. *Frontiers in Plant Science, 6*, 21.

Xu, L., Ajimura, M., Padmore, R., Klein, C., & Kleckner, N. (1995). *NDT80*, a meiosis-specific gene required for exit from pachytene in *Saccharomyces cerevisiae*. *Molecular and Cellular Biology, 15*(12), 6572–6581.

Xue, Z., Liu, C., Shi, W., Miao, Y., Shen, Y., Tang, D., Li, Y., You, A., Xu, Y., Chong, K., & Cheng, Z. (2019). *OsMTOPVIB* is required for meiotic bipolar spindle assembly. *Proceedings of the National Academy of Sciences, 116*(32), 15967–15972.

Yamamoto, M. (1996). The molecular control mechanisms of meiosis in fission yeast. *Trends in Biochemical Sciences, 21*(1), 18–22.

Yamashita, H., Xu, J., Erwin, R. A., Farrar, W. L., Kirken, R. A., & Rui, H. (1998). Differential control of the phosphorylation state of proline-juxtaposed serine residues Ser725 of Stat5a and Ser730 of Stat5b in prolactin-sensitive cells. *Journal of Biological Chemistry*, *273*(46), 30218-30224.

Yang, S. L., Xie, L. F., Mao, H. Z., Puah, C. S., Yang, W. C., Jiang, L., Sundaresan, V., & Ye, D. (2003). *Tapetum determinant1* is required for cell specialization in the *Arabidopsis* anther. *The Plant Cell, 15*(12), 2792–2804.

Yang, W. C., Ye, D., Xu, J., & Sundaresan, V. (1999). The *SPOROCYTELESS* gene of *Arabidopsis* is required for initiation of sporogenesis and encodes a novel nuclear protein. *Genes & Development, 13*(16), 2108–2117.

Yoshida, K., Kondoh, G., Matsuda, Y., Habu, T., Nishimune, Y., & Morita, T. (1998). The mouse RecA-like gene *Dmc1* is required for homologous chromosome synapsis

during meiosis. *Molecular Cell, 1*(5), 707–717.

Yu, H., Wang, M., Tang, D., Wang, K., Chen, F., Gong, Z., Gu, M., & Cheng, Z. (2010). *OsSPO11-1* is essential for both homologous chromosome pairing and crossover formation in rice. *Chromosoma, 119*(6), 625–636.

Yuan, L., Liu, J. G., Zhao, J., Brundell, E., Daneholt, B., & Höög, C. (2000). The murine *SCP3* gene is required for synaptonemal complex assembly, chromosome synapsis, and male fertility. *Molecular Cell, 5*(1), 73–83.

Yuan, W., Li, X., Chang, Y., Wen, R., Chen, G., Zhang, Q., & Wu, C. (2009). Mutation of the rice gene *PAIR3* results in lack of bivalent formation in meiosis. *The Plant Journal, 59*(2), 303–315.

Zhang, C., Song, Y., Cheng, Z. H., Wang, Y. X., Zhu, J., Ma, H., Xu, L., & Yang, Z. N. (2012). The *Arabidopsis thaliana* DSB formation (*AtDFO*) gene is required for meiotic double-strand break formation. *The Plant Journal, 72*(2), 271–281.

Zhang, F., Ma, L., Zhang, C., Du, G., Shen, Y., Tang, D., Li, Y., Yu, H., Ma, B., & Cheng, Z. (2020). The SUN domain proteins *OsSUN1* and *OsSUN2* play critical but partially redundant roles in meiosis. *Plant Physiology, 183*(4), 1517–1530. https://doi.org/10.1104/pp.20.00227

Zhang, L., Wang, J., Tang, Z., Lin, Z., Su, R., Hu, N., Tang, Y., Ge, G., Fan, J., Tong, M. H., & Xue, Y. (2025). The nuclear exosome co-factor *MTR4* shapes the transcriptome for meiotic initiation. *Nature Communications, 16*(1), 2605.

Zhao, D., Ni, W., Feng, B., Han, T., Petrasek, M. G., & Ma, H. (2003). Members of the *Arabidopsis*-SKP1-like gene family exhibit a variety of expression patterns and may play diverse roles in *Arabidopsis*. *Plant Physiology, 133*(1), 203–217.

Zhao, G. Q., & Garbers, D. L. (2002). Male germ cell specification and differentiation. *Developmental Cell, 2*(5), 537–547.

Zickler, D., & Kleckner, N. (1999). Meiotic chromosomes: Integrating structure and function. *Annual Review of Genetics, 33*(1), 603–754.

Peer-review history:
The peer review history for this paper can be accessed here:
https://pr.sdiarticle5.com/review-history/135465