Title: Cytoskeletal dynamics of gamete nuclear migration in flowering plants, animals, and yeast

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Abstract

Gamete nuclear migration is a critical process during fertilization in flowering plants, yet its molecular mechanisms remain poorly understood. Recent studies have highlighted the essential role of cytoskeletal elements, particularly F-actin, in directing sperm nuclear migration, which differ from the microtubule-driven migration in animals. We summarize the process of sperm nuclear migration in plants and the involvement of Class XI myosin XI-G in *Arabidopsis*, along with the ROP8-SCAR2 pathway's ARP2/3-independent mechanism for F-actin nucleation. We also provide a comparative overview of examples from sea urchins, *C. elegans*, mice and yeast contrasting these mechanisms with those in plants. Finally, we outline possible future research directions related to sperm nuclear migration in plants. This review highlights the need for further exploration of pre- and post-fertilization processes, emphasizing their importance in plant cytoskeleton biology and the coordinated development of seeds.

Introduction

Each generation of sexually reproducing species relies on the fusion of maternal and paternal genomes through fertilization. For this fusion to occur, the nuclei of male and female gametes must undergo directed migration. In flowering plants, it is typically the male gametes that migrate towards the female gametes, whereas in animals and yeast, both male and female gamete nuclei migrate cooperatively toward the center of the cell. Beyond this distinction, there are several other mechanistic differences among plants, animals, and yeast. Notably, in animals and yeast, the centrosome transitions with the male gamete during nuclear migration, and this migration is regulated by microtubules and spindle bodies organized by the centrosomes (Manandhar et al., 2005). In contrast, flowering plants lack centrosomes, and nuclear migration is governed by filamentous actin (F-actin) rather than microtubules (Carvalho-Santos et al., 2011; Kawashima et al., 2014). This raises an important question: How do microtubules and F-actin control the migration of male and female gamete nuclei in animals and flowering plants? Advances in microscopy have significantly enhanced our understanding of gamete nuclear migration (Shin et al., 2022). The use of cytoskeletal inhibitors has provided valuable insights into the role of cytoskeletal elements in this process, while molecular biology tools have enabled detailed investigations into the underlying mechanisms.

This review will focus on the recent discoveries in flowering plants and compare the distinct mechanisms that govern gamete nuclear migration in plants and animals. In animals, gamete nuclei are referred to as pronuclei during fertilization. By contrast, in plants, the term "nuclei" is used, as meiosis is completed in the plant gametes prior to fertilization. Since nuclear fusion does not occur immediately after gamete fusion, female gametes are still referred to as central cells or egg cells during the nuclear migration, rather than as zygotes.

Sperm nuclear migration in flowering plants

Double fertilization is a crucial process for the reproduction of flowering plants. When pollen contacts the stigma, it begins to hydrate and germinate, forming a pollen tube. The sperm cells travel along this tube to the micropylar end of the unfertilized ovule. Upon reaching the ovule, the tip of the pollen tube ruptures, releasing the sperm cells into the space between the central cell and the egg cell. The plasma membranes and cytoplasm of the two sperm cells then fuse with those of the egg cell and central cell, completing plasmogamy. Subsequently, the sperm nuclei enter the egg cell and central cell, where they fuse with the female nuclei, guided by actin cables to complete karyogamy (Kawashima et al., 2014). One sperm nucleus fuses with the egg cell nucleus, resulting in a zygote that develops into an embryo. The second sperm nucleus fuses with the diploid central cell nucleus to form triploid endosperm, which nourishes the developing embryo (Fig. 1) (Raghavan, 2003; Hamamura et al., 2012).

After plasmogamy, the sperm nuclei are captured by F-actin meshwork surrounding the female nucleus, which is anchored to the female gamete membrane (Kawashima et al., 2014). In the female gametes of *Arabidopsis thaliana* and the egg cell of rice, an F-actin meshwork structure radiates, while in the central cell of *Asparagaceae*, an F-actin mega-cable and parallel actin filaments have been observed (Kawashima et al., 2014; Ohnishi & Okamoto, 2017; González-Gutiérrez et al., 2021). The inward movement of the F-actin meshwork drives the male nucleus toward the female nucleus, ultimately leading to their fusion and the completion of karyogamy, which has been shown in *Arabidopsis*, rice, tobacco and maize (Kawashima et al., 2014; Ohnishi et al., 2014; Ohnishi and Okamoto, 2017; Peng et al., 2017). This process significantly differs from animals, where migration is primarily guided by microtubules. In flowering plants, formins and ARP2/3 are well-characterized actin nucleators that polymerize G-actin into F-actin. ROP and WASP/SCAR regulate F-actin dynamics. The LINC complex is known to bridge the nucleus and F-actin, and motor proteins like myosin also involves in F-actin dynamic movement. This section will cover these factors individually, with a primary focus on findings in *Arabidopsis* and rice. Fertilization mechanisms in algae have been reviewed in Fatema et al. (2019).

F-actin is essential for sperm nuclear migration in both the egg cell and central cell.

In most animals and yeast, microtubules control pronuclear migration (see sections on Animals and Yeast). However, in flowering plants, sperm nuclear migration depends on F-actin dynamics. In the *Arabidopsis* unfertilized ovule, a constant inward movement of the F-actin meshwork surrounding the central cell nucleus is observed. Regardless of pollen tube arrival or sperm cell release, the central cell initiates and maintains this inward F-actin movement and subsequently stops and disassembles the actin cables once fertilization is complete. These observations suggest that F-actin dynamics are primed to facilitate sperm nuclear migration. After plasmogamy with the central cell, actin cables

capture the sperm nucleus and continuously migrate it toward the central cell nucleus, driven by ongoing inward movement (Fig. 1) (Kawashima et al., 2014).

In *Arabidopsis* transgenic lines with semi-dominant negative *ACTIN* (*DN-ACTIN*), where actin assembly is specifically disrupted in female gametes, F-actin dynamics halt, and sperm nuclei fail to migrate toward the nuclei of the egg cell and central cell (Kawashima et al., 2014). Similarly, in rice egg cells, the use of the F-actin inhibitor latrunculin B disrupts sperm nuclear migration (Ohnishi et al., 2014). In maize egg cells and tobacco central cells, treatment with F-actin inhibitors such as cytochalasin B and latrunculin A (Lat A) also restricts sperm nuclear migration (Peng et al., 2017). These results collectively demonstrate that F-actin dynamics are crucial for sperm nuclear migration.

By contrast, microtubules are not essential for sperm nuclear migration in *Arabidopsis*, as indicated by the fact that fertilization occurs in microtubule-defective *PORCINO/+* (*por/+*) mutants (Kawashima et al., 2014). Similarly, sperm nuclear migration is not effected in the egg cells of rice, maize, and tobacco when treated with microtubule inhibitors like oryzalin and colchicine (Ohnishi and Okamoto, 2017; Peng et al., 2017). These genetic and pharmacological findings collectively indicate that sperm nuclear migration is independent of microtubules in flowering plants.

Formins, but not ARP2/3, contribute to F-actin assembly in female gametes.

In plants, formins and the ARP2/3 complex are well-characterized factors involved in actin nucleation (MILLARD et al., 2004; Kovar et al., 2006; Basu et al., 2008). The ARP2/3 complex, originally discovered in *Acanthamoeba*, consists of seven subunits, including two actin-related proteins, ARP2 and ARP3, and five additional subunits (Machesky et al., 1994). ARP2/3 complex functions as an actin nucleator for the formation of new filament branches (Blanchoin et al., 2000; Dayel et al., 2001; Fišerová et al., 2006). Mutants lacking ARP2/3 complex subunits exhibit defects in epidermal cell morphology and trichome distortion due to the inability to nucleate branched actin filaments (Le et al., 2003; Mathur et al., 2003; Zhang et al., 2013; Yanagisawa et al., 2015; Xu et al., 2024). Despite the presence of ARP2 transcripts in *Arabidopsis* central cells, inhibition of the ARP2/3 complex with CK-666 or mutation of ARP2/3 complex genes (*apr2* single and *arp2arp3* double mutants) did not affect the inward F-actin meshwork movement or seed development, indicating that ARP2/3 is not involved in sperm nuclear migration (Peng et al., 2017; Ali et al., 2020).

Formins are another group of actin nucleators in flowering plants (Deeks et al., 2002; Cvrčková et al., 2004). Formins primarily produce linear actin filaments and do not require pre-existing filaments for polymerization (Valencia and Quinlan, 2021). Inhibition of formins using SMIFH2, a small molecule inhibitor, resulted in reduced F-actin movement in *Arabidopsis* central cell. Additionally, the accumulation of F-actin around the central cell nucleus was not observed, further supporting the role of formins in regulating F-actin dynamics through their actin nucleation function during sperm nuclear migration (Ali and Kawashima, 2021).

ROPs and WAVE/SCAR promote F-actin movement in an ARP2/3-independent manner.

The ARP2/3 complex is activated initially by Rho-GTPases and Wiskott–Aldrich syndrome protein (WASP) family proteins, including the WAVE/SCAR family (Machesky et al., 1999; Machesky and Insall, 1998; Weaver et al., 2003). The WASP family consists of five members: WASP, N-WASP, and the WAVE/SCAR proteins—WAVE/SCAR1, WAVE/SCAR2, and WAVE/SCAR3 (Stradal et al., 2004). WAVE/SCAR proteins are known to activate ARP2/3 and contribute to F-actin formation. The use of wiskostatin, a chemical inhibitor of the WASP domain, impairs the movement of the central cell F-actin meshwork in *Arabidopsis* (Ali et al., 2020) and has similarly affected egg cells in tobacco and maize during *in vitro* fertilization (Peng et al., 2017). Furthermore, the movement of the central cell F-actin meshwork is significantly slower in *scar2-1* and *scar2-1scar4-1* mutants compared to wild-type plants, indicating that SCAR2 is the primary SCAR factor crucial for regulating F-actin movement during sperm nuclear migration (Ali et al., 2020).

Several Rho-GTPases in plants (ROPs) influence the organization of actin filaments in various contexts, including tip-growing cells and pollen tubes (Craddock et al., 2012; Ou and Yi, 2022). *ROP8*, expressed in the central cell of *Arabidopsis*, is essential for F-actin dynamics, as *DN-ROP8* dominant-negative mutant showed impaired F-actin assembly (Kawashima et al., 2014). Although extensive research has been conducted on other Rho-GTPase family proteins, studies specifically related to sperm nuclear migration are limited (Gu et al., 2003; Ou and Yi, 2022).

In summary, an ARP2/3-independent ROP-SCAR pathway exists in female gametes, controlling inward F-actin meshwork movement necessary for sperm nuclear migration in flowering plants. Recently, a new factor/pathway affecting actin nucleation in *Arabidopsis* epidermal cells has been proposed, where inhibition of both formins and ARP2/3 increased actin filament nucleation (Xu et al., 2024). It remains to be determined whether this new pathway also operates in gamete cells. Identifying and characterizing such factors will significantly enhance our understanding of both plant reproduction and cell biology.

Class XI myosin XI-G is involved in the sperm nuclear migration in *Arabidopsis* central cell.

The forces driving F-actin dynamics are generated through the interaction between actin and myosin. Myosin serves as a key link between the F-actin meshwork and the nuclei. In *Arabidopsis* central cell, Class XI myosin *XI-G* is expressed, and the *xi-g* knockout mutant exhibits significantly slower F-actin meshwork movement compared to the wild-type (Ali et al., 2020). Additionally, after applying the 50 μM 2,3-butanedione monoxime (BDM) to *Arabidopsis* and tobacco central cells inhibits myosin activity and impairs F-actin meshwork movement (Kawashima et al., 2014; Ali et al., 2020). This indicates that Class XI myosin is a crucial factor in regulating active F-actin movement in plant gamete cells. Further, treating rice egg cells with both 50 mM BDM and 20 μM N-ethylmaleimide (NEM), another myosin inhibitor, also inhibits F-actin meshwork movement and arrests sperm nuclear

migration (Ohnishi and Okamoto, 2017).

In *Arabidopsis* somatic cells, myosin XI-I interacts with outer nuclear membrane proteins, tail-anchored protein 1 (WIT1) and WIT2, anchoring to the nuclear membrane (Meier et al., 2017). Defects in nuclear movement have been observed in *xi-i* mutants (Tamura et al., 2013). WIT1 proteins also interact with WPP domain-interacting proteins (WIP), which form part of the Linker of Nucleoskeleton and Cytoskeleton (LINC) complex along with Sad1/UNC-84 (SUN) proteins (Evans et al., 2014; Zhou et al., 2012). Members of the LINC complex have been recently identified in maize (Gumber et al., 2019). While the *xi-i* mutant does not show fertilization defects (Tamura et al., 2013), it remains unclear whether XI-G interacts with WIT1/2. Further investigation is needed to elucidate the specific role of the LINC complex in sperm nuclear migration, if any.

Calcium concentration levels are associated with the speed of actin meshwork movement.

In *Arabidopsis*, calcium concentration increases in the fertilized egg cell following plasmogamy (Denninger et al., 2014). In maize, karyogamy fails when the Ca^{2+}-channel inhibitor gadolinium (Gd^{3+}) is applied (Antoine et al., 2001). In rice, the F-actin meshwork surrounds the entire egg cell and nucleus, facilitating sperm nucleus migration toward the egg nucleus within approximately 20 to 30 minutes after plasmogamy. Following sperm-egg cell fusion, the movement speed of actin filaments is 1.4 times faster compared to unfused cells, and this increase in speed appears to correlate with elevated Ca^{2+} levels in the fused gametes. Notably, the nuclear fusion of two egg nuclei is significantly accelerated with the exogenous application of Ca^{2+} (Ohnishi and Okamoto, 2017; Ohnishi et al., 2019). In *Arabidopsis* and tobacco, tip-localized ROPs regulate both the dynamics of F-actin and the oscillation of the Ca^{2+} gradient during tip growth (Fu et al., 2001; Gu et al., 2003). However, whether calcium plays a role in ROP-mediated signaling during nuclear migration remains to be elucidated.

Pronuclear migration in animals

In flowering plants, the organization of sperm nuclear migration is directed by the dynamics of F-actin meshwork. By contrast, in most animals, microtubules guide pronuclear migration during fertilization. Sperm cell swim with sperm motility dependent on the sperm flagella or cilia, which are composed of microtubules (Gibbons, 1981). Upon reaching the egg cell, the sperm cell membrane ruptures, allowing the sperm pronucleus, along with the centrosome (absent in the case of mice), to enter the egg cell, completing sperm-egg fusion. In the sperm fused egg cell, male and female pronuclei migrate to the cell center and undergo the first embryonic mitosis (Meaders and Burgess, 2020; Scheffler et al., 2021; Dunkley et al., 2022).

Research on early embryos has largely focused on the polarized distribution of anterior-posterior and asymmetric division, with relatively limited studies on pronuclear migration (Galli and Heuvel, 2008; Xiong et al., 2011; Chaigne et al., 2017). Additionally, pronuclear migration varies across different animal species, complicating the identification of conserved mechanisms. Model organisms such as sea urchins, *Caenorhabditis elegans* (*C. elegans*), and mice have been frequently used to explore the intricate details of sperm-egg fusion.

Microtubules Drive the Migration of Male and Female Pronuclei

The sea urchin was the first animal in which pronuclear migration was observed (Chambers, 1939). In sea urchins, the sperm aster, formed by microtubules, plays a role in positioning the male and female pronuclei, and the pronuclear migration occurs in three distinct phases. In the first phase, the sperm pronucleus penetrates the egg and migrates slowly with no clear direction. In the second phase, the microtubule sperm aster captures the female pronucleus and directs it toward the egg center. In the third phase, the male and female pronuclei approach the egg center together at a slow speed (Fig. 2) (Chambers, 1939; Tanimoto et al., 2016). The migration of the male pronucleus is inhibited by the application of microtubule inhibitors such as nocodazole and the dynein inhibitor ciliobrevin D. However, pronuclear migration still occurs in the presence of the F-actin inhibitor Lat B (Tanimoto et al., 2016).

In *C. elegans*, the male and female pronuclei are initially positioned at opposite ends of the egg cell, with the female pronucleus at the anterior and the male pronucleus at the posterior. Establishing these poles is crucial for subsequent nuclear migration. Similar to sea urchins, there are three main phases of pronuclear migration in *C. elegans*. In the first phase, both the male pronucleus that associated with two centrosomes, and the female pronucleus migrate slowly toward the cell center. In the second phase, spindle microtubules generated by the centrosomes, capture and pull the female pronucleus toward the male pronucleus at an accelerated rate. The distance between the united pronuclei and the posterior pole at this stage is critical for ensuring proper nuclear migration and successful fertilization. In the third phase, the male and female pronuclei rotate 90° from the anterior-posterior axis to a vertical

orientation while slowly migrating to the cell center, facilitating chromosome alignment and zygote formation (Fig. 3) (Kimura & Kimura, 2011; Shinar et al., 2011). Pronuclear migration defects have been observed in RNA-mediated interference (RNAi) experiments targeting gut on the exterior (*gex*), where the female pronucleus continued to migrate toward the posterior side after contacting the male pronucleus in the second phase (Xiong et al., 2011). Additional defects in nuclear migration were confirmed in RNAi mutants of microtubule-stabilizing factors such as transforming acidic coiled-coil protein (*tac-1*), dynein heavy chain-1 (*dhc-1*), and the human type I lissencephaly responsible gene *lis-1* (Gönczy et al., 1999; Faulkner et al., 2000; Cockell et al., 2004; Vazquez-Pianzola et al., 2022).

In conclusion, microtubules play a decisive role in pronuclear migration. Due to the lack of time-lapse live imaging data for other animals, the detailed mechanisms of male and female pronuclear migration remain elusive.

Both actin filaments and microtubules are involved in pronuclear migration in mice

In mice, both actin filaments and microtubules are essential for pronuclear migration, distinguishing this process from other animal species. Although the role of F-actin in controlling zygotic microtubule spindle positioning and asymmetric division in mice has been demonstrated (Chaigne et al., 2017, 2016), its specific function in pronuclear migration has been less explored. However, the 2021 study by Scheffler *et al.* utilized time-lapse live-cell confocal and super-resolution microscopy, combined with *in vitro* fertilization techniques, to observe that F-actin and microtubules are involved in distinct phases of pronuclear migration in mice.

During the first phase, a fertilization cone forms at the egg cell's surface upon sperm contact. After the sperm pronucleus entering the egg cell, it moves toward the cell center at a speed six times faster than the female pronucleus. This rapid movement is dependent on cortical actin filament nucleation factors Formin2 and Spire2 (Fig. 4A) (Montaville et al., 2014; Schuh, 2011). Formin2 and Spire2, enriched behind the male pronucleus, generate actin filaments that provide the force to push the male pronucleus towards the cell center. Overexpression of Spire2 enhances F-actin formation and accelerates the male pronucleus's movement. Conversely, expression of the dominant-negative-FH2 form of Formin2 impairs its interaction with Spire2, decreases cytoplasmic F-actin velocity, and slows the male pronucleus's movement, although it does not prevent the pronucleus from eventually reaching the cell center. This indicates that Formin2 and Spire2 primarily regulate F-actin on the cortex during the first phase. Additionally, the actin depolymerizing drug cytochalasin D inhibits pronuclear migration, suggesting that both cortical and cytoplasmic actin filaments are involved throughout this phase. On the other hand, the male pronucleus continues to migrate rapidly despite the application of the microtubule inhibitor nocodazole, indicating that microtubules are not crucial during the first phase (Scheffler et al., 2021). Moreover, the expression of the dominant-negative Myosin-Vb tail in fertilized mouse eggs results in defective nuclear migration, further implicating myosin playing important role

in pronuclear migration (Chaigne et al., 2016).

In the second phase, once both pronuclei have moved near the cell center, they are guided together to complete their movement at a slower pace (Fig. 4B and C). Although nocodazole application does not affect the speed of male pronuclear migration in the first phase, it dramatically decreases the speed of pronuclear movement in the second phase. The pronuclei fail to fuse due to excessive distance apart, indicating that microtubules are essential for this phase. Furthermore, the application of the dynein inhibitor p150-CC1 peptide reduces the movement of both male and female pronuclei, suggesting that the motor protein dynein together with microtubules participates in pronuclear migration (Scheffler et al., 2021). In summary, F-actin plays a continuous role throughout the entire pronuclear migration process in mice, while microtubules and dynein are crucial for guiding the pronuclei, especially during the second phase.

The interaction between SUN-domain and KASH-domain proteins, dependent on kinesin or dynein, is required for pronuclear migration.

In animals, SUN-domain and KASH-domain protein families on the nuclear envelope of male and female pronuclei are crucial for linking the F-actin and microtubule networks during pronuclear migration. In *C. elegans*, SUN-1 interacts with the KASH protein ZYG-12. Disruption of ZYG-12 leads to the detachment of the centrosome from the male pronucleus, illustrating its role in pronuclear positioning (Malone et al., 2003; Minn et al., 2009). Additionally, another SUN-domain protein, UNC-84, interacts with the KASH-domain proteins UNC-83 and ANC-1 in *C. elegans* (Malone et al., 1999; Starr et al., 2001; Starr and Han, 2002). The interaction between UNC-84 and UNC-83 is mediated by kinesin-1 and dynein (Meyerzon et al., 2009; Fridolfsson et al., 2010). Mutants lacking UNC-84 exhibit defects in pronuclear rotation and centration, highlighting the importance of these interactions in proper pronuclear migration (Xiong et al., 2011). In summary, SUN-domain and KASH-domain proteins have been biologically demonstrated to play crucial roles in pronuclear migration in *C. elegans*. However, similar experimental evidence in plants is still lacking, and future research may provide insights into the roles of SUN and KASH proteins in plant cells.

Nuclear migration in yeast

In the sexual reproduction of yeast (*Saccharomyces cerevisiae*), two haploid yeast cells of different mating types (Mat a and Mat α) undergo cell-cell fusion. The haploid nuclei then engage in a process referred to as "nuclear mating" or "nuclear congression," where they move toward each other and complete karyogamy to form a diploid zygote (Herskowitz, 1988). Unlike the movement of the male nucleus towards the female nucleus in flowering plants and most animals, the nuclei in sexual cells Mat a and Mat α of yeast move towards the cell's center simultaneously, which was revealed by microscopy live-cell imaging (Fig. 5) (Gibeaux et al., 2013). This nuclear mating process depends on microtubules, which are polymerized and controlled by the spindle pole body (Rose et al., 1986). The nuclei, connected to the spindle pole bodies, move along the microtubules until the spindle pole bodies contact each other, leading to nuclear fusion.

Spc72 interacts with Kar1 and Kar3 to generate the microtubule-spindle pole body complex and facilitate movement along microtubules.

Using the microtubule inhibitor nocodazole, significant blockage of nuclear mating was observed (Hašek et al., 1987). In mutants related to karyogamy, such as Kar1, Kar3, Kar4, and Kar9, which encode kinesin motors (Conde and Fink, 1976; Kurihara et al., 1994), as well as the β-tubulin gene Tub2 mutant (Huffaker et al., 1988), or the Bik1 mutant, which encodes a microtubule-associated protein (Berlin et al., 1990), all exhibit microtubule defects resulting in nuclear mating failure. These studies highlight that the spindle pole body acts as the microtubule organizing center and guides the nuclei towards each other. Spc72 is a γ-tubulin complex-binding protein localized at the spindle pole body, while Kar1 is a kinesin motor protein also localized at the spindle pole body and microtubules. In Mat α, Kar1Δ15 mutants with defective Spc72 interaction domains, and wild-type Mat a, microtubules polymerized from Mat α disconnect from the opposite side of the spindle pole bodies during nuclear mating. This indicates that Spc72 interacts with Kar1 to form a microtubule-spindle pole body complex, guiding the two nuclei from opposite sides closer to the center (Fig. 5) (Pereira et al., 1999; Gibeaux et al., 2013). Spc72 also binds with Kar3 to make pulling forces on microtubules for nuclear mating (Gibeaux et al., 2013). In yeast, the centrosome embeds directly into the nuclear envelope, which differs from animals. The Sad1 protein, an inner nuclear membrane SUN-family protein, accumulates at the nuclear periphery and spindle pole body, playing a role in the structure of the spindle pole body by maintaining its functional interface with the nuclear membrane and providing an anchor for microtubule motor proteins (Hagan and Yanagida, 1995). In yeast, even when one microtubule-spindle pole body is defective, the coordinated pulling forces making by both spindle poles enhance the overall robustness of nuclear congression, ensuring successful nuclear fusion and providing greater stability compared to mechanisms observed in plants and animals.

Conclusion

Recent advances in understanding gamete nuclear migration in flowering plants have provided valuable insights into this complex process, yet several questions remain unresolved. Key discoveries include the identification of Class XI myosin XI-G as crucial for nuclear migration and the characterization of the ROP8-SCAR2 pathway, which promotes F-actin nucleation through an ARP2/3-independent mechanism (Ali et al., 2020). This finding contrasts with the ARP2/3-dependent mechanisms observed in somatic cells (Xu et al., 2024). However, experimental evidence linking F-actin interactions with the KASH-SUN complex and motor proteins during nuclear migration in sexual reproduction is still lacking, despite observations of such interactions in stomatal cells (Moser et al., 2024). The specific genes regulating F-actin dynamics in *Arabidopsis* egg cells have not been identified. Although *in vitro* fertilization experiments have provided insights into sperm nuclear migration in species like rice, tobacco, and maize (Peng et al., 2017; Ali et al., 2020), detailed mechanisms in central cells remain unclear. The role of calcium signaling in modulating the rate of inward F-actin movement during sperm nuclear migration also need further investigation (Ohnishi and Okamoto, 2017).

We are only beginning to unravel the molecular intricacies of gamete nuclear migration in flowering plants. In flowering plants, only F-actin is employed, whereas in animals, either microtubules or both cytoskeletal elements are recruited.Moreover, F-actin is already polymerized and exhibits dynamic movement in unfertilized ovules, whereas in most animals, microtubule dynamics typically begin after gamete fusion. In flowering plants, the immotility of sperm cells necessitates reliance on F-actin of the egg and central cell to facilitate nuclear migration. Conversely, in animals, sperm cells are motile, utilizing microtubule-based flagella for movement toward the egg, with microtubules subsequently driving pronuclear migration after fusion. A key question is whether the immotility of plant sperm cells has driven the evolution of actin-dependent nuclear migration systems. This highlights the need to explore the evolutionary and functional reasons behind these distinct strategies in flowering plants and animals. Exploring plant-to-animal evolutionary process may offer insight into how these divergent mechanisms have evolved to suit the distinct reproductive strategies of the two kingdoms.

The coordination of processes from pollen migration and plasmogamy to sperm nuclear migration, karyogamy, and the initiation of embryo and endosperm development is critical for successful seed development. In flowering plants, a distinct mechanism has evolved where F-actin plays a central role instead of microtubules (reviewed in Davidson & Wood, 2016; Dresselhaus et al., 2016; Paez-Garcia et al., 2018). Further investigation into nuclear migration and related pre- and post-fertilization processes will not only deepen our understanding of plant reproduction but also provide valuable insights into plant cytoskeleton biology and the evolutionary pathways of plant reproduction.

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Figures Legend

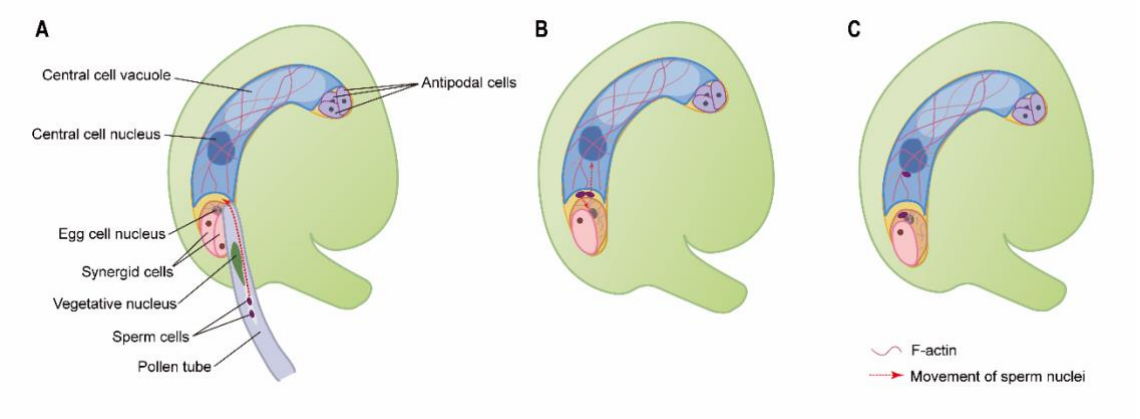

Figure 1. Double fertilization and nuclear migration in *Arabidopsis*.

(A) Sperm cells are released from the pollen tube and positioned between the egg cell and the central cell. (B) After plasmogamy, the two sperm nuclei are guided by F-actin towards the central cell and egg cell nuclei, respectively. (C) One sperm nucleus fuse with the central cell nucleus, while the other fuses with the egg cell nucleus.

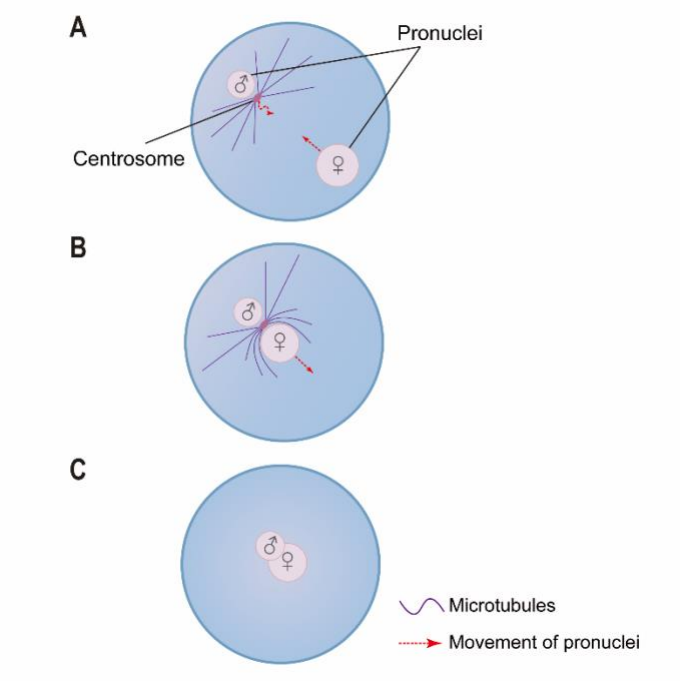

Figure 2. Pronuclear migration in sea urchin egg cells.

(A) The sperm pronucleus migrates in a slow speed with no direction in the first phase. (B) The microtubule sperm aster captures the female pronucleus and migrates to the cell center with male pronucleus in the second phase. (C) In the third phase, male and female pronuclei migrate to the cell center at slow speed, where nuclear fusion occurs.

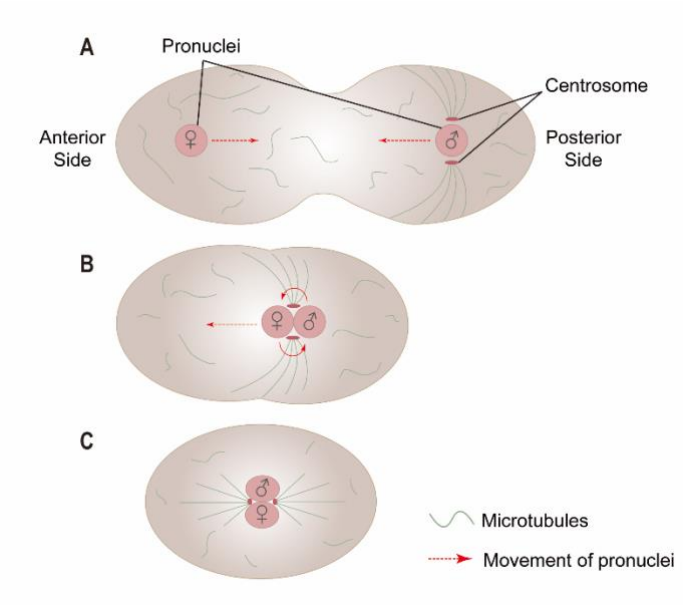

Figure 3. Pronuclear migration in *C. elegans*.

(A) In the first phase, female pronucleus and two centrosomes with the male pronucleus migrate towards the center of egg cell. (B) Microtubules capture and pull the female pronucleus toward the male pronucleus. The combination of the male and female pronuclei rotates 90° and migrates to the cell center. (C) Nuclear fusion occurs at the cell center.

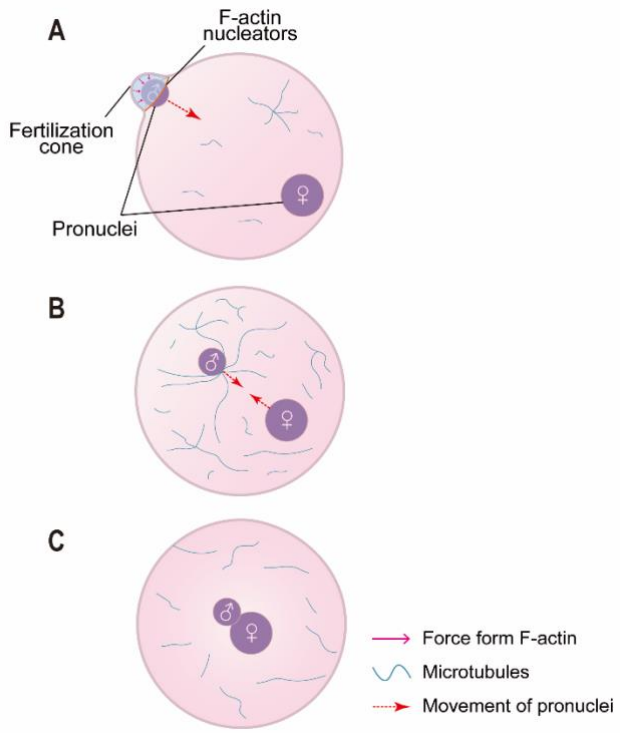

Figure 4. Pronuclear migration in mouse egg cells.

(A) In the first phase, male pronucleus is pushed by F-actin polymerized in the fertilization cone to the cell center. (B) In the second phase, both male and female pronuclei migrate towards egg cell center slowly. (C) Nuclear fusion occurs at the cell center.

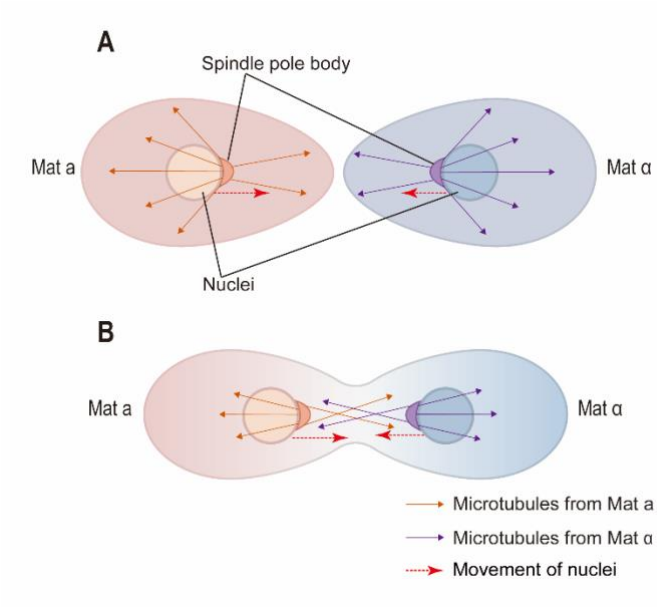

Figure 5. Nuclear mating in yeast sexual cells.

(A and B) Microtubules generating from spindle pole bodies on the nuclei of Mat a and Mat α guide nuclei migrate towards the cell's center simultaneously.