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a wretched tale

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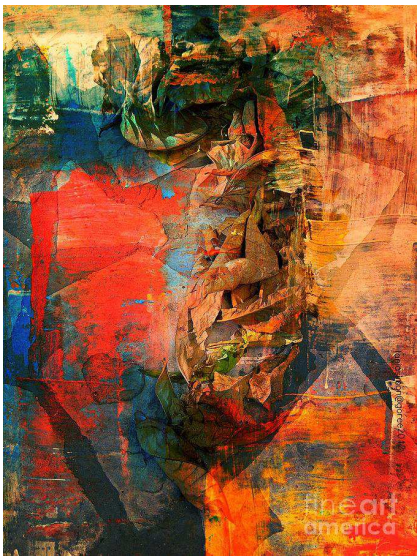
We all need guidance in life. And sperm cells are no exception to the rule. In plants, as in all living beings that depend on sex to multiply, a male gamete has to reach a female gamete in order to fuse with it. All sorts of mechanisms are used for this to occur. And plants are among the most imaginative organisms on the planet, simply because their mobility is so reduced. As such, they depend on forms of mobility that surround them: wind, bees, wild animals… And they have exploited this remarkably. At the molecular level, however, plants are far more mobile. An example is pollen tube elongation. In mouse-ear cress (*Arabidopsis thaliana*), for instance, once the pollen is ready to germinate, a bulge protrudes from its surface, elongates – and forms what is known as the pollen tube. Hordes of molecules are involved in pollen tube elongation. But you also need something which can actually guide the tube towards the ovule. And its name is protein HAPLESS 2, or HAP2.



Malaria, by Fania Simon (USA, Africa)

Courtesy of the artist

The notion that plants resorted to sex to flourish was first established by the German botanist and physician Rudolf Camerarius (1665-1721) who wrote, in a letter dated from 1694, that '*no ovules of plants could ever develop into seeds from the female style and ovary without first being prepared by the pollen from the stamens, the male sexual organ of the plant*'. Almost a century later, the German theologist and naturalist Christian Sprengel (1750-1816), who spent most of his life delving into the mysteries of plant sexuality, described the tricks of plant pollination – such as nectar guides and the art of mimicry in all its forms. Research on plant sexuality has evolved a lot ever since. Naturally. And today a far greater understanding of all the mechanisms plants use – both from the macromolecular and the molecular levels – are being unveiled thanks to novel technologies.

The amount of mechanisms thought up by plants to bring a male gamete closer to a female one is bewildering. And botanists have most certainly not observed them all. Plants make passive use of the wind and the fur of occasional wild animals to get their pollen to travel – in the hope that it will be deposited on a plant of the same species. Birds are used in the same way and pollen grains can be transported over huge distances. Plants have also learned how to lure insects into their flowers to pick up their pollen – by using cues such as colour, odour, scent and shape. Temptation can even come in the very subtle form of insect sex pheromone mimicry*, where plants become hyper selective and direct their lures towards a certain species of insect – thereby ensuring that it will deposit the pollen onto the same species of plant.

All these techniques, however, are for the initial phase of 'gamete approach'. Once a grain of pollen has been deposited on a flower, the next step is for the male gamete – harboured within the pollen grain – to reach the female gamete. So the grain germinates – as long as the surrounding conditions are appropriate. A bulge appears on the surface, and gradually becomes a tube – the pollen tube – which

elongates. Inside this tube is found the male gamete (or in the case of *Arabidopsis* and all angiosperms, two male gametes, one of which will fertilize the ovule). When it meets the ovule, the end of the pollen tube 'explodes' and one of the gametes will fuse with the ovule. An arrangement which is not all that far removed from the human reproductive system when you think about it.

The whole system is complex. There are hosts of molecules at work for all the different stages. Namely, germination, pollen tube elongation, what could be termed 'botanical ejaculation' and gamete fusion. Protein HAP2 has a role both in pollen tube guidance – not elongation – and gamete fusion. Indeed, mutant hap2 has no effect on pollen tube growth but the wild type HAP2 is necessary for the tube to elongate in the right direction, i.e. in the vicinity of the ovule. This particular talent may be a sort of 'quality control' mechanism; if the sperm is of poor quality, pollen tube guidance is faulty, and the gamete never reaches the ovule. Thus demonstrating an active role for sperm cells in the process of fertilization; a notion that is gathering momentum within the world of research.

HAP2 is hence needed both for pollen tube guidance and gamete fusion. The protein is largely expressed in pollen grains about to undergo germination, and is found in the plasma membranes of the sperm cells and in the sperm cell cytoplasm, lodged in the endoplasmic reticulum membrane. How does HAP2 help to guide the pollen tube towards the ovule? The N-terminal tip of the plasma membrane protein is in direct contact with the pollen tube cell's cytoplasm – perhaps even with the cell's cytoskeleton – and consequently well positioned to influence tube direction. The sperm cells also migrate towards the tip of the pollen tube by way of the cell's cytoskeleton. When the tube bursts, it releases the sperm, and HAP2 participates in gamete fusion – in fact, HAP2 is the first known gene to have a direct function in plant reproduction.

A surprising fact: HAP2 seems to exist in many eukaryotes, but not in higher animals. This would imply that the system is deep-rooted and that a different system evolved in higher animals – perhaps more sophisticated, more adapted to their needs. In particular, HAP2 is found in the mammalian parasite *Plasmodium* – the organism that transmits malaria – and is believed to be involved in gamete fusion, which occurs in the gut of the female mosquito once she has sucked up the blood of a victim, and before she finds another… One way of trying to block *Plasmodium* transmission to a human, and contributing to the eradication of malaria, would be by finding a vaccine that is able to deactivate HAP2, thus preventing *Plasmodium* reproduction. This brings hope to an illness which – according to WHO's latest estimates – afflicted almost 220 million people in 2010 and killed about 660,000.

N.B. Read Protein Spotlight issue 145, "unusual liaisons"

Cross-references to UniProt

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