



# Gender studies—a cell biological viewpoint

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In the public opinion, sexuality is commonly linked with reproduction. However, sexual propagation is actually a fairly inefficient way to reproduce. While two cells that propagate asexually will generate eight cells as offspring, where each cell is an exact reproduction of the progenitor, during sexuality, first, two cells will merge by a highly risky process that is therefore extremely time-consuming (the first meiotic prophase often lasts for many hours), and the sexual process will then give rise to only four cells, whereby none of these cells equals any of the progenitors. The selective advantage of sexuality must therefore be sought outside of reproduction. In fact, sexuality is a very efficient means to generate genetic variation and, thus, to boost the speed of evolutionary change. Its advantage does not become manifest on the level of the individual, but only on the level of the population. The evolution of genders can be understood as a further variation of this theme—the existence of two genders (it should be kept in mind that this model, while dominating the human perception of sexuality, is not the only possible strategy) will reinforce obligate heterosexuality and further accelerate genetic mixing. However, it also poses an extreme risk to the individual. In case that there is no mating partner endowed with the opposite sex, there will be no reproduction whatsoever. In organisms, where this risk is high, genders are expected to be more permissive. Two contributions to the current issue deal with cellular aspects underlying evolutionary strategies to cope with the risks of heterosexuality.

Flowering plants as sessile organisms are normally hermaphrodites—in most cases, male and female organs are even coexisting in the very same flower; occasionally, there exist male and female flowers on the same individual. Only a minority of plant species are diecious with male and female

individuals. Since the angiosperm flower is composed of leaf-bearing whorls, where the identity of each whorl is defined by combinatorial transcription factors (for a recent review, see Theißen et al. 2016), a gender switch is readily achieved by inactivation of one of these factors. The genetic base of plant genders is far less understood than in animals, though. Only in very few cases have sex chromosomes been discovered—for instance, in the moss *Marchantia* or the dicot *Silene* (reviewed in Ainsworth et al. 1998). A third case has been the *Rumex* genus, where an XY gender system exists. In contrast to the mammalian gender system, where the Y chromosome determines gender in a dominant manner, in *Rumex acetosa*, the ratio between the X and the autosomal chromosomes has been found to be relevant. The work by Kasjaniuk et al. (2018) in the current issue is now analysing a peculiar case of a further *Rumex* species, where two subspecies exist that differ in the number of their sex chromosomes. While the Texas subspecies of *R. hastatulus* shows a simple XX/XY system, where the genders have the same number of chromosomes, the North Carolina subspecies is endowed with a curious XY1Y2 gender system (where male and female plants have different numbers of chromosomes). Since the two subspecies were separated fairly recently, this genetic snapshot allows some insight into the evolution of gender determination. Authors generated symmetric hybrids between the two subspecies and followed the behaviour of the chromosomes during pollen meiosis. They show evidence for an autosomal origin of the extra-chromosomal segment in the neo-sex chromosome of the North Carolina subspecies. They further show that the viability of the resulting pollen was not symmetric, but dependent on the subspecies, who donated the Y chromosomes. This observation is interesting beyond the peculiar case of two plant subspecies, because it highlights the role of genders for the formation of new species—reduced fitness of a hybrid is a first manifestation of an incipient propagation barrier. This barrier is more pronounced in the heterozygous sex—a phenomenon that is known as Haldane's rule: 'When in the offspring of two different animal races one sex is absent, rare, or sterile, that sex is the heterozygous [heterogametic] sex'. (Haldane 1922).

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While the case of *Rumex hastatulus* describes the split of two subspecies by means of genders, the contribution by Farder-Gomes et al. (2018) in the current issue deals with a case of physiological hermaphroditism. The gender system of the *Hymenoptera* is based on a mechanism, where haploid offspring is male, while diploid offspring is female (in most cases). The mother can decide the gender of its offspring by either fertilising or not fertilising the egg. In these insects, mating and fertilisation are, therefore, uncoupled; the females keep the semen alive in specific spermatheca, such that they can dispose of the sperm any time. In case of the honeybee, several years can elapse between the mating flight and the fertilisation of the egg. This allows to profit from the benefits of sexuality, while at the same time minimising the dependence on the availability of a mating partner at the time of oviposition. Authors investigate the reproductive organs of a parasitic wasp that attacks leaf-cutter ants, which means that the need to separate mating from oviposition is accentuated for these highly specialised parasites. It is not sufficient that the spermathecae protect the sperms; they also have to keep them viable over a long time, which requires nutrition by the haemolymph of the hosting female. This nutritional feature is provided by specific glands lining the spermathecum. Interestingly, the lumen is also lined by a distinct cuticle, which might be a manner to protect the ‘non-self’ sperm from immunity of the hosting animal. Thus, while the wasp is female by its genetic composition, it can cultivate viable sperms over a long time, which means nothing else that, from a physiological viewpoint, it can be described as hermaphrodite.

Sexuality is certainly one of the most striking phenomena of evolution—while other traits unfold their selective advantage directly on the level of the individual, the fitness gain of

sexuality becomes evident only on a ‘meta-level’, i.e. if evolutionary change over several generations is followed. The two contributions described above shift the cellular base of gender into the focus. When talking about genetic sex determination, the attempt to mathematically describe and explain genetic change requires a certain degree of reductionism. But we should never forget that these genes are hosted by germ cells and that a full understanding of genetics and evolution is not possible without insight into the cellular base.

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