Editorial

Long-drawn-out story

The referee suggested that we "… better define and explain 'alternate segregation' and 'adjacent-1 segregation'. A simple figure illustrating these alternatives would help a great deal". Back in 1964, La Chance, Riemann, and Hopkins (*Genetics* **49** 959–972) wearied that '… chromosome pairing … in a translocation heterozygote … (has) been diagrammed and discussed in many publications …'. Geneticists working with translocations must continue to bear the cross of making 'alt / adj-1' figures afresh.

La Chance *et al*. reported an autosomal dominant mutant strain of the screw-worm fly *Cochliomyia hominivorax*. Females lay eggs in the wounds of warm-blooded animals, the maggots hatch and burrow through a feast of warm flesh, producing foul-smelling pus that attracts more flies. Mature larvae drop from the wound, pupate in the soil, bluish-green adults eclose, mate, and repeat nature's 'red in ovipositor and mouth-hook' cycle. In mutant flies, a wing segment called the R-cell was blackened by pigmentation. The Brc (black R-cell) mutant phenotype was associated with a reciprocal translocation. Several generations of Brc × Brc crosses failed to establish a pure-breeding strain, suggesting that translocation-homozygotes were inviable. Remarkably, in each generation the ratio of Brc to wild-type flies was 3:1 instead of the expected 2:1 (1 lethal Brc/Brc : 2 Brc/ + heterozygotes : 1 +/+ wild-type homozygote). They proposed that in Brc males alternate segregation is twice as frequent as adjacent-1, a kind of chromosomal meiotic drive.

Segregation Distorter (SD) of *Drosophila melanogaster* is the best-studied meiotic drive (*Genetics* **192** 33–53, 2012). All sperm from SD/SD^{+} males pass on the *SD*-bearing chromosome-2 to their progeny. The *Sd* gene, in chromosome-2L, is a 3' truncated version of the *Ran GTPase activating protein* (*RanGAP*) gene created by a tandem duplication of a segment of the *RanGAP* gene. The C-terminally truncated Sd-RanGAP protein is enzymatically active but lacks the wild-type RanGAP's localization signals. While wild-type RanGAP is tethered to the cytoplasmic side of the nuclear envelope, Sd-RanGAP accumulates in the nucleus and the cytoplasm. Mislocalization of Sd-RanGAP depletes nuclear RanGTP and impairs nuclear transport. *SD* chromosomes are *Sd* Rsp^{i} in genotype, whereas most SD^{+} chromosomes are Sd^{+} Rsp^{s}. The Rsp^{s} (Responder-sensitive) locus in drive-sensitive Sd^{+} spermatids has several hundred copies of a 240 bp satellite DNA repeat, whereas the Rsp^{i} allele in insensitive spermatids has very few or no satellite repeats. The following model was proposed for *Rsp*'s role (*Genetics* **193** 771–784, 2013). Under non-distorting (i.e. SD^{+}/SD^{+}) conditions, precursor *Rsp* piRNA transcripts are exported from the nucleus, processed into mature piRNAs, and reenter the nucleus as part of a Rsp-piRNA–primed RNA–protein silencing complex (Rsp RNP) that silences the Rsp^{s} locus and enables Rsp^{s}-bearing chromosomes to condense chromatin. Under distorting (i.e. SD/SD^{+}) conditions, perturbation of nuclear transport retains the Rsp precursor piRNAs in the nucleus, and/or blocks nuclear entry of the Rsp RNP. Consequently, Rsp^{s} is not silenced, the Rsp^{s}-bearing spermatids fail to condense chromatin, and are eliminated. In contrast, Rsp^{i} spermatids can condense chromatin in either distorting or non-distorting conditions.

In fungi, meiotic drive was shown to propel species divergence (*eLife* **3** e02630, 2014), and *Spore-killer* genes that kill meiotic products not containing them are known (*PNAS* **109** 12093–12098, 2012; *PLOS Genet.* **10** e1004387, 2014). We were excited to report yet another drive: crosses heterozygous for *Neurospora crassa* translocations introgressed into *N. tetrasperma* make fewer homokaryotic ascospores following alternate than adjacent-1 segregation (*G3* **5** 1263–1272, 2015). Admittedly a more recondite finding, our referee was only trying to help us to disseminate it.

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