TR-1 neocentromeres are controlled by a kinesin-14 motor in maize Ab10 meiotic drive

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Mendel's first law, that any allele has a 50% chance of being transmitted to progeny, is one of the most fundamental tenets of genetics. However, many genetic systems have been described that consistently violate this rule and transmit alleles greater than half the time. A classic example of this phenomenon called "meiotic drive" exists in the major cereal crop maize (*Zea mays* L.) and is thought to have significantly altered the course of evolution in the *Zea* genus[1].

Maize chromosomes contain features called knobs that are easily visible when viewed under the microscope For example, Barbara McClintock followed a knob on chromosome 9 to show that crossing-over is the cytological process responsible for genetic recombination[2]. Aside from their practical use as a cytogenetic tool, knobs have a biological function: they are hubs for meiotic drive. Rhoades discovered that when a particular chromosome 10 haplotype--called Abnormal chromosome 10 (Ab10)--is present, knobs and their linked alleles are preferentially transmitted through the female germline, thus causing meiotic drive[3]. He also made the observation that Ab10 caused "neocentromeres" to form during meiotic anaphase, where the knobs were pulled towards the chromosome poles and arrived before centromeres. Rhoades connected neocentromere activity to meiotic drive in a model where the chromatid containing a knob preferentially enters the basal megaspore cell, by virtue of its neocentromere activity, and is thus transmitted more than half the time.

We have recently come to learn more about the molecular nature of knobs. Knobs are composed of two distinct tandemly-repetitive sequences called knob180 and TR-1. Knobs can be found on every chromosome in diverse maize lineages. Some knobs are composed entirely of either knob180 or TR-1, but most knobs contain a combination of both sequences. The Dawe lab had previously described a multi-gene complex on Ab10 encoding a kinesin-14 motor protein that is responsible for the neocentromere activity of knob180 repeats[4]. Using a new genome assembly of the Ab10 haplotype[5], Swentowsky et al[6] identified a gene for a second kinesin-14 required for TR-1 neocentromere activity.

The new gene was named *Trkin* (*TR-1 kinesin*). When diverse Ab10 accessions were observed in meiosis, the presence of the full-length *Trkin* transcript was associated with TR-1 neocentromere activity. Key evidence that TRKIN is the motor that powers TR-1 neocentromeres was obtained using modern fluorescence microscopy techniques. By combining Fluorescence *in situ* Hybridization (FISH) to visualize tandem repeats and immunofluorescence of TRKIN, Swentowsky used Structured Illumination Microscopy (SIM) to observed precise co-localization of TRKIN and TR-1 knobs (**Figure 1**). Collaborating with a group at Oregon State University, the authors went on to use an *in vitro* gliding assay to demonstrate that the TRKIN protein is a functional microtubule-based motor of the type necessary to drive for neocentromere formation.

Several avenues of research are opened up with our new knowledge of the two neocentromere motors. Since knobs can be found on every maize chromosome arm, Ab10 meiotic drive is thought to have affected the segregation of the majority of genes in the genome and profoundly impacted maize evolution. Most knobs are mixed but it remains unclear how the two knob repeats cooperate to accomplish meiotic drive. Now that both motor proteins have been identified, further genetic and cell biological studies can be pursued using *trkin* mutants to determine how the two tandem repetitive elements contribute to meiotic drive. In the longer term, an improved understanding of Ab10 will open new avenues for creating artificial neocentromere and meiotic drive systems, which may have practical applications for plant breeding or to combat the spread of invasive species[7,8].

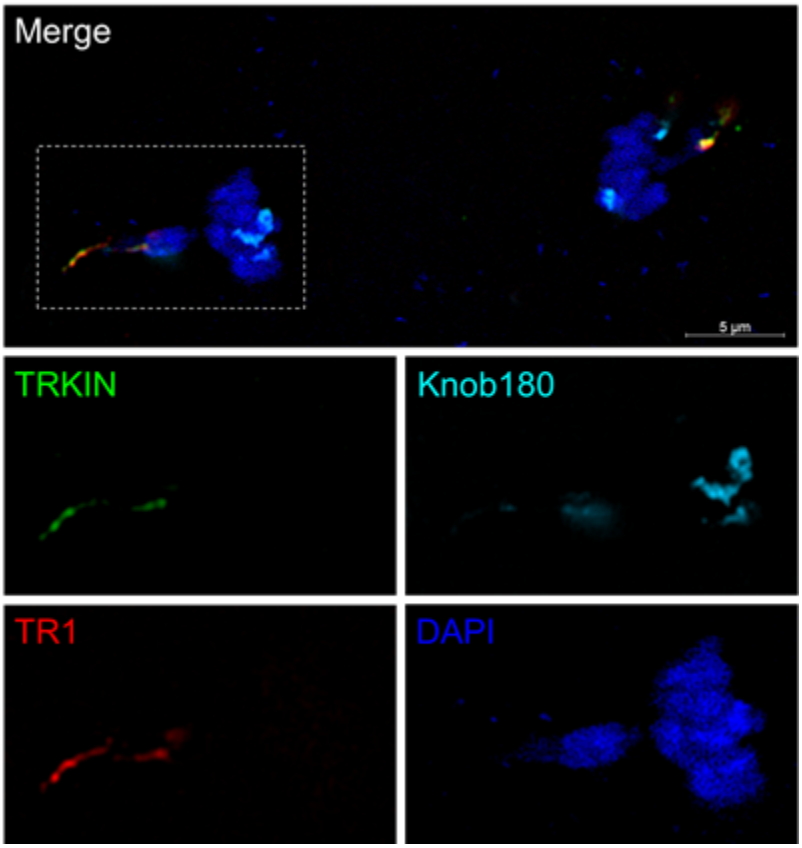

Figure 1. TRKIN localizes specifically to TR-1 neocentromeres. An Ab10 meiocyte undergoing anaphase II was stained using FISH-immunofluorescence for TRKIN (green), TR-1 (red), Knob180 (cyan), and DNA (blue). Top image shows four channels overlaid and individual channels within the dashed rectangle are shown below. This shows precise co-localization of the TRKIN protein to TR-1 but not knob180 neocentromeres.

References

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