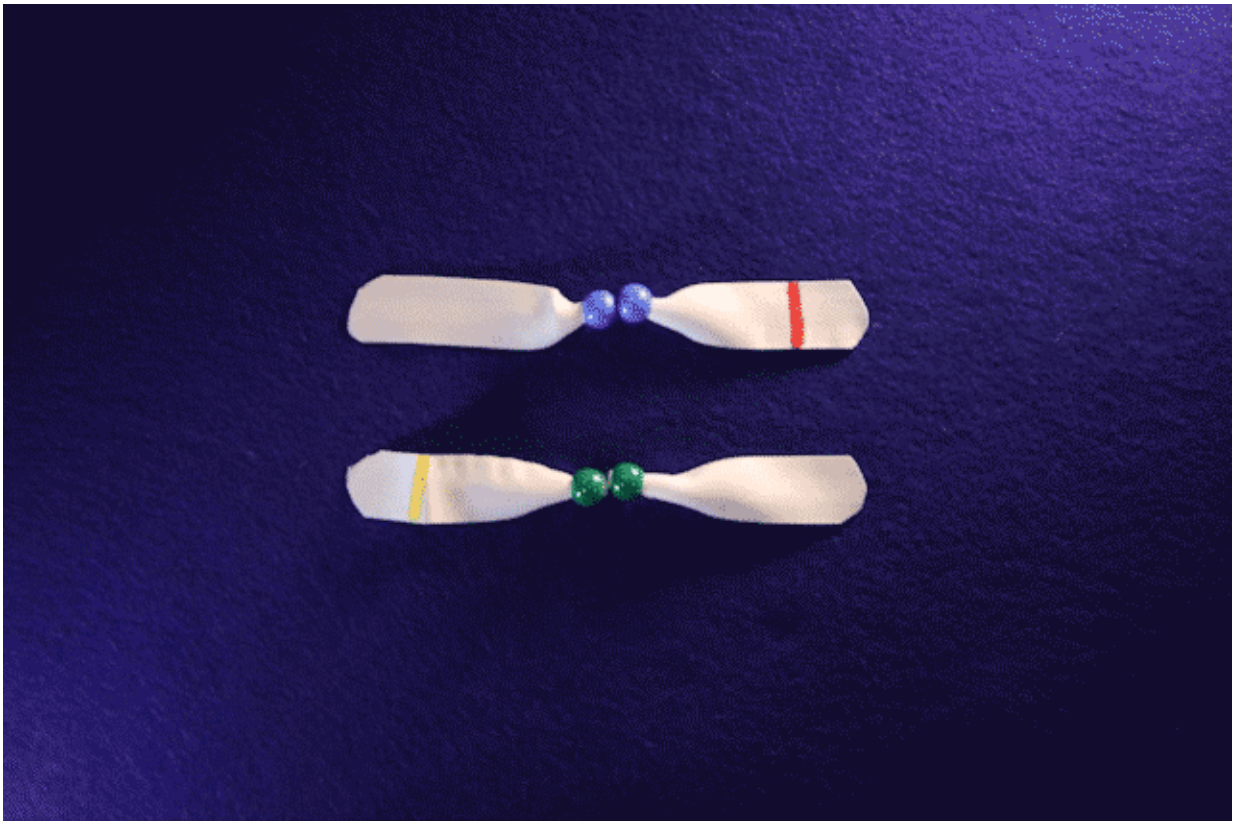


Scientists map sex chromosome evolution in pathogenic fungi

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A new paper from Duke molecular genetics and microbiology shows how pathogenic *Cryptococcus* fungi evolved from having many sexes to just two through 50 million years of gene swapping. Credit: Kara Manke

Biologically speaking, nearly every species on Earth has two opposite sexes, male and female. But with some fungi and other microbes, sex

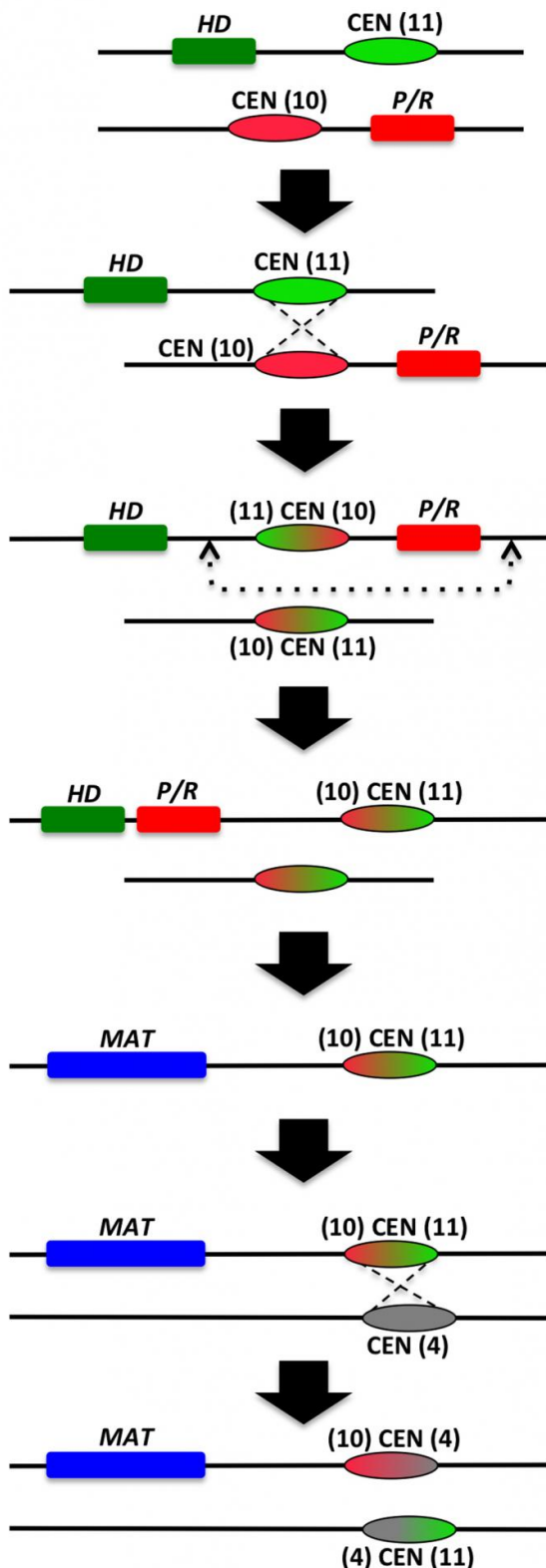
can be a lot more complicated. Some members of *Cryptococcus*, a family of fungus linked to human disease, can have tens of thousands of different mating types.

In a study appearing early online Aug. 11 in *PLOS Biology*, Duke researchers have mapped the evolutionary turning point that transformed the pathogenic form of *Cryptococcus* from an organism of many sexes to one with only two. They found that during evolution, a reshuffling of DNA known as translocation brought together separate chunks of sex-determining genes onto a single chromosome, essentially mimicking the human X or Y chromosome.

Surprisingly, they've shown that these crucial translocations occurred at the centromeres, the twisty ties that hold together chromosomes at the center of an x-shaped pair. These regions of the chromosome are so dense that they were once thought to be removed from recombination.

"Recombination at the centromere doesn't have to happen frequently, it just has to happen often enough that it punctuates the evolution of the organism," said Joseph Heitman, MD, PhD, senior study author and professor and chair of molecular genetics and microbiology at Duke University School of Medicine. "With each translocation, the genome is altered again and again, until you have evolved an entirely new species."

Scientists have been studying the evolution of sex chromosomes for more than a century. In the 1960's, Japanese-American geneticist and evolutionary biologist Susumu Ohno proposed a theory in which the genes determining sex first arose at various spots scattered across the [entire genome](#), but over time were "captured" on the sex chromosomes. In humans, those chromosomes go by the familiar X and Y; in birds, they are known as Z and W; in moss, they are called U and V.



I. Ancestral tetrapolar state

II. Ectopic recombination in the CEN regions mediated by common transposable/repetitive elements.

III. The outcome of the ectopic recombination is that the two *MAT* loci (*P/R* and *HD*) are now located on the same chromosome, separated by CEN in the middle.

IV. Subsequent chromosomal rearrangements, such as inversions or transpositions, bring the two *MAT* loci next to each other.

V. Eventually, the two *MAT* loci fuse to form one single contiguous large *MAT* locus that is present in the pathogenic *Cryptococcus* species.

VI. The resulting chromosome on which the fused *MAT* locus is located could undergo additional inter-centromeric recombination with a different chromosome, eroding the signature of intercentromeric recombination between the two *MAT* loci bearing chromosomes in the tetrapolar species. This could also occur after step IV and before step V.

A schematic figure from the paper illustrates how recombination occurred at the centromere and then genes migrated and fused to leave *Cryptococcus* with just two sexes, when before it had many. Credit: Sheng Sun, Duke University

Regardless of the name or species, Heitman contends that some universal principles could govern the evolution of all sex chromosomes. He and an international team of researchers focused on the last [common ancestor](#) of the human pathogen *Cryptococcus neoformans* and its nearest sibling species, a non-pathogen called *Cryptococcus amylo lentus*.

In *C. amylo lentus*, dozens of genes at two different locations on the chromosomes control what's called a tetrapolar, or four-part, mating system. At one location or locus known as P/R, genes encode pheromones and pheromone receptors that help the fungus recognize compatible mating types. At the other locus, called HD, genes govern the development of sexual structures and reproductive spores.

The researchers sequenced the entire genome of *C. amylo lentus*, mapping the location of all the genes as well as the centromeres on each of the organism's 14 chromosomes.

They found that the genomes had undergone quite a bit of rearrangement since the two species shared a common ancestor, at least 50 million years ago. For example, chromosome 1 of *C. neoformans* contained pieces of four different [chromosomes](#) from *C. amylo lentus*, providing evidence of multiple translocations, some within the centromere.

"That was very surprising. The dogma has been that recombination is repressed in centromeric regions," said Sheng Sun, PhD, lead study author and assistant research professor at Duke University School of Medicine.

In the 1980's, a seminal paper by Duke colleague Tom Petes demonstrated recombination could occur across the centromeres in *Saccharomyces cerevisiae*, but some attributed the finding to a quirk of the favored model organism with its tiny point centromeres. But since then, other studies have emerged suggesting that the phenomenon was wider spread.

In this study, the researchers showed that in *Cryptococcus amyloletus*, the ancestral state, the P/R locus resided on chromosome 10 and the HD locus on chromosome 11. But in *Cryptococcus neoformans*, the evolved state, those loci ended up in one place. According to their model, multiple translocations deposited the two sex determinants on the same chromosome, with a centromere in between. Subsequent rearrangements put P/R and HD next to each other. The result was an organism with a bipolar mating system, much like the male and female sexes that embody most species.

"In any kind of model like this, you are thinking about what could have been the organization in the last common ancestor, which is now extinct so you can't know definitively," said Heitman. "But in each of these lineages, there are multiple evolutionary events that have occurred, and you can use genomics to turn back the hands of time and deduce the trajectory."

Heitman says their study suggests that other researchers should actively look for translocations, both in the expected locations as well as within centromeres. These chromosomal rearrangements are a common cause of birth defects and cancer in humans.

He and his colleagues are currently investigating whether similar translocations occur in the evolution of [sex chromosomes](#) in other fungal families, such as *Ustilago* and *Malassezia*.

More information: "Fungal genome and mating system transitions facilitated by chromosomal translocations involving intercentromeric recombination," Sheng Sun, Vikas Yadav, R. Blake Billmyre, Christina A. Cuomo, Minou Nowrousian, Liuyang Wang, Jean-Luc Souciet, Teun Boekhout, Betina Porcel, Patrick Wincker, Joshua A. Granek, Kaustuv Sanyal and Joseph Heitman. *PLOS Biology*, Early online Aug. 11, 2017. [DOI: 10.1371/journal.pbio.2002527](https://doi.org/10.1371/journal.pbio.2002527)

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