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Genome Watch

Yeasts and how they came to be

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This month's Genome Watch highlights a large-scale sequencing project that enriches our understanding of yeast evolution and diversity.

In contrast to most eukaryotes, fungi have relatively small and simple genomes, making them an attractive resource for large-scale genomic studies. Even more attractive, the budding yeast subphylum (Saccharomycotina) has some of the most straightforward genomes to assemble and annotate, as they are generally small (10-20Mb) and intron-poor. The Saccharomycotina also harbor some of the most important fungi for bioindustry, being essential for converting sugars into ethanol and other valuable chemicals.

The genome of *Saccharomyces cerevisiae* was the first sequenced eukaryotic genome, which led to many breakthroughs in understanding eukaryotic biology and enabling genetic engineering.[1] Now, as part of the y1000+ project, with the ambitious goal to sequence over 1000 yeast genomes Shen *et al*.[2] sequenced and annotated 220 of these fungi. Despite their small genomes, budding yeasts exhibit an extraordinary range across their functional repertoire. Combining these data with 100 published yeast genomes and phenotypic information on metabolic capabilities for all species in their study, the authors were able to make key connections between gene pathways and particular metabolic traits. For example, they inferred that the common ancestral budding yeast could assimilate nitrate, xylose and galactose, but lacked the ability to ferment glucose.

This study also explored how distribution of these traits across the subphylum came to be. Through phylogeny reconstruction paired with results of their metabolic analysis, they were able to trace the loss and gain of new traits through subphylum history. By inferring the traits of the budding yeast common ancestor, the authors implicate gene loss as a main driver of diversification. Since this work has been published, several follow-up studies have been conducted that use subsets of the genomic data from this project to explore budding yeast diversity and evolution.

To follow up on gene loss as the evolutionary driver of diversity, Steenwyk *et al*.[3] explored a fast evolving lineage in the genus *Hanseniaspora*, a cosmopolitan lineage that is often found in high abundance on grapes and in wine must. They found that this lineage lost many cell cycle and DNA repair genes and represents an unusual example of long-term survival of a hypermutator lineage. These hypermutator species exhibit additional extensive gene loss, harboring the lowest number of genes compared to any other budding yeast. Furthermore, the observed gene losses were consistent with their known metabolic traits (for example, the inability to grow on various carbon sources).

Although gene losses are important for driving diversification in budding yeasts, horizontal gene transfer (HGT) is another interesting contributor to their evolution. Kominek *et al*.[4] identified the first example of an HGT event involving transfer of a full operon from bacteria into yeasts. This operon contained siderophore biosynthesis pathway genes, was functional, and enabled these yeasts to acquire a new metabolic trait for iron uptake. By exploring conservation of iron uptake and storage systems across 175 fungi including 17 closely related genomes from the clade encompassing *Wickerhamiella and Starmerella* yeasts, the authors found that this biosynthetic capability came from a single HGT event at the root of *Wickerhamiella/Starmerella*. From 186 budding yeast genomes, over 800 genes were predicted to be acquired from bacteria by HGT, and most of these genes are associated with metabolism.[2]

Thanks to the sequencing efforts of Shen *et al*. and others, we now have a rich sampling of an ancient (~400 million years old) eukaryotic subphylum. This provides us with the first opportunity to explore eukaryotic evolution at this magnitude and has already provided various important insights into the basic biology of eukaryotes. In addition to those discussed above, these data have been used to characterize variation and alterations of codon usage[5] and reinvention of mating-type switching.[6] We expect that the completion of the y1000+ project will provide an even fuller picture of the subphylum and has the potential to reveal many new and important insights into the biology of yeasts and eukaryotes at large.

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Competing interests
The authors declare no competing interests.

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