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Into the wild—Exploring the life cycles of yeasts

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This Special Issue on the life cycles of yeasts is dedicated to the memory and legacy of Prof. Angelika Amon who, driven by scientific curiosity, creativity, passion, and brilliance, pioneered many of the fundamental discoveries of the cell cycle using *Saccharomyces cerevisiae* as a model organism. Prof. Amon made impressive discoveries on the processes of cell growth, division, and aging, along with their associated extracellular and intracellular cues. Some notable discoveries she made include the role of cyclin degradation in promoting cells to exit mitosis and on how aneuploidy associated cellular stresses affect cell proliferation. Through her everlasting impact on the field, Prof. Amon's scientific legacy will live on eternally.

Yeasts have been the faithful companions of humans for centuries. The study of yeast laboratory strains has enabled outstanding scientific discoveries including a comprehensive understanding of the life cycles of eukaryotic cells. It might seem like we have discovered everything there is to know about the life cycles of yeasts; however, recent studies published in this Special Issue and elsewhere suggest that even for model yeast species like *S. cerevisiae*, we are still missing some of the basics in terms of our understanding of their life cycles. Population genomic analyses of *S. cerevisiae* have revealed a level of heterozygosity and polyploidy that are incompatible with the dogmatic haplo-diplobiontic life cycles that we are typically taught in school and that often serve as a reference for downstream discoveries in the field.

In a remarkable little book called *The Life of Yeasts*, Herman Phaff, Martin Miller and Emil Mrak described with great clarity the extraordinary diversity of life cycles that occur in different yeast species (Phaff, Miller, & Mrak, 1966). They described seven different types of yeast life cycles —four in diploid species and three in haploid species. It is humbling to realize that, more than 50 years later and with numerous genome sequences in hand, we

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still know very little about the molecular bases of these profound phenotypic differences, particularly for haploid species.

A number of studies in this Special Issue highlight the major gaps in our knowledge on the life cycles of yeasts and emphasize the idea that we must expand our studies beyond standard laboratory yeasts to include non-conventional species and "wild" yeast strains, where novel and unexpected findings are beginning to be revealed.

The collection of papers in this Special Issue include basic science studies focusing on features of the life cycles of yeasts. A paper by Zhou Li, Boisnard, Enache-Angoulvant, and Fairhead (2020) compared the life cycle of the wild yeast *Nakaseomyces delphensis* with that of the laboratory yeast *S. cerevisiae*. Surprisingly, the authors found that, unlike *S. cerevisiae*, which is largely diploid, N. delphensis exists predominantly in the haploid state. Similarly, in a paper by Toyomura, Hisatomi, Yokoyama, and Miyamoto (2020) the authors found that although the *HO*-dependent mating type switch is well established in *S. cerevisiae*, a new gene, *MTI1*, regulates mating-type interconversion in the yeast *Kazachstania naganishii*.

To date, few papers in the field have focused on the non-dividing sections of the life cycles of yeasts. Following meiosis, yeast species produce spores that can remain dormant for long periods of time and then germinate when environmental conditions are favorable. Depending on the yeast species, such signals include the presence of different carbon sources, temperatures, etc. A paper by Plante and Landry (2020) found that although dextrose is sufficient to trigger spore germination in S. cerevisiae, in certain wild lineages of Saccharomyces paradoxus, dextrose is necessary but not sufficient to trigger spore formation, and inorganic phosphate is also required for the process. These findings highlight the differences in environmental conditions required for two closely related budding yeast species to undergo spore germination. Further, Heasley, Singer, Cooperman, and McMurray (2020) demonstrate that contrary to the common assumption that Saccharomyces spores lack positional cues for outgrowth, these spores are actually prepolarized to grow away from their sibling spores in an ascus. In a related paper, Marek, Opalek, Kałdon, Mickowska, and Wloch-Salamon (2020) describe how S. cerevisiae cells transition to a quiescent state under starvation conditions. The authors found a role for SSY1, a gene that encodes a component of an amino acid sensor system, in the transition to this quiescent state. Together, these studies are relevant for our understanding of quiescent states in the cell cycle of other eukaryotic cells such as neurons, stem cells, and reproductive cells.

Another paper in this Special Issue highlights the connection between metabolism and the cell cycle. Venkatesh, Murray, Coughlan, and Wolfe (2020) characterized giant *GAL* gene clusters in *Torulaspora* species that are much larger and more polymorphic than the classical *GAL1*, *GAL10*, *GAL7* genes of *S. cerevisiae*. Their findings suggest that metabolic gene clusters are likely dynamic in yeast species and can affect their abilities to utilize different carbon sources for growth.

Additionally, there are several comprehensive and timely review articles in this Special Issue that emphasize different features of the cell cycles of yeasts, such as the widespread

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nature of heterozygosity and polyploidy (see Fischer, Liti, & Llorente, 2020), quiescence in budding yeast (see Miles, Bradley, & Breeden, 2021; Sun & Gresham, 2020), and how the DNA mismatch repair proteins have evolved in yeasts in the context of the vegetative and sexual phases of their life cycles (see Furman, Elbashir, & Alani, 2020). Finally, there is a perspective piece (see Steenwyk, 2020) on the blending of the arts and sciences to describe the natural world, where visual art is used to depict the beauty of the life cycles of yeasts. An artistic portrait of the budding yeast *S. cerevisiae* from this perspective was aptly chosen for the cover of this special issue.

We hope you enjoy reading this Special Issue and that it inspires you and the next generation of scientists to continue to probe the life cycles of yeasts.

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