IN SILICO IDENTIFICATION OF *Meyerozyma guilliermondii* STRAIN SO POTENTIAL VIRULENCE FACTORS AND PATHOGENICITY VERIFICATION OF GENERATED MUTANTS IN ZEBRAFISH MODEL

By

LIM SI JIE

Thesis Submitted to the School of Graduate Studies, Universiti Putra Malaysia, in Fulfilment of the Requirements for the Degree of Doctor of Philosophy

January 2024

IB 2024 7

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Chairman : Siti Nurbaya Binti Oslan, PhD

Institute : Bioscience

Candidiasis, a fungal infection caused by *Candida* species, has been a global health concern that caused 40-60% mortality in the bloodstream infected patients. The virulence factors (VFs) in the most isolated *C. albicans* and other prominent *Candida* species, have been widely investigated. However, the reduction of antifungal drug susceptibility in non-prominent *Candida* spp., especially *C. guilliermondii*, is concerning. The roles of VFs in fungal pathogenicity in relevance to its structural data have been undermined for drug developments. The proper quantification on the fungal VFs was also lacking in the literature. A locally isolated *Meyerozyma guilliermondii* from spoiled orange (strain SO) that has been proven as a promising expression host for industrially important enzymes, exhibited ≥99% proteome similarity to other

natural and clinical isolates but its VFs responsible for its pathogenicity towards zebrafish embryos remained unknown. Therefore, this research was aimed to comprehensively characterize and verify the VFs in *M. guilliermondii* strain SO using structure-guided mutants. A 19 out of 36 hits from 7 families [secreted aspartyl proteinase (Sap), agglutinin-like sequence, enolase, lipase, phytase, phospholipase, and heat-shock protein] detected using Hidden-Markov Model, exhibited the same conserved domain and stronger phylogenetic relationships with *C. albicans* SC5314. Next, the predicted and validated three-dimensional structures and their sequences were analyzed to verify the most potent VFs for fungal pathogenicity. The cell wall or cell membrane associated *Mg*Sap341 and extracellular *Mg*Sap1972 were targeted for deletion due to the predicted catalytic site enlargement, broader substrate specificity, and druggable active site clefts with the largest molecular surface area. Four general or VF-specific virulence assays were established to determine the pathogenicity of *M. guilliermondii* strain SO. The fungus demonstrated higher endoplasmic reticulum (ER), cell wall integrity but lower osmotic tolerances than *Saccharomyces cerevisiae* BY4742. Besides killing 75% more zebrafish embryos *in vivo*, it also produced 11× higher proteinase activity and 7.5× higher biofilm mass than *S. cerevisiae*. To determine the pathogenic roles of *Mg*Sap341 and *Mg*Sap1972, three mutants (Δ*SAP341*, Δ*SAP1972* and Δ*SAP1972* Δ*SAP341*) were constructed *via* homologous recombination strategy and they showed higher sensitivity towards osmotic, cell wall perturbing, and ER stresses than the wild type. *Mg*Sap1972 and *Mg*Sap341 contributed most to the reduction in biofilm mass (34.1%) and specific proteolytic activity (61.8%), respectively. All mutants showed virulence

reduction (mortality and invasion rates) in the zebrafish embryos model: double mutant>single mutants>wild type. Thus, *Mg*Sap341 and *Mg*Sap1972 that were analyzed and targeted through computational approaches, indeed contributed to the fungal pathogenicity of *M. guilliermondii* strain SO. More potent VFs in *M. guilliermondii* were detected than the literature, signifying the proper and high coverage documentation strategy before the comprehensive, VF-specific *in silico* analyses were performed to examine the structure-function relationship, subsequently bridging its potential pathogenic roles and antifungal drug development. The quantitative virulence assessments established allowed the comparison of fungal pathogenicity level at inter- and intra-species strata in diagnostic and pathology laboratories. Lastly, the establishment of *FLP-SAT1* strategy allows other VFs' pathogenic roles mining, providing insights into VF-specific antifungal drug screening and fungal pathogenic mechanisms.

Keywords: Candidiasis, Fungal Pathogenicity, Hidden-Markov Model, *Meyerozyma guilliermondii,* Virulence Factors

SDG: GOAL 3: Good Health and Well-beings

Abstrak tesis yang dikemukakan kepada Senat Universiti Putra Malaysia sebagai memenuhi keperluan untuk ijazah Doktor Falsafah

PENGENALAN FAKTOR-FAKTOR KEVIRULINAN BERPOTENSI SECARA *IN SILICO* DALAM *Meyerozyma guilliermondii* STRAIN SO DAN PENGESAHAN PATOGENESITI MUTAN-MUTAN YANG DIBINA DENGAN MENGGUNAKAN MODEL IKAN ZEBRA

Oleh

LIM SI JIE

Januari 2024

Pengerusi : Siti Nurbaya Binti Oslan, PhD

Institut : Biosains

Candidiasis merupakan jangkitan kulat yang disebabkan oleh spesies *Candida*. Jangkitan ini telah menjadi kebimbangan kesihatan dunia yang membawa 40-60% kematian dalam pesakit yang dijangkiti saluran darah. Faktor-faktor kevirulinan (VF) dalam *C. albicans* yang paling sering dipencilkan dan spesies lain yang popular telah dikaji dengan meluas. Namun, pengurangan kerentanan ubat antikulat dalam spesies *Candida* yang kurang popular, terutamanya *C. guilliermondii*, adalah sangat kritikal. Kajian struktur VF dalam kevirulinan *Candida* telah diabaikan untuk pembangunan ubat. Kuantifikasi VF yang tepat juga kurang diberi perhatian. Pencilan oren rosak (strain SO) *Meyerozyma guilliermondii* yang telah dibuktikan perumah

pengekspresan protein rekombinan yang menjanjikan, menunjukkan kesamaan proteom ≥99% dengan pencilan-pencilan semulajadi dan klinikal. Namun, VF yang bertanggungjawab terhadap kematian embrio ikan zebra masih belum diketahui. Maka, penyelidikan ini bertujuan untuk mengkaji dan mengesahkan VF dalam *M. guilliermondii* strain SO dengan bantuan struktur protein. Terdapat 19 daripada 36 padanan dalam 7 keluarga VF [*secreted aspartyl proteinase* (Sap), *agglutinin-like sequence*, *enolase*, *lipase*, *phytase*, *phospholipase* dan *heat-shock protein*] yang dikesan dengan model *Hidden Markov*, menunjukkan domain terpelihara yang sama dan hubungan filogenetik yang lebih kuat dengan *C. albicans* SC5314. Seterusnya, struktur-struktur tiga dimensi VF serta jujukan-jujukan mereka telah dianalisa untuk mengesahkan VF yang paling penting kepada sifat patogenik kulat tesebut. *Mg*Sap341 (dinding atau membran sel) dan *Mg*Sap1972 (ekstraselular) telah menjadi sasaran untuk dipadamkan disebabkan pembesaran tapak pemangkin serta pengkhususan substrat yang lebih meluas di samping tapak-tapak aktif yang berpotensi untuk menjadi sasaran ubat yang memiliki keluasan permukaan molekul terbesar. Empat ujian virulen yang umum atau spesifik dengan VF telah ditubuhkan untuk menentukan sifat patogenik *M. guilliermondii* strain SO dimana kulat ini menunjukkan toleransi terhadap tekanan jalinan endoplasma (ER) dan integriti dinding sel yang lebih tinggi tetapi tekanan osmotik yang lebih rendah daripada *Saccharomyces cerevisiae* BY4742. Selain membunuh 75% lebih banyak embrio ikan zebra *in vivo*, kulat ini juga menghasilkan 11× aktiviti proteinase dan 7.5× jisim biofilm yang lebih tinggi daripada *S. cerevisiae*. Untuk menentukan peranan patogenik *Mg*Sap341 dan *Mg*Sap1972, tiga mutan (Δ*SAP341*, Δ*SAP1972* dan

Δ*SAP1972* Δ*SAP341*) yang dihasilkan melalui strategi rekombinasi homolog telah menunjukkan rintangan yang lebih tinggi terhadap tekanan osmotik dan ER serta gangguan dinding sel berbanding dengan jenis liar. *Mg*Sap1972 dan *Mg*Sap341 telah masing-masing terbukti memberikan sumbangan terbesar kepada pengurangan jisim biofilm (34.1%) dan aktiviti proteolitik khusus (61.8%). Pengurangan virulen (kadar kematian dan kadar penyerangan) ditunjukkan dalam semua mutan dalam urutan menurun- mutant berganda>mutan-mutan tunggal>jenis liar dalam model embrio ikan zebra. Maka, *Mg*Sap341 dan *Mg*Sap1972 yang telah dikenalpasti, dikaji dan disasar melalui pendekatan pengkomputeran adalah jelas menyumbang kepada sifat patogenik *M. guilliermondii* strain SO. Lebih banyak VF telah dikesan dalam *M. guilliermondii* berbanding dengan literatur. Strategi dokumentasi yang tepat dan berliputan luas adalah sangat penting sebelum analisis jujukan dan struktur dijalankan untuk mengkaji hubungan struktur-fungsi yang dapat mengaitkan peranan patogenik potensinya dengan pembangunan ubat antikulat. Ujian virulen kuantitatif yang ditubuhkan membolehkan tahap patogenisiti kulat dibandingkan dalam inter- dan intra-spesies di makmal diagnostik dan patologi. Akhirnya, penubuhan strategi *FLP-SAT*1 boleh digunapakai untuk mengenalpasti peranan patogenik VF lain dan memberikan wawasan kepada penyaringan ubat antikulat khusus-VF dan mekanisme patogenik kulat.

Kata Kunci: *Candidiasis*, Patogenesiti Kulat, *Hidden-Markov Model*, *Meyerozyma guilliermondii*, Faktor-faktor Kevirulinan

SDG: *GOAL 3: Good Health and Well-beings*

ACKNOWLEDGEMENTS

First and foremost, I would like to express my sincere gratitude to my supervisor, Assoc. Prof. Dr. Siti Nurbaya Oslan for her invaluable guidance and constant support throughout the completion of my doctoral studies. She provided constructive advice and comments; I would never be able to stay firm and complete this project without her endless encouragement and efforts. I would also like to extend my appreciation to my co-supervisors, Prof. Dr. Mohd Shukuri Mohamad Ali, Assoc. Prof. Dr. Suriana Sabri and Dr. Noor Dina Muhd Noor for their valuable advice, suggestions, and feedback; special thanks to Dato' Dr. Abu Bakar Salleh for providing professional views and critical feedback on my research work and manuscripts. Their vast knowledge and experience have been invaluable to me throughout my academic research.

Furthermore, I would like to acknowledge the generous financial support and research grants provided by the Ministry of Higher Education (MoHE) through Fundamental Research Grant Scheme (FRGS/1/2019/STG05/UPM/02/1) and UPM through Graduate Research Fellowship and Putra Initiative Grant (GP-IPS/2022/972300). I am thankful to Dr. Naseem Akhtar Gaur from the International Centre of Genetic Engineering and Biotechnology (ICGEB), New Delhi, India for his kind gift and advice on the usage of pSFS2A disruption vector that was also used by Assoc. Prof. Dr. Siti Nurbaya Oslan during her *Arturo Falaschi* fellowship at ICGEB. Besides, I would also like to express my sincere appreciation to all the principle investigators, postgraduate students and laboratory colleagues at the Institute of Bioscience (IBS), Enzyme and

Microbial Technology (EMTech) Research Centre, and Faculty of Biotechnology and Biomolecular Sciences including Dr. Eseoghene Lorrine Okojie, Dr. Tan Hui Teng, Dr. Khaw Yam Sim, Madam Iwana Izni Zainudin, Ms. Shilan S. Saleem, Mr. Diveyan Mohan, Ms. Puan Sheau Ling, Ms. Lim Zheng Syuen, Madam Rasidnie Razin Wong, Mr. Yap How Swen and Mr. Koh Wei Chin for their kind help and support during my study.

I am also grateful for the moral support and encouragement from my great friends, including Mr. Choong Thonzen, Mr. Tan Yizhang, Mr. Oh Poe Zhi, Ms. Cheng Chin Yee, Ms. Wong Chen Yee, Madam Thian Jia Yi, Mr. Wong Jun Xian and Mr. Benny Lim Shi Huang. Last but not least, I am deeply grateful to my family members for their unwavering love and support during this challenging time. In closing, I would like to extend my appreciation to everyone who has directly or indirectly lent their support to me throughout this journey.

This thesis was submitted to the Senate of Universiti Putra Malaysia and has been accepted as fulfilment of the requirement for the degree of Doctor of Philosophy. The members of the Supervisory Committee were as follows:

Siti Nurbaya binti Oslan, PhD
Associate Professor
Faculty of Biotechnology and Biomolecular Sciences
Universiti Putra Malaysia
(Chairman)

Mohd Shukuri bin Mohamad Ali, PhD
Professor
Faculty of Biotechnology and Biomolecular Sciences
Universiti Putra Malaysia
(Member)

Suriana binti Sabri, PhD
Associate Professor
Faculty of Biotechnology and Biomolecular Sciences
Universiti Putra Malaysia
(Member)

Noor Dina binti Muhd Noor, PhD
Senior Lecturer
Faculty of Biotechnology and Biomolecular Sciences
Universiti Putra Malaysia
(Member)

_____
ZALILAH MOHD SHARIFF, PhD
Professor and Dean
School of Graduate Studies
Universiti Putra Malaysia

Date: 14 March 2024

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2D	Two dimensional
3D	Three-dimensional
β-ME	β-Mercaptoethanol
Als	Agglutinin-like sequence
AMR	Antimicrobial resistance
ANOVA	Analysis of variance
Bpm	Beat per minute
BSA	Bovine serum albumin
BSI	Bloodstream infection
Cas	CRISPR-associated protein
CC	Competent cell
CDC	Centers for Disease Control and Prevention
CFS	Cell-free supernatant
CFU	Colony forming unit
CFW	Calcofluor white
CHK1	Hybrid histidine kinase 1
CIP	Calf Intestinal Alkaline Phosphatase
CR	Congo Red
CRE	Recombinase
CRISPR	Clustered regularly interspaced short palindromic repeat
CTE	C-terminal entrance loop
CV	Crystal violet
CWP	Cell wall protein

DMSO	Dimethyl sulfoxide
DNA	Deoxyribonucleic acid
DTT	Dithiothreitol
Ece1	Candidalysin
ECM	Extracellular matrix
Eno	Enolase
EPS	Extracellular polymers
ER	Endoplasmic reticulum
EV	Extracellular vesicle
FLD	Formaldehyde dehydrogenase
FLP	Flippase
FN	Fibronectin
FOH	Farnesol
FRT	Flippase recombination target
GI	Gastrointestinal
GMQE	Global Model Quality Estimate
GPI	Glycophosphatidylinositol
GRAS	Generally Recognized as Safe
HMM	Hidden-Markov model
Hpe	Hours post exposure
Hpf	Hours post fertilization
HPG	Human plasminogen
HR	Homologous recombination
HAS	Human serum albumin
Hsp	Heat-shock protein

IACUC	Institutional Animal Care and Use Committee
ICU	Intensive care unit
IEC	Intestinal epithelial cell
Ig	Immunoglobulins/Antibodies
IMP	Inositol monophosphatase
LB	Luria-Bertani
Lip	Lipase
mAB	Monoclonal antibody
MAPK	Mitogen activated protein kinase
MCS	Multiple cloning site
MD	Molecular dynamics
MEGA	Molecular Evolutionary Genetics Analysis
MPO	Proteinaceous myeloperoxidase
mRNA	Messenger RNA
MSA	Multiple sequence alignment
NAT	Nourseothricin
NCBI	National Center for Biotechnology Information
NET	Neutrophil extracellular trap
NHEJ	Non-homologous end-joining
NICU	Neonatal intensive care unit
NMR	Nuclear magnetic resonance
NTC	No-template control
NTE	N-terminal entrance loop
NU	Neonatal unit
OD	Optical density

ODc	Cut-off optical density
Opt	Oligopeptide transporter
PAGE	Polyacrylamide gel electrophoresis
PBC	Peptide binding cavity
PBS	Phosphate buffered saline
PCR	Polymerase chain reaction
PE	Pericardial edema
PDB	Protein Databank
Pho	Phytase
Pkc	Protein kinase C
Plb	Phospholipase B
PSI-BLAST	Position-specific iterative basic local alignment search tool
PSSM	Positions-specific scoring matrix
RMSD	Root-mean-square deviation
RNA	Ribonucleic acid
ROS	Reactive oxygen species
Rpm	Revolution per minute
RPMI	Roswell Park Memorial Institute
Sap	Secreted aspartyl proteinase
SAT1	Nourseothricin-selectable marker
SDS	Sodium dodecyl sulphate
SL	Sphingolipid
SO	Spoiled orange
ST	Short tail
TCA	Trichloroacetic acid

TF	Transcription factor
TOR	Target of rapamycin
tRNA	Transfer RNA
UPR	Unfolded protein response
VF	Virulence factor
VTN	Vitronectin
XTT	2,3-bis-(2-methoxy-4-nitro-5-sulfophenyl)-2H-tetrazolium-5-carboxanilide
YASARA	Yet Another Scientific Artificial Reality Application
YBD	Yeast extract-BSA-dextrose
YCB	Yeast carbon base
YE	Yolk sac edema
YNB	Yeast nitrogen base
YPD	Yeast extract-peptone-dextrose
ZFET	Zebrafish embryo toxicity

CHAPTER 1

INTRODUCTION

1.1 Background

Fungal diseases have emerged as a pressing public health concern, driven by factors such as the increasing number of immunocompromised individuals, evolving healthcare practices that contribute to antifungal drug resistance, and shifting environmental conditions (CDC, 2023). Among these dangerous infections (candidiasis, aspergillosis, cryptococcosis, (para)coccidioidomycosis, histoplasmosis and blastomycosis), candidiasis stands out as a formidable threat (Reddy et al., 2022). *Candida* spp., as the human skin and gut microflora, can cause superficial and invasive opportunistic infection (candidiasis) (Pote et al., 2020), contributing to ≥70% mortality in the infected patients (Brown et al., 2012; Pappas et al., 2018).

Candidemia has been one of the most deadly nosocomial bloodstream infections and is capable of causing organ-infecting, deep-seated candidiasis (Antinori et al., 2016). It has drawn attention to the virulence factors (VFs) of several prominent *Candida* spp. (*C. albicans*, *C. glabrata*, *C. parapsilosis* and *C. tropicalis*) that were deposited in *Candida* Genome Database since 2004 (Skrzypek et al., 2017). Proteins and enzymes are studied in-depth besides the transcriptional regulation of yeast-to-hyphae transition (Brunke et al., 2016; Mba & Nweze, 2020). Crystal structures of these VFs, including agglutinin-like sequences, secreted aspartyl proteinases (Sap) and enolase (Dostál et al.,

2021; Li et al., 2022; Lin et al., 2014) were resolved for their virulence-associated structure-function relationships. The increasing numbers of gene sequences and genomes deposited in GenBank have eased the *in silico* analyses, including comparative analyses of sequences and three-dimensional (3D) structures (Lin et al., 2014; Qiu et al., 2023; Zainudin et al., 2023).

Besides the prominent *Candida* spp., *C. guilliermondii* (CTG-clade; teleomorph: *Meyerozyma guilliermondii*) was reported for up to 66.6% mortality (Ahangarkani et al., 2019; Gabaldón et al., 2016). Albeit its natural repertoires (de Marco et al., 2018; Ganapathy et al., 2019; Oslan et al., 2012), *M. guilliermondii* and its anamorph have also been isolated from clinical samples with increasing antifungal drug resistance (Chaves et al., 2020; Hirayama et al., 2020). Its reported pathogenicity dampened its huge industrial potential in volatile flavor compounds production, pentoses fermentation and effluent biodegradation (Ganapathy et al., 2019; Martini et al., 2016; Wah et al., 2013). A recent comparative genomic analysis of a local isolate of *M. guilliermondii* from spoiled orange (SO) showed ≥99% proteome similarity compared to other available soil isolates (YLG18 and RP-YS-11) and the clinical isolate (ATCC 6260) (Zainudin, 2022). Despite its proven promising capability in expressing recombinant industrially important enzymes (Abu et al., 2020; Nasir et al., 2020; Oslan et al., 2015), a preliminary toxicity study then elucidated its pathogenicity towards zebrafish embryos, but the contributing VFs were not well-documented and verified (Zainudin et al., 2023).

Precise attributions of fungal pathogenicity to the VFs *via* gene deletion studies are crucial for the in-depth understanding of fungal virulence mechanisms; this knowledge in turn promote the development of VF-specific antifungal drugs and vaccines. Among the available fungal genome editing tools, homologous recombination strategy has been used to study gene functions and virulence (Mancera et al., 2019; Song et al., 2020). Most studies began to employ the antibiotic markers with *FLP* flippase (Liu et al., 2023; Yang et al., 2023) instead of the auxotrophic markers and *CRE* recombinase (Moyes et al., 2016; Tsang et al., 2017). However, the strategy has only been reported in prominent *Candida* species but not the rare *C. guilliermondii*, highlighting the need to enrich its molecular toolbox. Following the *VF* genes deletion, *in vitro* and *in vivo* animal studies are undeniably significant to validate the virulence reduction in the constructed mutants and thus, the dispensability of the deleted *VF*s in fungal pathogenicity.

1.2 Problem Statements

The pathogenicity of *M. guilliermondii*, particularly strain SO, remains inadequately understood, with limited knowledge of its VFs and their impacts on fungal growth and pathogenicity when deleted. Furthermore, the role of cell wall associated and extracellular VFs in *Candida* pathogenicity, especially in less-studied species like *C. guilliermondii*, lacks comprehensive investigation and quantification of their virulence attributes. To address these gaps, precise attribution of VFs to their virulence roles is essential for the development of

highly specific antifungal drugs with reduced host side effects. Additionally, there is a need to explore and adapt advanced genome engineering techniques, such as *FLP* flippase and nourseothricin-selectable marker strategies, for targeted gene deletions in *M. guilliermondii*. This combined research effort aims to elucidate the virulence mechanisms of *M. guilliermondii*, optimize genome engineering tools, and pave the way for the development of effective antifungal therapies with improved specificity and safety profile.

1.3 Research Objectives

The main objective of this research was to comprehensively characterize and verify the VFs in *M. guilliermondii* strain SO, with the following sub-objectives:

i. To identify and analyze the virulence factors in *M. guilliermondii* strain SO using Hidden-Markov Model search;

ii. To verify and target the putative virulence factors through sequence and structural analyses;

iii. To characterize and determine the virulence features exhibited by *M. guilliermondii* strain SO;

iv. To construct a virulence factor-deficient *M. guilliermondii* strain SO using homologous recombination strategy and determine the virulence features

1.4 Hypothesis

Deletion of specific *VF* genes (*MgSAP341* and *MgSAP1972*) in *M. guilliermondii* strain SO will lead to a demonstrable reduction in virulence, thereby confirming their roles as critical virulence factors.

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