UNIVERSITI PUTRA MALAYSIA

MECHANISM OF TRANSCRIPTOME PROFILING OF CYNOMOLGUS MACAQUE (Macaca fascicularis Raffles) FROM PENINSULAR MALAYSIA

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TRANSCRIPTOME PROFILING OF CYNOMOLGUS MACAQUE (*Macaca fascicularis* Raffles) FROM PENINSULAR MALAYSIA

By

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

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TRANSCRIPTOME PROFILING OF CYNOMOLGUS MACAQUE (*Macaca fascicularis* Raffles) FROM PENINSULAR MALAYSIA

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Chairman: Associate Professor Noorjahan Banu binti Mohammed Alitheen, PhD
Faculty: Biotechnology and Biomolecular Sciences

The cynomolgus macaque (*Macaca fascicularis*) is an extensively utilised nonhuman primate model for biomedical research due to its biological, behavioural, and genetic similarities to humans. Genomic information of cynomolgus macaque is vital for research in various fields, however, there is presently a shortage of genomic information on the Malaysian cynomolgus macaque. This study aimed to sequence, assemble, annotate, and profile the Peninsular Malaysian cynomolgus macaque transcriptome derived from five tissues, kidney, liver, lymph node, spleen, and thymus using RNA sequencing (RNA-Seq) technology. Tissues were harvested from three male wild cynomolgus macaques and were subjected to RNA extraction, RNA-Seq library preparation, and sequencing utilising the Illumina Hi-Seq 2500 sequencer. A total of 268,287,769 paired-end 75 base pair sequencing reads were obtained from the sequencing run. Filtered sequence reads were mapped to the *M. fascicularis* reference genome using CLC Genomics Workbench, with the overall mapping percentage of the sequence reads ranging from 44-69%. Differential gene expression analysis between four tissue comparisons revealed 5473 differentially expressed genes (DEGs) between kidney and liver, 574 DEGs between lymph and spleen, 5402 DEGs between lymph and thymus, and 7008 DEGs between spleen and thymus. The number of tissue-specific genes identified in kidney, liver, lymph, spleen, and thymus tissues were 310, 154, 2156, 169, and 143 genes respectively. Expressed genes were categorised to Gene Ontology (GO) and KEGG pathway categories using Panther Database and DAVID Bioinformatics Resources respectively. GO terms with the highest number of associated expressed genes were Cellular Process, Catalytic Activity, and Cell Part categories in the GO Biological Process, Molecular Function, and Cellular Component domains respectively. For pathway categorisation, the majority of expressed genes fall under Metabolism pathway (kidney and liver), Organismal systems (lymph), and Genetic information processing (spleen and thymus). Six metabolism-related pathway categories were enriched, which include Metabolic pathways, Biosynthesis of amino acids, Amino sugar and nucleotide sugar metabolism, Inositol phosphate metabolism, Pyruvate metabolism, and Oxidative phosphorylation, while five immune-related pathways were enriched, which include Complement and coagulation cascades, Platelet activation, Antigen processing and

presentation, B cell receptor signalling pathway, and Intestinal immune network for IgA production. An additional eight immune-related pathways were identified, which include TNF signalling pathway, RNA degradation, Ras signalling pathway, Rap1 signalling pathway, Protein processing in endoplasmic reticulum, N-Glycan biosynthesis, Wnt signalling pathway, and NF-kappa B signalling pathway. RNA-Seq gene expression data were validated with NanoString nCounter Elements XT and real-time quantitative PCR assays. This study represents the first time the transcriptome of the Peninsular Malaysian cynomolgus macaque is sequenced via RNA-seq. Novel transcriptomic data will further enrich the present *M. fascicularis* genomic database and provide future research potentials involving the cynomolgus macaques, including novel transcript discovery, comparative genomic and / or transcriptomic studies with other closely related macaques, and the development of molecular markers for population genetic studies of the cynomolgus macaques in Malaysia and other regions.

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

PEMPROFILAN TRANSKRIPTOM KERA CYNOMOLGUS (*Macaca fascicularis* Raffles) SEMENANJUNG MALAYSIA

Oleh

JOEY EE ULI

Julai 2017

Pengerusi: Profesor Madya Noorjahan Banu binti Mohammed Alitheen, PhD
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Kera cynomolgus (*Macaca fascicularis*) kerap digunakan sebagai model primat bukan manusia untuk penyelidikan bioperubatan disebabkan oleh kemiripannya kepada manusia dari aspek biologi, tingkah laku, dan genetik. Maklumat genomik kera cynomolgus adalah mustahak untuk penyelidikan di berbagai bidang sains, namun terdapat kekurangan maklumat genomik kera cynomolgus sejak kebelakangan ini. Kajian ini bertujuan untuk menjujuk, membina, menganotasi, dan memprofil transkriptom kera cynomolgus Semenanjung Malaysia yang diperolehi daripada lima sumber tisu, iaitu ginjal, hati, nod limfa, limpa, dan timus melalui teknologi penjujukan RNA (*RNA sequencing*, RNA-Seq). Tisu-tisu diperolehi daripada tiga individu kera cynomolgus jantan liar. Sejurusnya, pengekstrakan RNA, pembinaan sumber RNA-Seq, dan penjujukan dijalankan dengan menggunakan teknologi penjujuk Illumina Hi-Seq 2500. Sebanyak 268,287,769 jujukan berpasangan 75 bp diperolehi daripada proses penjujukan. Jujukan yang telah disaring dipetakan kepada genom rujukan *M. fascicularis* melalui program "CLC Genomics Workbench". Peratusan pemetaan keseluruhan bagi kelima-lima tisu adalah di antara 44-69%. Analisis *differential gene expression* bagi empat jenis perbandingan tisu menunjukkan bahawa terdapat 5473 gen yang diekspreskan secara berbeza (DEG) di antara ginjal dan hati, 574 DEG di antara nod limfa dan limpa, 5402 DEG di antara nod limfa dan timus, dan 7008 DEG di antara limpa dan timus. Jumlah gen yang diekspres secara khusus di tisu ginjal, hati, nod limfa, limpa, dan timus adalah masing-masing 310, 154, 2156, 169, dan 143 gen. Seterusnya, gen-gen yang diekspres di dalam tisu masing-masing dikategorikan ke dalam kategori-kategori *Gene Ontology* (GO) dan *KEGG pathway* melalui program Panther Database dan DAVID Bioinformatics Resources. Istilah GO yang kerap dikaitkan dengan gen-gen yang diekspres termasuk Proses Sel, Aktiviti Katalitik, dan Bahagian Sel yang masing-masing berada di dalam domain GO Proses Biologi, Fungsi Molekul, dan Komponen Sel. Bagi pengkategorian tapak laluan, majoriti gen-gen yang diekspres dikategorikan di dalam Tapak laluan metabolik (ginjal dan hati), Sistem organisma (nod limfa), dan Pemprosesan maklumat genetik (limpa dan timus). Enam laluan metabolisme telah dikenalpastikan, iaitu Tapak laluan metabolik, Biosintesis amino acid, Gula amino dan metabolisma gula nukleotid, Metabolisma inositol fosfat, Metabolisma piruvat, dan

Fosforilasi oksidatif. Sementara itu, lima laluan sistem imun juga dikenalpasti, iaitu Aliran komplemen dan koagulasi, Pengaktifan platlet, Pemprosesan dan persembahan antigen, Laluan isyarat reseptor sel B, dan Jaringan imun usus kecil untuk penghasilan IgA. Di samping itu, lapan lagi laluan yang berkaitan dengan sistem imun dikenalpasti, termasuk Laluan isyarat TNF, Degradasi RNA, Laluan isyarat Ras, Laluan isyarat Rap1, Pemprosesan protein dalam endoplasmik retikulum, Biosintesis N-Glycan, Laluan isyarat Wnt, dan Laluan isyarat NF-kappa B. Data-data ekspresi gen yang dijanakan melalui teknik RNA-Seq disahkan dengan eksperimen NanoString nCounter Elements XT dan kaedah kuantitatif tindak balas berantai polimerase masa nyata (RT-qPCR). Kajian ini merupakan kali pertama transkriptom kera cynomolgus Semenanjung Malaysia dijujukkan melalui teknik RNA-Seq. Data-data transkriptomik yang baharu ini akan menambah kepada maklumat genomik *M. fascicularis* yang kian ada, dan juga memberi peluang untuk kajian-kajian selanjutnya. Kajian-kajian yang melibatkan kera cynomolgus termasuk penemuan transkrip baharu, bandingan genomik dan transkriptomik di antara kera-kera berkait rapat, dan pembangunan penanda molekular untuk pengajian populasi genetik kera cynomolgus di Malaysia dan kawasan-kawasan selanjutnya.

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I certify that a Thesis Examination Committee has met on 21st July 2017 to conduct the final examination of Joey Ee Uli on his thesis entitled "Transcriptome Profiling of Cynomolgus Macaque (*Macaca fascicularis* Raffles) From Peninsular Malaysia" in accordance with the Universities and University Colleges Act 1971 and the Constitution of the Universiti Putra Malaysia [P.U.(A) 106] 15 March 1998. The Committee recommends that the student be awarded the Doctor of Philosophy.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

LIST OF ABBREVIATIONS

µg	Microgramme
µl	Microlitre
µM	Micromolar
18S / 28S	Svedberg Unit
Acetyl-CoA	Acetyl Coenzyme A
ADP	Adenosine Diphosphate
Akt	Protein Kinase B
ANP	Atrial Natriuretic Peptides
AP-1	Activator Protein 1
APRIL	A Proliferation-Inducing Ligand
ATP	Adenosine Triphosphate
BAFF	B-cell Activating Factor
BCE	Before the Common or Current Era
BCR	B Cell Receptor
BLAST	Basic Local Alignment Search Tool
BLASTn	Nucleotide Basic Local Alignment Search Tool
bp	Base Pair
BP	Biological Process
Ca^{2+}	Calcium Ion
CAMs	Cell Adhesion Molecules
CC	Cellular Component
cDNA	Complementary DNA
cGMP-PKG	Cyclic Guanosine Monophosphate-Protein Kinase G
CLCGW	CLC Genomics Workbench

CPM	Counts per Million
cq	Quantification Cycle
CSR	Class Switch Recombination
cSRC	Sarcoma Proto-Oncogene, Non-Receptor Tyrosine Kinase
CYP2C19	Cytochrome P450 2C19
DAVID	Database for Annotation, Visualization and Integrated Discovery
DEG	Differentially Expressed Genes
dNTP	Deoxynucleotide Triphosphate
DTT	Dithiothreitol
DWNP	Department of Wildlife and Natural Parks
EDGE	Empirical Analysis of Differential Gene Expression
ENCODE	The Encyclopedia of DNA Elements
EST	Expressed Sequence Tag
EST-SSR	Expressed Sequence Tag-Simple Sequence Repeat
FDR	False Discovery Rate
FFPE	Formalin-Fixed Paraffin-Embedded
FOV	Field of View
FPKM	Fragments per Kilobase of Exon Model per Million Mapped Reads
FU	Fluorescent Unit
GO	Gene Ontology
HIV	Human Immunodeficiency Virus
HVSI	Hypervariable Segment I
IACUC	Institutional Animal Care and Use Committee
IgA	Immunoglobulin A

IKK	Inhibitory Kappa B Kinase
IL	Interleukin
IUCN	International Union for Conservation of Nature
K	Potassium
KEGG	Kyoto Encyclopedia of Genes and Genomes
LTA	Lymphotoxin Alpha
M	Molar
MAPK	Mitogen-Activated Protein Kinase
MF	Molecular Function
MHC	Major Histocompatibility Complex
mM	Micromolar
mRNA	Messenger RNA
MSA	Multi-Species Annotation
mtDNA	Mitochondrial DNA
Na	Sodium
Na^+	Sodium Ion
NADH	Reduced Nicotinamide Adenine Dinucleotide
NCBI	National Center for Biotechnology Information
Neu5Ac	N-Acetylneuraminic Acid
NF-kappa	Nuclear Factor-Kappa
NF-κB	Nuclear Factor-Kappa B
ng	Nanogramme
NGS	Next-Generation Sequencing
NHP	Nonhuman Primate
NHPRTR	Nonhuman Primate Reference Transcriptome Resource

NK	Natural Killer
nM	Nanomolar
Nt	Nucleotide
NTC	No Template Control
Oligo-dT	Oligo-Deoxythymine
OXPHOS	Oxidative Phosphorylation
p	Probability
PCA	Principal Component Analysis
PCR	Polymerase Chain Reaction
PI3K	Phosphatidalyinositol-3-Kinase
PI3P	Phosphatidylinositol 3-Phosphate
PI5P	1-Phosphatidyl-1D-*myo*-Inositol 5-Phosphate
PIP_2	Phosphatidylinositol 4,5-Bisphosphate
PLC-γ2	Phospholipase C-γ2
pM	Picomolar
PRR	(Pro)Renin Receptors
pS	Picosiemens
QC	Quality Check
Q_x	Phred Quality Score
r	Pearson Correlation Coefficient
R^2	Pearson Correlation Coefficient
RALGDS	Ral Guanine Nucleotide Dissociation Stimulator
RefSeq	The Reference Sequence Database
RhoA	Ras Homolog Gene Family, Member A
RIG-I	Retinoic Acid-Inducible Gene I
RIN	RNA Integrity Number

RNA-Seq	RNA Sequencing
rRNA	Ribosomal Ribonucleic Acid
RRP44	Ribosomal RNA-Processing Protein 44
RT-PCR	Reverse-Transcription Polymerase Chain Reaction
RT-qPCR	Quantitative Real-Time Polymerase Chain Reaction
SdhA	Succinate Dehydrogenase Complex, Subunit A
SdhB	Succinate Dehydrogenase Complex, Subunit B
sFPKM	Significant Fragments per Kilobase of Exon Model per Million Mapped Reads
SIV	Simian Immunodeficiency Virus
SNP	Single Nucleotide Polymorphism
SQ	Starting Quantity
SRA	Short Read Archive
STR	Short Tandem Repeats
Syk	Spleen Associated Tyrosine Kinase
TAB1	Transforming Growth Factor Beta-Activated Kinase Binding Protein 1
TAE	Tris-Acetate-Ethylenediaminetetraacetic Acid
TAK1	Transforming Growth Factor Beta-Activated Kinase
TE	Tris-Ethylenediaminetetraacetic Acid
TGFβ	Transforming Growth Factor Beta
TNF	Tumour Necrosis Factor
TNFR1	Tumour Necrosis Factor Receptor 1
TNFR2	Tumour Necrosis Factor Receptor 2
TPM	Transcripts per Million
TRAF6	Tumor Necrosis Factor Receptor-Associated Factors 6
U	Unit

UDP-GlcNAc	Uridine Diphosphate N-Acetyl-Alpha-D-Glucosamine
UniProt	Universal Protein Resource
V	Volts
Vs.	Versus
X	Times
Xg	Times Gravity
$\Delta\Delta C_t$	Comparative Threshold Cycle

CHAPTER 1

INTRODUCTION

1.1 Background

The cynomolgus macaque (*Macaca fascicularis*, Raffles), also known as the long-tailed macaque, or kera in Bahasa Malaysia, are nonhuman primates (NHP) that are important to the biomedical field of research. Researchers primarily utilise the macaques as NHP models due to the macaque's genomic similarity with humans which are reflected in both organisms sharing similar physiology, behaviour, and genetics (Carlsson *et al*., 20024). Such biological similarities are taken advantage of by researchers for translational studies as the macaques tend to recapitulate symptoms of diseases observed in humans, which are theoretically translatable to human subjects. While the murine model remains as a research staple, in some instances, macaques are generally more practical for certain experimental designs. For instance, investigations into the infection mechanism of specific viruses cannot be conducted if the model organism's organs of which the infection occurs on are vastly different. In other situations, a viral infection simply cannot occur in animal models other than primates, for example, simian immunodeficiency virus/human immunodeficiency virus (SIV/HIV) (Ambrose *et al*., 2007). This makes the cynomolgus macaque a valuable asset to biomedical research. A myriad of biomedical disciplines utilise the cynomolgus macaques as NHP models, including pharmacokinetic studies of drugs, vaccine development, immunology, neuroscience, and the evaluation of drug efficacy and toxicity (Theriault *et al*., 1999; Nunamaker *et al*., 2013; Lee *et al*., 2014b; Silverstein *et al*., 2014; Berry *et al*., 2015).

Biomedical studies fundamentally require an understanding of gene expression patterns which are observable through the profiling of transcripts and/or transcriptomes. Classical methods to sequence entire transcriptomes rely on cloning and sequencing of vast numbers of transcripts, while conventional gene expression studies utilise real-time quantitative PCR (RT-qPCR) and DNA microarrays to observe changes in expression levels of a particular panel of genes that are related to a condition or phenotype of interest. Global gene expression profiling is crucial to better understand the effects of drug treatments or pathogenic infections towards model organisms (Lamb *et al*., 2006). While RT-qPCR remains as the golden standard for gene expression studies, its output remains medium-throughput, at the same time microarrays are limited by their incapability for exploratory studies (Zhao *et al*., 2014). In addition, classical sequencing of entire transcriptomes is time consuming, labour intensive, and costly. In the past decade, a high throughput methodology called RNA sequencing (RNA-Seq) has emerged as the go-to method to profile entire transcriptomes in a single sequencing run. Generally, only a small amount of starting material is required for the library construction and the platform also allows for pooling of samples into a single reaction (Rajkumar *et al*., 2015). Furthermore, the RNA-Seq platform eschews cloning of nucleotide sequences, and is suitable for novel investigations of non-model organisms. The output consists of a global gene expression profiling of entire transcriptomes that ultimately saves time, money, and resources. Furthermore, with careful experimental design, datasets obtained from RNA-Seq experiments can be utilised not only for gene

expression profiling studies, but also for other studies such as novel gene discovery, studies into alternative splicing events, molecular marker development, transcriptomic comparisons, and gene co-expression studies (Wang *et al*., 2012a; Loraine *et al*., 2013; Li *et al*., 2014; Ballouz *et al*., 2015).

While the technology and model organism of interest are crucial to biomedical research, a fundamental aspect in experimental design that requires no less attention is the genetic history of the model organism. Rodents are bred in controlled laboratory conditions whereby researchers can manipulate the genotype of the rodent model organism to suit their experimental objectives and methodologies. A great number of cynomolgus macaque models are captured from the wild and are housed in primate research facilities around the world. In situations where model organisms are captured from wild populations, it is vital to profile the genomic and transcriptomic information of model organisms that originate from different geographical locations. It is not uncommon for organisms of the same species that originate from different localities to exhibit different phenotypical traits (Haus *et al*., 2014). Careful experimental considerations are required to take into account the origins of the model organisms. A group of organisms with higher genetic diversity is likely to exhibit a wider range of phenotypical traits, while organisms with relatively lower genetic diversity are easier to predict the outcome of experiments. Ultimately, it is important that the genomic and transcriptomic information of model organisms, particularly the cynomolgus macaque, originating from different geographical locations are made known for the benefit of the scientific community and biomedical research.

1.2 Problem Statement

Previous studies have shown that the Malaysian cynomolgus macaque have higher levels of nucleotide diversity, and are monophyletic and cluster separately from other Southeast Asian populations of cynomolgus macaques (Smith *et al*., 2007; Abdul-Latiff *et al*., 2014). Taking into consideration the genetic diversity and uniqueness of the Malaysian cynomolgus macaque, they are potentially useful as NHP model organisms for translational studies. Presently, the transcriptomes of the Chinese, Mauritian, and Vietnamese cynomolgus macaques have been sequenced via various high-throughput methodologies (Huh *et al*., 2012; Peng *et al*., 2014a; Osada *et al*., 2015), however the Malaysian cynomolgus macaque has yet to be sequenced. A closer look into the expression profile of the Malaysian cynomolgus macaque is important as a stepping stone in utilising the Malaysian cynomolgus macaque as a NHP model organism. As such, this project was conceived and carried out to sequence the entire transcriptome of wild Malaysian cynomolgus macaque via RNA-Seq methodologies, with the expected outcome of the project to provide fully sequenced and annotated transcriptomes of kidney, liver, lymph node, spleen, and thymus tissues harvested from wild Malaysian cynomolgus macaque individuals. The dataset obtained will be valuable for potential future biomedical science studies that utilise the Malaysian cynomolgus macaque as NHP model organisms. In addition to biomedical research, the transcriptomic dataset produced will be valuable for other studies, including comparative transcriptomic studies, splicing quantitative trait loci studies, phylogenomic studies, and also the development of genic molecular markers for population genetic studies.

1.3 Objectives

Therefore, the general objective of this study is to sequence the transcriptome of five metabolism and immune-related tissues harvested from the cynomolgus macaque (*Macaca fascicularis*) from Peninsular Malaysia via RNA sequencing (RNA-Seq). The specific objectives of this study include:

1. To construct a transcriptome dataset from five tissues (kidney, liver, lymph node, spleen, and thymus) harvested from the cynomolgus macaque from Peninsular Malaysia.

2. To identify and functionally annotate transcribed genes in the transcriptome of cynomolgus macaque.

3. To perform gene ontology and pathway analyses on the transcriptome dataset.

4. To identify and investigate differential expressions of tissue function-related genes in different tissues in cynomolgus macaque.

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