



UNIVERSITI PUTRA MALAYSIA

**OLFACTORY DETECTION OF METHYL EUGENOL BY MALE ORIENTAL
FRUIT FLY, BACTROCERA DORSALIS (HENDEL)
(DIPTERA: TEPHRITIDAE)**

ANNA CHIENG CHUI TING

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By

ANNA CHIENG CHUI TING

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

April 2019

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Abstract of thesis presented to the Senate of Universiti Putra Malaysia in fulfillment of the requirement for the degree of Doctor of Philosophy

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By

ANNA CHIENG CHUI TING

April 2019

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Oriental fruit fly, *Bactrocera dorsalis* (Hendel) is one of the world's most destructive pests of fruits and vegetables. Methyl eugenol (ME), a potent male attractant that is also found as a plant volatile compound, when mixed with insecticides is widely used to manage and control those pestiferous flies. Upon detection of ME, *B. dorsalis* male will respond rapidly by flying in zig-zag pattern to, landing and subsequent feeding on ME. Hitherto, with tremendous progress in molecular biology, there is now improved understanding in the molecular basis of insect detection of odourants such as ME by the antennae (ANT) of male *B. dorsalis*. However, little is known about the role of the maxillary palp (MP) in odourant detection. The general aim of this study was to evaluate the role of olfactory organs, ANT and MP in male *B. dorsalis* detection of ME. Therefore, the specific objectives of this study were to: 1) ascertain the function of MP in detection of ME by male *B. dorsalis*; 2) evaluate electrophoretic protein pattern in both MP and ANT, and following male attraction to ME, 3) evaluate associated proteome changes, 4) evaluate transcriptome changes followed by 5) an integrated proteo-transcriptome analysis. First, it has been demonstrated in those males from wind tunnel and cage behavioural assays that both olfactory organs were functionally complementary in detecting ME. The ANT was involved in long-range detection of ME while the MP at close range, manoeuvres the male towards the ME source for feeding. Second, exposure to ME appeared to have increased the protein concentration of both olfactory organs compared to those non-ME-exposed. When protein profiles of the male olfactory organs were obtained using gradient PAGE, a number of proteins present were below 66 kDa. Similarly, SDS-PAGE analyses showed most protein bands were between 20-100 kDa with 2 major bands below 20 kDa. No marked differences were seen in the protein patterns of both organs when compared between before, and

after exposure to ME. Finally, a complementary approach using shotgun proteomics followed by transcriptomics (reference-based alignment) revealed the existence of 30 genes/ proteins having tissue specific expression with 7 being odourant binding proteins and 1 belonging to alcohol dehydrogenase. Six genes were significantly expressed in those organs with 5 up-regulated and 1 down-regulated. Of those 5 genes, *BdorOBP69a* was induced in both olfactory organs following the exposure to ME. Whilst *BdorOBP69a* was not detected in the proteome of both organs, another OBP *BdorOBP84a-2* was significantly up-regulated in the MP only following exposure to ME. The presence of those different genes and proteins that were induced in different organs following exposure to ME suggests that the proteo-transcriptomic basis of gene-protein is an intricate pattern of operation. In genes that were involved in detoxification of xenobiotics including ME i.e., P450 members, two different types of those annotated genes were up-regulated at proteome level in both olfactory organs following exposure to ME. This suggests the role of MP in detecting and feeding on ME.

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

**PENGESANAN BAU METIL EUGENOL OLEH LALAT BUAH ORIENTAL,
BACTROCERA DORSALIS (HENDEL) (DIPTERA: TEPHRITIDAE)**

Oleh

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Lalat buah Oriental, *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) adalah salah satu serangga perosak buah-buahan dan sayur-sayuran yang paling serius di dunia. Metil eugenol (ME), sejenis bahan penarik poten lalat buah jantan yang juga ditemui sebagai sebatian tumbuhan yang mudah meruap, apabila dicampur dengan racun serangga perosak telah digunakan secara meluas dalam pengurusan dan pengawalan serangga perosak tersebut. Apabila ME dikesan oleh lalat jantan *B. dorsalis*, lalat tersebut akan bergerak balas dengan pantas melalui penerbangan secara zig-zag yang diikuti dengan pendaratan dan pemakanan sebatian ME itu. Kini, berikutan perkembangan yang pantas dalam biologi molekul, pemahaman yang berasaskan molekul mengenai pengesanan bau seperti ME oleh organ antena (ANT) lalat buah jantan *B. dorsalis* adalah lebih baik. Walau bagaimanapun, pemahaman mengenai peranan palpa maksilari (MP) dalam pengesanan bau sebatian meruap masih lagi kurang. Oleh itu, matlamat umum kajian ini adalah untuk menilai peranan ANT dan MP dalam pengesanan ME oleh lalat jantan *B. dorsalis*. Sehubungan itu, maka objektif khusus kajian ini adalah untuk: 1) menentu fungsi MP dalam pengesanan ME oleh jantan *B. dorsalis*; 2) menilai corak protein elektroforetik dalam kedua-dua MP dan ANT; 3) menilai perubahan proteome; 4) menilai perubahan transcriptome diikuti dengan 5) perubahan proteo-transcriptome yang berkaitan berikutan penarikan jantan *B. dorsalis* ke ME. Pertama, melalui kajian kelakuan dengan menggunakan asai terowong angin dan sangkar, organ ANT dan MP telah ditunjukkan berfungsi secara saling melengkapi dalam pengesanan ME. ANT adalah terlibat dalam pengesanan jarak jauh ME manakala MP adalah untuk pengesanan ME secara jarak dekat dengan memimpin lalat jantan ke arah sumber ME untuk dimakan. Kedua, pendedahan lalat jantan kepada ME telah menghasilkan peningkatan dalam kepekatan protein kedua-dua organ ANT dan MP lalat jantan *B. dorsalis* berbanding dengan lalat jantan yang tidak terdedah kepada ME. Apabila profil protein ANT dan MP jantan diperolehi melalui kaedah elektroforesis gel

poliakrilamida (PAGE) tak nyahasli (native), beberapa protein yang dijumpai adalah di bawah 66 kDa. Begitu juga dengan SDS-PAGE yang menunjukkan kebanyakan jalur protein berada di antara 20-100 kDa dengan 2 jalur utama di bawah 20 kDa. Tiada perbezaan ketara didapati dalam kedua-dua corak protein ANT dan MP apabila perbandingan dibuat di antara corak protein sebelum dan selepas pendedahan kepada ME. Akhirnya, pendekatan pelengkap dengan menggunakan kaedah proteomik rawak ("shotgun proteomics") diikuti dengan transkriptomik penyejajaran berasaskan rujukan mendedahkan kewujudan pengekspresan 30 gen/ protein berasaskan tisu dengan 7 protein pengikat pembau ("odourant") dan 1 alkohol dehidrogenase. Pengekspresan gen berlaku dengan ketara dalam 6 gen dalam ANT dan MP dengan peningkatan dalam 5 gen dan penurunan dalam 1 gen. Daripada 5 gen tersebut, *BdorOBP69a* telah didorong dalam kedua-dua ANT dan MP selepas pendedahan kepada ME. Walaupun *BdorOBP69a* tidak dikesan dalam proteome kedua-dua organ, satu lagi OBP *BdorOBP84a-2* telah menunjukan kenaikan yang ketara dalam MP sahaja selepas pendedahan kepada ME. Kemunculan gen-gen dan protein yang berlainan yang diinduksi dalam organ-organ yang berlainan berikutan pendedahan kepada ME menunjukkan asas proteo-transkriptomik gen-protein adalah corak operasi yang rumit dan penilaian terhadap kesan temporal pada ANT dan MP berikutan pendedahan jantan *B. dorsalis* kepada ME adalah diperlukan. Analisis lanjut juga menunjukkan bahawa dalam gen yang terlibat dalam detoksifikasi xenobiotik termasuk ME i.e., ahli P450, dua jenis gen yang dianotasi telah menunjukan kenaikan di tahap proteome dalam ANT dan MP masing-masing berikutan pendedahan kepada ME. Ini turut mencadangkan peranan MP dalam pengesanan dan pemakanan ME.

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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:

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LIST OF ABBREVIATIONS

7TM	7-transmembrane domain
ADH	alcohol dehydrogenase
ANT	antenna/ antennea
APS	ammonium persulfate
BSA	Bovine serum albumin
cDNA	complementary DNA
CF	(<i>E</i>)-coniferyl alcohol
CL	cuelure
CSP	chemosensory protein
CYPs	cytochromes P450
DAE	day of emergence
DAP	differentially abundant protein
DEG	differentially expressed gene
DMC	(<i>Z</i>)-3,4-dimethoxycinnamyl alcohol
DMP	2-allyl-4,5-dimethoxyphenol
GPCR	G-protein coupled receptor
GR	gustatory receptor
GST	glutathione S-transferases
iGluR	ionotropic 'glutamate' receptor
IR	ionotropic receptor
kDA	kilodalton
LC-MS	liquid chromatography mass spectrometry
m/z	mass/ ion
MAT	male annihilation techniques
ME	methyl eugenol
ME-exp	methyl eugenol exposed
ME-unexp	methyl eugenol unexposed (control)
MP	maxillary palp(s)
mRNA	messengers RNA
NADH	reduced nicotinamide adenine dinucleotide
NADPH	reduced nicotinamide adenine dinucleotide phosphate
OBP	Odourant binding protein
OR	Odourant receptor
ORCO	Odourant receptor co-receptor
ORN	olfactory receptor neurone
ODE	Odourant degradation enzyme
PBP	pheromone binding protein
PBPRP	pheromone binding protein related protein
PCB	polychlorinated biphenyls
R _f	relative front
RK	raspberry ketone
RKF	raspberry ketone formate
rpm	revolutions per minute
SDS-PAGE	sodium dodecyl sulphate-polyacrylamide gel electrophoresis
SIT	sterile insect techniques
SNMP	sensory neurone membrane protein
TCA	trichloroacetic acid

TEMED	tetramethylethylenediamine
TML	tridmedlure
UGT	UDP-glucuronosyltransferases



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CHAPTER 1

INTRODUCTION

True fruit flies (Diptera: Tephritidae) consist of some of the world's most serious insect pests of horticultural production throughout the subtropical and tropical regions (Drew, 1989). Within the past decades, there has been an increase in economic loss towards the production of commercial fruits and vegetables due to severe fruit fly infestations and invasion (Allwood *et al.*, 2002). Thus, with certain species of Tephritidae such as the Oriental fruit fly and Mediterranean fruit fly possessing high mobility, dispersal and high degree of polyphagy, they have been documented as major invaders in a list of quarantine targets (Clarke *et al.*, 2005; Vayssières *et al.*, 2014; Wan *et al.*, 2017). Hitherto, global losses attributed to fruit fly damage have been estimated to be over US\$ 2 billion annually (Shelly *et al.*, 2014).

As one of the largest genera in the fruit fly family of Tephritidae (subfamily: Dacinae), the genus *Bactrocera* includes around 500 described species (Drew, 1989; Drew and Hancock, 2000). Within the genus *Bactrocera*, there exists the *B. dorsalis* complex that consists of 85 morphologically similar species such as the highly invasive and damaging *B. dorsalis*, *B. dorsalis* (Hendel) (Clarke *et al.*, 2005; Drew and Romig, 2013). However, the close similarities between the *B. dorsalis* and its sibling species such as *B. invadens* Drew, Tsuruta & White, *B. papayae* Drew & Hancock and *B. philippinensis* Drew & Hancock that are all major fruit pests have created much confusion over their identities (Lux *et al.*, 2003; Schutze *et al.*, 2012) that impacts global quarantine fruit restrictions. However, with the synonymization of *B. dorsalis* with the three aforementioned species recently as a single *B. dorsalis* species (Schutze *et al.*, 2015), this allows the improvement of pest management tools which is restricted previously due to the species limits (Schutze *et al.*, 2015).

The detection and control of *B. dorsalis* relies heavily on methyl eugenol (ME), 1,2-dimethoxy-4-(2-propenyl) benzene (phenylpropanoid) that is a unique and potent attractant for male tephritid fruit flies (Metcalf *et al.*, 1975) since its discovery over a century ago (Howlett, 1915). As a component of plant compound, ME is known to occur in over 480 plant species (Tan and Nishida, 2012). Following *B. dorsalis* male consumption of ME, the heightened during courtship period at dusk attraction of female towards those conspecific males has been attributed to production of attractive chemical cues in the form of sex pheromone, (*E*)-coniferyl alcohol (CF), along with 2-allyl-4,5-dimethoxyphenol (DMP) and (*Z*)-3,4-dimethoxycinnamyl alcohol (DMC) from ME that were emitted from the rectal gland during wing fanning at dusk (Nishida *et al.*, 1988a, 1988b).

In managing the *B. dorsalis*, multiple tactics with the aim to achieve low pest prevalence or pest free status have been developed by using of ME as attractant. The tactics which are used to manage and control these pestiferous tephritid fruit flies through the manipulation of certain facets of the biology of these flies that include the sterile insect technique (SIT), male annihilation technique (MAT), protein bait sprays and biological control (Piñero *et al.*, 2009b; Vargas *et al.*, 2015). The application of ME as a supplement in feeding the sterile males which are released in SIT programmes can aid in male signalling and thus increasing the mating competitiveness of the ME-fed male over non-ME-fed wild male (Hee and Tan, 1998; McInnis *et al.*, 2011; Tan *et al.*, 2014) with conspecific feral females (Pereira *et al.*, 2013). As millions of sterile males are released in SIT in order to suppress the reproduction of the feral female pests, the efficacy of SIT is further enhanced when MAT which uses insecticide intoxicated ME in attracting, killing and eventually reducing the number of wild males is implemented prior to the commencement of SIT.

As most tactics for monitoring and controlling of *B. dorsalis* involve the continuous use of ME as male attractant, there have been concerns that lines of non-ME-attracted males may be generated (Ito and Iwahashi, 1974; Shelly, 1997). Further, sequential MAT releases of insecticide baited ME followed by releases of SIT irradiated males may result in those sterile males themselves attracted and killed by those ME baits (Barclay *et al.*, 2014). This underscores the need for enhanced understanding on mechanisms of male detection of ME at the behavioural, physiological and molecular levels. Therefore, the understanding of the olfactory system provides the basis designing novel tephritid pest control approaches such as silencing of sequence-specific gene using RNA interference (RNAi) (Mamta and Rajam, 2017) through the manipulation of olfactory mechanism of *B. dorsalis*.

The *B. dorsalis*, like other insects, owns two bilateral symmetrical pairs of olfactory organs on its head, namely, antenna (ANT) and maxillary palp (MP). Although there has been significant important development in elucidating the molecular basis of antennal function of *B. dorsalis* in recent years (Zheng *et al.*, 2013; Wu *et al.*, 2015; Wu *et al.*, 2016; Liu *et al.*, 2016; Liu *et al.*, 2017; Liu *et al.*, 2018), there has been no information on the function of *B. dorsalis* MP in detecting ME. The MP is also another pair of olfactory organs which have been shown to house specific receptors in responding to behaviourally important odourants in *D. melanogaster* (Dweck *et al.*, 2016) and *B. tryoni* (Verschutt *et al.*, 2018). Therefore, it is believed that specific odourant receptors which respond selectively to ME might also present on the MP of *B. dorsalis* since both olfactory organs contain similar types of olfactory sensilla (Dickens *et al.*, 1988; Lee *et al.*, 1994) that may accommodate receptors tuned to ME.

Thus, in this study, my first objective (Chapter 3) was to evaluate if the MP is also involved in the male *B. dorsalis* attraction to ME. Cage behavioural assays and wind tunnel assays involving response of *B. dorsalis* to ME with ANT and/or MP ablation were conducted. My second objective (Chapter 4) was to examine for any changes in the electrophoretic protein pattern in both ANT and

MP of the *B. dorsalis* following exposure to ME. This is due to the fact that in olfactory organs, a number of proteins have been implicated to be involved in detection of volatile compounds such as odourants. Changes in the electrophoretic patterns of protein expression in the ANT and MP were observed. Finally, an integrated analysis of generated proteomic and transcriptomic profiles of both ANT and MP of *B. dorsalis* male was performed in order to understand mechanism(s) of olfactory processing (perireceptor events) in those organs following attraction to ME which still remain largely unclear to date (i.e., proteome analysis [Chapter 5], transcriptome analysis [Chapter 6] and integrated proteo-transcriptome analysis [chapter 7]). It was expected that result from this research will shed new light on the role of the MP of *B. dorsalis* in detection of ME and the associated changes in the proteome and transcriptome level of the MP and ANT following attraction to ME. This information will be beneficial for development of novel proteo-transcriptome based strategies to control those pests.

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BIODATA OF STUDENT

Anna Chieng Chui Ting was born on 10th March 1990 in Kuching, Sarawak, Malaysia. After completing her secondary school education and obtaining the Sijil Pelajaran Malaysia (SPM) certificate from SMK Jalan Arang, she continued to attain the higher school certificate, Sijil Tinggi Persekolahan Malaysia (STPM) from SMK Batu Lintang, Kuching. In July 2010, she was enrolled for tertiary education in Universiti Putra Malaysia (UPM) and received her B.Sc. (First Class Hons.) degree, majoring in Biology from Faculty of Science, Universiti Putra Malaysia in 2014. With an excellent track record, she was accepted as a PhD student in Entomology under that tutelage of Dr Alvin KW Hee in the same faculty of her alma mater. Over the course of her doctoral candidature, she has successfully published two key papers in Insect Biochemistry and Molecular Biology as well as Journal of Insect Science.

LIST OF PUBLICATIONS

- Chieng, A. C. T.**, Hee, A. K. W., & Wee, S. L. (2018). Involvement of the antennal and maxillary palp structures in detection and response to methyl eugenol by male *Bactrocera dorsalis* (Diptera: Tephritidae). *Journal of Insect Science*, 18, 19.
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