



Functional characterisation of *Sirex noctilio*
chemosensation genes

“Functional characterisation of *Sirex noctilio* chemosensation genes”

By

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Declaration of Authorship

I, Leandri Klynsmith (Maiden name: Bezuidenhoudt), declare that the dissertation, which I hereby submit for the degree of Masters in Science in Genetics at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signed,

At the University of Pretoria, on _____ 20____

by _____ Leandri Klynsmith (Bezuidenhoudt).

Dedicated to my family

"Science is organized knowledge. Wisdom is organized life"

- Immanuel Kant

Table of contents

Declaration of Authorship.....	1
Table of contents	3
Acknowledgements	5
Preface.....	6
List of abbreviations.....	8
Chapter I: Literature Review.....	9
Potential of reverse chemical ecology in insect pest management and control: From omics to lures	9
Abstract	10
1.1. Introduction.....	11
1.2. A molecular view of the insect chemosensory system	12
1.2.1. Olfaction versus gustation	12
1.2.2. Mechanistic and molecular pathway of odour reception: From air to action	14
1.3. The role of semiochemicals in pest management	17
1.3.1. What is a semiochemical?	17
1.3.2. Sustainable pest management via semiochemicals.....	19
1.4. Deciphering insect chemosensation: interdisciplinary approaches.....	21
1.4.1. Conventional/classical chemical ecology.....	21
1.4.2. Alternative and complementary approaches to classical chemical ecology.....	23
1.5. The invasive woodwasp, <i>Sirex noctilio</i>	29
1.5.1. Life history and biology.....	29
1.5.2. Control mechanisms.....	30
1.5.3. Chemical ecology of <i>Sirex noctilio</i>	31
1.6. Conclusion	35
1.7. References.....	36
1.8. List of figures.....	51

Chapter II: Research chapter	57
Transcriptome profiling of olfactory and non-olfactory appendages in <i>Sirex noctilio</i> (Hymenoptera: Siricidae) reveals sex- and tissue-specific chemosensory genes.....	57
Abstract	58
2.1. Introduction	60
2.2. Methods.....	63
Insect collection and storage	63
RNA isolation.....	63
Illumina sequencing	65
Identification of chemosensation genes	65
Quality control, read mapping and read counting	65
Expression quantification and differential expression analysis.....	65
2.3. Results	66
Overview of olfactory and non-olfactory transcriptomes of <i>Sirex noctilio</i>	66
Chemosensation gene identification, characterisation and curation	67
Identification of differentially expressed genes	67
Expression profiling identified tissue-, sex- and developmental stage-specific chemosensation genes	68
2.4. Discussion	71
<i>Sirex noctilio</i> versus Hymenoptera chemosensation gene repertoires.....	71
Tissue type, sex and developmental stage influences on overall gene expression profiles.	73
Chemosensation genes displaying sex- and/or tissue-biased expression	76
2.5. Conclusion and future work.....	84
2.7. Acknowledgements	85
2.8. Declarations.....	85
2.9. References	86
2.10. List of Figures.....	98
2.11. Supplementary material	123
Supplementary figures.....	123
Supplementary tables	134
Supplementary files	169
Addendum 1: Journey through this Masters	170

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Preface

South Africa's forestry sector has significant economic and social importance. The commercial afforested area makes up 1% (1.21 million ha) of South Africa's land area. A total of 157 500 people are directly employed by the forestry sector with an additional 59 800 jobs in the forest sub-sector and 27 500 indirect forestry related jobs contributing to human resource development for this country. Poverty in rural communities is alleviated through forestry livelihood programmes by providing timber, medicinal plant products, food and firewood. On top of this, forest products (such as timber, paper and pulp) contribute 0.6% to South Africa's GDP and is one of the top exported products.

Non-native *Pinus* spp. are one of the main tree species planted in South Africa for its quality timber. Unfortunately, these pine plantations are affected by several invasive pests and pathogens that can cause major economic losses. This dissertation focuses on one of the most serious of these invasive pests, the woodwasp, *Sirex noctilio* (Hymenoptera: Siricidae), which is a threat to pine production throughout the Southern Hemisphere.

Sirex noctilio is native to Eurasia and North Africa, but established in the Western Cape region of South Africa in 1994. Since its discovery, *S. noctilio* has spread along the Southern Cape, and eventually through the Eastern Cape, Kwazulu-Natal and Mpumalanga to Limpopo. A South African *Sirex* Control Programme was initiated in 2002 in response to this insect threat. The aim of this programme is to reduce the wasp population to an acceptable level that minimises the impact of this pest. This programme is based on monitoring, biological control and research.

Pheromones have been used for the last six decades to monitor, manipulate, and trap insect pests and have been an integral part of integrated pest management. A better understanding of the chemical communication of *S. noctilio* will aid the development of chemical control strategies that can supplement the current management strategies used to ensure low population levels of the pest. For more than four decades the chemical ecology of *S. noctilio* has been investigated to develop lure-and-trap systems to allow implementation of monitoring and management practices. This work has elucidated several chemical cues/signals that mediate *S. noctilio* behaviour. Chemical ecology studies have demonstrated that female woodwasps are attracted to physiologically stressed pine trees through the release of host stress volatiles and male woodwasps attempt copulation in response to a female-produced,

cuticular lipid sex pheromone. Using classic chemical ecology methods researchers discovered that *S. noctilio* ovipositors are electrophysiologically active and respond to pine needle extracts and ethanol. Most recently a putative male-produced volatile pheromone that possibly mediates lek formation and location has been identified.

In this dissertation, chapter one explores insect chemosensation and the molecular techniques used to investigate this biological process. First, the molecular components required for chemosensation are discussed. These components are proteins that are critical to pest management strategies through gene manipulation and functional studies. The current role of semiochemicals in pest management is also discussed in the context of chemosensation. Furthermore, interdisciplinary approaches that can be used to decipher chemosensation in insects are considered. Finally, the current knowledge of the biology and chemical ecology of *S. noctilio* is synthesized and interpreted in the light of the information that is reviewed from other systems, and as a foundation for chapter two.

There are some behaviours such as male aggregation and mating behaviour that raise the question of potential pheromone receptors. Pest management by targeting the chemosensation system of *S. noctilio* is of great potential value to forestry world-wide, but better knowledge about this system is needed. Chapter two, therefore, investigates chemosensation of *S. noctilio* on a molecular level through gene expression analyses. *Sirex noctilio* wasps are sexually dimorphic and we explore how this dimorphism extends to the wasps' chemosensation. The *S. noctilio* genome, produced by our in-house research group, enabled us to identify chemosensation genes involved in the uptake, binding, and transport of chemical molecules to lay the foundation for gene expression investigation. By using RNA sequencing of different sexes, developmental stages and tissues, we aim to identify and characterise the expression patterns of chemosensation genes. This study sets the stage for future reverse chemical ecology studies for this forest pest. The study also adds basic knowledge about chemosensation in a basal Hymenoptera species and non-social wasps

List of abbreviations

Abbreviation	Description
CRCE	Computational reverse chemical ecology
CSP	Chemosensory protein
DEG	Differentially expressed gene
EAG	Electroantennogram
GC-EAD	Gas chromatographic electroantennographic detection
GC-MS	Gas chromatography-mass spectrometry
GR	Gustatory receptor
GRN	Gustatory receptor neuron
HPLC	High-performance liquid chromatography
IR	Ionotropic receptor
LFC	Log ₂ fold change
OBP	Odourant binding protein
ODE	Odourant degrading enzyme
OR	Olfactory receptor
ORCO	Odourant receptor co-receptor
ORN	Olfactory receptor neuron
PBP	Pheromone binding protein
PCR	Polymerase chain reaction
RCE	Reverse chemical ecology
RNA	Ribonucleic acid
RT-qPCR	Real-time quantitative polymerase chain reaction
SNMP	Sensory neuron membrane protein
SSR	Single sensillum recordings
TPM	Transcripts per kilobase per million reads

* if an 's' is added to the end of an abbreviation it refers to plural form

Chapter I: Literature Review

Potential of reverse chemical ecology in insect pest management and control: From omics to lures

Abstract

Olfaction is the dominant modality that insects use to obtain information about their biotic and abiotic environment. Consequently, insect olfaction can be exploited for insect pest management if the identity of the chemical cues and signals involved are known. Classical chemical ecology approaches for semiochemical discovery are time consuming and labour intensive. The genomics era is, however, offering opportunities to perform insect chemical ecology research on a larger and more inclusive scale for model and non-model organisms. For example, chemical ecogenomics is the integration of ecological genomics and chemical ecology that employs findings from genomic and transcriptomic data to understand chemosensation. Results from chemical ecogenomic studies can contribute to the understanding of fundamental mechanisms underlying the chemosensory system and help identify the molecules involved in chemosensation processes as potential novel targets against agricultural pests and disease vectors. The increasing number of identified insect chemosensory genes, such as those encoding chemoreceptors and odorant binding proteins, create the need for high-throughput techniques for the identification of the semiochemicals or ligands specific to these proteins. For this purpose, the field of reverse chemical ecology is rapidly developing as a way to identify behaviourally active ligands for certain chemosensation proteins in a more targeted way. Here we review the current techniques used to investigate insect chemosensation, where they are applied and what they promise to contribute to the future of integrative approaches that would target the chemosensory systems of insect pests for novel and effective management strategies.

Key words: Chemosensation, semiochemicals, ecogenomics, invasive pests, pest management

1.1. Introduction

Of all the senses, the perception of chemicals is likely the oldest, most common and important for insect survival [1]. Essential behaviours such as mate- and host-seeking, oviposition, predator avoidance and inter- and intra-species communication are predominantly mediated through chemical detection via sensory organs (like antennae) [2–4]. The perception of chemical stimuli, whether from biotic or abiotic sources, is therefore, vital for insect survival and the process of perception has to be extremely efficient. A delay, for example, in mate or host detection can have severe fitness consequences especially for insects that are short-lived as adults. Chemical detection can thus attenuate the potential fitness consequences by facilitating rapid detection of a mate or a host.

Chemical messages are decrypted by the well-developed and complex chemosensory system of insects. Initial decryption occurs at the level of odourant binding proteins (OBPs) and chemosensory proteins (CSP) that bind and transport chemical molecules to chemoreceptors located in neuron membranes. This is where the second level of decryption occurs when the chemical molecule binds to its corresponding receptor which could be either an olfactory (OR), gustatory (GR) or ionotropic (IR) receptor [5, 6]. Final decryption of the chemical message occurs in the brain where the appropriate behaviour in response to the message will be determined [7]. There has been significant growth in our understanding of the chemosensation system of insects in recent years. While most of that understanding is still derived from the study of model insects, there is also a growing body of knowledge on non-model systems.

Because chemosensation has strong influences on insect behaviour, insect pests can be managed by manipulating their chemical communication, which can be achieved by exploiting our understanding of this process. To this end, one needs to understand how the perception of a chemical signal affects an insect's behaviour. Chemical ecology integrates biology, chemistry and ecology to address these questions in an interdisciplinary manner [1]. Classical chemical ecology methods used to identify behaviourally active semiochemicals include the extraction, identification and synthesis of the chemical of interest, followed by behavioural bioassays to determine the behavioural response. This is a time intensive and expensive approach, which also requires a substantial number of insect specimens. Such a system can be

lethargic and impractical in cases where sample collection is not possible and for the rapidly increasing number of globally emerging pests.

The elucidation of molecular mechanisms and proteins involved in insect chemosensation accompanied by technological advances in genetics and biochemistry are facilitating new approaches to investigate chemosensation. Reverse chemical ecology (RCE) utilises high-throughput methods for the identification of ligand-protein interacting partners in order to functionally deorphanise chemosensation proteins [4]. Chemoreceptor deorphanisation is the process of identifying chemical ligands responsible for activating a receptor thus a receptor for which the ligand is still unknown can be referred to as an orphan receptor. Heterologous expression systems have been developed for large-scale deorphanisation of insect chemoreceptors and OBPs/CSPs which can even be used for non-model organisms [8].

In this review, we reflect on the molecular processes involved in the perireceptive events of insect chemosensation. We also consider the role of semiochemicals on pest control strategies and the various approaches used to study chemosensation of insect pests. Finally, we reflect on how emerging approaches like reverse chemical ecology and heterologous expression systems used to study chemosensation of insects will aid the development of potential novel control methods for important insect pests even non-model pests. The chemosensory system of insects is key to their survival but, manipulated correctly, can also be the key to their demise.

1.2. A molecular view of the insect chemosensory system

1.2.1. Olfaction versus gustation

Insects live in a chemical world where the chemosensory system is essential for survival. Chemosensation is divided into two categories based on the nature of the chemical that is detected: olfaction is the detection of air-borne chemicals/odorants (smell), and gustation is the detection of aqueous chemicals/tastants (taste). For insect physiology, alternative terms are also used where smell/olfaction is regarded as distant chemoreception and taste/gustation as contact chemoreception [9].

Sensilla are cuticular hair-like protrusions on the surface of the insect body that house chemosensation proteins, receptors and neurons [10]. The perireceptive events of chemosensation (discussed in the following section) occur within these cuticular structures.

Chemosensory sensilla have specific distributions and morphologies which influences their function in the chemosensory system (figure 1.1) [9]. Gustatory sensilla are used for contact chemoreception and are widely distributed across the entire body of the insect including the wing margins, mouthparts, legs, genitalia and ovipositor with the labellum being the main gustatory organ [11–13]. Conversely, olfactory sensilla detect volatiles and have a more confined distribution on the antennae, maxillary palps and labial palps of the insect, with antennae being the primary site of olfaction [10, 12, 14].

Olfactory sensilla are classified into four major morphological categories namely, coeloconic, basiconic, trichoid, and auriculate sensilla (figure 1.1) which were identified through ultrastructure studies using light, transmission and electron microscopy [15–18]. Olfactory sensilla of insects show functional division for the different morphological categories due to the specific sensory neurons that are housed in each sensillum category (figure 1.1) [16–21].

Odourants and tastants have inherent differences in their chemical properties, and consequently, insects have a diverse chemoreceptor superfamily of ionotropic receptors (IR), gustatory receptors (GR) and olfactory receptors (OR) [5, 22, 23]. The IRs and ORs are expressed within the membranes of the olfactory receptor neurons (ORN) which are housed in olfactory sensilla. The GRs, however, are expressed in gustatory receptor neuron (GRN) membranes that are housed within gustatory sensilla [5, 14]. The evolution and diversification of these receptors have occurred in response to the ecological and biological needs of each insect species [24].

Ionotropic receptors are an ancient group of receptor proteins similar to ORs and with a molecular structure comparable to ionotropic glutamate proteins [4, 10, 13]. Insect IRs respond to acid-based odours and amines that are not detected by ORs [10, 25, 26]. Within the group of IRs, there are ‘antennal’ IRs which are conserved within the insect clade, as well as ‘divergent’ IRs that are more species-specific [14]. Ionotropic receptors form a receptor protein complex of up to three subunits. One of these protein subunits is an IR that is specific to a single odour. The rest of the protein complex is made up of one or two receptors (either IR25a, IR8a or IR76b) that are broadly expressed as co-receptors [27, 28].

Gustatory and olfactory receptors have a common origin, but have evolved into divergent and highly variable multi-gene protein families [5]. Gustatory receptors have roughly 400 amino acids and encode seven transmembrane domains to function as ligand-gated ion channels [22,

29, 30]. Gustatory receptors are involved in the detection of a wide spectrum of chemical compounds, which include amino acids, sugars, repulsive compounds, carbon dioxide and pheromones [5, 13, 31, 32]. It is also believed that gustatory reception forms part of the somatosensory system (responsible for the perception of various tactile and thermal stimuli) to allow multisensory information processing [31, 33].

General odours and pheromones are detected by the multi-transmembrane ORs. Similar to GRs, ORs have seven transmembrane domains and are around 400 amino acids in length. Olfactory receptors are highly divergent across insect orders with regard to the number of ORs, as well as the amino acid sequences of the proteins. These divergent ORs are referred to as odourant-specific or tuning ORs, which are specific to certain odourant stimuli [34]. Insect ORs function as heteromeric complexes to form odourant-gated ion channels. These complexes consist of an obligate, highly conserved co-receptor and a tuning OR [22, 29].

1.2.2. Mechanistic and molecular pathway of odour reception: From air to action

The olfactory system of insects has evolved for discrimination and sensitivity to a plethora of chemical stimuli. Olfaction is the main sense used by insects to detect and locate hosts, food, mates, oviposition sites and predators [10, 35–37]. This review, therefore, focuses on the molecular reception pathway of an odour molecule during olfaction to illustrate the function of chemosensation proteins. The related topic of insect gustation [31, 38] and the neurological processing of the chemical signals and cues [39, 40] are reviewed elsewhere.

Olfaction is initiated with the reception of an odour molecule that enters the olfactory sensilla (on the antennae, maxillary palps or labial palps). Odour reception events include the physical uptake, binding, transport, inactivation and degradation of an odour, which are collectively known as the perireceptive events (figure 1.2) [22, 41]. Several chemosensation proteins are involved in perireceptive events which include odourant binding proteins (OBP), chemosensory proteins (CSP), chemosensory receptors (ORs, GRs, IRs), co-receptors, sensory neuron membrane proteins (SNMP) and odourant degrading enzymes (ODE) [10, 14, 22].

Most odour molecules are hydrophobic, therefore, they are first solubilised by OBPs and CSPs, enabling their movement through the hemolymph towards the olfactory receptors housed within the ORNs [10, 14, 22]. Odour binding proteins (also referred to as pheromone binding proteins (PBPs)) and CSPs are globular proteins that are mainly responsible for odourant

transport, but to some extent assist with odour discrimination to enhance the sensitivity and selectivity of insect olfaction [22, 42–44]. These proteins have α -helical domains which produce a hydrophobic cavity used for odour binding [13, 45]. It has also been suggested that OBPs and CSPs are involved in the transport of semiochemicals [46], as well as other physiological processes [47, 48]. The tertiary structure of OBPs is stabilised by three interlocked disulphide-bridges located between conserved cysteine residues whereas the CSP proteins have two disulphide bonds [45]. This conserved tertiary structure of these two protein classes allows for their phylogenetic separation from one another [42]. Based on primary protein sequences of OBPs, four groups have been classified namely classical, plus-C, minus-C and atypical [44].

Three mechanisms are proposed by which the interactions between OBPs or CSPs and odours lead to the activation or inhibition of olfactory receptors. The first proposed mechanism is the binding of the OBP/CSP–odour molecule complex to the OR [13, 22]. The second proposed mechanism suggests that once the OBP/CSP–odour complex has reached the vicinity of the OR, pH changes cause an α -helix to free the odour molecule from the ligand-binding pocket, after which the odour molecule binds to the receptor [13, 45]. The third proposed mechanism involves the binding of the odour molecule to the OBP/CSP at high pH levels after which a ‘lid’ is formed over the ligand-binding pocket with the C-terminus of the OBP/CSP [13, 22, 49]. Once this complex reaches the negatively charged membrane of the ORN, where there is a low pH, the ‘lid’ is opened and the odour molecule is released onto the OR [13, 49].

The OR repertoires of insects has been shaped by the gain and loss of genes for adaptation to their specific life history, biology and ecology [8]. The first OR was discovered in the model species *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) in 1999 [50–52]. Since this discovery, the OR repertoires of several insect species have been identified through the use of transcriptome analysis [36, 53], genomes and *in silico* prediction analysis [54]. Through comparative genetic studies, OR repertoires of insect species have been found to be highly diverse in amino acid sequence and have undergone species-specific retractions and expansions [55]. Insect OR repertoires vary from as little as four (including ORCO) in dragonflies [56] to more than 300 in ants that are highly social insects [57]. It is currently believed that evolutionary adaption has shaped the OR repertoire present within various insect species [10, 27, 58, 59].

One of the most intriguing aspects of insect olfaction is how the olfactory system can distinguish between the diversity of odours insects are exposed to. To date, evidence suggests it is due to a combinatorial receptor code produced by the differential activation of ORs that allows for enhanced specificity and selectivity [8, 22]. This code refers to the phenomenon whereby a subset of tuning ORs are activated by a single odour or an overlapping subset of odours activate a single tuning OR [22, 32, 34, 44, 60]. Therefore, some ORs are broadly tuned to a large set of odours making them generalist ORs whereas specialist ORs are more narrowly tuned to a single or small set of odours (as in the case of pheromone specific odour receptors) [8, 22, 32, 44, 60, 61]. It has also been reported that OR classes have restricted expression patterns in the ORNs, which may subsequently determine the specificity of these neurons as not all neurons express the same groups of ORs [5, 10, 13].

Olfactory receptors form heteromeric complexes with the commonly known odourant receptor co-receptor, ORCO. ORCO is a highly conserved, seven-transmembrane co-receptor that was first identified in *D. melanogaster* (as *Or83b*) and orthologs of this protein have since been discovered in various other insects from different orders, including Lepidoptera, Hemiptera, Orthoptera, Coleoptera, Hymenoptera and Zygentoma [8]. The ORCO protein is, in many ways, essential to insect olfaction. Studies have shown that the absence of ORCO prevents the localisation of ORs to the neuron membrane [25, 62]. In *ORCO*-deficient fruit flies, it was seen that the flies have an attenuated electrical response to odour molecules which suggest ORCO improves the responsiveness of ORs without affecting its specificity [8].

Response to pheromones not only requires pheromone-specific ORs, but also an additional element, namely sensory neuron membrane proteins (SNMP) [63]. These SNMPs were first identified in the ORNs of the Silk Moth, *Antheraea polyphemus* Cramer (Lepidoptera: Saturniidae). The SNMPs are two-transmembrane proteins that belong to the CD36 receptor family which binds lipoproteins and fatty acids in mammals [64–66]. Based on the function of CD36 receptors and the fact that SNMPs have homology to these proteins it is suggested that SNMPs are essential for reception of lipophilic pheromones [67, 68]. There are three representative genes, known as (1) SNMP-1 that is expressed in the ORNs and (2) SNMP-2 that are expressed in the accessory/supporting cells of olfactory sensilla (figure 1.1) and SNMP-3 [68–70]. The roles of SNMP-2 and SNMP-3 genes in insect olfaction is still under investigation, however, studies in *D. melanogaster* have found that SNMP-1 is essential for rapid activation

of cis-vaccenyl acetate pheromone reception as well as for rapid termination of the olfactory response [63, 67].

Interaction between an OR and an odour molecule leads to the generation of an electrical impulse. When an odour molecule or OBP/CSP-odour molecule complex binds to the appropriate OR the OR/ORCO protein complex allows the movement of ions such as Ca^{2+} , Na^{+} and K^{+} across the neuron membrane [8, 29]. This ion flux leads to depolarisation in the ORN membrane. Through this depolarisation, the chemical signal is converted into an electric nerve impulse which is further carried along neurons to the nervous system of the insect where a cascade of neural activities determines the appropriate behavioural response [60]. Through this process, the odours present in the air around the insect are perceived and interpreted to elicit an appropriate behavioural action.

Inactivation of odour molecules is crucial to insect chemosensation. Following the successful reception and interpretation of a chemical signal, odours must rapidly be deactivated to prevent sensory adaptation and ensure continuous and rapid detection of ensuing chemical stimuli [71]. This allows the insect to have a constant response to its altering chemical environment [22]. The most popular theory for odour inactivation is through enzymatic degradation by odourant-degrading enzymes (ODE) [4, 22]. Several enzymes from detoxification enzyme families which include esterases, alcohol dehydrogenases, aldehyde oxidases, UDP-glycosyltransferases, glutathione-S-transferases and cytochrome P450 have been implicated in the inactivation of odour molecules [71–74]. For enzymes to be regarded as an ODE, two criteria must be met, first the enzyme must reside within the same areas (e.g. sensilliary lymph) where olfaction (or gustation) occurs and second the enzyme must also have the ability to degrade/inactivate the chemical signal molecules [71, 75].

1.3. The role of semiochemicals in pest management

1.3.1. What is a semiochemical?

Pesticides are widely used to eradicate the threat and limit the damage associated with insect pests. As early as 1914 the first case of pesticide resistance was reported [76]. The systematic emergence of pesticide resistance and the toxicity of synthetic pesticides to the environment create the need for better, integrative and environmentally safe control strategies [77]. Insight

into insect chemosensation has the potential to create more sustainable and environmentally friendly pest management strategies, such as using lures and traps that manipulate the chemical communication of specific insect pests [78].

The term, semiochemical, describes a chemical or a chemical mixture that emanates from one organism and ultimately affects the physiology and behaviour of a receiving organism [79, 80]. Semiochemicals are classified into different categories based on their modes of action and the interactions they mediate. Semiochemicals are divided into two main groups namely pheromones and allelochemicals (figure 1.3). Pheromones mediate interactions between conspecifics [81]. Based on the behavioural response elicited, pheromones are divided into several subgroups including trail, recruitment, home recognition, alarm, aggregation, oviposition, royal and sex pheromones, each of which is responsible for a specific behaviour [82, 83]. Heterospecific interactions are mediated by allelochemicals [81]. Most allelochemicals are classified on the basis of whether the receiver (kairomones), the emitter (allomones) or both the receiver and emitter (synomones) benefit. Some allelochemicals are emitted from non-living sources (apneumones) or induce a repellent response in the receiver towards the emitter (antimones) [82–84].

Using the woodwasp, *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), as an example the potential role of semiochemicals can be illustrated (figure 1.3). Lek formation observed with *S. noctilio* males (aggregating at the tree canopy) may be mediated by visual cues and aggregation pheromones (figure 1.3 – A2) [85]. Oviposition pheromones can also be used by *S. noctilio* females to determine the chemical suitability of a pine host tree (figure 1.3 – A3). The relationship between *S. noctilio* and the fungus, *Amylostereum areolatum* Boidin (Russulales: Amylostereaceae), is an example of a symbiotic interaction where synomones from the fungus may be used by the wasp during site-selection for egg laying (figure 1.3 – B3) [86, 87]. *Ibalia leucospoides* Hochenwarth (Hymenoptera: Ibalidae), a parasitoid of *S. noctilio*, exploit kairomones released from *A. areolatum* and potentially also from *S. noctilio* to locate eggs or 1st instar larvae of *S. noctilio* for oviposition (figure 1.3 – B1) [88–90]. Whilst it is clear that semiochemicals are involved in life situations of *S. noctilio*, the identity and type of semiochemicals mediating these interactions (e.g. symbiotic interactions) are still unclear and need to be elucidated.

The use of semiochemicals has several benefits over the use of pesticides in pest management. Pesticides can have detrimental off-target effects on, amongst others, other arthropods as well as vertebrates [91]. Conversely, unlike broad spectrum insecticides, semiochemicals can be very specific [92]. Another advantage is that semiochemicals are required in very low dosages and they are less persistent in the environment thereby making them more environmentally friendly [80, 82]. Insects are less likely to develop resistance to semiochemicals as they form part of the insects' biology and is essential to their survival [77]. These benefits make semiochemicals good resources for pest management, however, to exploit these benefits we need a greater understanding of the chemosensory system of the target pest.

1.3.2. Sustainable pest management via semiochemicals

Semiochemicals can be used in indirect control or direct control tactics [83]. Indirect control tactics employ semiochemicals to detect and monitor insect pest populations. Direct control strategies include mass trapping and disruption. Mass trapping aims to reduce the abundance of pests by luring them towards a trap by the use of a semiochemical that acts as an attractant. Disruption strategies are achieved by oviposition deterrents, stimulo-deterrent diversionary strategy (commonly referred to as push-pull strategy) and mating disruption [84, 92].

Detection and monitoring practices are used to track population density, developmental stage and dispersal range of a pest population so that correct management intervention will occur at the appropriate point in time. For detection and monitoring, general attractants can be used, however, pest control usually focuses on a specific pest and therefore attractants with high specificity (e.g. pheromones) are predominantly used [93, 94]. This indirect control strategy is also vital in management of insects that have cryptic lifestyles, such as white grubs that are root-feeding, soil dwellers or woodwasp larvae that feed inside host tree wood since the detection of the adult stages is key to effective pest control strategy implementation.

Pheromone-baited mass trapping uses species-specific pheromones (e.g. aggregation or trail pheromones) to lure the target insect pest into a trap where it is then physically entrapped [95, 96]. Mass trapping can also be used to capture a single sex of the pest species and it is, therefore, essential to understand how the use of sex pheromones will influence mass trapping results (for example the sex pheromone may only be attractive to either males or females) [97]. Mass trapping does not only help control the targeted insect pest but it can also aid in the

detection of pests that may be present or introduced in the environment, as has been seen in control strategies of lepidopteran pests [98]. This strategy is most successful for low-density populations [83] and species that live as adults for a long time before egg deposition [80].

Lure-and-kill, lure-and-sterilise and lure-and-infect strategies rely on the principles of mass trapping (the use of an attractant semiochemical) but each with some variation [80]. In lure-and-kill strategies, attractants are used to lure the insect pest into a trap where it is subsequently exposed to a killing agent [83]. This method is primarily employed during long-term pest management or when invasive pests have to be eradicated [95]. Lure-and-sterilise and lure-and-infect strategies function the same as lure-and-kill, but instead of using a killing agent, a sterilant or pathogen is used, respectively [80]. Lure-and-sterilise effectively removes the insect from the population similarly to lure-and-kill [95], whereas lure-and-infect allow insect survival for a short time period during which they spread the entomopathogen to cause an epizoonotic outbreak in the population [99–102].

Sex pheromones advertise availability and location to potential mates and are widely used for mating disruption. Sex pheromones are used to inform a potential conspecific mate of another's availability as well as its location [83]. Pheromone dispensers disrupt mating in two ways either by 1) directly creating a false pheromone trail to follow or 2) through indirect mechanisms, such as masking of the pheromone trail of the emitting partner (confusing the receiver) or sensory desensitisation due to overexposure to the pheromone [83, 103, 104]. The decrease in mating can result in reduced population growth [104, 105]. This method is most common for Coleoptera and Lepidoptera species since major strides have been made in the identification of pheromones of these orders [106].

Push-pull control strategies use chemical manipulation to make the plant resource unappealing to the insect pest thus pushing them away and simultaneously pulling them towards a specific area (trap or trap crop) so that they can be removed [107]. This behavioural manipulation can also be targeted to natural enemies of the insect pest to serve as a complementary control strategy. The key to successful push-pull management is to have a comprehensive understanding of the target pests' biology, chemical ecology and biotic interactions [83]. This management strategy mostly utilises naturally occurring semiochemicals making it a good alternative to insecticides used in integrated pest management [107]. One of the most prominent examples of push-pull pest management is the intercropping system for maize used

against maize stemborers. The repellent source used in this system is either molasses grass, *Melinis minutiflora* Beauvois (Poaceae) or a legume *Desmodium uncinatum* Jacq. (Fabaceae). The repellent plants are situated through the maize crop fields. The attractant used in this system, wild Napier grass *Pennisetum purpureum* Schumach (Poaceae), is planted on the outskirts of the maize crop field to pull the stemborer moths away from the maize crops [108].

In order to use semiochemicals for pest control and insect monitoring, we need to know how these chemicals affect insect behaviours such as mate and host finding, oviposition and larval feeding. Semiochemical reception forms the basis of several pest control systems. With increasing threat of insect pests and the emergence of pesticide resistance, it is becoming more crucial to gain a better understanding of the molecular pathways involved for semiochemical detection in order to understand how the genetics of insect chemosensation can be combined with chemical control practices to create a more integrative pest management system.

1.4. Deciphering insect chemosensation: interdisciplinary approaches

1.4.1. Conventional/classical chemical ecology

In the last 60 years, the study of chemical languages has become a very prominent and well-developed field of research. Chemical ecology is an interdisciplinary science that investigates everything from the characterisation and synthesis of biologically active chemicals, the production, transmission and detection mechanisms of both the sender and receiver up to the behavioural and physiological responses induced by chemical molecules [1]. The promise of using semiochemicals for pest management was one of the primary impetuses for developing the now well-developed field of chemical ecology.

Since the development of the electroantennogram in 1955 by Dietrich Schneider, numerous chemical compounds which influence insect behaviour have been identified [109]. A prominent example is the identification of the *Bombyx mori* Linnaeus (Lepidoptera: Bombycidae) sex pheromone, Bombykol. The identification of this pheromone set the stage for similar studies which has since led to the identification of various chemicals that are of behavioural and ecological importance [1, 110–113].

The chemoelectrical properties of insect chemosensation enabled the exploration of chemoreceptor responses to various chemical stimuli in order to identify electrophysiologically active chemicals [114]. Ion fluxes generated during chemical ligand-chemoreceptor interactions lead to the generation of an electrical impulse that can be detected by methods such as electroantennograms (EAG) [115]. In order to use EAG, pure chemical ingredients (synthetic or natural chemicals) are required to screen chemoreceptor responses, which is problematic when chemical messages are mixtures of several different chemical ingredients [114]. As a result, several classical chemical ecology techniques such as coupled gas chromatographic-electroantennographic detection (GC-EAD), gas chromatography-mass spectrometry (GC-MS) and high-performance liquid chromatography (HPLC) are employed to study chemical communication of insects.

GC-EAD employs both EAG and gas chromatography for simultaneous separation and detection of electrophysiologically active chemicals within complex mixtures [114, 116, 117]. By using GC-EAD the predicament of having to use pure chemicals for EAG analyses are circumvented [118]. First, the chemical secretions from the sender or its headspace are collected, after which secretions are separated into fractions via the gas chromatograph. Next the active chemical ingredients present in these fractions are identified via the use of a biosensor (e.g. antennae) as the signal receiver. The final step is to determine the chemical structure of the active ingredient and to synthesise it [46, 114, 119]. An electrophysiologically active chemical is not necessarily a behaviourally active chemical. Hence bioassays are required to determine if the appropriate behaviour is induced by the chemical.

Using the entire antenna or body as a biosensor during coupled GC-EAD does not produce selective responses for a single volatile and a sensillum. Olfactory sensilla vary in the type of olfactory receptor neurons (ORNs) housed by them and only express up to five ORNs in a single sensillum [120, 121]. These properties of an olfactory sensillum accompanied by the odour specificity of ORNs (due to the select expression of certain ORs in the neuron membrane) [5, 13] enable more selective investigation of olfactory responses through single sensillum recordings (SSR) [120]. The SSR technique can also be coupled with gas chromatography (GC-SSR) to allow simultaneous separation and detection of active ingredients, as well as the ORs present in the sensillum [120, 122]. The main benefit of this technique is the fact that it can be

used to investigate electrophysiological features of a single OR present in a single sensillum, as well as the chemicals they respond to [122].

1.4.2. Alternative and complementary approaches to classical chemical ecology

Functional validation of chemosensory genes

Next-generation sequencing technologies have advanced to such a level that they are not only used to generate genomes and transcriptomes, but also to investigate minuscule differences in gene expression patterns [123]. By using quantitative RNA sequencing, a comprehensive investigation can be done of these differences in gene expression for model and non-model species under various conditions and different sexes, developmental stages and tissues [124, 125]. Real-time quantitative polymerase chain reaction (RT-qPCR) is another technology readily employed to analyse gene expression and to functionally validate genes of interest [124, 126, 127].

Investigating chemosensation genes between sexes, tissues and developmental stages (life stages) will lay the foundation for novel pest management strategies. For example, pheromones are mostly detected by specific ORs, therefore, these specialised ORs will often be differentially expressed in certain conditions [125]. In a scenario where a female insect secretes a pheromone that is detected only by the conspecific male (i.e. females do not detect the pheromone), one would expect a male-biased expression of the OR [128]. Similarly, if a specific odour is only detected through olfaction then one might hypothesise that ORs specific for this odour will have tissue-biased expression, meaning it will be present in olfactory tissues (e.g. antennae) but not non-olfactory tissues (e.g. legs).

Sex-related transcriptomes

It is important to understand chemosensation of insects especially ones that act as disease vectors so that control mechanisms with high efficiency and specificity can be designed for these vectors. *Anopheles gambiae* Giles (Diptera: Culicidae) is of great medical importance as it is the chief vector of human malaria in sub-Saharan Africa [129]. By using transcriptome sequencing, Pitts *et al.* [129] compared the expression profiles of chemosensory tissues (maxillary palps and antennae) to non-chemosensory tissues (whole body) of both male and female adult *An. gambiae*. They were able to identify chemosensation genes due to their enriched expression in the chemosensory tissues compared to the entire body. From this study,

it was concluded that the chemoreceptive spectrum of males and females are similar, but variation in transcript quantity of the chemosensation genes existed. It was observed that the male antennae had enhanced expression of genes involved in audition. Altogether the results suggest that sexual dimorphism in the antennae of male and female mosquitoes exists, with female antennae dedicated to olfaction and male antennae to audition [129]. Sex-related transcriptome analyses shed light on the differences in molecular processes of chemosensation between male and female insects.

Molecular processes of chemosensation are investigated to understand the chemical communication of agricultural pests to permit genetic manipulation of insects' chemosensory abilities. Several studies using RNA sequencing and RT-qPCR for gene expression validation have been done on agricultural pests such as the brown planthopper, *Nilaparvata lugens* Stål (Hemiptera: Delphacidae) [130], the Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae) [131], the Diamondback moth, *Plutella xylostella* Linnaeus (Lepidoptera: Plutellidae) [132], a scarab beetle, *Holotrichia oblita* Faldermann (Coleoptera: Scarabaeidae) [36], the Oriental armyworm, *Mythimna separate* Walker (Lepidoptera: Noctuidae) [133] and the sweet potato whitefly, *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) [127]. In these studies, researchers analysed the differences in the antennal transcriptome between adult male and female insects to determine sex-specific or sex-biased olfactory gene expression. Sex-biased gene expression can suggest proteins that detect chemicals which are more important to one sex. These data can, therefore, be used to refine chemical control strategies to be more specific not only at the species level but also to target one sex within a species.

Similar to agricultural pests, investigating the molecular basis of chemosensation for biological control agents, such as parasitic wasps, can improve biocontrol strategies through genetic manipulation for enhanced detection of host chemical cues [126]. *Chouioia cunea* Yang (Hymenoptera: Eulophidae) is an endoparasitic wasp that is used to reduce populations of *Hyphantria cunea* Drury (Lepidoptera: Erebididae) which is a forest pest in China [134, 135]. Through antennae transcriptome analysis of adult male and female wasps, Zhao *et al.* [134] annotated and subsequently quantified the expression level of the chemosensation genes in *C. cunea* for various tissue parts (antennae, head, thorax and abdomen) by reverse transcription PCR and RT-qPCR. From this study, the authors were able to identify genes that have enhanced

or specific expression in the antennae of female wasps, which can help to understand how these parasitoids locate their hosts for oviposition [134]. Similar work has been done for the endoparasitoids of the European corn borer, *Macrocentrus cingulum* Brischke (Hymenoptera: Braconidae) and *Meteorus pulchricornis* Wesmael (Hymenoptera: Braconidae) [14]. Investigations of sex-related transcriptomes can therefore reveal genes that are important for host recognition and oviposition.

Tissue, developmental and caste-related transcriptomes

Antennal transcriptome analysis is one of the main ways in which insect chemosensation is studied since the antennae are the main site of insect olfaction [136]. Comparison between antennal transcriptomes and other non-olfactory tissues (e.g. legs, wings and body) can reveal key olfaction genes that are potential targets for pest control. In an RNA sequencing study by Yang *et al.* [132], the chemoreception gene repertoire (ORs, GRs, IRs, OBPs, CSPs and SNMPs) of *P. xylostella* antennae were identified. Subsequent to identifying these genes, reverse transcription PCR analyses were used to determine the tissue-specific expression of ORs and IRs between antenna and leg tissues [132]. The study revealed tissue-specific expression of pheromone specific ORs of which some were found to have male-biased or specific expression. This phenomenon of tissue- and sex-biased expression of ORs is common in lepidopteran species and is most likely important during mate-seeking by the males and oviposition by females [53, 137–139].

Essential life behaviours are prioritised differently during the various life stages of an insect. For example, insects that spend most of their life cycle in larval form would prioritise feeding during the larval stage and mating during the short-lived adult stage. Because of these prioritisations, developmental stage or life stage-specific transcripts can be identified. Investigating and comparing the chemosensory gene repertoire of an insect across its life stages (i.e. egg, larva, pupa and adult stages) can reveal genes that facilitate chemically induced behaviours specific to a life stage [3]. For example, RNA interference (RNAi) can be implemented as a pest control strategy by altering the genetic composition of a host plant to make it pest tolerant or resistant. Introducing RNAi constructs into a host plant that targets and interfere with the function of larval chemosensory genes used during feeding inside the host plant can restrict larval development as well as pest damage [54]. Thus, life stage-specific genes can be targeted to

manipulate the associated behaviour of the genes, which may ultimately lead to the management or population collapse of the insect species.

Eusocial insects live in complex societies where each individual of a caste has a specific function to ensure the survival of the colony. Complex caste-specific social behaviours are predominantly mediated by chemical cues and, therefore, an equally complex chemosensory system is used to regulate these behaviours [47]. Mitaka *et al.* [140] investigated the expression patterns of chemoreceptors among different castes and sexes of the termite *Zootermopsis nevadensis* Hagen (Blattodea: Termopsidae) using RNA sequencing. The chemoreceptor gene repertoire of primary queens and kings, mature primary kings, mature secondary queens, as well as for both male and female alates, soldiers and worker termites, were assessed [140]. Investigation of the chemoreception genes not only revealed the caste- and sex-biased expression of these genes but also indicated that there are age-dependent expression differences within the reproductive castes. Therefore, the study revealed how the need to detect caste-specific chemical cues influences chemosensory gene expression patterns.

Deorphanisation of chemosensation genes through reverse chemical ecology

Conventional reverse chemical ecology

The in-depth investigation of the molecular and cellular biology of insect chemosensation in an increasing number of insect genomes [141], coupled with heterologous expression systems created a novel method for rapid and dynamic deorphanisation (identify a receptors' ligand partner) of chemosensory proteins. This approach is referred to as reverse chemical ecology (RCE). RCE can be used to search for prospective active semiochemicals that can be used for pest management strategies by screening interactions of a molecular target (chemoreception proteins: OBPs and ORs) with various chemical ligands [142, 143]. RCE studies use either laboratory based chemical biology approaches (e.g. expression systems) or computational simulations that involve *in silico* molecular docking and molecular dynamic simulations to identify potential ligands [136].

RCE techniques are high throughput and can screen a myriad of semiochemical or synthetic chemical ligands for their binding activity and affinity with OBPs or ORs. Similar to GC-EAD analyses, ligand binding to OBPs or ORs activation does not imply that the chemical analysed will be behaviourally active in the insect, therefore, bioassays are still required to confirm activity [143]. Prior knowledge of insect chemoreception proteins (i.e. OBPs and ORs) and

hence chemoreception genes are required for RCE [136]. In order to study the interactions that OBPs/ORs have with semiochemical ligands, the proteins are expressed *in vitro* or *in vivo* in heterologous expression systems.

A study illustrating the potential of RCE was done by Choo *et al.* [143]. These researchers used olfactory proteins to guide them to an active semiochemical (acetaldehyde) that was determined to be an oviposition attractant for female *Culex quinquefasciatus* Say (Diptera: Culicidae). They identified the ten most highly expressed ORs of female *C. quinquefasciatus* using RNA sequencing and RT-qPCR, and selected the ORs that were not yet deorphanised for expression in *Xenopus* oocytes to screen ligand interactions. The binding activity between 230 odourants and the expressed ORs were investigated, but not one CquiOR showed any activation to the odourant panel [143]. The researchers accidentally applied an old nonanal solution to the oocytes after which they observed a strong response by CquiOR36. After confirming the active ingredient in the old nonanal solution as acetaldehyde, the activation of CquiOR36 by this ingredient was confirmed with EAGs using antennae over-expressing this receptor as well as wild-type female antennae. Final confirmation of the oviposition attracting properties of acetaldehyde was determined by behavioural bioassays, assessing oviposition rates and dual-choice assays.

Heterologous expression systems used for RCE can either be *in vivo* or *in vitro* systems. Frog oocytes, insect cell lines and mammalian cell lines are for *in vitro* deorphanisation of ORs and functional characterisation of OBPs, while empty neuron systems of *Drosophila* are used for *in vivo* deorphanisation/characterisation. Each of these systems have their unique advantages and disadvantages [8]. Cell-free expression systems using *Escherichia coli* cells [144] or giant biomembrane capsules [145] have also been designed for OR synthesis.

Xenopus laevis Daudin (Anura: Pipidae) oocytes combined with voltage-clamp electrophysiology is one of the most frequently employed techniques used for ion channel receptor deorphanisation [146]. *Xenopus* oocytes have been used to study the molecular basis of chemoreception in insect species such as *D. melanogaster* [147], *Apis mellifera* Linnaeus (Hymenoptera: Apidae) [148], *Megacyllene caryae* Gahan (Coleoptera: Cerambycidae) [149], *Cimex lectularius* Linnaeus (Hemiptera: Cimicidae) [150], *A. gambiae* [151] and *Athetis lepigone* Möschler (Lepidoptera: Noctuidae) [152]. This *in vitro* system has even been employed for investigating the mechanisms by which an OR-ORCO protein complex is activated [153].

Several chemoreception proteins have successfully been deorphanised and characterised using mammalian and insect cell lines along with calcium imaging. Mammalian cell lines such as HeLa [154] and human embryonic kidney cell line 293 (HEK293) [155] and insect cell lines produced from *B. mori* cells (Bm5), *Trichoplusia ni* cells (Highfive cells) [156], ovaries of *Spodoptera frugiperda* (Sf9) [157, 158] and *D. melanogaster* Schneider 2 cells can be used to investigate ligand-protein interactions.

The *in vivo Drosophila* empty neuron system combined with single sensillum recordings (SSR) is used in the same manner as with classical chemical ecology methods [8]. However, a mutant fly for which specific receptor genes of an ORN have been removed is used to express a receptor gene of interest (of any species) in the “empty” ORN [32, 159, 160].

Computational reverse chemical ecology

Binding interactions between molecular targets (ORs and OBPs) and an odourant ligand can be analysed with virtual simulations of the ligand docking and molecular dynamics of these interactions. This is known as computational reverse chemical ecology (CRCE) [2, 79]. CRCE techniques can be employed prior to RCE and behavioural assays in order to limit the cost and time of functional assays. Including CRCE in chemoreception studies will also accelerate and focus deorphanisation attempts by identifying and using a smaller subset of potentially active odourants during the screening process [161].

Odourant ligands bind to OBPs and ORs in a ligand-binding cavity formed in the three-dimensional structure of the proteins, therefore, ligand-protein interaction simulations require the tertiary structure of the molecular targets as well as the structure of the odourant ligand. Elucidation of protein structures is mainly done through nuclear magnetic resonance spectroscopy [162], X-ray crystallography [163] and mass spectrometry [164]. These techniques are, however, expensive and crystallised proteins are not always attainable [2].

Comparative homology modelling is one way to circumvent the challenges faced during identification of protein structure and binding activity. Target protein structures can be predicted based on structures of evolutionarily similar proteins of known structure [2, 161]. Constructing a homology model requires sequence alignments, generation and refinement of the three-dimensional protein model, ligand docking and molecular dynamics simulations [165]. Once the three-dimensional structures have been modelled, docking analyses are done

(using computer programs e.g. AutoDock or Docking Server) to assess the ligands' pose in the ligand-binding site, as well as the binding affinity of the interaction [166]. Based on scoring schemes of the pose and the binding affinities, potentially active ligands are identified [79, 166].

Virtual screening studies of chemoreception proteins have now been done for a few insect species such as *Periplaneta americana* Linnaeus (Blattodea: Blattidae) [167], *Locusta migratoria* Linnaeus (Orthoptera: Acrididae) [168], *A. cerana* Fabricius (Hymenoptera: Apidae) [169], *Bactrocera dorsalis* Hendel (Diptera: Tephritidae) [79], *Hylamorpha elegans* Burmeister (Coleoptera: Scarabaeidae) [170] and *P. xylostella* [161]. Both RCE and CRCE, conducted with chemosensation proteins as targets, allow for the identification of interacting chemical ligands of these proteins and can be used to gain a better understanding of the molecular mechanisms underlying chemoreception [4, 32].

Caballero-Vidal *et al.* [171] employed machine learning along with RCE to demonstrate the potential of these emerging techniques as a rational approach to identify behaviourally active ligands that can ultimately be used for semiochemical control of insect pests. Using machine learning (with virtual ligand screening and modelling), antagonists of two *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae) olfactory receptors were identified [171]. Subsequent electrophysiological analyses using the *Drosophila* empty neuron system and behavioural assays validated the *in silico* results. This study proved that RCE holds great potential to identify active semiochemicals for agricultural and forestry insect pests [171].

1.5. The invasive woodwasp, *Sirex noctilio*

1.5.1. Life history and biology

Sirex noctilio has gained increasing attention over the years due to its destructive impact on *Pinus* plantations in the Southern Hemisphere [172]. The woodwasp is not regarded as a pest in its native ranges of Eurasia and North Africa [173]. However, accidental introductions into New Zealand [174, 175], Australia [176, 177], Uruguay, Argentina [178], Brazil [179], South Africa [180], Chile [181], the United States [182], Canada [183] and China [184] have shown that *S. noctilio* can be an important, global invasive pest of coniferous trees outside its native range (figure 1.4).

Sirex noctilio has several recorded host trees belonging to different genera namely *Abies*, *Larix*, *Araucaria*, *Picea* and *Pseudotsuga* but pine species are its preferred hosts [173, 185]. Pine trees are non-native to the Southern Hemisphere and are used as plantation species in monoculture plantations. As monoculture plantations have less genetic diversity, it is easy for a pest, such as *S. noctilio*, to establish and spread if the plantation species are susceptible.

Sirex noctilio lives a cryptic lifestyle. Female wasps oviposit eggs into host trees in which the larvae spend their life and overwinter in the wood of the tree (sometimes even up to three years) [186, 187]. Adults emerge the following summer and can live up to 12 days [186]. Like most wasps, the woodwasp has haplo-diploid sex determination where unfertilised, haploid eggs develop into males and fertilised, diploid eggs develop into females [185].

During oviposition, *S. noctilio* females not only inject eggs into the tree stem but they also transfer a phytotoxic mucus (or venom) and fungal inoculum into the tree [188, 189]. The fungus, *A. areolatum*, is a symbiotic partner of *S. noctilio* that enhances larval growth and survival within the trees by aiding in the digestion of cellulose [190–193]. *Amylostereum areolatum* is a weak white-rot pathogen that by itself has a negative impact on pine production [194]. However, it is the combination of the fungus, the woodwasp larvae and the phytotoxic wasp mucus that poses a great threat to the trees [185]. The insect-fungus complex of *S. noctilio* and *A. areolatum* has been extensively reviewed since it became an economic threat to pine plantations [190, 195].

1.5.2. Control mechanisms

Implementation of silvicultural practices can reduce damage caused by *S. noctilio*. Silvicultural practices aim to improve forest health by promoting the growth of resilient and robust trees that are less susceptible to woodwasp attack which will ultimately reduce stress in the forest stands [196]. These practices ultimately manage the population size of *S. noctilio* and hence the damage caused by this forest pest. Silvicultural practices such as removal of susceptible hosts, creation of optimal pine growth conditions and thinning are recommended to reduce damage caused by *S. noctilio* in pine plantations [196, 197].

Biological control has been a primary control strategy for *S. noctilio*. Given the serious threat posed by *S. noctilio* to pine plantations, the Australian Congress of Scientific and Industrial Research Organisation and the Commonwealth Institute of Biological Control started a

worldwide campaign during the 1960s and the 1970s to search for natural enemies of *S. noctilio* in its native ranges [177, 198]. This program identified parasitic wasps and nematode species that were used as biocontrol agents [198, 199].

The entomophagous-mycetophagous nematode, *Deladenus siricidicola* Bedding (Nematoda: Neotylenchidae), is the main biocontrol agent against *S. noctilio* [200]. *Deladenus siricidicola* is an effective control agent due to its complex bi-cyclic lifecycle with a fungus-feeding as well as a parasitic phase [201, 202]. During the fungus-feeding phase, nematodes are free-living during which they feed on *A. areolatum*, the symbiotic fungal partner of *S. noctilio* [201–204]. In the parasitic phase of *D. siricidicola*, nematodes can either infect and parasitise *S. noctilio* larvae or adult woodwasps (which cause females to become sterile) [199, 202].

Besides *D. siricidicola*, parasitic wasps are the second most important biological control agents for *S. noctilio* [199, 200]. In the past, three parasitic wasps have been identified to be effective against *S. noctilio* namely, *Rhyssa persuasoria* Linnaeus (Hymenoptera: ichneumonidae), *Megarhyssa nortoni* Cresson (Hymenoptera: Ichneumonidae) and *I. leucospoides* of which the latter is the most effective parasitic wasp for *S. noctilio* control [200]. Both *R. persuasoria* and *M. nortoni* are ectoparasitic wasps, therefore, they parasitise late instar *Sirex* larvae by laying their eggs on the surface of the larval body [200]. On the other hand, *I. leucospoides* is an endoparasitic wasp that parasitises embryos and first instar larvae by feeding on these two *Sirex* life forms as well as laying their eggs inside of the embryos and larvae [200].

Biological control agents employed against *S. noctilio* show variable degrees of efficacy, which questions the future of these control strategies. In the past, the use of *D. siricidicola* and parasitic wasps have been shown to be effective in controlling the damage caused by *S. noctilio*, however, various factors influence the efficacy of the control strategy, such as environmental conditions, rearing, handling and storage of the biological control agents, biological variations, nematode virulence, *S. noctilio* resistance and population incompatibility [172, 177, 202, 204, 205]. Due to variation in the efficacy of biological control, refinement of current control strategies and the development of new strategies are needed.

1.5.3. Chemical ecology of *Sirex noctilio*

EAG and GC-EAD techniques have been used to study the antennal response of *S. noctilio* towards host-based chemical cues. The difficulty with predicting behaviourally active host

volatiles is the fact that *S. noctilio* antennae respond to several pine volatiles, making it difficult to narrow down the chemicals of interest [206]. The long life cycle and long list of potential chemicals make identification of behaviourally active volatiles through behavioural assays expensive and time-consuming.

Despite challenges in studying the chemical ecology of *S. noctilio*, attractive host volatiles have been identified. Once a woodwasp located a potential host tree, antennae are used as chemical biosensors in a behaviour known as antennal tapping to assess the suitability of the host tree. *Sirex noctilio* is primarily attracted to monoterpene alcohols and monoterpene hydrocarbons found in pine trees [206]. Coyle *et al.* [207] conducted field studies and found that α -pinene and β -pinene can be used as an attractant lure for Siricidae. During this field trial, they also studied the attractiveness of the hosts' stress compound, ethanol, along with α -pinene and found it also acts as an effective lure [207]. A more recent study by Erbilgin *et al.* [208], confirmed that an ethanol and (-)- α -pinene blend is effective for attracting siricid woodwasps. Additionally, they also found that the monoterpene hydrocarbon, (+)-3-carene, is most attractive to woodwasps followed by (-)- β -pinene and (-)- α -pinene [208].

The symbiosis between *S. noctilio* and *A. areolatum* is also an important avenue for chemical ecology studies. Due to the significance of *A. areolatum* for the survival of *S. noctilio*, Fernández *et al.* [87] tested whether female wasps use volatiles from *A. areolatum* to locate oviposition sites on trees. Using Y-tube olfactometer behavioural assays, Fernández *et al.* [87] showed that *S. noctilio* females are indeed attracted to volatiles of their fungal symbiont (figure 1.3 – B3). This suggests that fungal volatiles are used to locate host trees that have already been infected by *S. noctilio* [87]. Similarly, studies with the *S. noctilio* parasitoid, *I. leucospoides*, have proved that this parasitoid utilises volatiles of *A. areolatum* as cues to locate hosts, assess the host quality and increase parasitoid activity [89, 90].

Studies have investigated the chemical cues involved in the mating of *S. noctilio*. Böröczky *et al.* [209] studied the chemical basis of mate recognition by males. Based on previous studies that showed cuticular lipids to be involved in mate recognition, Böröczky *et al.* [209] examined the cuticular lipid coating of both male and female *S. noctilio* wasps (figure 1.3 – A4). Through behavioural assays using females that either had the cuticular lipids present on their body or not, it was found that copulation was indeed induced by the cuticular lipid compounds [209]. It has also been proposed that decreased female attractiveness could be related to decrease

cuticular lipids concentrations of older females [210]. Following this discovery, Böröczky and colleagues analysed the cuticular extracts and identified three components of the female, short-range, contact sex-pheromone namely, (*Z*)-7-nonacosene (*Z*)-7-heptacosene, and (*Z*)-9-nonacosene [209].

The ovipositor of *S. noctilio* females have been shown to have chemosensory function which may be used to assess the suitability of a host tree prior to oviposition (figure 1.3 – A3). Followed by antennal tapping, ovipositor probing is used by *S. noctilio* wasps to assess the chemical suitability of a host. The study by Hayes *et al.* [86] showed that the ovipositor of a female woodwasp is responsive to pine host volatiles and ethanol. Ethanol is a commonly produced plant stress-compound also produced by dying trees and is a known attractant for wood-boring insects [211–213]. It has also been found that ethanol is produced by *A. areolatum* [90]. Therefore, the ability to detect ethanol in the bark or wood of a host tree via an ovipositor could allow *S. noctilio* females to assess the stress levels of the host tree as well as the presence or absence of *A. areolatum*. This will ultimately determine whether the host tree is suitable for oviposition [86]. Proteome and transcriptome analysis of *S. noctilio* [214] and *S. nitobei* [215] venom have been conducted to identify expressed proteins in this phytotoxic mucus. Among the proteins identified were CSP and OBP proteins [214, 215]. Taking into account that the venom is deposited into the host tree via the ovipositor the role of the ovipositor as a chemosensory instrument used for host tree and oviposition-site selection is further consolidated.

Very little is known about how male and female woodwasps locate one another for mating which occurs at the tree canopy. Following emergence, male wasps move up to the tree canopy where male aggregations form (figure 1.3 – A2) [209, 216]. Females emerge a few days later, disperse and eventually locate a mate [209]. It is hypothesised that the aggregation/swarming behaviour of male woodwasps is regulated by a male-produced aggregation pheromone. Behavioural bioassays revealed that males exposed to two to five day-old males displayed excitatory behaviours compared to males exposed to one day-old males [216]. Investigation of male headspace odours identified the male-produced pheromone, (*Z*)-3-decen-1-ol, which attracts males. A blend of (*Z*)-3-decen-1-ol which with two minor components, (*Z*)-4-decenol and (*E,E*)-2,4-decadienal was also shown to be attractive to both males and females in lab bioassays [216]. Field assays investigated whether this male-produced pheromone can act as a

long-range sex pheromone for *S. noctilio*. Hurley *et al.* [217] evaluated the efficacy of the putative pheromone in baited traps during field trials in South African pine plantations and concluded that it is an ineffective attractant for male and female woodwasps. These mixed results may be affected by low population densities, presence of host volatiles in the field or novel chemicals not detected [208] by Cooperband *et al.* [216]. Regardless, the search for a long-range sex pheromone of *S. noctilio* is still underway and a recent study investigated the biology of a male-produced, putative aggregation/sex pheromone [218]. From this study the presence of (Z)-3-decen-1-ol and (Z)-4-decenol in male headspace was confirmed and additionally (Z)-3-octenol and (Z)-3-dodecenol were identified. Dose-response experiments revealed that although both males and females respond to all four compounds the strength of the response varied between doses, compounds and sexes. Guignard *et al.* [218] also identified the male hind-legs as the site of storage and/or synthesis and also showed that the release rate of the pheromone by males is 15 times higher what is usually release by lures. Therefore, results from Cooperband *et al.* [216] and Guignard *et al.* [218] support the theory that these compounds mediate aggregation of males and lek location by females.

A recent study by Guo *et al.* [219] investigated the olfactory gene repertoire for *S. noctilio* and *S. nitobei* through antennal transcriptome analysis. In this study, the researchers also investigated the expression profile of *Sirex* OBPs in antennae, legs, genitals and heads through RT-qPCR analysis in order to identify genes that exhibit sex- or species-specific expression [219]. Results from this study revealed expression of species-specific olfactory genes suggesting that *S. noctilio* and *S. nitobei* may have different olfactory discrimination capabilities. OBPs exhibiting tissue- and sex-biased expression were also identified. This study is the start of understanding *Sirex* chemosensation. However, broader investigation of chemosensation gene expression as well as protein expression and binding assays are still required to elucidate the molecular processes involved in *S. noctilio*.

Knowledge of the type of chemical cues used by *S. noctilio* can help develop better pest management strategies as well as monitoring systems by using more effective chemical lures. Genomic and transcriptomic analyses of *S. noctilio* will lay a foundation for future RCE and deorphanisation studies. By knowing which genes are involved in chemosensation of this woodwasp, one can investigate from the gene level up how known and novel semiochemicals influence molecular and protein interactions. This will in turn illuminate how certain

semiochemicals influence the behaviour of this important forest pest. Once the chemosensory genes have been identified through transcriptomic analyses, interesting gene targets can be used in expression systems to identify ligands that bind or activate the expressed protein product. This can help identify ligands that have the potential for being used in pine plantations as part of chemical control strategies.

1.6. Conclusion

Chemoreception is an indispensable system for all animals, therefore, it is important to have an understanding of genetic and physiological processes involved in this system. Studies investigating the genetic basis of insect chemoreception can determine whether ecological and physiological adaptations of an insect is echoed throughout the chemoreception system. If a genetic cause can be determined for a specialised behaviour it creates a new avenue to manipulate an insect's life situation especially if a control strategy is sought after for pest insects. The chemical cues and signals that insects respond to have exceptional potential for integrated pest management, which should be exploited in future research. Targeting the chemoreception of insect pests for novel control strategies can be engineered to target specific species without affecting beneficial organisms. *Sirex noctilio* is an important target and example in this regard, given its importance as a pest, wide distribution and the broad base of basic knowledge accumulated over the years. Investigating the transcriptome of different developmental stages and sexes of *S. noctilio* will aid in the development of potential novel control methods for this important insect pest. In order to use reverse chemical ecology to understand the how, when, and why of *S. noctilio* chemosensation (more specifically olfaction), we require information about the genes underlying this process. Therefore, identification, characterisation and deorphanisation of the chemoreception genes and proteins of *S. noctilio* is a potentially valuable target for future studies.

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1.8. List of figures

Figure1.1. Simplified view of olfactory (top left) and gustatory (top right) sensilla. Olfactory sensilla have multiple pores whereas gustatory sensilla have only one single pore at the top of the cuticular protrusion. 1A-1D indicate the four major categories of olfactory sensilla. Adapted from Shields and Hildebrand (2001) and Gullan and Cranston (2010). 53

Figure1. 2. Molecular pathway involved with odorant reception. Chemosensation comprises of two phases namely reception and neurological processing. Reception is the perireceptive events involved in the uptake, binding, transport, inactivation and degradation of odour molecules. Neurological processing is the neurological events involved in odour recognition and alteration of behaviours. Adapted from Masiga *et al.* [41]. 54

Figure1.3. Potential ways in which semiochemicals may play a role in *S. noctilio* chemosensation. This figure represents scenarios in *S. noctilio* life where semiochemicals determine the insect's behavioural response. Behaviours illustrated in A1, A2 and B2 are hypothetical as no semiochemical has been linked to these behavioural responses, yet. Behaviours illustrated in A3 (Hayes *et al.* [86]), A4 (Böröczky *et al.* [209]), B1 (Martínez *et al.* [89]; Jofré *et al.* [90]) and B3 (Fernández Ajó *et al.* [87]) have been showed to be influenced by semiochemicals. Pheromones facilitate intraspecific communication and mediate essential behaviours of *S. noctilio* (left-hand side – A). Interspecific communication and interaction with the environment are mediated by allelochemicals (right-hand side – B). Different developmental stages of an insect (top left corner – Adult, pupa and larva) may react differently to semiochemicals or rely on a specific semiochemical to initiate a specific behavioural response for example mating or oviposition. The environment of an insect (top right corner) includes everything from predators to parasitoids, and interactions with this environment depend to a large extent on semiochemicals but is also influenced by tactile and visual cues. The (+) indicates whether the sender or the receiver benefits from the allelochemical cue. 55

Figure1.4. Global distribution of *S. noctilio*. The oval indicates the native range of *S. noctilio* where it is not regarded as a serious forest insect pest. Invaded range of *S. noctilio* is indicated by the wasps, along with the date at which the wasp was discovered in that

region. The first discovery of *S. noctilio* outside of its native range was in New Zealand in the early 1900. Following the identification of *S. noctilio* in New Zealand, it has subsequently spread across the Southern Hemisphere as it was discovered in Tasmania (1952) mainland Australia (1961), Uruguay (1980), Argentina (1985), Brazil (1988), South Africa (1994) and Chile (2001). Until the early 2000's *S. noctilio* was not found in the Northern Hemisphere except for its native range (black oval), however, in 2004 the woodwasp was discovered in the United States of America shortly before its discovery in Canada (2005). More recently *S. noctilio* has also been discovered in China (2013) where it is regarded as an invasive insect..... 56

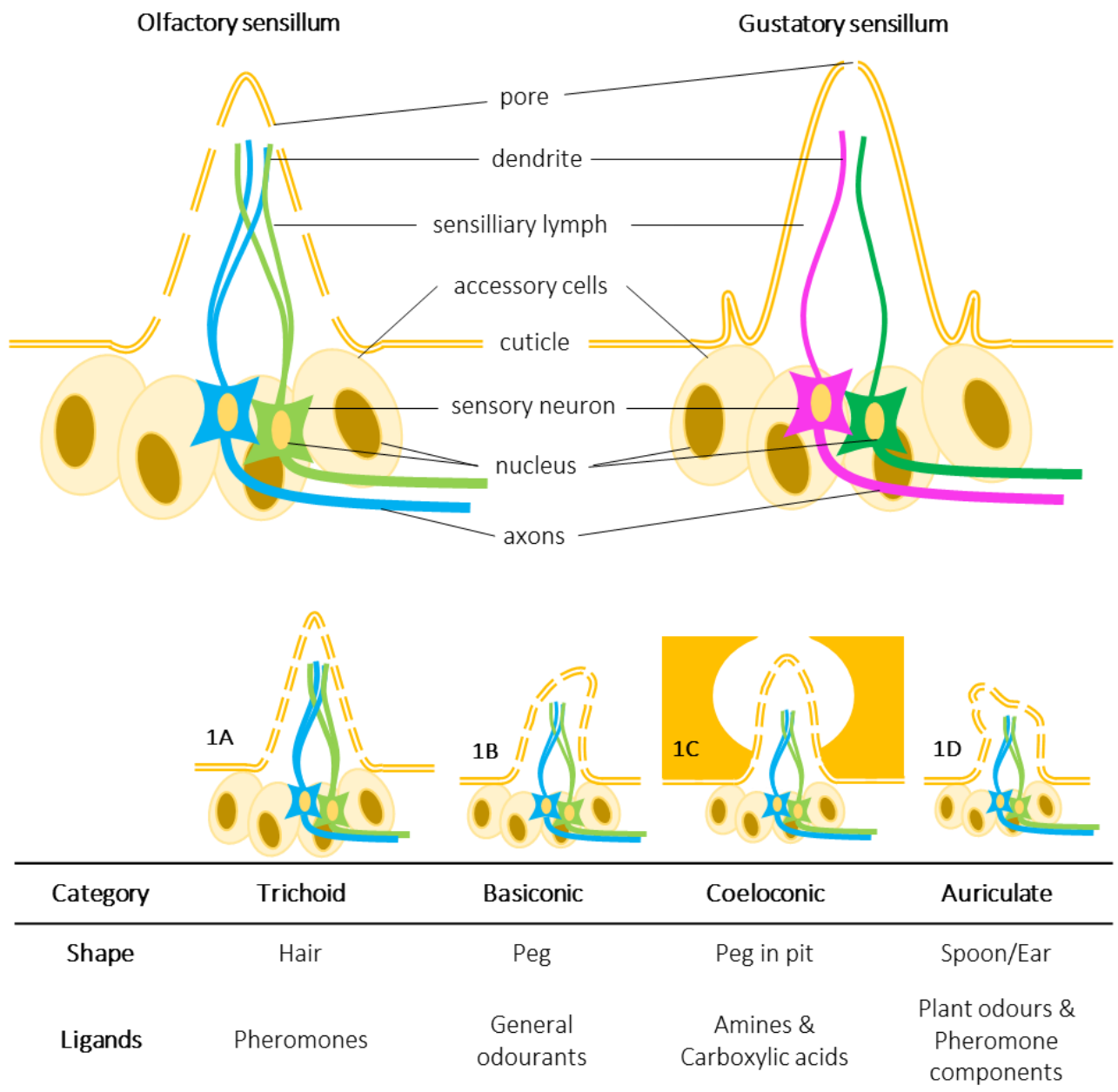


Figure1.1. Simplified view of olfactory (top left) and gustatory (top right) sensilla.

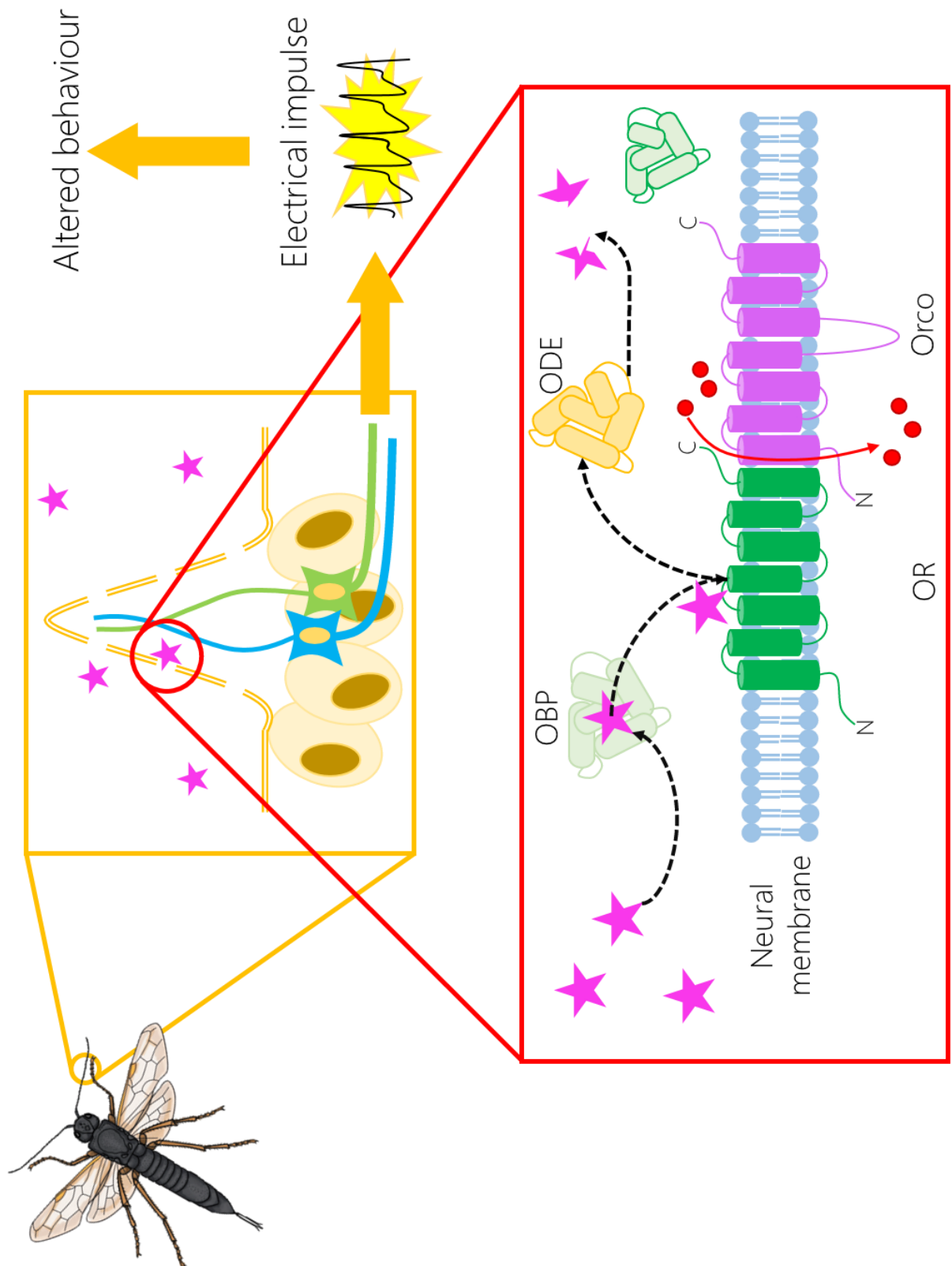


Figure1. 2. Molecular pathway involved with odorant reception.

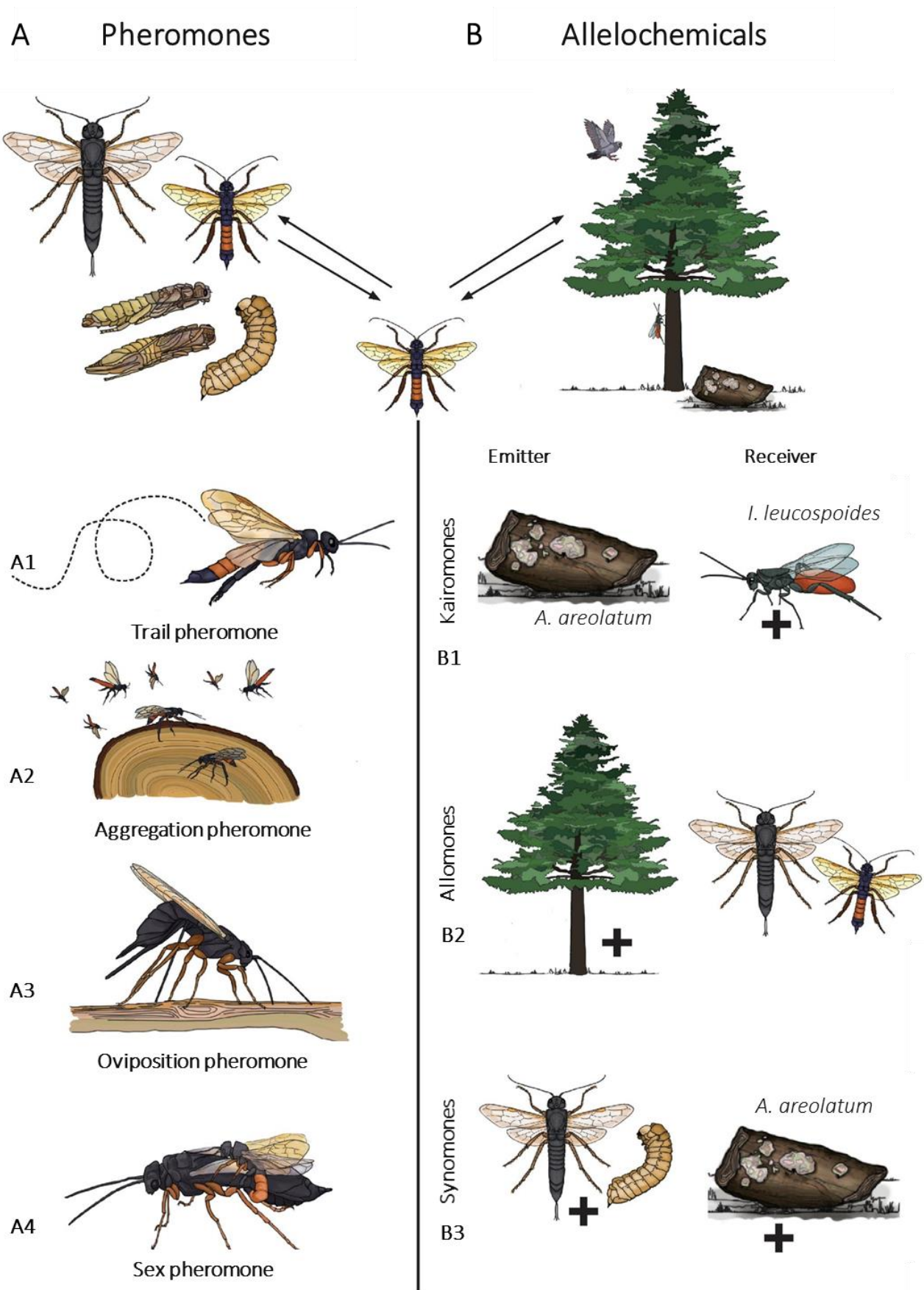


Figure1.3. Potential ways in which semiochemicals may play a role in *S. noctilio* chemosensation.

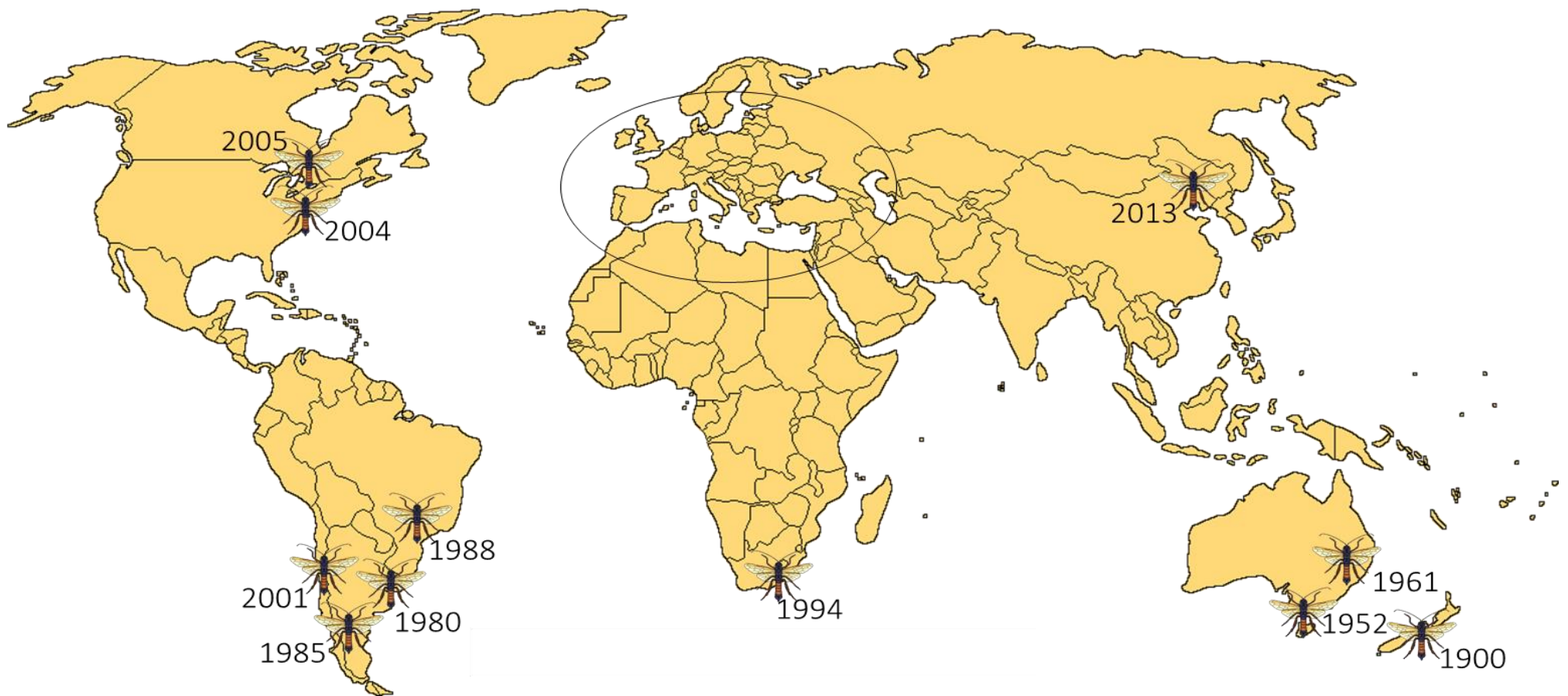


Figure1.4. Global distribution of *S. noctilio*

Chapter II: Research chapter

Transcriptome profiling of olfactory and non-olfactory appendages in *Sirex noctilio* (Hymenoptera: Siricidae) reveals sex- and tissue-specific chemosensory genes

Abstract

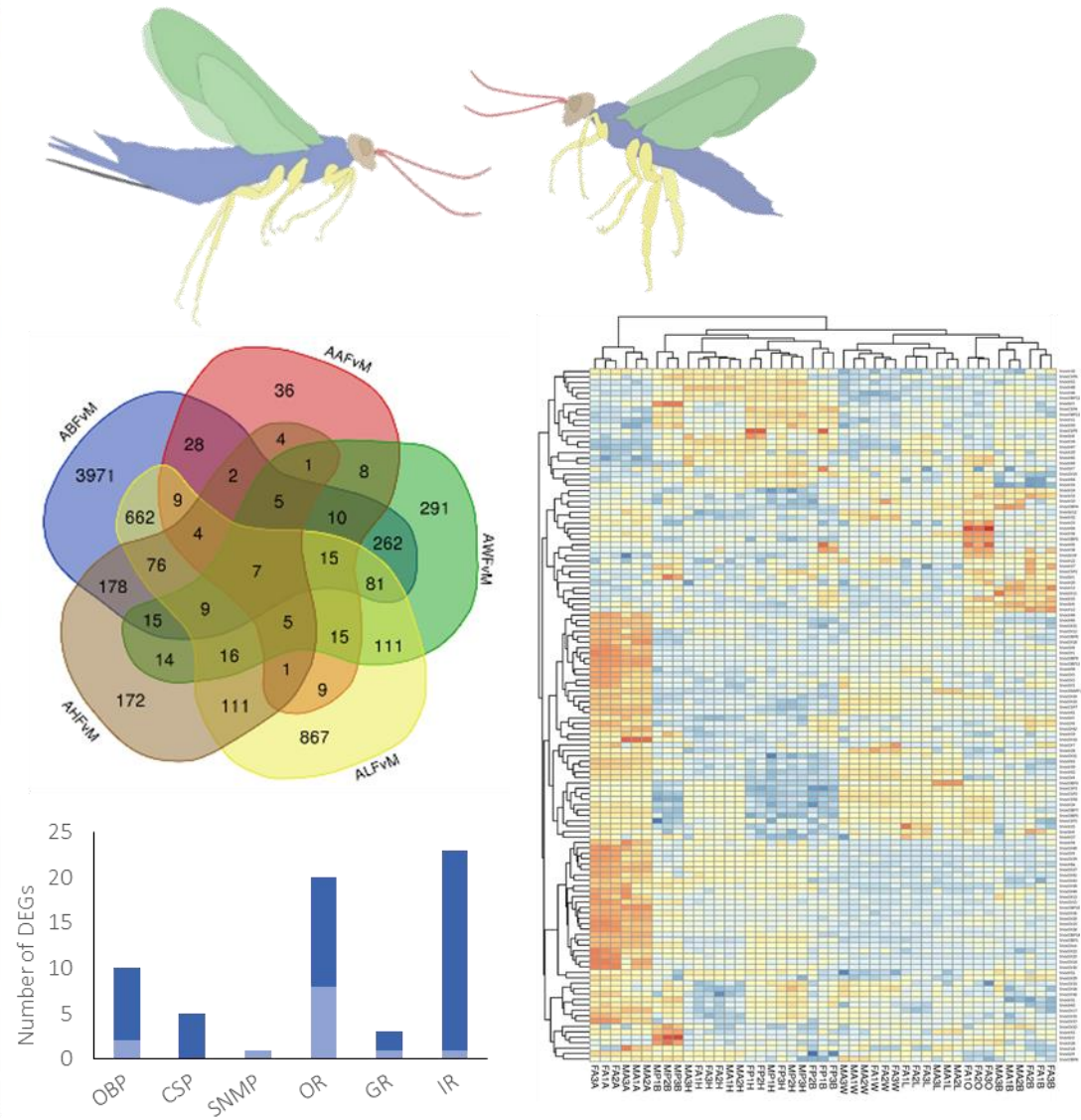
Background: Insects rely on olfaction and gustation to interact with their surrounding environment. The highly sophisticated and complex chemosensory system behind smell and taste has received considerable attention due to its potential to contribute to the development of pest control strategies. This is because elucidating the molecular basis of chemosensation can be exploited in the design of behaviour-modifying chemical molecules. To gain a better understanding of the molecular basis of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) chemosensation we used RNA sequencing to create the most comprehensive comparison to date of chemosensation gene expression between olfactory and non-olfactory appendages of this representative of an ancient hymenopteran group.

Results: We compared gene expression between 15 transcriptome datasets to identify sex-, tissue-, and developmental stage-specific chemosensation genes. *Sirex noctilio* has 129 candidate chemosensation genes consisting of 45 olfactory receptors (OR), 12 gustatory receptors (GR), 48 ionotropic receptors (IR), 14 odourant binding proteins (OBP), 9 chemosensory proteins (CSP), and one sensory neuron membrane protein (SNMP). ORs and OBPs were enriched in olfactory appendages whereas GRs, IRs, CSPs, and the SNMP exhibited variable expression profiles across tissues. Developmental stage and tissue type, and to a lesser extent sex, influenced the expression of chemosensory genes. Several differentially expressed genes were identified. The antennae-, ovipositor- and leg-biased chemosensation genes identified are of particular interest due to the olfactory function, oviposition site-selection function and sexual dimorphism of these tissues, respectively.

Conclusions: Based on expressed OR transcripts the chemoreceptive spectrum is largely similar between males and females. However, if relative expression levels of ORs correlate with sensitivity then females could have enhanced odour sensitivity. Sex- and tissue-specific genes are promising targets for future deorphanisation studies which could aid the identification of novel attractants or repellents for biorational pest management.

Key words: Chemoreceptors, chemosensory carrier proteins, expression profiling, invasive insect, olfaction, *Sirex noctilio*, transcriptomics

Chemosensation in *Sirex noctilio*



2.1. Introduction

The primary sensory modality through which insects perceive their biotic environment is chemosensation. As a result, chemosensation is vital to their survival, making it an attractive target for novel pest control strategies. Detection of chemical cues and signals enable insects to identify food sources and hosts, avoid predators, select oviposition sites and mediate social interactions [1, 2]. To detect semiochemicals most insects have highly sophisticated chemosensory systems involving olfaction (detection of volatile chemicals) and gustation (detection of aqueous chemicals) [3–5].

Until recently, the most prominent method used to investigate insect chemosensation was through classical chemical ecology methods such as EAG, GC-EAD, GC-MS, and HPLC coupled with behavioural assays [6]. In large part, the discipline of chemical ecology aims to identify, characterise, synthesise and determine the biological significance of semiochemicals and the phenomena they mediate [7]. Classical chemical ecology methods, however, only reveal which chemicals are biologically active, leaving knowledge gaps in the genetic and molecular mechanisms involved in insect chemosensation. *In silico* molecular docking analysis, expression systems, and next-generation sequencing technologies have created a new way to deorphanise receptor-ligand partners and identify genetic targets of chemosensation [8].

A diverse array of chemosensory genes is used to ensure precise recognition and high sensitivity of the chemosensory system. First, two amphipathic proteins, odourant binding proteins (OBPs) and chemosensory proteins (CSPs), ferry the chemical molecules through the hemolymph of a sensillum where they activate chemoreceptors [9, 10]. Chemoreceptors are seven trans-membrane proteins located on the dendrites of receptor neurons. Three classes of chemoreceptors are known, olfactory receptors (ORs), ionotropic receptors (IRs), and gustatory receptors (GRs) [4, 11, 12]. These chemoreceptors convert the chemical signal into an electrical impulse that stimulates the perceiving insect to elicit a corresponding behaviour. In addition to these proteins, the odourant receptor co-receptor (ORCO), sensory neuron membrane proteins (SNMPs), and odourant degrading enzymes (ODEs) are also essential to insect chemosensation. ORs function as heteromeric complexes with ORCO [13, 14], SNMPs are required along with ORs for pheromone detection [15] and ODEs are crucial to the inactivation of odour molecules to ensure that the chemical signal is deactivated to ensure high sensitivity and continuous detection of chemical messages [16].

The woodwasp, *Sirex noctilio*, from the Symphyta suborder, is native to Eurasia and northern Africa where it preferentially attacks stressed or dying trees and is not considered as a forest pest [17, 18]. The intricate, mutualistic association between *S. noctilio* and *Amylostereum areolatum* Boidin (Russulales: Amylostereaceae) has, however, become a global forest pest as a result of its anthropogenically driven range expansion. During oviposition, a phytotoxic mucus (aids development of the fungal symbiont) [19] and *A. areolatum* inoculum (essential for larval development as the larvae feed on the fungus whilst tunnelling through the wood) [20, 21] are introduced into pine trees [22]. The combined action of the mucus and fungus weakens host tree defences, increasing vulnerability to larval feeding and can lead to tree mortality. The threat posed by the *Sirex* – *Amylostereum* complex is combatted primarily through biocontrol with *Deladeunus siricidicola* Bedding (Nematoda: Neotylenchidae) and silvicultural practices [23]. However, the efficacy of these strategies is variable [24, 25]. Semiochemicals that mediate host and mate location have immense potential to provide new biorational tactics and facilitate more efficacious timing of existing management tactics.

Classical chemical ecology techniques have been used to explore host and mate location in *S. noctilio* and resulted in the development of a host kairomone lure used to monitor populations [26]. Studies have found that *S. noctilio* is attracted to a blend of volatiles emitted from stressed or dying pine trees that include monoterpene alcohols and hydrocarbons [27–29]. Semiochemical baited traps are used to assess the distribution of the woodwasp and the efficacy of current control strategies [30, 31]. Olfactometer bioassays have demonstrated the attraction of *S. noctilio* females to volatiles from the fungal symbiont, *A. areolaum*, but the chemical compounds involved remain unknown [32]. Cuticular lipids behaving as short-range contact sex-pheromones to induce copulation have been identified [33], but uncertainty exists regarding the presence of long-range sex and aggregation pheromones. Potential male-produced pheromones have been identified and may mediate the aggregation of male woodwasps and assist the location of these male leks by female wasps [34, 35]. While this putative pheromone was active in laboratory bioassays, field trials have been unable to demonstrate activity [28]. Hayes *et al.* [36] demonstrated with electrophysiological analyses, that the ovipositor of *S. noctilio* has chemosensory capabilities, most likely used during oviposition. Proteome analyses identified OBPs and CSPs in the venom and venom sac of *S. noctilio*, which could be essential during oviposition [37, 38].

There is limited information on the molecular mechanisms involved in *S. noctilio* chemosensation. This can be partly attributed to the lack of quality transcriptomes. A recent study investigated the gene repertoire of *S. noctilio* and *S. nitobei* Matsumura (Hymenoptera: Siricidae) through antennal transcriptome analysis and RT-qPCR analysis of OBPs [39]. Antennal transcriptome analysis is a common approach for insect chemosensation research, however, chemosensory genes are differentially expressed in an array of tissues which can influence gene identification and bias results. To investigate the diversification of chemosensation gene families, as well as to functionally characterise these genes, both genome and transcriptome data should be included in the identification of chemosensation genes. Investigating the molecular basis of *S. noctilio* chemosensation through the identification of chemosensory genes, phylogenetic analyses, and expression profiling are essential first steps required to perform targeted gene function analyses through techniques such as reverse chemical ecology [40]. Expression profiling of chemosensation genes in different developmental stages, tissues and sexes holds valuable information about the potential functions of these genes [41–47].

Wasps from the Symphyta suborder have divergent lifestyles and niches ranging from ectophytophagy (*Athalia rosae* Linnaeus (Hymenoptera: Tenthredinidae)) to parasitism (*Orussus abietinus* Newman (Hymenoptera: Orussidae)) to endophytophagy (*Cephus cinctus* Norton (Hymenoptera: Cephidae) and *S. noctilio*). How life-history traits relate to chemosensory gene repertoire remains elusive, largely due to the lack of knowledge surrounding the molecular mechanisms underlying chemosensation.

Sirex noctilio is sexually dimorphic and it is not known if this variation extends to expression patterns of chemosensation genes. Adult wasps are short-lived and therefore, require an efficient chemosensory system to find mates and hosts. Pupae live a cryptic life within the wood and are expected to differ in their chemosensory requirements from other developmental stages. Woodwasp mating is influenced by several sensory modalities, but the role of chemosensation during this process is unclear. Therefore, in this study, we performed transcriptome profiling of six major chemosensation gene families identified from the *S. noctilio* genome. Transcriptome profiling can elucidate how life history and behaviour may relate to chemosensation gene expression. Gene expression was profiled to identify biased expression of chemosensation genes in (a) olfactory and non-olfactory tissues for (b) male and female *S. noctilio* wasps of (c) different developmental stages.

2.2. Methods

An overview of study protocol is shown in figure 2.1.

Insect collection and storage

Pine logs infested with *S. noctilio* were collected from KwaZulu-Natal (April 2018), Western-Cape (June 2018), and Eastern-Cape (January 2019) provinces of South Africa (figure 2.2). Logs were stored in outdoor netted cages for pupal collections and in indoor netted cages maintained at $23\text{ }^{\circ}\text{C} \pm 1\text{ }^{\circ}\text{C}$ for adult wasp collections (Forestry and Agricultural Biotechnology Institute biocontrol farm, University of Pretoria, South Africa). Pupal samples were extracted between May 2018 and November 2018 and this was done using a manual hydraulic log splitter. Emerged adult wasps were collected daily from netted cages between August 2018 and January 2019.

For transcriptome sequencing, tissues from different developmental stages (Adults: abdomens-thoraces (hereafter referred to as body), antennae, head without antennae, wings, legs and ovipositors; Pupae: Head with antennae and body with appendages), and sexes (adult male and female wasps, male and female pupae) (figure 2.1) were excised upon collection and immediately flash-frozen in liquid nitrogen and stored at $-80\text{ }^{\circ}\text{C}$ until further processing. A total of 45 samples across 15 different tissues (three biological replicates per tissue) were used for transcriptome sequencing. For adult wasps, 25 individuals were pooled into one sample per biological replicate per tissue, whereas four individuals were pooled for each pupal sample.

RNA isolation

Samples were freeze-dried prior to grinding to facilitate the breakdown of the tissues and thereby increase recovery of the RNA. To account for weight loss in samples due to freeze-drying, samples were weighed before and after freeze-drying to adjust the amount of starting material used for RNA extractions. Small tissue samples (antennae, heads, wings, legs and ovipositors) were ground into a fine powder with the mixer mill MM301 (Retsch®) (1 min at maximum frequency) whereas large tissue samples (pupa bodies and adult thoraces and abdomens) were ground into a fine powder in liquid nitrogen using a mortar and pestle.

Total RNA was extracted from the ground samples using the TriZol® reagent (Ambion, Life Technologies) according to the manufacturer's instructions (figure 2.3). All recommended steps

were included during the extraction protocol. Isolated RNA was re-suspended in RNA storage solution (1 mM Sodium Citrate pH 6.4, Ambion) and kept at -80 °C until used. RNA quality was assessed using 1% agarose gel electrophoresis (110V, 20 min), stained with GelRed (Biotium) and visualised using a Gel Doc™ Ez Imager (BioRad) and the Image Lab 4.0 software. RNA quantity was quantified with the Qubit® 2.0 Fluorometer (Invitrogen, Life Technologies) using the Qubit® RNA BR Assay Kit (Invitrogen) according to the manufacturer's instructions.

RNA samples obtained from TriZol extractions were subjected to DNase I (RNase-free, 1 U/μL Thermo Scientific™) treatment (figure 2.4). DNase treatment reactions, in which 7ug RNA was used per treatment, were carried out according to the manufacturers' instructions. RiboLock RNase Inhibitor (Thermo Scientific) was included at a concentration of 1 U/μl to prevent RNA degradation during DNase treatment. DNase treated RNA samples were subsequently cleaned up using the RNeasy Mini kit (Qiagen) according to the manufacturer's instructions. All optional steps were included during the purification protocol and a second elution was performed to increase the yield of eluted RNA. Quality and quantity of purified RNA were assessed using agarose gel electrophoresis and Qubit assay as mentioned above.

Following DNase treatment and clean-up, polymerase chain reaction (PCR) analyses were used to assess if there is still genomic DNA contamination. PCR reactions were set up using both purified RNA samples as well as RNA samples that had not undergone DNase treatment and column purification in order to compare amplification profiles. Both *Actin* (Makua *et al.* unpublished) (Forward primer: 5'-CGGCATTCACGAGACTAC-3', T_m = 52.9; Reverse primer: 5'-ACGGTGTGTCATAAAGG-3', T_m = 52.9) and *Cytochrome oxidase I* [48] (HCO2198: 5'-TAAACTTCAGGGTGACCAAAAAATCA-3'; LCO1490: 5'-GGTCAAC AAATCATAAAGATATTGG-3') gene primers were used for PCR amplification. PCR reactions were carried out in a final volume of 25 μl containing 0.4 μM forward and reverse primer respectively, 1 U FastStart Taq DNA Polymerase, 1x PCR buffer without MgCl₂, 200 μM of each dNTP, 3 mM MgCl₂ and 1 μl RNA. The final reaction volume was made up with DEPC-treated dH₂O. PCR cycling conditions were one cycle at 95 °C for 5 min followed by 40 cycles of 30 sec at 94 °C, 30 sec at 52 °C for primer annealing, 1 minute at 72 °C for elongation, and a final elongation step at 72 °C for 7 min and finally, the samples were maintained at 4 °C. PCR products were analysed using 1% agarose gel electrophoresis (110V, 30 min) along with 6x loading dye (ThermoFisher Scientific) stained with GelRed and visualised using a BioRad Gel Doc™ Ez Imager.

Illumina sequencing

To study the expression profile of chemosensory genes within olfactory and non-olfactory appendages, cDNA library construction and Illumina sequencing of the 45 RNA samples were carried out by Macrogen HQ, Seoul, Republic of Korea (table S2.1). Following quality control, RNA samples were subjected to library construction using the TruSeq Stranded mRNA LT Sample Prep Kit for Illumina. Library quality was assessed with the Agilent Technologies 2100 Bioanalyzer using a DNA 1000 chip. Finally, the RNA libraries were subjected to the Illumina NovaSeq 6000 platform for generation of pair-end 101 bp stranded, mRNA reads.

Identification of chemosensation genes

Chemosensation multi-gene families (9 OBPs, 10 CSPs, 56 ORs, 12 GRs, 54 IRs, and 8 SNMPs) were identified through BLAST [49], InterProScan [50], TMHMM [51], and SignalP [52] analyses by Postma *et al.* (in preparation) (figure S2.1). Candidate chemosensation genes were analysed through phylogenetic analysis to identify sub-families and *Sirex*-specific gene expansions or contractions (Postma *et al.* in preparation). Candidate chemosensation genes were manually curated as part of this study using a web-based genomic annotation editing platform, Apollo (version 2.0.6) [53] with RNA-sequence data mapped to the assembly as supporting evidence for gene structure.

Quality control, read mapping and read counting

FastQC v0.11.7 (<https://www.bioinformatics.babraham.ac.uk/projects/fastqc/>) and MultiQC version 1.6 [54] were used to assess the quality of raw reads. RNA-sequenced reads were mapped to an in-house reference genome assembly of *S. noctilio* using HISAT v2.1.0 [55] (detail parameters are provided in supplementary material). The program, featureCounts (R version, 3.6.0 Subread version 1.5.2, <http://subread.sourceforge.net>) was used to count reads that mapped to genomic features (detail parameters are provided in supplementary material). To assess the quality and characteristics of the RNA sequence data principal component analyses (PCA) were performed.

Expression quantification and differential expression analysis

Read counts obtained from featureCounts were used to perform differential expression analysis using DESeq2 version 1.24.0 [56] in Rstudio. Count data was transformed through variance stabilizing transformation in the DESeq2 package of R. Genes with an adjusted p-value < 0.05 (padj-value > 0.05) and a $|\log_2\text{FoldChange}| > 1$ ($|\text{LFC}| > 1$) were classified as significantly

differentially expressed genes (DEGs) [57–59]. Antenna tissue was used as control condition for DESeq2 analyses since it is the main olfactory tissue of insects. To qualitatively investigate the expression profiles of chemosensation genes across different tissue, the TPM (transcripts per kilobase per million reads) values were used [60]. TPM values were calculated using StringTie v1.3.4 [61].

2.3. Results

Overview of olfactory and non-olfactory transcriptomes of *Sirex noctilio*

A total of 45 cDNA libraries constructed from various *S. noctilio* tissue samples (three biological replicates per tissue sample) were successfully sequenced with the Illumina NovaSeq 6000 platform. Transcriptome sequencing produced more than 51 million paired-end reads (51,364,080 to 89,413,056 million reads) for each sequenced library (table S2.1). The GC content and Q20 percentage of RNA sequenced data ranged from 97.03% to 98.51% and from 32.79% to 43.55%, respectively. An average alignment rate of 91.7% was obtained across all libraries.

Genes exhibit similar expression profiles primarily influenced by tissue type and developmental stage (figure 2.5). Compared to tissue type, sex had a minor influence on the overall gene expression profiles. Separation between pupal and adult wasp gene expression was observed in PCA (figure 2.5). PCA displayed different separation patterns for developmental stages around the principal component axes when comparing global gene expression (separated around PC1) versus only chemosensation genes (separated around PC2). For global gene expression of adult wasps, body tissues can be clearly distinguished from all other tissues. Antenna, wing, and head tissues also formed distinct clusters in PCA of global gene expression. The separation between leg and ovipositor tissues, however, was not clearly distinct and female leg and ovipositor tissues cluster closely together (figure 2.5). Global gene expression of pupal tissues showed distinct clustering for pupal head and body tissues which are in contrast to the combined clustering of these tissues in the PCA of expressed chemosensation genes (figure 2.5). Clustering in the PCA of chemosensation genes (figure 2.5) revealed a different clustering pattern compared to global gene expression. PCA of chemosensation gene PCA revealed that adult wings clustered along with legs and ovipositor tissues. Adult body and head tissue formed a cluster for the chemosensation gene PCA compared to the distinct clustering observed in the

PCA of all genes. Adult antennae formed a distinct cluster (well separated from all other tissues) and male and female antennae form distinct clusters, unlike in the PCA of all genes (figure 2.5).

Chemosensation gene identification, characterisation and curation

A total of 129 candidate chemosensation genes were investigated through transcriptome profiling (figure S2.9). Genes of the chemosensory multi-gene families previously identified by Postma *et al.* (in preparation) (figure S2.1-figure S2.4), were manually curated to avoid fusion of transcripts due to adjacent gene models. This is not uncommon since several chemosensory genes are located as gene clusters in insect genomes as a result of tandem duplications [62, 63].

Identification of differentially expressed genes

DESeq2 analysis

To explore gene expression dynamics, tissues were compared in a pair-wise manner between and within each sex (using antennae and body tissues as control tissues) for all expressed genes (figure 2.6). Differential expression analysis between olfactory and gustatory tissues, provide important genetic information that can shed light on the processes of olfaction and gustation. The highest number of DEGs were observed for female wings vs. female body followed by ovipositors vs. female body and female antennae vs. female body whereas the lowest number of DEGs were observed for female antennae vs. male antennae followed by female head vs. male head, and female pupa head vs. male pupa head (figure 2.6, A). The clustering observed in the PCA (figure 2.5) is in accordance with the expression profiles produced from DESeq2 analyses.

There were more differentially expressed chemosensation genes between pairwise comparisons of antennae with other tissues (head, legs, wings, ovipositors, and body) (figure 2.6, B). Considering global gene expression, there were more DEGs in pairwise comparisons between body tissues versus other tissues (antennae, head, legs, wings, and ovipositors). For adult female versus male pairwise comparisons, a positive LFC value meant that the gene had higher expression in females, whereas a negative LFC value meant the gene had higher expression in males (table S2.2). Similarly, for comparisons with antennae as control, a positive LFC meant higher expression in the compared tissue and a negative LFC value meant higher expression in antennal tissues. Several chemosensation genes were identified as either up- or down-regulated in specific tissues. Chemosensation genes that were found to be exclusively

differentially expressed between specific DESeq2 datasets, were identified using Venn diagrams (figure 2.7, figure 2.8, and figure S2.5-S2.8).

Expression profiling identified tissue-, sex- and developmental stage-specific chemosensation genes

Odourant binding protein (OBPs)

The expression profiles of 14 predicted OBPs were investigated for *S. noctilio* (figure 2.9). Three main clusters were identified from the hierarchically clustered heatmap: Cluster A (pink block) representing genes with higher expression in pupal tissues, cluster B (green block) representing genes with higher expression in adult tissues and cluster C (blue block) which are genes with higher expression in antennae. Six SnocOBPs displayed antennae-biased expression; SnocOBP1, SnocOBP8, SnocOBP11 and SnocOBP14 were enriched in both female and male antennae (figure 2.10), whereas SnocOBP7 and SnocOBP10 were expressed significantly higher in female and male antennae, respectively (figure 2.7, table S2.2). Within male tissue comparisons, SnocOBP5 and SnocOBP9 also showed antennal bias, however, not for female antennae because these genes had no significant differential expression between antennae, ovipositor, and legs of female wasps (figure 2.8). Three genes displayed tissue bias in non-olfactory chemosensory tissues (figure 2.8, figure 2.10); SnocOBP2 (ovipositor biased, 1508.23 TPM), SnocOBP3 (leg biased, also significantly higher expression in male legs (193629.75 TPM) compared to females (547.94 TPM)) and SnocOBP4 (male body biased, 558.91 TPM). Two genes, SnocOBP12 and SnocOBP13, showed developmental stage-biased expression with significantly higher expression in pupal tissues (table S2.2) and SnocOBP12 also displayed biased expression in head tissues (figure 2.9, figure 2.10).

Chemosensory binding proteins (CSPs)

A total of 9 CSPs were identified and characterised (figure 2.11). Genes encoding CSPs displayed variable expression across the investigated tissues with no prominent enrichment in a single sensory tissue. Four clusters were identified from the hierarchical clustering analysis: Cluster A showed lower expression in pupal and adult body tissues and higher expression in body appendages. Cluster B were genes with higher expression in adult tissues whereas cluster D represents genes with higher expression in pupal tissues. Cluster C represents genes that had higher expression in body and head tissues. SnocCSP7 displayed antennae-biased expression

(figure 2.8, figure 2.11, and figure 2.12). SnocCSP5 and SnocCSP8 were highly expressed across all tissues but SnocCSP5 had significantly higher expression in adult wings and SnocCSP8 had significantly higher expression in wing and female ovipositor tissues (table S2.2). SnocCSP3 displayed male-biased leg expression (27170.82 TPM) (figure 2.7, figure 2.12, table S2.2). SnocCSP4 and SnocCSP9 displayed developmental stage-biased expression in all pupal tissues and female pupal tissues, respectively (figure 2.11, cluster D). SnocCSP2 displayed ovipositor enhanced expression and SnocCSP6 enhanced expression in head tissues, however, both genes had low transcript abundances for CSP genes (figure 2.12 and table S2.3).

Sensory neuron membrane protein (SNMP)

Only one gene was identified as a putative SNMP in *S. noctilio*. Several tissues of both adult and pupal wasps had expression of SnocSNMP1, however, the highest transcript abundance was in male legs followed by male antennae and female antennae (figure 2.13). This gene (SnocSNMP1) displayed sex-biased expression with significantly higher expression in female body and wing tissues whereas displaying significantly higher expression in male leg tissues (figure 2.7, table S2.2).

Olfactory proteins (ORs)

Hitherto, the OR gene repertoire of *S. noctilio* consists of 45 ORs including the highly conserved co-receptor, ORCO. Overall, *S. noctilio* ORs revealed an antennae-biased pattern of expression for almost all ORs (figure 2.14, cluster A). For adult male wasps, 28 out of 45 ORs (SnocOR1, SnocOR5-6, SnocOR8-9, SnocOR14-18, SnocOR20-23, SnocOR25-28, SnocOR30, SnocOR37-44 and SnocORCO) were up-regulated in antennae whereas for female adult wasps, 32 ORs (SnocOR1-3, SnocOR5-6, SnocOR8-9, SnocOR13-15, SnocOR17-18, SnocOR20-28, SnocOR30, SnocOR35-SnocOR41, SnocOR43-44, and SnocORCO) were up-regulated in antennae ($|\text{LFC}| > 1$) (figure 2.8). It is also noted that many of the *S. noctilio* OR transcript abundances (TPM values) were higher in female antennae compared to male antennae (figure 2.15 and table S2.3). Several antennae-biased genes also displayed sex bias; six genes displayed female bias (SnocOR6, SnocOR9, SnocOR22-23, SnocOR28 and SnocOR39) whereas only one gene displayed male bias (SnocOR16) (figure 2.7 and figure 2.15). Twelve ORs also showed differential expression between female and male heads, legs and bodies (figure 2.7, figure 2.15, and table S2.2). SnocOR11 was shown to be significantly up-regulated in body tissues compared

to antennae, however, this gene had very low expression (TPM) and was therefore not further considered (table S2.2). Similarly, SnocOR19 showed significantly enhanced expression in adult wings and female ovipositor tissues (table S2.2), however, transcript abundance of this gene was very low (table S2.3). Some *S. noctilio* ORs with antennae-biased expression also displayed high transcript abundances in other adult chemosensation tissues that may be of biological relevance; SnocOR4 in wings, SnocOR8 in female body tissues, SnocOR10 in wings, SnocOR12 in female heads, SnocOR21 and SnocOR24 in ovipositors and SnocOR29 in body and female head tissues (table S2.3). The co-receptor, SnocORCO, displayed antennae-biased expression with no significant expression differences between male and female antennae (figure 2.15, table S2.2).

Gustatory receptors (GRs)

The GR gene repertoire of *S. noctilio* consists of 12 genes and unlike the OR genes, there was no clear enhanced expression of GRs in a single tissue type (figure 2.16). The overall transcript abundances of the GR genes were relatively low with the highest TPM at around 57 (table S2.3). One of the GR genes (SnocGR11) was not included in the hierarchical clustering heatmap as it had low/no expression (zero read counts) across all tissues investigated. SnocGR9 displayed antennae-biased expression for adult females, however, there was no significant difference between the expression of this gene in head and antennal tissues of adult males, and thus it seems to be equally co-expressed in male heads and antennae (figure 2.8, figure 2.17, and table S2.2). SnocGR12 was up-regulated in male head and antennal tissues (figure 2.7) but also displayed ovipositor-biased expression (figure 2.17 and table S2.2). Body tissue-biased expression was observed for SnocGR6 in adult wasps (figure 2.8). SnocGR8 did not only exhibit developmental stage-biased expression in female pupa but it also displayed tissue-biased expression in the head tissues of *S. noctilio* (figure 2.17 and table S2.2). Developmental stage-biased expression was observed for SnocGR2 and SnocGR3 which were up-regulated in bodies of male pupae (figure 2.16 and table S2.2). The expression of SnocGR4 was not significantly up-regulated in ovipositor tissues, however, this gene showed higher transcript abundance in ovipositors compared to other tissues (figure 2.17 and table S2.3). SnocGR5 was significantly up-regulated in antennal tissues compared to other adult tissues except when compared to body tissues. SnocGR10 displayed enhanced expression in female ovipositors, however, the transcript abundance for this gene is extremely low (table S2.3).

Ionotropic receptors (IRs)

The IR multi-gene family has the largest chemosensation gene repertoire in *S. noctilio*, consisting of 48 receptors. Much like the GRs, the IRs did not exhibit enhanced expression in a single tissue type but rather had variable expression across tissues (figure 2.18). For adult female wasps, 8 out of 48 IRs (SnocIR01, SnocIR03, SnocIR8a, SnocIR09, SnocIR39 and SnocIR43-45) were up-regulated in antennae whereas for male adult wasps 10 IRs (all the same as in female antennae with two additional IRs: SnocIR19 and SnocIR54) were up-regulated in antennae (figure 2.8). Sex-biased genes identified in pairwise comparisons between similar tissues included SnocIR09 in female wings and legs and SnocIR18 in male antennae (figure 2.7). Five IR genes (SnocIR05, SnocIR06, SnocIR23, SnocIR36 and SnocIR38) displayed ovipositor-biased expression (figure 2.18), however, only SnocIR23 and SnocIR36 were significantly up-regulated (figure 2.8 and table S2.2). Several SnocIR genes showed high expression in ovipositor tissues and in addition were also highly expressed in other tissue types (e.g. SnocIR04, SnocIR14, SnocIR42, and SnocIR49). *Sirex noctilio* IRs also displayed leg-biased expression for both female and male wasps, whereas in wing tissues, SnocIRs were only up-regulated in female wing tissues (figure 2.7). SnocIR52, SnocIR46, and SnocIR48 showed higher expression in adult heads (figure 2.19).

2.4. Discussion

In this study, we report on a comprehensive set of high-quality transcriptomes from antennae, heads (with antennae removed), legs, wings, ovipositors and bodies (referring to thoraces and abdomens) of adult *S. noctilio* woodwasps. We also report on the first transcriptome of a siricid species for both male and female pupa. Together, the transcriptomes generated in this study augment the current genetic information available for *S. noctilio*. Supported by gene curation and phylogenetic analyses, the expression profile of six major gene families, a total of 129 genes, encoding chemosensation proteins involved in the uptake, transport and binding of chemical molecules were characterized.

***Sirex noctilio* versus Hymenoptera chemosensation gene repertoires**

In this study, 129 chemosensation genes were identified in the genome of *S. noctilio*, including 45 ORs, 12 GRs, 48 IRs, 14 OBPs, 9 CSPs and one SNMP gene. We identified 43 genes that were not previously identified in a recently published study on *S. noctilio* and *S. nitobei*

chemosensation genes [39]. That study identified 86 chemosensation genes for *S. noctilio* which included 41 ORs, 8 GRs, 16 IRs, 16 OBPs, 7 CSPs and one SNMP [39]. The number of candidate OR (45) and GR (12) genes of *S. noctilio* are less than that identified in the transcriptome and genome of the closely related species the wheat stem sawfly, *C. cinctus* (72 ORs and 35 GRs). The number of IR (48) and OBP (14) genes are, however, comparable to *C. cinctus* (49 IRs and 15 OBPs) [47]. Differences in the chemosensory gene complements of insect species are most likely due to adaptation to different niches.

Several genes from our study (two OBPs, three CSPs, 11 ORs, 6 GRs, and 33 IRs) were not identified by Guo *et al.* [39] in *S. noctilio* and *S. nitobei*. This discrepancy in chemosensation gene repertoires between these studies could be due to the different methods used. The current study employed both the genome and transcriptomes of various tissues and life stages of *S. noctilio*, whereas only antennal transcriptomes were used by Guo *et al.* [39]. For example, SnocOR11 was not identified by Guo *et al.* [39]. SnocOR11 was significantly up-regulated in adult bodies compared to the expression in antennae. SnocOR11 is most closely related to CcinOR59 and CcinOR60 which also seem to be expressed outside of the expected olfactory organs [47]. Other differences between these studies include the inclusion of *S. nitobei* in antennal transcriptome analysis, as well as the use of quantitative real-time PCR analysis for gene expression validation of selected OBPs in antennae, heads, legs and external genitalia in Guo *et al.* [39]. Both studies did, however, find that chemoreceptor co-receptors (ORCO and IRco) have the highest expression in antennae tissues.

Sirex noctilio has a relatively small chemosensation gene repertoire compared to other Hymenoptera. For example, the chemoreceptor gene repertoire alone (excluding OBPs, CSPs and SNMPs) of *Apis mellifera* Linnaeus (Hymenoptera: Apidae) consists of approximately 183 genes [64], while *Bombus terrestris* Linnaeus (Hymenoptera: Apidae) has 206 genes [65], *Nasonia vitripennis* Walker (Hymenoptera: Pteromalidae) has 282 genes [66], *Pogonomyrmex barbatus* Smith (Hymenoptera: Formicidae) has 429 genes, and *Harpegnathos saltator* Jerdon (Hymenoptera: Formicidae) has 387 genes and this only includes the chemoreceptor genes [67, 68]. The lower number of chemosensation genes compared to other Hymenoptera could be explained by the sensory drive hypothesis that suggests variation in signal production, transmission and detection is driven by natural selection in heterogeneous environments [69, 70]. It is, however, still unclear whether selection acts directly on the chemosensation system

or the behavioural responses of an insect [71]. The small chemoreceptor gene repertoire of *S. noctilio* could be attributed to the fact that this is a basal Hymenoptera woodwasp living in a relatively homogenous environment (i.e. coniferous forest) with less complex social interactions and adults that do not feed. *Sirex*-specific chemosensation genes identified through phylogenetic analysis by Postma *et al.* (in preparation) are of particular interest since these genes would most likely be geared towards specific life scenarios and behaviours of *Sirex*.

Tissue type, sex and developmental stage influences on overall gene expression profiles

Olfactory and gustatory tissues in *S. noctilio* showed extensive overlap in gene expression profiles of the different transcriptomes, but also critical distinctions. The influence of olfactory and non-olfactory appendages are reflected by the antenna-biased expression pattern observed for the majority of SnocORs and SnocOBPs, reflecting the fact that antennae are the main site of olfaction [1, 72]. The distinctiveness of antennae from the rest of the transcriptomes and the homogeneity between male and female chemosensation genes in these tissues were similar to observations in the Hessian fly, *Mayetiola destructor* Say (Diptera: Cecidomyiidae) [73]. Genes that were predominantly expressed in antennae (such as antennae-biased OBPs and the noticeable expression of the majority of SnocORs) are implicated in olfaction, as this is the primary chemosensation organ of an insect [74]. Head tissues, specifically mouthparts, have also been implicated in olfaction, but to a lesser extent than antennae [75, 76]. The diverse expression patterns of CSPs, GRs and IRs across tissues are indicative of the gustatory function of these tissues.

Based on expressed chemosensation genes male legs consistently clustered away from wings, ovipositor and female legs. This finding reflects the sexual dimorphism observed in adult legs (males have larger hind legs) [34, 35]. *Sirex noctilio* legs, specifically the hind legs of males, seems to be an essential organ in the chemical communication of this woodwasp since it has been shown to be the site of synthesis and/or storage of a male-produced pheromone blend [34]. Based on the chemistry and emitting sex of this pheromone blend, as well as attraction in both male and female wasps during lab bioassays, Guignard *et al.* [34] suggested that this pheromone could act as an aggregation-pheromone (instead of a sex pheromone), mediating lek formation in males and lek location in females. In support of this conclusion, Queffelec *et al.* [77] found a delay in mating readiness of emerged males which is most likely due to sexual immaturity unrelated to this pheromone since the pheromone blend identified by Guignard *et*

al. [34] is produced in young and mature males. Delayed sexual maturity in *S. noctilio* males suggest that there may also be chemosensation genes that are not yet expressed or responsive to pheromones in emerged males compared to matured males.

The clustering of *S. noctilio* legs, ovipositors and wings based on the pattern of chemosensation gene expression indicates that these appendages may have similar or overlapping functions in chemosensation. Unique functions are, however, evident based on differential expression analyses. Ovipositors, wings and legs have been shown to have olfactory functions and ovipositors and legs are also involved in gustation [78–80]. A gene expression study in *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) also identified expressed chemosensation genes in female and male tarsi and the pheromone gland-ovipositor complex [78]. Dou *et al.* [78] also found differentially expressed chemosensation genes (especially OBPs and CSPs) between female tarsi and the pheromone gland-ovipositor complex. In contrast to the study in *H. zea* where no significantly differentially expressed chemosensation genes were identified between male and female tarsi [78], in the current study *S. noctilio* had several significantly DEGs in legs, once again echoing the leg dimorphism of *S. noctilio* [34].

The chemosensation gene expression was highly similar for males and females, including in the antenna [73]. There were, however, differences in the transcript abundance of some genes in the chemosensation gene repertoire based on sex, rather than transcript type. This pattern was also seen in *Anopheles gambiae sensu lato* (Diptera: Culicidae) [1], where the relative expression of chemosensory genes was higher in females than males and that might cause increased sensitivity to odours (if receptor expression levels correlate to sensitivity). In *Drosophila melanogaster* Meigen (Diptera: Drosophilidae), single nucleotide polymorphisms of OR genes contributed to behavioural variation in response to odours, which corresponded to different levels of OR expression [70]. The higher relative expression levels of SnocORs observed in female antennae compared to males potentially indicate variation in odour sensitivity or shifts in olfactory perception. While few in number, sex-biased, significantly DEGs (especially in antennae) represent exciting targets for functional studies in *S. noctilio* [1].

Developmental stages formed well defined gene expression clusters, reiterating the distinct niches and behaviours associated with these life stages. Due to the diverse physiological functions of chemosensation carrier proteins, expression of OBPs and CSPs in pupae are anticipated. Limited expression of chemoreceptors are predicted as onset of chemoreceptor

expression will most likely only start during pupal development as the cuticle develops [81]. Conversely, chemosensation gene expression is expected to be higher in adult wasps, since there is reduced feeding and developmental activities and exaggerated focus on mate, host and oviposition-site selection. Compared to adults, *S. noctilio* pupae had low expression of ORs, but this could be expected to increase closer to eclosion or with antennae development as seen in *A. cerana cerana* Fabricius (Hymenoptera: Apidae) [82]. Transcriptome profiling of developmental stages of the pine moth, *Dendrolimus punctatus* Walker (Lepidoptera: Lasiocampidae), also showed enrichment of chemosensory genes as pupae metamorphosed into adults [83]. SNMPs and GRs had similar or moderate levels of expression between *S. noctilio* adults and pupa, but CSPs and IRs had similar or higher expression in pupa compared to adults. This is not surprising since these genes are multifunctional.

The expression profiles identified for the chemosensation gene repertoire of *S. noctilio* in this study is expected to be a snapshot of the variation across the developmental stages and ages of this woodwasp. This is because chemosensory-plasticity, in response to changes in environmental and physiological conditions, is known to influence gene expression patterns. Previous studies have shown that age, reproductive state, mating state, feeding state and circadian rhythm can influence chemosensation gene expression that can ultimately make an insect more or less receptive to chemical stimuli [84–86]. Therefore, investigation of chemosensation gene expression under varying physiological states can aid elucidation of receptor and carrier protein functions.

An example of a physiological state that might be valuable to explore in terms of chemosensation is female age. *Sirex noctilio* females switch from a focus of mate selection to host location and selection, which is triggered in an age-dependant manner [77, 87, 88]. Since *S. noctilio* can oviposit eggs regardless of mating status (mated or unmated) a potential trigger could be ovarian maturity [89]. Chemosensation genes that are no longer expressed after mating or reproductive maturity could imply a function in sex-pheromone detection [86]. Therefore, chemoreceptor gene expression comparison between immature and mature female wasps could reveal genes essential to reception of oviposition site selection and host olfactory cues, after the physiological switch between mate and host selection has occurred.

Chemosensation genes displaying sex- and/or tissue-biased expression

Chemosensation carrier and supporting proteins (OBPs, CSPs and SNMPs)

In general, chemosensation carrier proteins (OBPs and CSPs) showed higher expression abundances (TPM values) compared to chemoreceptors (ORs, GRs and IRs). The highest expressed chemosensation gene was SnocOBP3 in adult male legs. The higher expression of chemosensation carrier proteins (OBPs and CSPs) compared to chemoreceptors (ORs, GRs, and IRs) was expected as studies have shown that these proteins are highly concentrated in the sensillar lymph of chemosensilla [11, 90, 91].

Six of the 14 *S. noctilio* OBPs had their highest expression in antennal tissues and another three were highly expressed in antennae. The first step of the perireceptive events of chemosensation is the uptake and transport of chemical molecules through the chemosensillar lymph mediated by these small, soluble binding proteins (OBPs and CSPs) [4, 92]. The involvement of OBPs in this essential first step of chemosensation along with antennae-biased expression is suggestive of an olfactory role for these genes to detect kairomones and pheromones [42, 47, 59, 93, 94].

SnocOBP14 is an antenna-biased gene potentially involved in pheromone detection. This gene was identified as OBP9 by Guo *et al.* [39] and proposed to be a PBP since it clustered with PBPs and specifically, AmelASP1 of *A. mellifera*. AmelASP1 is regarded as an antenna-specific protein (ASP) involved in the reception of the queen pheromone [57, 95]. OBPs further classified as pheromone binding proteins (PBPs) are involved in sex-pheromone detection making them attractive targets for chemosensation gene manipulation.

Antennae-biased OBPs, SnocOBP7 and SnocOBP10, are also sex-biased which suggest a sensory function, but may also echo differential attraction to sex-pheromones and host plant odours [37]. The female antennae-biased SnocOBP7 may be involved in the detection of volatiles mediating host and oviposition-site selection [45]. The male antennae-biased expression of SnocOBP10 could indicate potential involvement in mating behaviours through detection of female produced sex-pheromones or aggregation pheromones used for lek formation [96].

OBPs tightly regulated in specialised tissues were identified through the exhaustive investigation of adult tissues. Interestingly, sex bias was observed for all SnocOBPs expressed in non-antennal tissues contrary to observations in the hemipteran, *Apolygus lucorum* Meyer-

Dür (Heteroptera: Miridae), where limited sex-bias was observed for OBPs expressed outside of antennal tissues [96]. SnocOBP3 and SnocOBP4 displayed adult male-biased expression in legs and bodies, respectively, suggesting a gustatory function for these genes. Previous studies have suggested, leg-biased OBP expression may mediate behaviours such as host-seeking [97–99]. However, contrary to the male leg-biased expression of SnocOBP3, OBPs from these studies showed enhanced expression in both male and female legs. The male leg-biased expression of SnocOBP3 could imply a role in pheromone detection and/or the release and storing of chemical compounds [92]. Due to the hind leg sexual dimorphism of *S. noctilio* it is also possible that SnocOBP3 has a function outside of chemosensation such as leg development [34, 96], but functional and protein-ligand interaction studies are needed to confirm this function.

Expression profiles of SnocOBP2 and SnocOBP9 suggest chemosensory functions possibly related to oviposition-site selection specific to ovipositors (SnocOBP2) and shared with antennae (SnocOBP7). SnocOBP2 was ovipositor-biased, while SnocOBP5 and SnocOBP9 were highly expressed in ovipositors with highest expression in antennae. Female woodwasps use their ovipositors to probe a host tree to determine whether it is a suitable site for egg development. The ovipositor of *S. noctilio* has also been shown to have electrophysiological activity capable of pine volatile and ethanol detection [36]. Furthermore, Faal *et al.* [100] also showed that *S. noctilio* females are attracted to volatiles emitted from *A. areolatum*, thus these OBPs might be involved in detection of volatiles from fungal infections from previous wasp attacks.

Deposited along with the eggs is a phytotoxic venom and symbiotic fungal spores to weaken host defences and allow fungal colonisation, ultimately improving survival of the wasp progeny [37, 101]. OBPs have been identified in the venom of parasitoid wasps, *Anisopteromalus calandrae* Howard (Hymenoptera: Pteromalidae) [102], *Chelonus inanitus* Linnaeus (Hymenoptera: Braconidae) [103], *N. vitripennis* [104], and *Pteromalus puparum* Linnaeus (Hymenoptera: Pteromalidae) [105], as well as in *S. noctilio* venom sacs [37]. Phylogenetic analyses with venom sac protein data from Wang *et al.* [37] suggest SnocOBP2 and SnocOBP9 are not expressed in venom sacs of *S. noctilio*, but SnocOBP5 is expressed. This expression pattern of SnocOBP5 suggests multifunctionality.

A large subset SnocOBPs are antenna-biased while SnocCSPs show a complex expression pattern, either with ubiquitous or biased expression in specialized tissues. Chemosensation carrier proteins, OBPs and CSPs, show complex expression patterns that are highly variable between hymenopteran species. In some Hymenoptera species OBPs are mostly antenna-specific whereas in other species CSPs tend to be antenna-specific [106]. *Vespa crabro* Linnaeus (Hymenoptera: Vespidae) is one species with a 'reverse' expression profile for chemosensation carrier proteins where CSPs are antenna-specific and OBPs are equally expressed in different tissues [106]. The expression profiles of *S. noctilio* chemosensation carrier proteins, however, resemble that of *A. mellifera*, where neither protein class is exclusively antenna-specific which supports the multifunctionality (ranging from pheromone delivery to vision and even pesticide resistance) of these binding proteins [106–110].

SnocCSP7 was the only antenna-biased CSP in *S. noctilio*. A study in the migratory locust, *Locusta migratoria* Linnaeus (Orthoptera: Acrididae), showed that CSPs with antenna enhanced expression play a big role in the behavioural switch between the solitary and gregarious phase [111]. CSP knockdown in gregarious *L. migratoria* locusts, caused a shift to solitarious-like behaviours. This is an example of CSPs mediating aggregation pheromone detection. The antenna-biased CSP of *S. noctilio* could thus also be involved in pheromone detection. It would be valuable to investigate the expression of SnocCSP7 before and after exposure to conspecific males and females of mature age, respectively.

The *S. noctilio* CSP genes, SnocCSP1, SnocCSP3-5, and SnocCSP8 were ubiquitously expressed, but did have enhanced expression in a tissue that differed for the genes. SnocCSP5 and SnocCSP8 were significantly enhanced in wings compared to antennae, but in females these genes were also enhanced in legs (SnocCSP5) and ovipositors (SnocCSP8). In addition to odourant binding, CSPs are involved in leg regeneration [112], embryonic integument development [113], and are carriers of visual pigments [114]. Immunocytochemical investigation of CSPs in wings of *L. migratoria* revealed that CSPs were expressed in the sensillum lymph of contact chemoreceptors as well as in the epidermal cells [115] suggesting that not all chemosensory carrier proteins are involved in odour recognition. Therefore, determining where proteins like SnocCSP5 and SnocCSP8 are localised in insect tissues could reveal whether they are involved in chemosensation.

Antennae and male leg biased expression of SnocSNMP1 is consistent with the hypothesis that SNMPs are required along with pheromone detecting ORs to recognize lipophilic pheromones [116]. Three subtypes of SNMPs (SNMP1-3) have been identified throughout insect orders. Work done in moths, *Heliothis virescens* Fabricius (Lepidoptera: Noctuidae) and *Antheraea polyphemus* Cramer (Lepidoptera: Saturniidae), have shown that SNMP1 is expressed in olfactory neurons and SNMP2 is expressed in supporting cells surrounding olfactory neurons [116]. In *D. melanogaster* the SNMP is expressed in both supporting cells and neurons [117]. In both Lepidoptera species and *D. melanogaster* it is proposed that SNMP is required for pheromone detection [116–118]. The expression profile of SnocSNMP1 was also observed for *A. cerana cerana* where SNMP1 is highly expressed in antennae and legs [119] and *Microplitis mediator* Haliday (Hymenoptera: Braconidae) where it is highly expressed in antennae [118]. The study in *A. cerana cerana* suggested that the expression of SNMP1 in legs may indicate involvement in various sensory processes. However, the demonstration of *S. noctilio* male hind legs being the site of synthesis and/or storage of a potential aggregation sex-pheromone [34] may implicate the expression of SnocSNMP1 in male legs in pheromone detection.

Chemoreceptors (ORs, GRs and IRs)

Across all tissues investigated, the SnocORCO co-receptor gene was the most highly expressed OR gene. The antenna-biased expression of SnocORCO not only highlights the fact that the antennae are the main olfactory organ, but also the importance of this gene [4]. ORCO improves the responsiveness and sensitivity of ORs to ensure accurate detection of chemical stimuli [14]. In our study, ORCO was not only expressed in adult antennae, but also displayed low expression abundance (0.21 TPM) in the ovipositors of adult female wasps. Investigation of ORCO expression in *Drosophila suzukii* revealed that there is no expression of ORCO in ovipositors [120], however, sequencing coverage and quality can have an influence on the detection of genes especially if they are expressed at low levels. Expression profiling of ORCO in *H. zea* and *H. assulta* Guenée (Lepidoptera: Noctuidae), however, also found very low expression of ORCO in the pheromone gland-ovipositor complex [78, 121]. Co-expressing ORCO and *HassOR31* (which was highly expressed in the ovipositor) in *Xenopus* oocytes showed that *HassOR31* is responsive to plant odourants that may assist oviposition site selection for females [121]. Thus, ORCO may still be essential for the functioning of ORs in non-olfactory tissues and is important to realise as this can influence functional deorphanisation studies of ORs.

Some ORs had unexpected expression profiles. Even though SnocOR10, SnocOR12, and SnocOR18 had highest expression in antennae these genes also had uniform, high expression in all other tissues. Ubiquitously expressed ORs with higher expression in antennae were also observed in *Microplitis mediator* Haliday (Hymenoptera: Braconidae) [122]. These OR genes could potentially be involved in contact pheromone reception or host location, but they could also be involved in other physiological functions [123]. Similarly, SnocOR4, SnocOR24, SnocOR29 and SnocOR42-43 were most highly expressed in antennae, but these genes also had high expression in at least one other tissue type. Pitts *et al.* [124] showed that the malaria mosquito ORCO gene mediates spermatozoa activation in the testes. Thus it is possible that genes expressed in non-antennal tissues have a shared olfactory role with antennae, but it is also likely that these genes have additional physiological functions in non-olfactory tissues.

SnocOR16 was significantly up-regulated in male antennae compared to all other tissues which make it a candidate pheromone receptor. This genes' expression pattern conforms to the observation by Guo *et al.* [39]. The expression profile of SnocOR16 is of particular interest since phylogenetic analyses revealed that SnocOR16 belongs to the 9-exon subfamily of the larger OR multigene family (Postma *et al.* in preparation, figure S2.2). The 9-exon OR subfamily seems to be involved in the recognition and perception of cuticular hydrocarbon (CHC) pheromones in Hymenoptera [68, 125]. Cuticular hydrocarbons are used to make the insect's cuticle waterproof and mediate social behaviours, ranging from courtship and aggregation to colony organization (division of labour and task identification) and conspecific communication (caste and nestmate recognition) especially in eusocial insects [68, 125–129]. Discrimination of different CHC profiles in ants can occur without physical contact between individuals which suggests that CHCs can be potential olfactory signals that may be detected by ORs housed in the antennae [130]. Cuticular hydrocarbons (monoalkenes) identified on the cuticle of female *S. noctilio*, induce a copulatory response in male woodwasps [33]. Queffelec *et al.* [77] found that female attractiveness decreases with age and that male *S. noctilio* wasps exhibit potential mate choice. Queffelec *et al.* [77] proposed that production of CHCs by female wasps could decrease with age making older females less attractive and subsequently have fewer matings. Deorphanisation studies between SnocOR16 with CHC ligands are now needed to determine whether SnocOR16 is a sex-pheromone receptor.

SnocOR24 exhibited antennae biased expression, along with high expression in ovipositor tissues. Phylogenetic analyses revealed that SnocOR24 is at the base of a large clade that contains *A. mellifera* OR11 (AmelOR11), AmelOR1, and AmelOR3 (Postma *et al.* in preparation, figure S2.2). AmelOR11 is the honey bee OR responsible for the reception of the queen pheromone substance, 9-oxo-2-decenoic acid, and is one of the few olfactory receptors that have been deorphanised [131, 132]. The orthologs of AmelOR1 and AmelOR3 in *A. cerana cerana* (AcerOR1 and AcerOR3) have been proposed to perceive floral scents and to be necessary for male-related behaviours, respectively [82]. Based on the expression profile of SnocOR24 it is worth exploring the function of this gene as it might serve an important role in oviposition or mating.

Two genes related to the linalool, floral scent receptor, AmelOR151, of *A. mellifera* was identified in this study, namely SnocOR20 and SnocOR21. This is one of the few hymenopteran genes that has been successfully deorphanised [133]. Linalool is a floral terpene alcohol with diverse biological properties including anti-microbial, anti-oxidant, larvicidal, insecticidal and repellent activities as well as attractant properties for pollinators [134, 135]. Females of *S. noctilio* are also attracted to a four-compound blend of its fungal symbiont which includes linalool [100]. The most closely related *S. noctilio* genes to AmelOR151 are SnocOR20 and SnocOR21. Interestingly, SnocOR20-21 and SnocOR24 have very similar expression profiles with high expression levels in ovipositors and highest expression in antennae. It is possible that SnocOR20 and SnocOR21 play a role during oviposition to ensure eggs are deposited in suitable host trees. These receptors may either determine if the fungal symbiont *A. areolatum* is present or detect larvicidal and anti-microbial compounds.

Unlike ORs, gustatory receptors did not show enhanced expression in a single tissue condition which is consistent with the fact that these receptors perform a diverse range of functions. The detection of soluble chemical signals like amino acids, sugars, repellent compounds and non-volatile pheromones is achieved through GRs which are also believed to be involved in detection of tactile stimuli [3, 136, 137]. One known exception is the presence of a GR that is responsible for the detection of carbon dioxide [138].

Phylogenetic analyses identified a single CO₂ receptor ortholog for *S. noctilio* namely SnocGR11 (Postma *et al.* in preparation, figure S2.3). Two CO₂ chemoreceptor orthologs have been identified in *C. cinctus* [47]. The presence of these orthologs in the Symphyta is in stark contrast

to species in the Apocrita (e.g., *N. vitripennis*, *A. mellifera*, and *B. terrestris*) that do not have a CO₂ receptor ortholog [67]. Insects detect CO₂ for a variety of reasons ranging from avoidance behaviour [139], host location in mosquitoes, flower quality assessment in Lepidoptera, brood placement and maintenance in social insect colonies [140], as well as oviposition in phytophagous insects [141]. Unlike the carbon dioxide GRs of *C. cinctus* which were expressed in head tissues, there was no/poor evidence of expression in the transcriptome raw reads for SnocGR11. Thus this gene may have become a degraded pseudogene, may only be essential during a specific developmental stage (such as the larvae) or the expression may be regulated in an age- or mating-dependant manner [85].

SnocGR1 and SnocGR2 had low expression in pupal tissues. This is of interest since literature proposed that orthologs of these genes are conserved amongst Hymenoptera, but not found in non-eusocial species [142]. According to phylogenetic analyses SnocGR1 and SnocGR2 are orthologous to AmelGR10 (Postma *et al.* in preparation, figure S2.3). AmelGR10 is a broadly tuned amino acid receptor with high expression in the fat body of *A. mellifera* [142]. The fat body of insects is responsible for energy metabolism and nutrient storage and undergoes reorganisation during metamorphosis which is vital for pupa and adult formation [143]. Investigation of AmelGR10 expression revealed that this gene is differentially expressed in different developmental stages and is essential for nursing behaviour of honey bee workers [144]. SnocGR1 and SnocGR2 is, therefore, a potential growth and developmental regulator involved in monitoring amino acid concentration.

Putative sugar receptors displayed differential expression, where SnocGR5 had enriched expression in antennae while SnocGR6 was significantly enriched in bodies. SnocGR5 and SnocGR6 are orthologous to AmelGR2 and AmelGR1, respectively (Postma *et al.* in preparation, figure S2.3). The sugar receptors of *A. mellifera* have different functions; AmelGR1 is responsive to glucose, maltose, sucrose and trehalose, while AmelGR2 is not [145]. Co-expression of AmelGR1 and AmelGR2 altered sensitivity towards these sugars with an increased response to glucose and a decreased response to the other sugars compared to AmelGR1 alone [145]. Immunolocalisation of AmelGR1 and AmelGR2 suggest AmelGR1 functions as a monodimer or heterodimer and prompted the suggestion that AmelGR2 may function as a co-receptor for sugar responses [145]. The response of SnocGR1 and SnocGR2 should be tested against sugars present in pine trees to elucidate the functions of these putative sugar receptors.

SnocGR9 had enriched expression in antennae. This gene is only orthologous to genes of the Symphyta species *C. cinctus* and *A. rosae*. The putative function of SnocGR9 is completely unknown but the antennal enriched expression and phylogenetic relationship of this gene generate sufficient interest for future functional work [47].

Ionotropic receptors are an ancient chemoreceptor group involved in chemoreception of acids, amines, aldehydes and pheromone signals, but are also involved in hygro- [146] and thermosensation [147] and the regulation of sexual circuitry [80]. The IR genes of *S. noctilio* had complex expression across the various tissues. Several IR genes displayed sex or tissue-biased expression, however, the lack of information about these genes due to their fairly recent discovery makes it difficult to infer putative functions for these genes [148]. SnocIR34 was the most highly expressed IR gene, which was in head tissues. SnocIR36 was up-regulated in ovipositors. SnocIR28 had relatively high expression in antennae, wings and pupal tissues and forms part of the IR21a phylogenetic clade (Postma *et al.* in preparation, figure S2.4). DmelIR21a is involved in thermosensation to avoid cool temperatures [149]. The ubiquitously expressed IR93a ortholog, SnocIR31, is not only involved in hygrosensation, but also thermosensation in *D. melanogaster* [147]. There is, however, a sparsity of information on these IR genes and a clear need for further investigation to determine gene function in hymenopteran species.

The highly conserved IR co-receptors, IR25a (SnocIR45), IR8a (SnocIR8a) and IR76b (SnocIR09) were antenna-biased, as well as the top three expressed genes in antennae [150, 151]. This biased expression, much like SnocORCO, suggests a co-receptor function. The expression of these co-receptors are similar to that of *Aphidius gifuensis* Ashmead (Hymenoptera: Braconidae) [152], but not *C. cinctus* where IR25a and IR76b were most highly expressed in heads and IR8a had relatively low expression [47].

SnocIR09 was up-regulated in female legs and wings compared to male tissues suggesting sex-related functions for this gene. Investigation of IR expression in sour gustatory receptor neurons in tarsi of *D. melanogaster* showed that DmelIR76b (ortholog for SnocIR09) and DmelIR25a (ortholog for SnocIR45) are essential in sour gustatory receptor neurons for oviposition preference in acid containing foods [153]. SnocIR09 could be a putative mediator of oviposition and should be investigated for its potential involvement during oviposition.

SnocIR45 was not significantly differentially expressed between sexes, however, the relative expression of the gene was higher in female wasps. SnocIR45 was also expressed in ovipositors. IR25a (orthologous to SnocIR45), as well as three other genes (IR93a orthologous to SnocIR31, IR40a, and IR68a orthologous to SnocIR54) are involved in hygrosensation [146, 154, 155]. *Sirex noctilio* has no ortholog for IR40a and SnocIR54 had very low expression, which is in agreement with observations for *C. cinctus* [47]. Ambient conditions such as relative humidity and temperature affect egg deposition of *S. noctilio* [22]. SnocIR45 is thus an intriguing gene as it may be critical during host tree selection and oviposition site-selection performed by woodwasp females.

Tandem arrayed SnocIR01 and SnocIR02 were up-regulated in male legs and bodies compared to female tissues. SnocIR01-02 are related to Dmel64a and DmelIR84a (Postma *et al.* in preparation, figure S2.4). DmelIR64a is tuned to acids and is required for avoidance behaviour in response to acid detection [156, 157]. DmelIR84a is activated by aromatics (used for feeding, breeding and oviposition) from food sources but is not activated by equivalent fly-derived odours [158]. DmelIR84a is required for male courtship and is proposed to induce male courtship in the presence of food thereby possibly complementing pheromone receptors in *D. melanogaster* [158]. Grosjean *et al.* [158] suggested that DmelIR84a coordinates feeding, oviposition site-selection and reproduction by integration of food and mate selection pathways through IR84a. The function of IR64a and IR84a in *D. melanogaster* and the sex bias expression of the *S. noctilio* orthologs raise the question whether SnocIR01-02 could have similar functions.

2.5. Conclusion and future work

The comprehensive transcriptome analysis performed in this study identified several intriguing gene targets for future studies on chemosensation in *S. noctilio* and potentially other Hymenoptera. The molecular insight gained from this study lays a foundation for future (reverse) chemical ecology, expression manipulation, and deorphanisation studies to elucidate the specific functions of chemosensory gene targets, both for biological understanding and that could be manipulated for pest control. Such studies can guide the more time intensive behavioural assays that will be required to validate expression data of chemosensation genes.

RT-qPCR of interesting gene targets will be valuable tools to gain clarity on potential gene functions and to determine which genes should be investigated through expression

manipulation and protein interaction studies. Expression profiles of genes identified in this study can be validated through RT-qPCR across different developmental stages (including eggs and larvae) and physiological states of the adult wasps. This will also identify genes that may no longer be functional (e.g. SnocGR11).

Computational reverse chemical ecology analyses could follow the data produced in this study [159]. Through computer simulated ligand docking and investigation of molecular dynamics, chemical ligand-protein partners can be identified for further behavioural studies. Furthermore, chemical ligands of the identified chemosensation genes can be identified through heterologous expression systems that make use of either insect or non-insect cell lines [160], ideally in a *Sirex* cell line and/or through *in vivo* gene manipulation studies.

Information held within this dataset relates not only to chemosensation, but also to immunity, sex-determination, reproduction and development amongst others. A deeper insight from this dataset into the molecular basis of these other elements of *Sirex* biology will further accelerate the design of insect-behaviour-modifying stimuli.

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2.8. Declarations

Ethics approval

No permits were required to perform research on this forest pest. Ethics approval was granted by the Faculty of Natural and Agricultural Sciences Ethics Committee (Reference number: NAS173/2020). This work did not involve endangered or protected species.

2.9. References

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2.10. List of Figures

Figure 2.1. Overview of study. This figure illustrates the broad overview of how the study was conducted and the questions that were of interest. 103

Figure 2.2. Map indicating where infested pine logs were collected in South Africa. White lines indicate borders between provinces. Dark yellow regions indicate provinces from which *S. noctilio* infested pine logs were collected. Wasps indicate specific regions within each province from where pine logs were collected. 104

Figure 2.3. Agarose gel electrophoresis results of total RNA extractions using the TRIzol protocol. R, biological replicate (1/2/3). Yellow arrow indicates where genomic DNA bands were observed in the crude RNA extractions. 1 µl RNA sample was loaded with 1 µl loading dye and gel electrophoresis ran for 20 mins at 110 V. 105

Figure 2.4. Agarose gel electrophoresis results of DNase treated RNA samples. Top gel: RNA quality after (lanes 1 and 2) and before (lanes 3) DNase treatment and column clean-up. Yellow arrow indicates genomic DNA contamination (only present in lane 3). Lane 1, first column clean-up elution; Lane 2, second column clean-up elution; Lane 3, crude RNA extract. Bottom gels: R, biological replicate (1/2/3). All lanes contain DNase treated RNA extracts. Samples are clean from genomic DNA. 1 µl RNA sample was loaded with 1 µl loading dye and gel electrophoresis ran for 20 mins at 110 V. 107

Figure 2.5. Principal component analysis (PCA) performed on the expression data of *S. noctilio* for chemosensation genes (left) and all expressed genes (right). Normalised count data was used with the plotPCA function of DESeq2 in R. Count data was produced from featureCounts and transformation of count data was accomplished through the built in variance stabilizing transformation of DESeq2. Tissue type: A, antennae; B, body; H, head; L, leg; O, ovipositor; W, wings. Tissue sample: FA, female antennae; FB, female body; FH, female head; FL, female legs; FO, female ovipositor; FPB, female pupae body; FPH, female pupae head; FW, female wings; MA, male antennae; MB, male body; MH, male head; ML, male legs; MPB, male pupae body; MPH, male pupae head; MW, male wings. 108

Figure 2.6. Significantly differentially expressed (DE) genes (adjusted p-value < 0.05) identified through pair-wise comparisons of different RNA tissue libraries of *S. noctilio*. (A) DE genes identified in 62 pair-wise comparisons. Up-regulated genes: log2FoldChange (LFC) > 0; Down-regulated genes: log2FoldChange (LFC) < 0. FA, adult female antennae; MA, adult male antennae; FH, adult female head; MH, adult male head; FL, adult female legs; ML, adult male legs; FW, adult female wings; MW, adult male wings; FB, adult female body; MB, adult male body; FO, adult female ovipositor; FPH, female pupa head; MPH, male pupa head; FPB, female pupa body; MPB, male pupa body; FH*, female adult head and antennae; MH*, female adult head and antennae; FB*, female adult body, legs, wings and ovipositor; MB*, male adult body, legs and wings. (B) DE chemosensation genes identified

in pair-wise comparisons of adult wasps using antenna and body (numbers within brackets) tissues as control condition, respectively. 109

Figure 2.7. Sex-biased chemosensation genes of female and male *S. noctilio* in different tissues.

Bar graph shows the number of significantly differentially expressed (DE) genes of each chemosensation gene class between females and males (dark blue) and the number of genes DE in adult antennae (for both male and female) for each gene class (light blue). Venn diagrams indicate the shared DE genes (whether up-regulated or down-regulated) between adult female and male pairwise comparisons for the different tissues. Genes indicated in the coloured blocks are chemosensation genes that are significantly DE in a specific tissue in pairwise comparisons between female and male tissues (adjusted p-value < 0.05 and |LFC| > 1). Tissues are represented by a specific colour throughout the figure. ABFvM, Adult Body Female vs Male; AAFvM, Adult Antennae Female vs Male; AWFvM, Adult Wings Female Vs Male; ALFvM, Adult Legs Female vs Male; AHFvM, Adult Head Female Vs Male. 110

Figure 2.8. Tissue-biased chemosensation genes of female and male *S. noctilio*.

Significantly differentially chemosensation genes (adjusted p-value < 0.05, |LFC| > 1) in female (top) and male (bottom) woodwasps identified through pairwise comparisons with antennae. Genes indicated are **exclusively up-regulated** in the corresponding tissue. Genes indicated in **bold** are genes that displayed up-regulation in both females and males in the same tissue type. Venn diagrams indicate the up-regulated and down-regulated genes shared in different tissues. AFBvA, Adult Female Body vs Antennae; AFHvA, Adult Female Head vs Antennae; AFLvA, Adult Female Legs vs Antennae; AFOvA, Adult Female Ovipositor vs Antennae; AFWvA, Adult Female Wings vs Antennae. AMBvA, Adult Male Body vs Antennae; AMHvA, Adult Male Head vs Antennae; AMLvA, Adult Male Legs vs Antennae; AMWvA, Adult Male Wings vs Antennae..... 111

Figure 2.9. Hierarchical clustered heatmap of *S. noctilio* odourant binding proteins (SnocOBP#)

gene expression across various tissue types of adult and pupa developmental stages. The tissue samples for which gene expression was analysed are represented in 3 biological replicates on the x-axis. Odourant binding protein genes of *S. noctilio* (SnocOBP#) are indicated on the y-axis. Four clusters were identified: Cluster A (pink block) are genes exhibiting higher expression in pupa tissues whereas cluster B (green block) are genes with higher expression in adult tissues and lower expression in pupa tissues. Cluster C (Orange block) consist of one gene which displayed a highly variable expression pattern across tissues. Cluster D (blue block) displayed antennae-biased expression. Count data produced through featureCounts were normalised and used to produce this figure using the pheatmap R package (<https://CRAN.Rproject.org/package=pheatmap>). Gene expression data were hierarchically clustered using a k-means approach and count data was transformed using variance stabilizing transformation, both using the R DESeq2 package. 112

Figure 2.10. Bar plots indicating the average TPM (transcripts per kilobase per million reads) per tissue type of adult female (red) and male (blue) *S. noctilio* wasps for each SnocOBP gene. Y-axis indicates transcripts per kilobase per million reads (TPM). X-axis indicates tissue type: A, Antennae; B, Body; H, Head; L, Legs; O, Ovipositor; W, Wings. TPM values were transformed as follow: $\text{mean}(\log(\text{tpm} + 1))$ 113

Figure 2.11. Hierarchical clustered heatmap of *S. noctilio* chemosensory proteins (SnocCSP#) gene expression across various tissue types of adult and pupa developmental stages. The tissue samples for which gene expression was analysed are represented in 3 biological replicates on the x-axis. Chemosensory protein genes of *S. noctilio* (SnocCSP#) are indicated on the y-axis. Four clusters were identified: Cluster A (pink block) are genes with lower expression in pupa and adult body tissues with higher expression in body appendages. Cluster B (green block) shows genes with higher expression in adult tissues whereas cluster D (orange block) represents genes with higher expression in pupa tissues. Cluster C (blue block) represents genes that have higher expression in body and head tissues. Count data produced through featureCounts were normalised and used to produce this figure using the pheatmap R package (<https://CRAN.Rproject.org/package=pheatmap>). Gene expression data were hierarchically clustered using a k-means approach and count data was transformed using variance stabilizing transformation, both using the R DESeq2 package. 114

Figure 2.12. Bar plots indicating the average TPM (transcripts per kilobase per million reads) across tissue types of adult female (red) and male (blue) *S. noctilio* wasps for each SnocCSP gene. Y-axis indicates transcripts per kilobase per million reads (TPM). X-axis indicates tissue type: A, Antennae; B, Body; H, Head; L, Legs; O, Ovipositor; W, Wings. TPM values were transformed as follow: $\text{mean}(\log(\text{tpm} + 1))$ 115

Figure 2. 13. Bar plots indicating the average TPM (transcripts per kilobase per million reads) across tissue types of adult female (red) and male (blue) *S. noctilio* wasps for the SnocSNMP1 gene. TPM across tissue types of adult female (red) and male (blue) *S. noctilio* wasps for the SnocSNMP1 gene. Y-axis indicate transcripts per kilobase per million reads (TPM). X-axis indicates tissue type: A, Antennae; B, Body; H, Head; L, Legs; O, Ovipositor; W, Wings. TPM values were transformed as follow: $\text{mean}(\log(\text{tpm} + 1))$ 116

Figure 2.14. Hierarchical clustered heatmap of *S. noctilio* olfactory receptor's (SnocOR#) gene expression across various tissue types of adult and pupa developmental stages. The tissue samples for which gene expression was analysed are represented in 3 biological replicates on the x-axis. Olfactory receptor genes of *S. noctilio* (SnocOR#) are indicated on the y-axis. Two clusters were identified: Cluster A (pink block) are genes predominantly expressed in adult antennae. Cluster B (blue block) are genes with generally higher expression in body, head wing and antennae tissues. Count data produced through featureCounts were normalised and used to produce this figure using the pheatmap R package

(<https://CRAN.Rproject.org/package=pheatmap>). Gene expression data were hierarchically clustered using a k-means approach and count data was transformed using variance stabilizing transformation, both using the R DESeq2 package. 117

Figure 2.15. Bar plots indicating the average TPM (transcripts per kilobase per million reads) across tissue types of adult female (red) and male (blue) *S. noctilio* wasps SnocOR for each gene. Y-axis indicates transcripts per kilobase per million reads (TPM). X-axis indicates tissue type: A, Antennae; B, Body; H, Head; L, Legs; O, Ovipositor; W, Wings. TPM values were transformed as follow: $\text{mean}(\log(\text{tpm} + 1))$ 118

Figure 2.16. Hierarchical clustered heatmap of *S. noctilio* gustatory receptor's (SnocGR#) gene expression across various tissue types of adult and pupa developmental stages. The tissue samples for which gene expression was analysed are represented in 3 biological replicates on the x-axis. Gustatory receptor genes of *S. noctilio* (SnocGR#) are indicated on the y-axis. Five clusters were identified: Cluster A (pink block) are genes with low expression in head, wing, leg and ovipositor tissues. Cluster B (green block) are genes with no clear pattern. Cluster C (blue block) genes have low expression in ovipositor and body tissues. Cluster D (red block) is only represented by one gene. Cluster E (orange block) are genes highly expressed in male pupa bodies. Count data produced through featureCounts were normalised and used to produce this figure using the pheatmap R package (<https://CRAN.Rproject.org/package=pheatmap>). Gene expression data were hierarchically clustered using a k-means approach and count data was transformed using variance stabilizing transformation, both using the R DESeq2 package. 119

Figure 2.17. Bar plots indicating the average TPM (transcripts per kilobase per million reads) per tissue type of adult female (red) and male (blue) *S. noctilio* wasps for each SnocGR gene. Y-axis indicates transcripts per kilobase per million reads (TPM). X-axis indicates tissue type: A, Antennae; B, Body; H, Head; L, Legs; O, Ovipositor; W, Wings. TPM values were transformed as follow: $\text{mean}(\log(\text{tpm} + 1))$ 120

Figure 2.18. Hierarchical clustered heatmap of *S. noctilio* ionotropic receptor's (SnocIR#) gene expression across various tissue types of adult and pupa developmental stages. The tissue samples for which gene expression was analysed are represented in 3 biological replicates on the x-axis. Ionotropic receptor genes of *S. noctilio* (SnocIR#) are indicated on the y-axis. Four clusters were identified: Cluster A (pink block) are genes with low expression antennae, wings, legs and ovipositor tissues. Cluster B (green block) are genes with higher expression in adult head tissues. Cluster C (dark blue block) genes have higher expression in adult body tissues. Cluster D (orange block) are genes highly expressed in ovipositor tissues. Cluster E (red block) are genes with unique expression patterns. Cluster F (light blue block) are genes with higher expression in antennae tissues. Cluster G (dark green block) are genes with low expression in body and head tissues and higher expression in antennae, legs, wings and ovipositor tissues. Count data produced through featureCounts

were normalised and used to produce this figure using the pheatmap R package (<https://CRAN.Rproject.org/package=pheatmap>). Gene expression data were hierarchically clustered using a k-means approach and count data was transformed using variance stabilizing transformation, both using the R DESeq2 package. 121

Figure 2.19. Bar plots indicating the average TPM (transcripts per kilobase per million reads) per tissue type of adult female (red) and male (blue) *S. noctilio* wasps for each SnocIR gene. Y-axis indicates transcripts per kilobase per million reads (TPM). X-axis indicates tissue type: A, Antennae; B, Body; H, Head; L, Legs; O, Ovipositor; W, Wings. TPM values were transformed as follow: $\text{mean}(\log(\text{tpm} + 1))$ 122

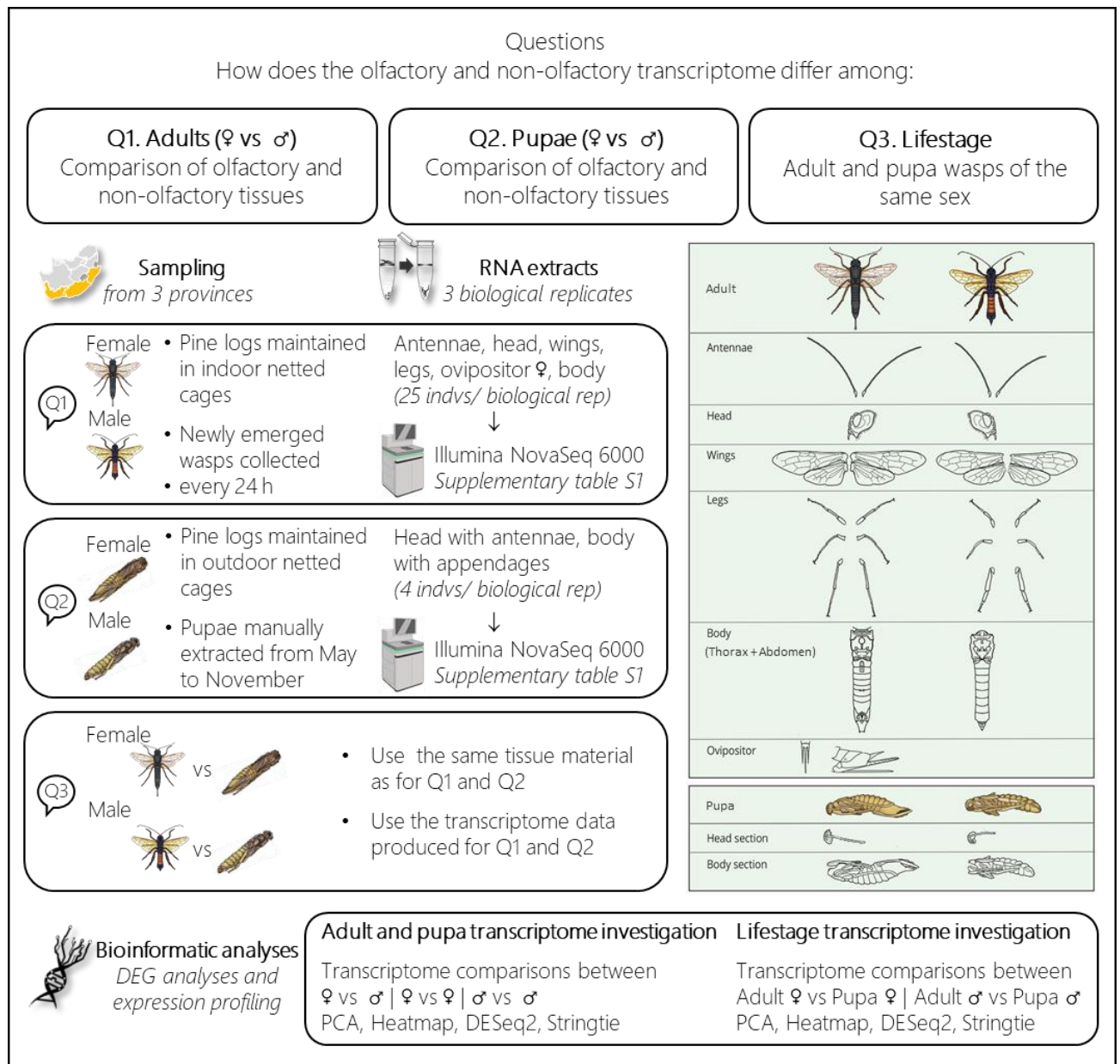


Figure 2.1. Overview of study.

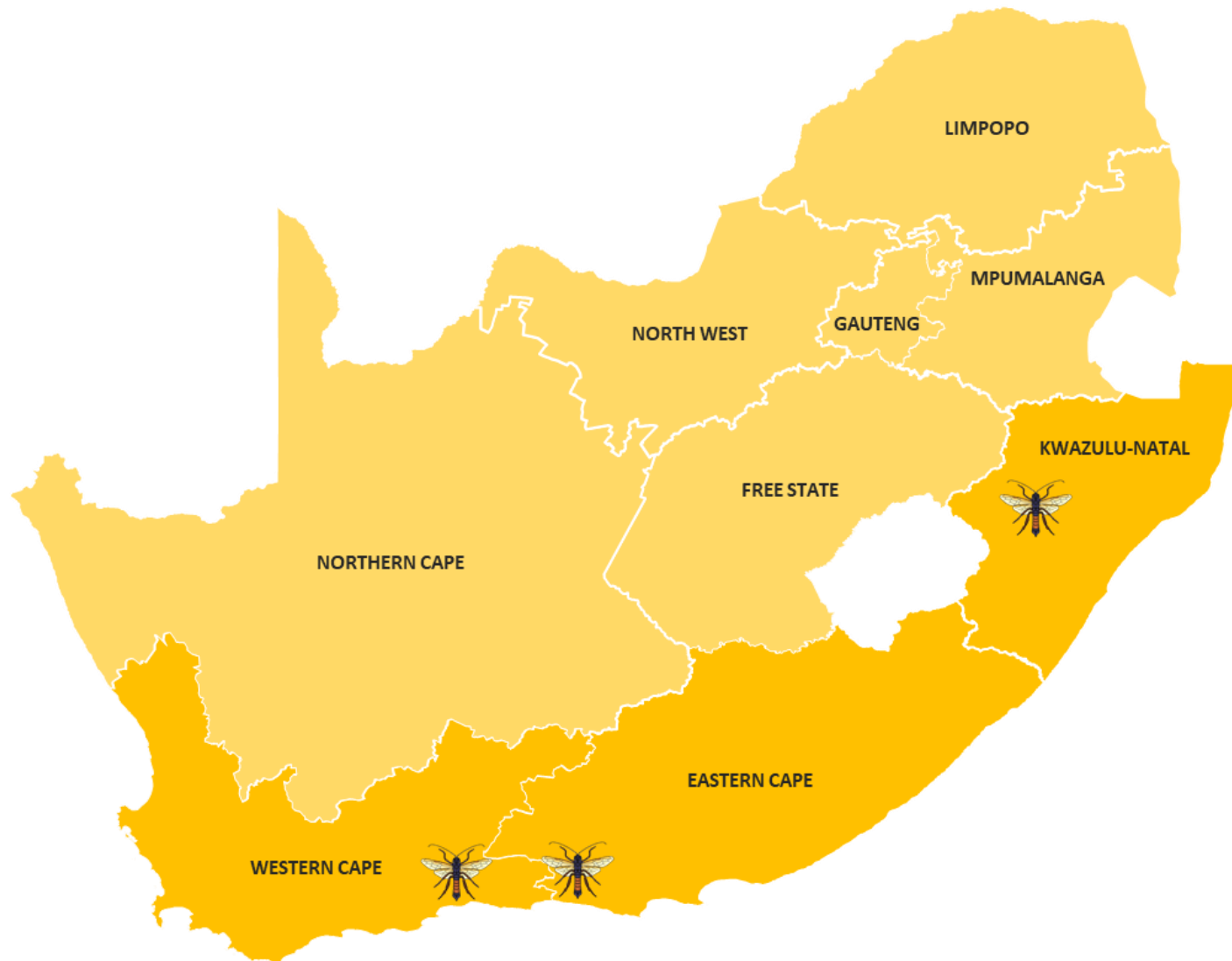


Figure 2.2. Map indicating where infested pine logs were collected in South Africa

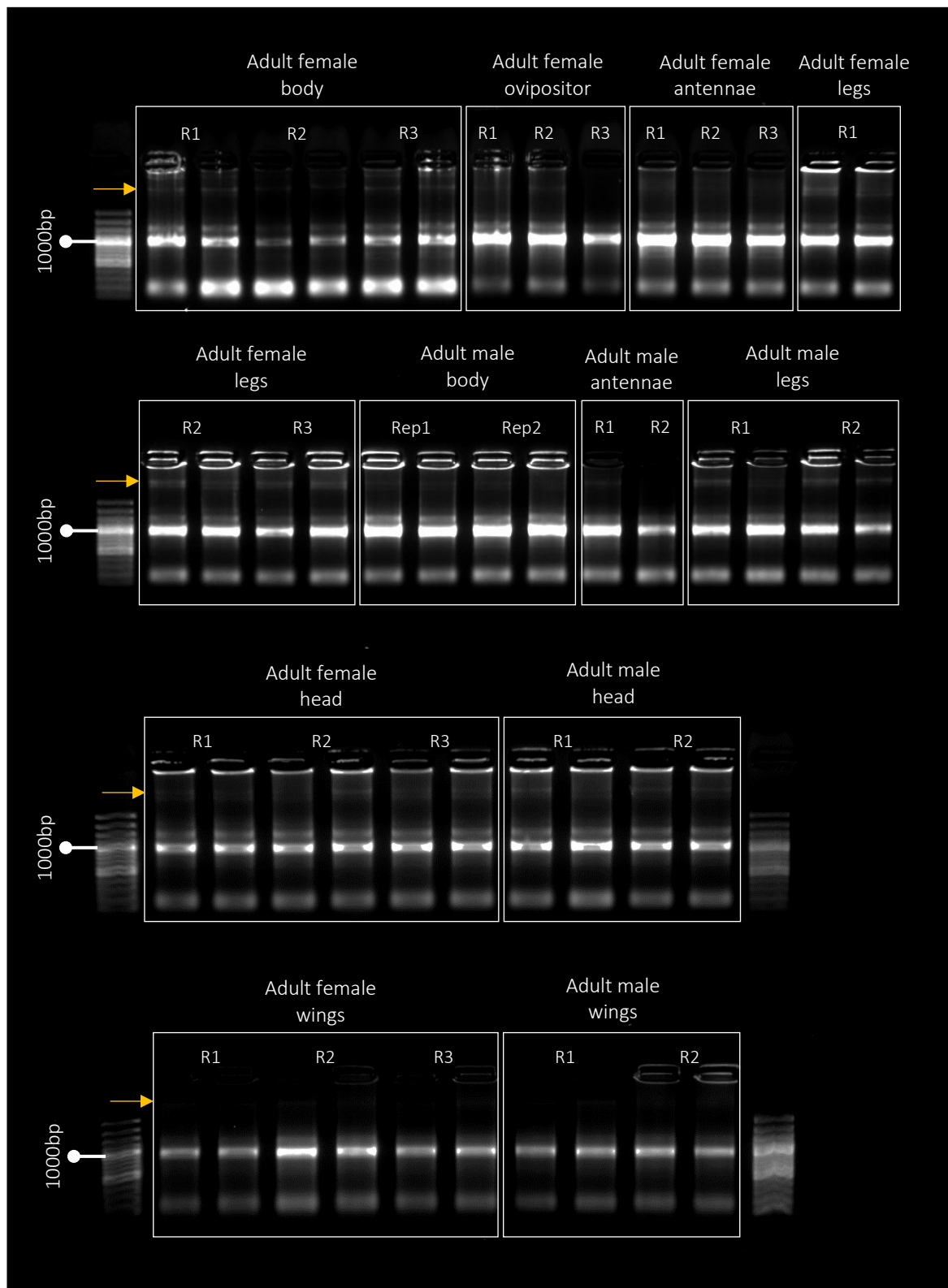


Figure 2.3. Agarose gel electrophoresis results of total RNA extractions using the TRIzol protocol.

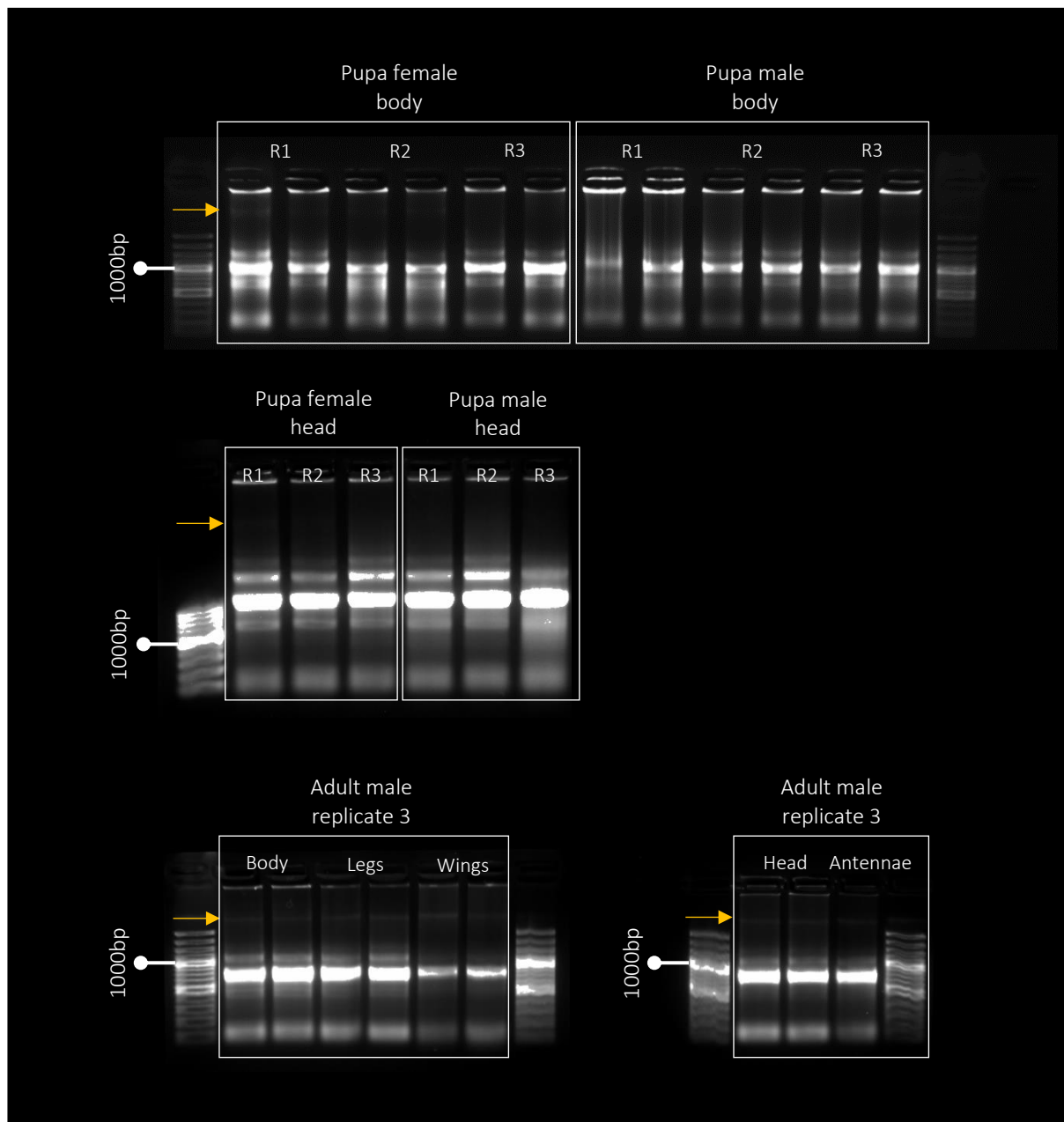


Figure 2.3. (Continue). Agarose gel electrophoresis results of total RNA extractions using the TRIzol protocol.

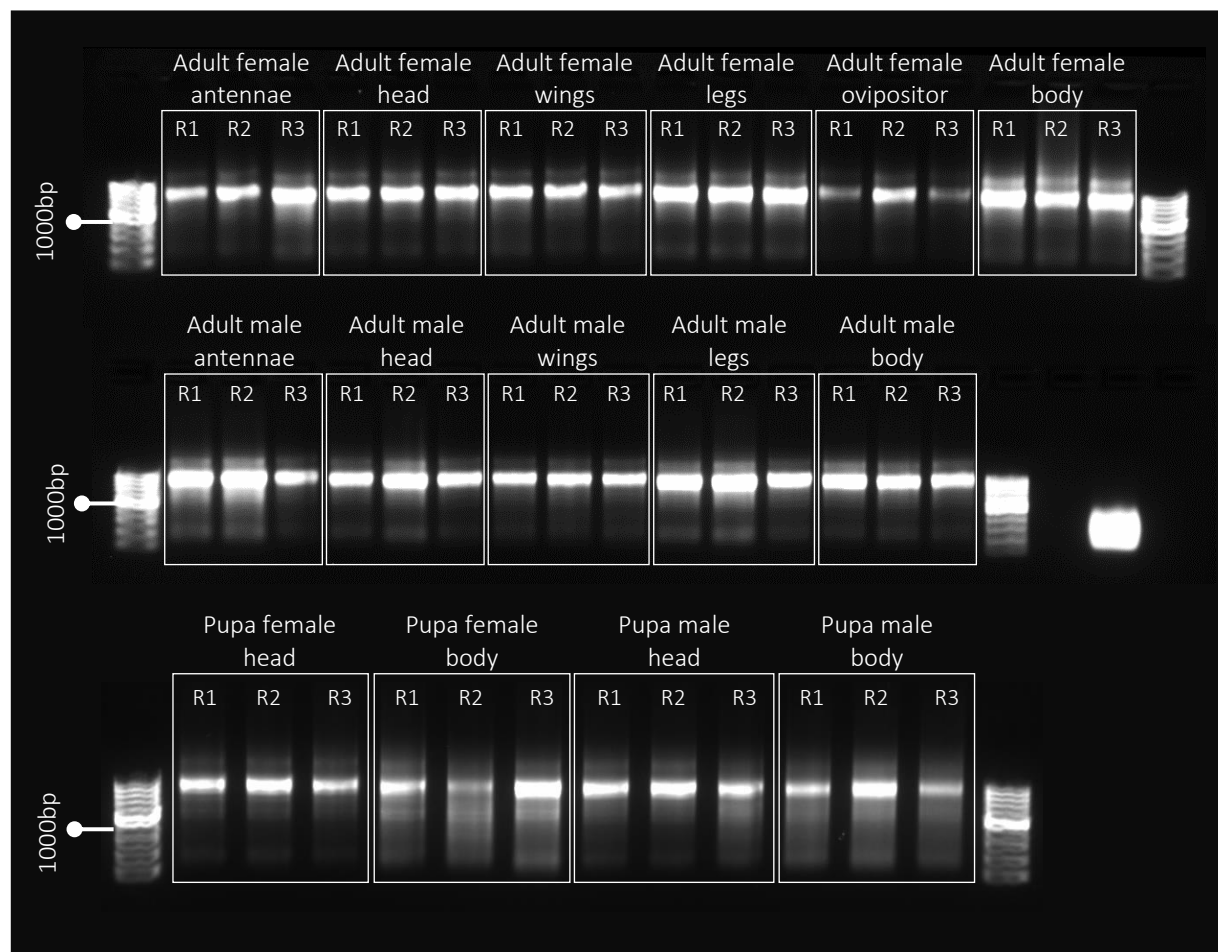


Figure 2.4. Agarose gel electrophoresis results of DNase treated RNA samples.

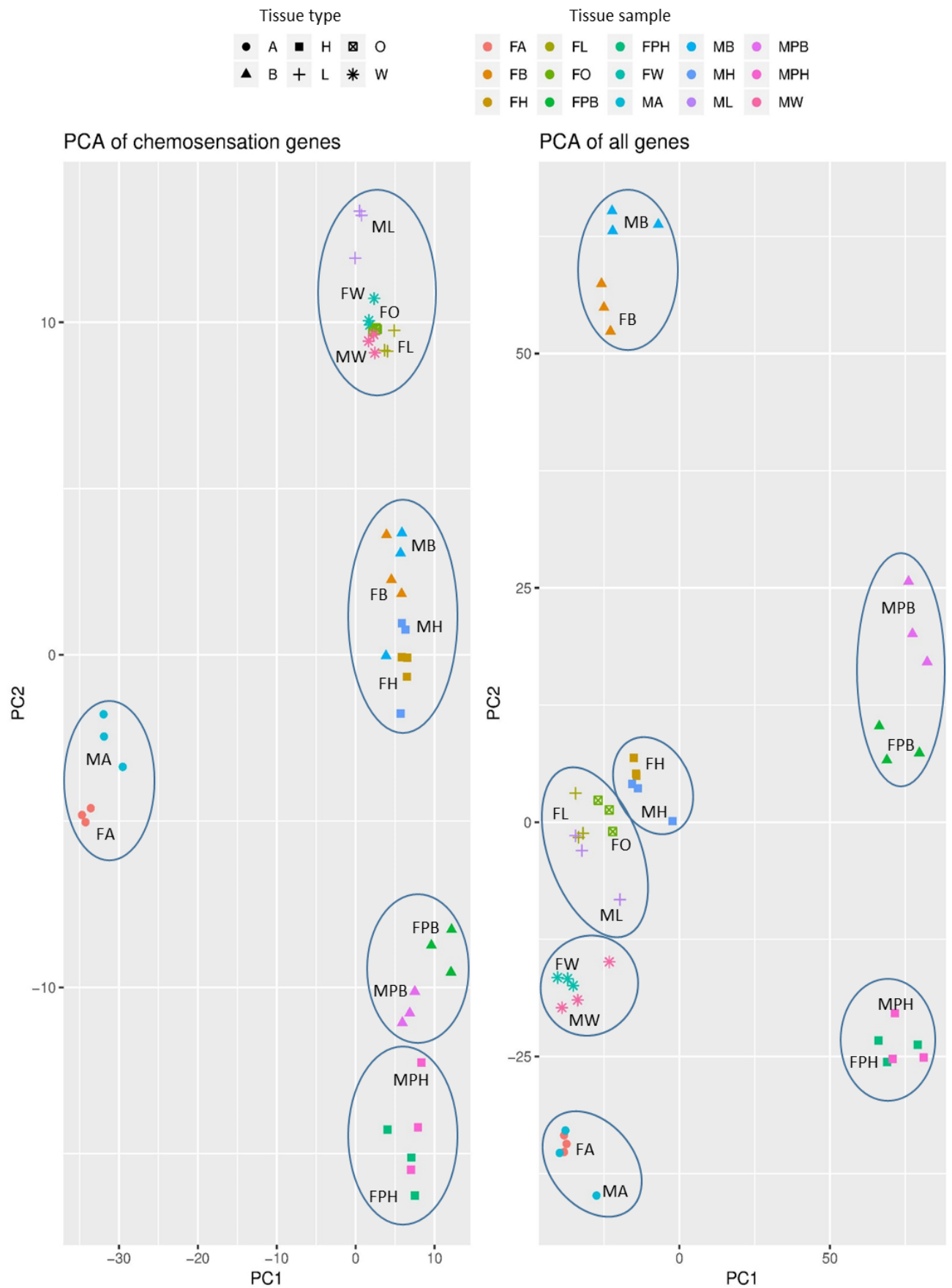


Figure 2.5. Principal component analysis (PCA) performed on the expression data of *S. noctilio* for chemosensation genes (left) and all expressed genes (right).

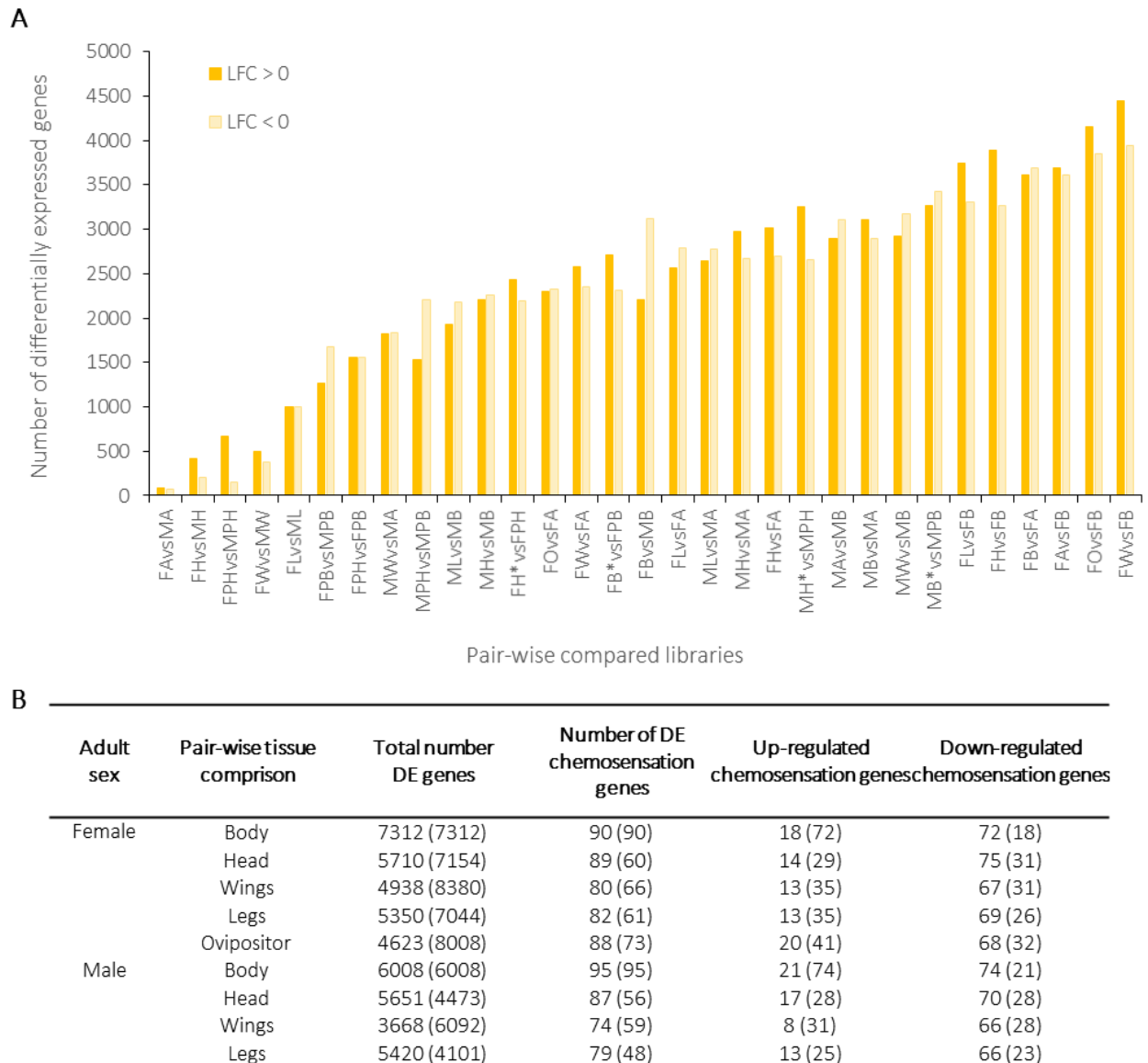


Figure 2.6. Significantly differentially expressed (DE) genes (adjusted p-value < 0.05) identified through pair-wise comparisons of different RNA tissue libraries of *S. noctilio*.

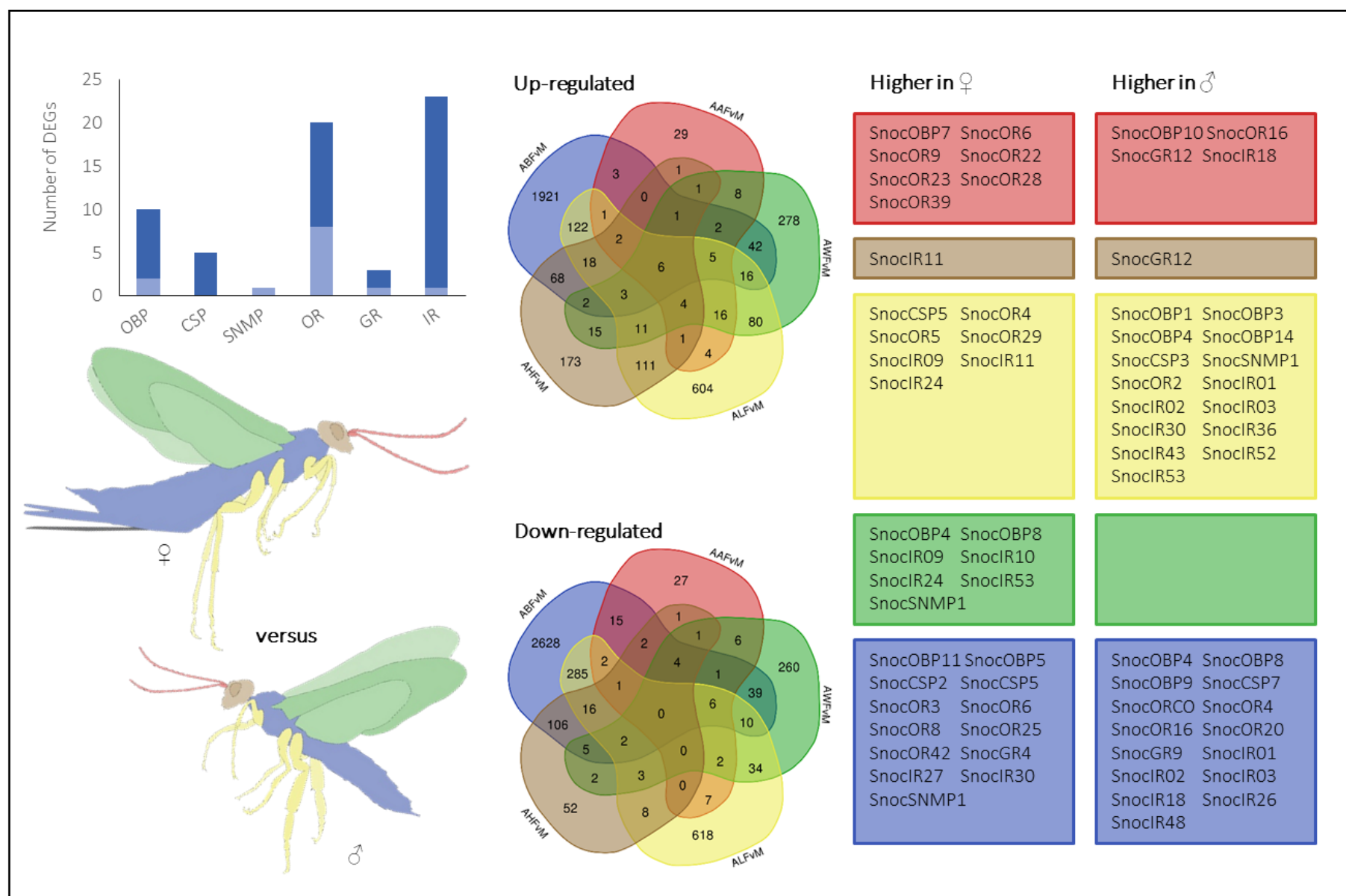


Figure 2.7. Sex-biased chemosensation genes of female and male *S. noctilio* in different tissues.

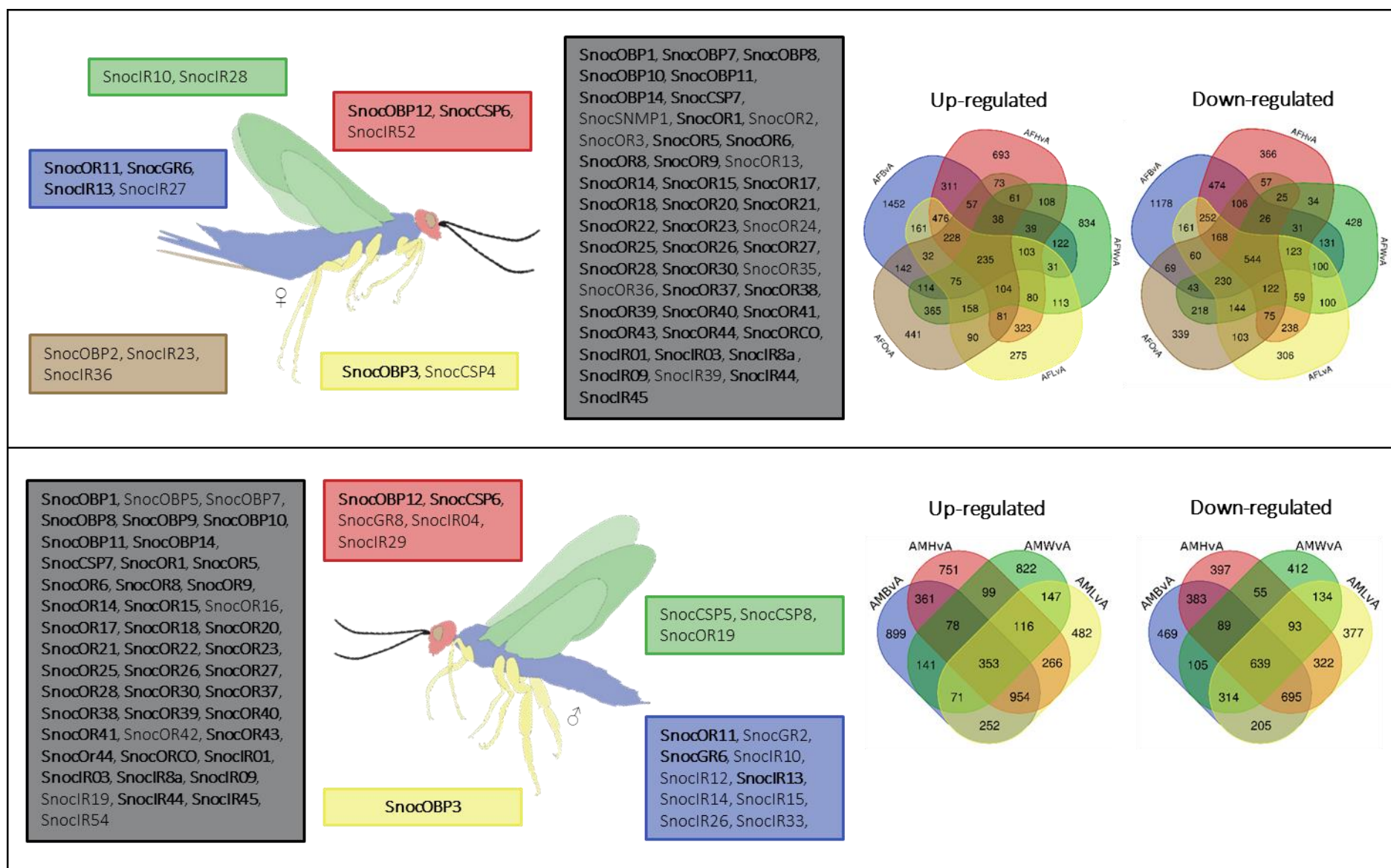
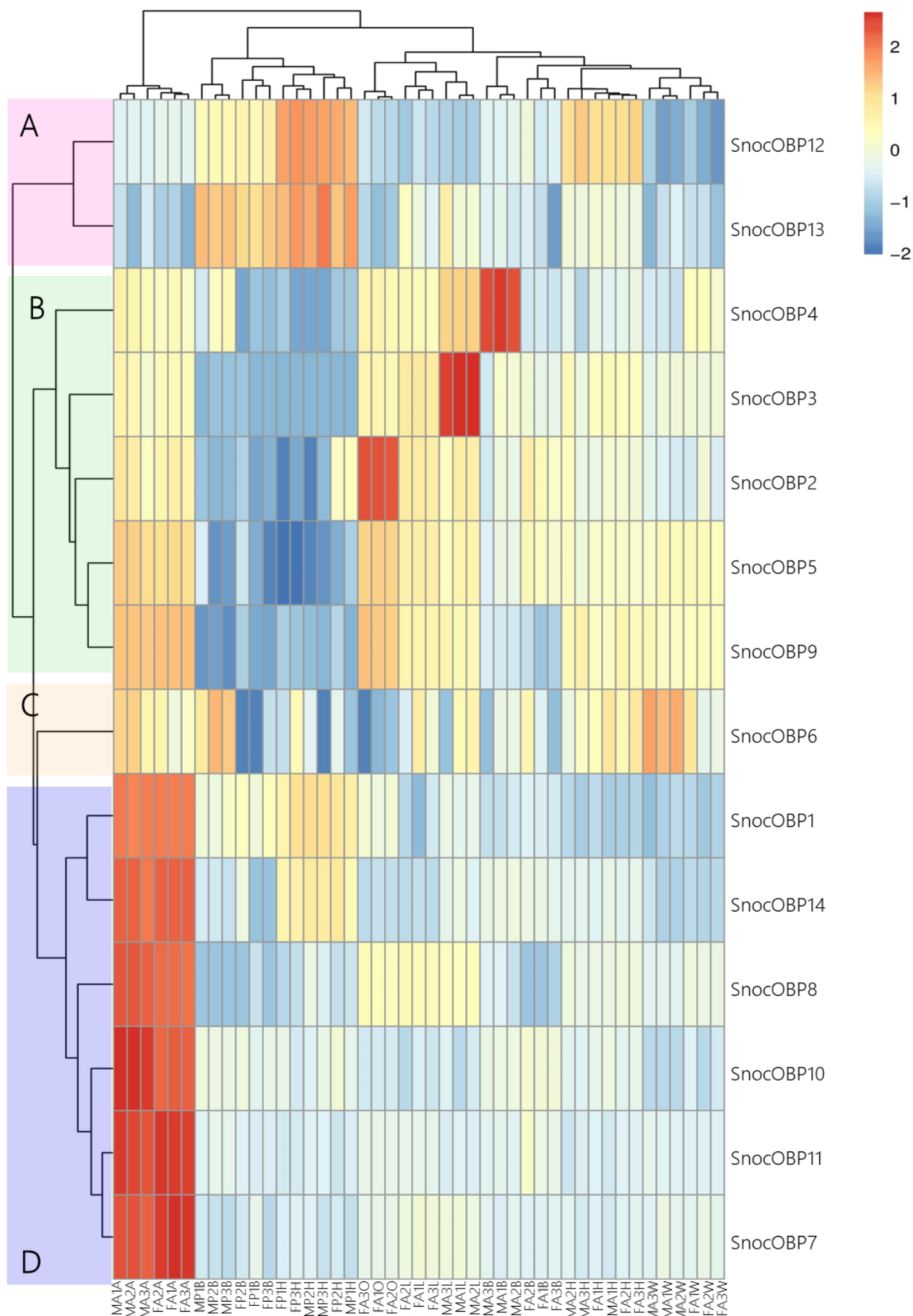


Figure 2.8. Tissue-biased chemosensation genes of female and male *S. noctilio*.



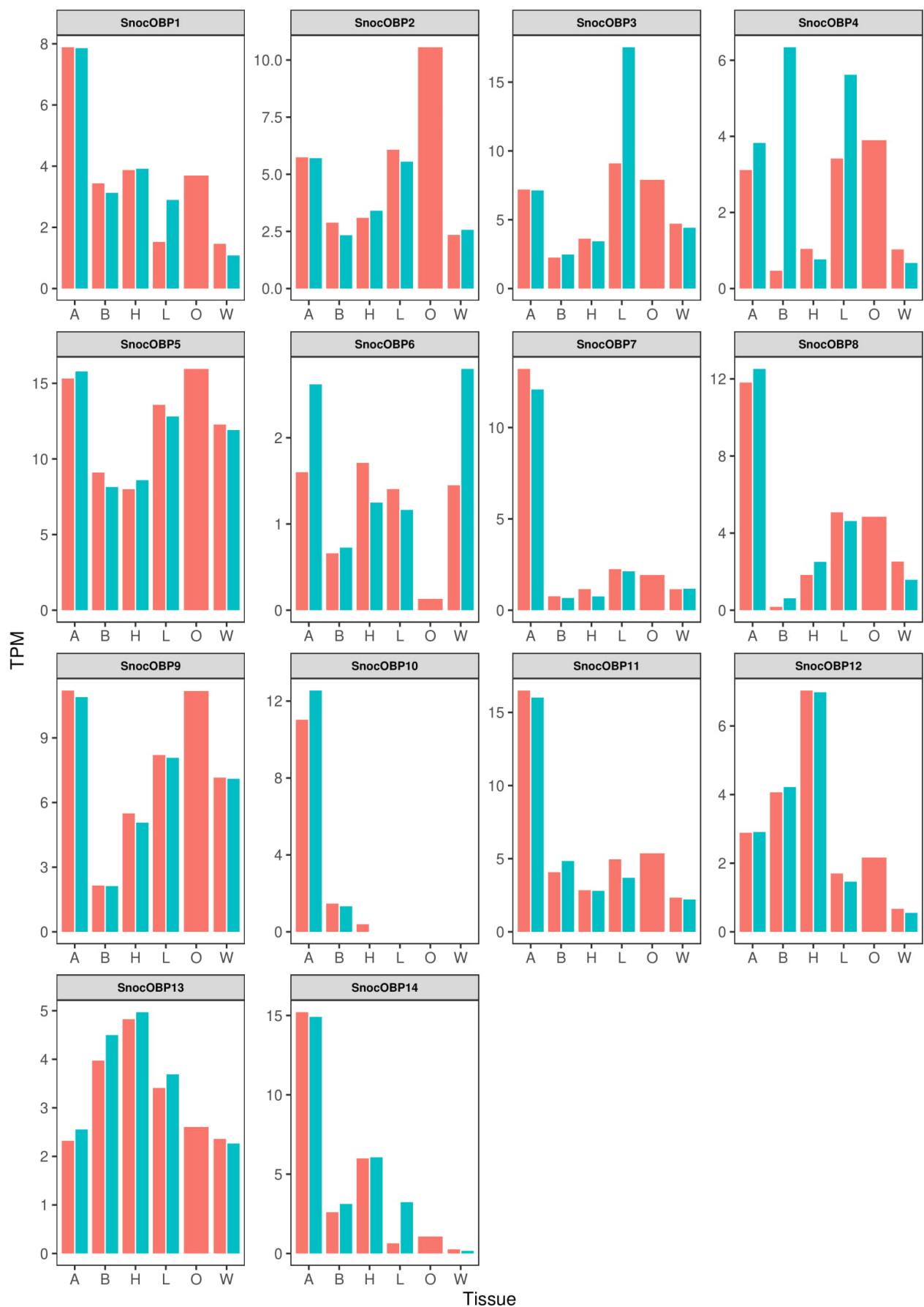


Figure 2.10. Bar plots indicating the average TPM (transcripts per kilobase per million reads) per tissue type of adult female (red) and male (blue) *S. noctilio* wasps for each SnocOBP gene.

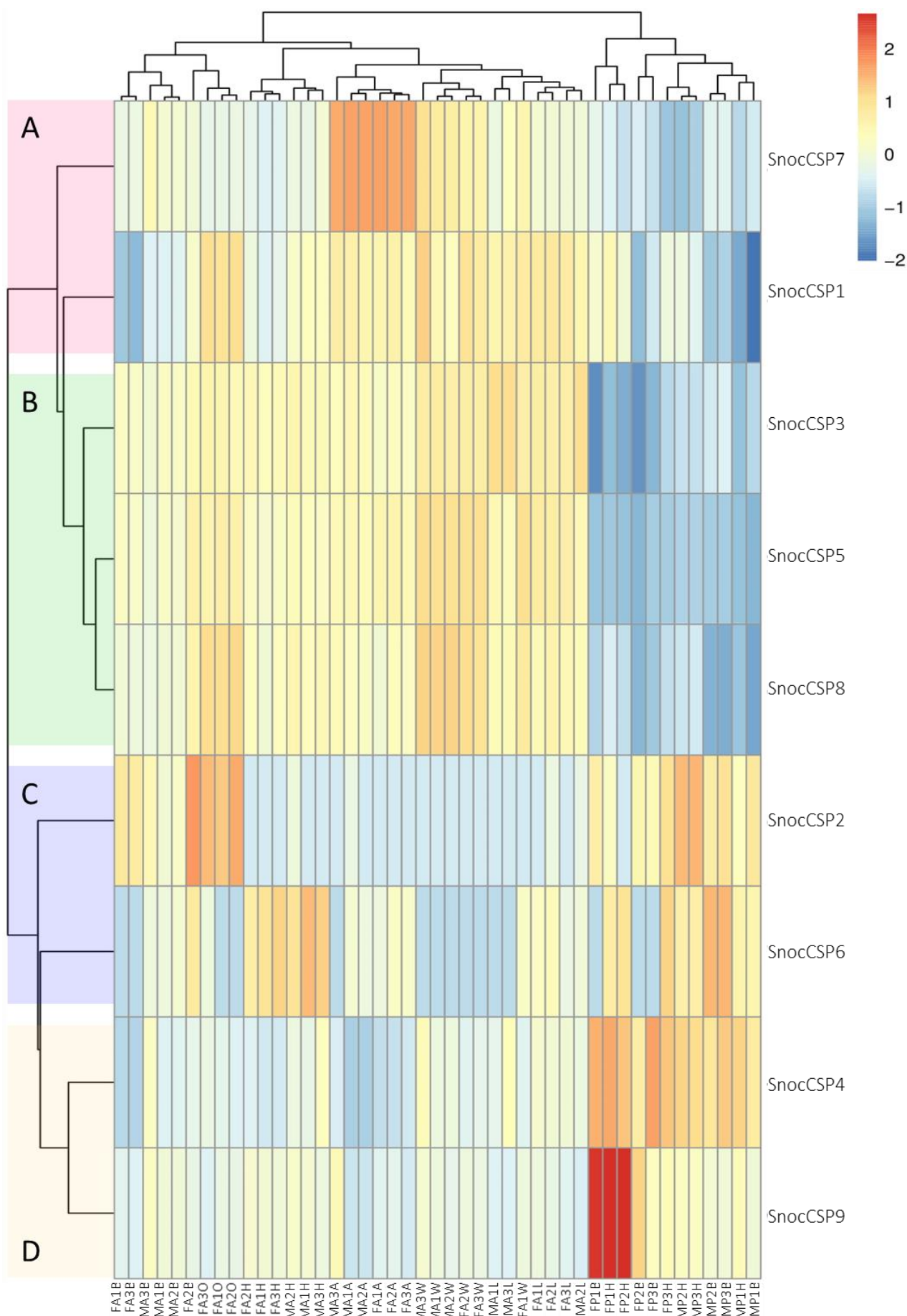


Figure 2.11. Hierarchical clustered heatmap of *S. noctilio* chemosensory proteins (SnocCSP#) gene expression across various tissue types of adult and pupa developmental stages.

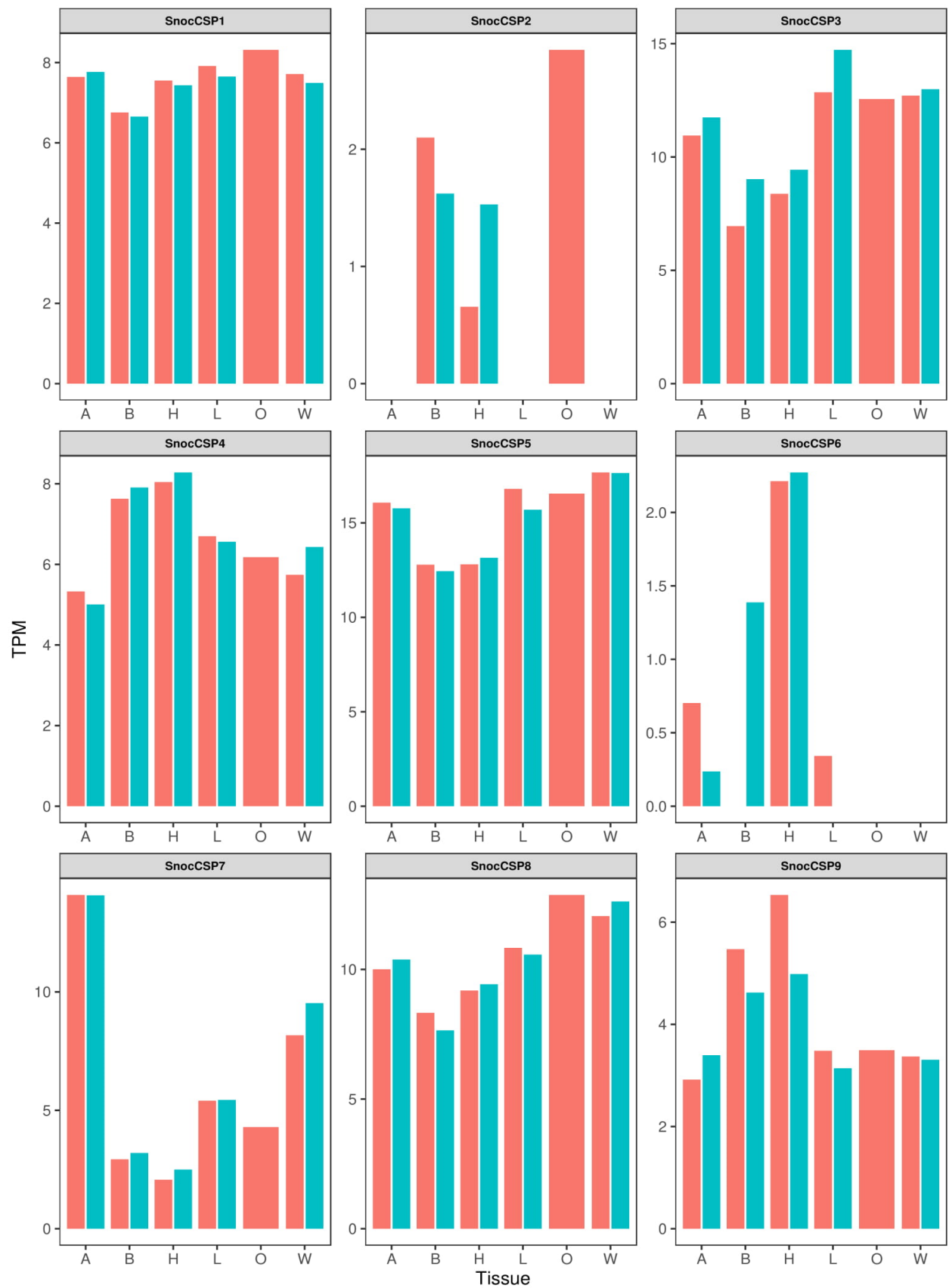


Figure 2.12. Bar plots indicating the average TPM (transcripts per kilobase per million reads) across tissue types of adult female (red) and male (blue) *S. noctilio* wasps for each SnocCSP gene.

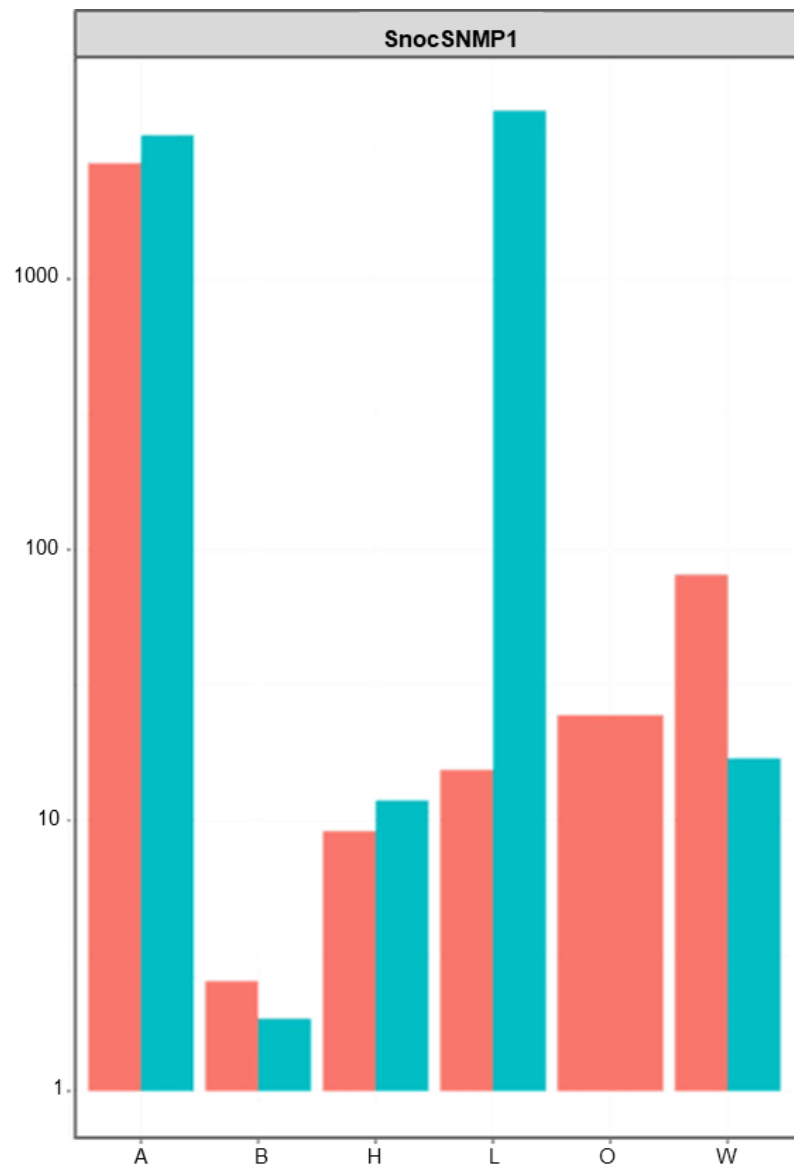


Figure 2. 13. Bar plots indicating the average TPM (transcripts per kilobase per million reads) across tissue types of adult female (red) and male (blue) *S. noctilio* wasps for the SnocSNMP1 gene.

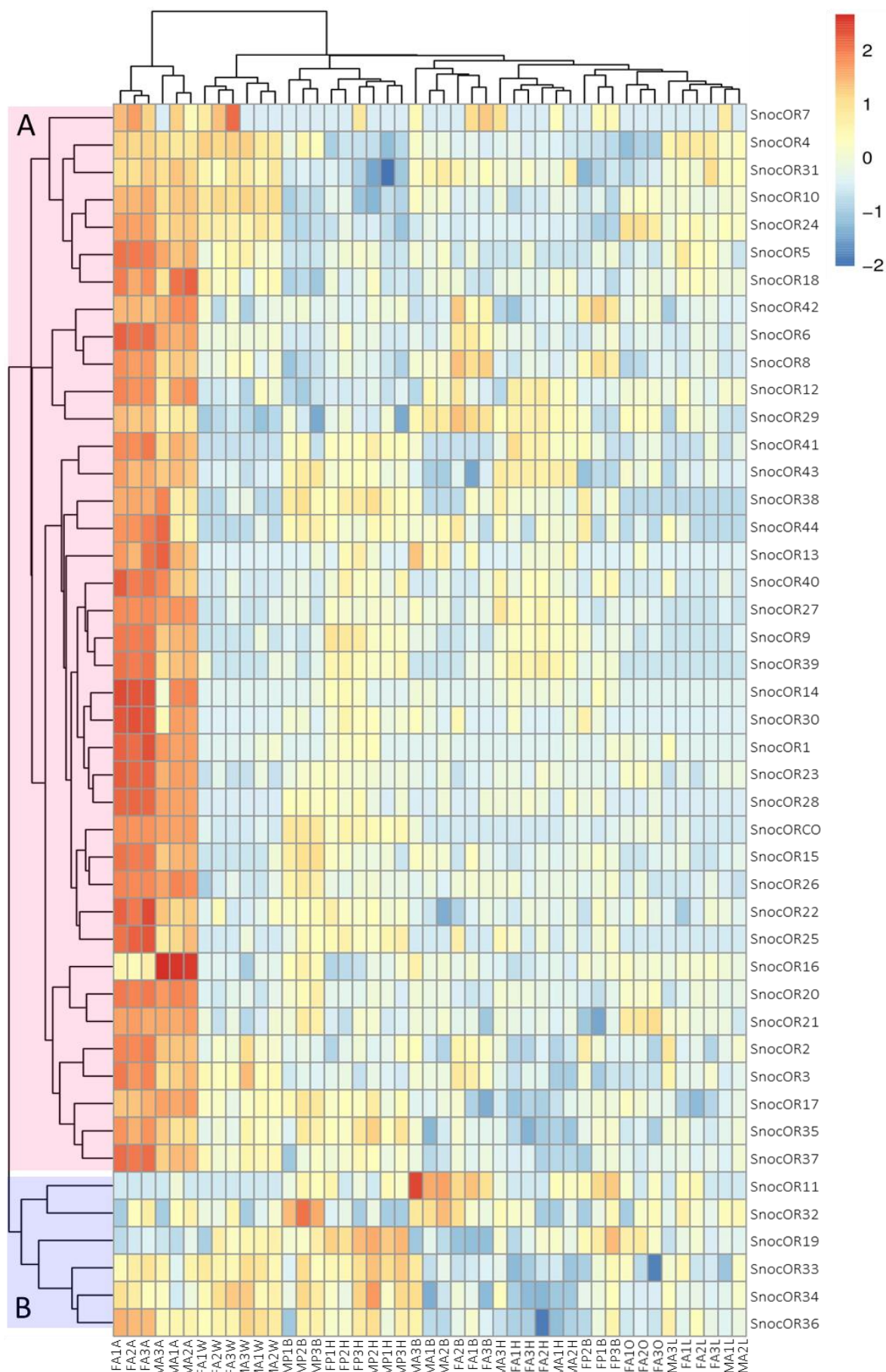


Figure 2.14. Hierarchical clustered heatmap of *S. noctilio* olfactory receptor's (SnocOR#) gene expression across various tissue types of adult and pupa developmental stages.



Figure 2.15. Bar plots indicating the average TPM (transcripts per kilobase per million reads) across tissue types of adult female (red) and male (blue) *S. noctilio* wasps SnocOR for each gene.

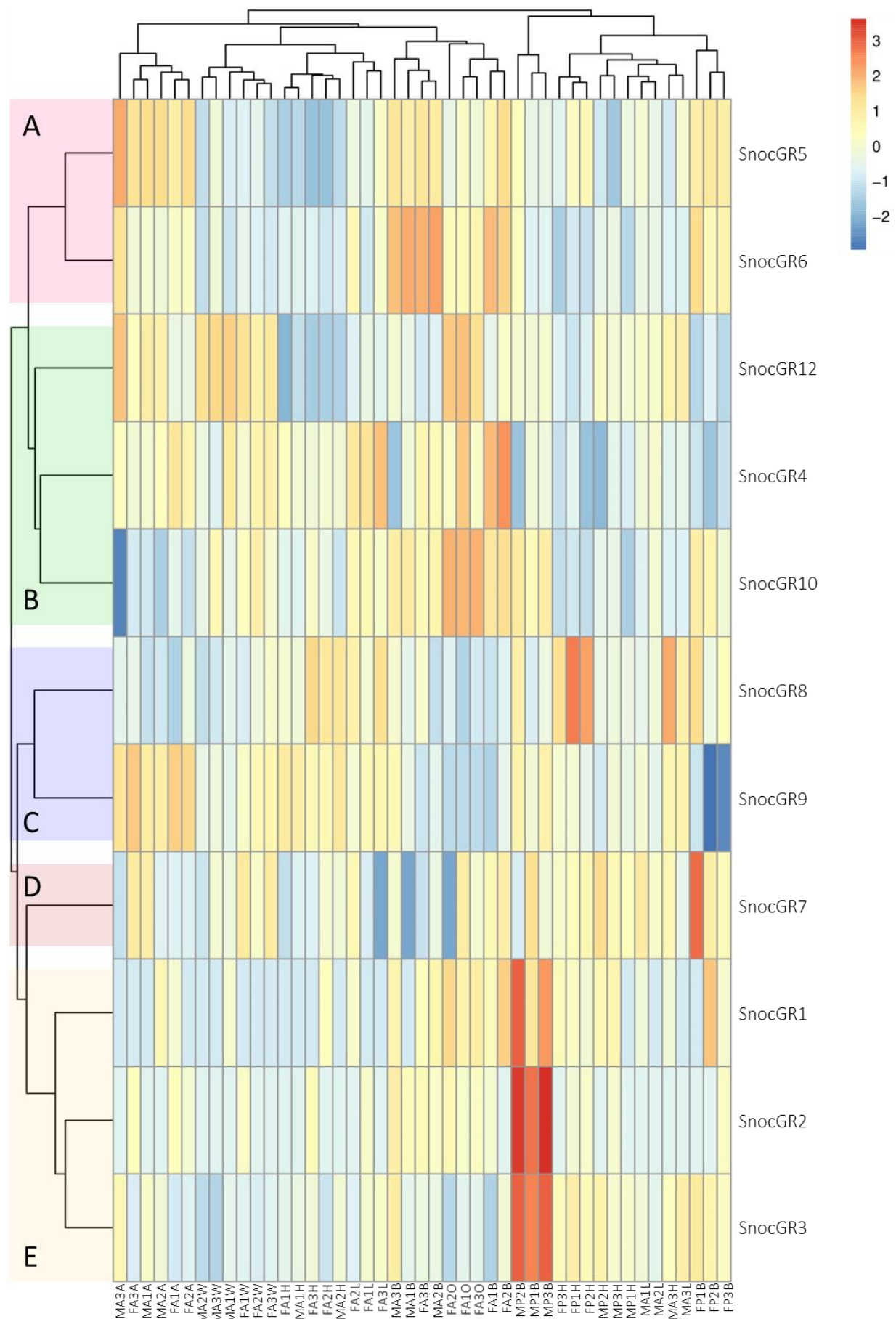


Figure 2.16. Hierarchical clustered heatmap of *S. noctilio* gustatory receptor's (SnocGR#) gene expression across various tissue types of adult and pupa developmental stages.

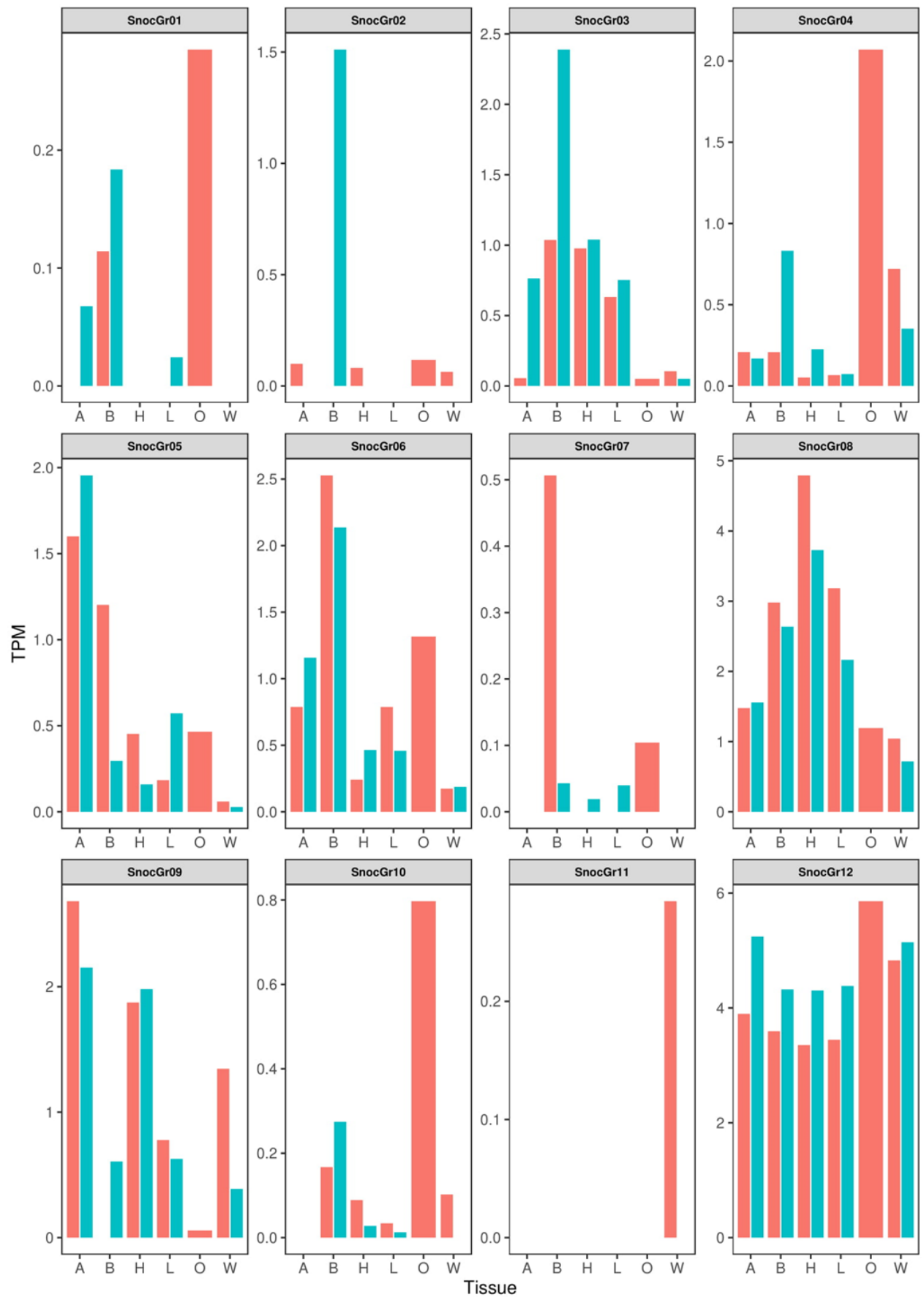


Figure 2.17. Bar plots indicating the average TPM (transcripts per kilobase per million reads) per tissue type of adult female (red) and male (blue) *S. noctilio* wasps for each SnocGR gene.

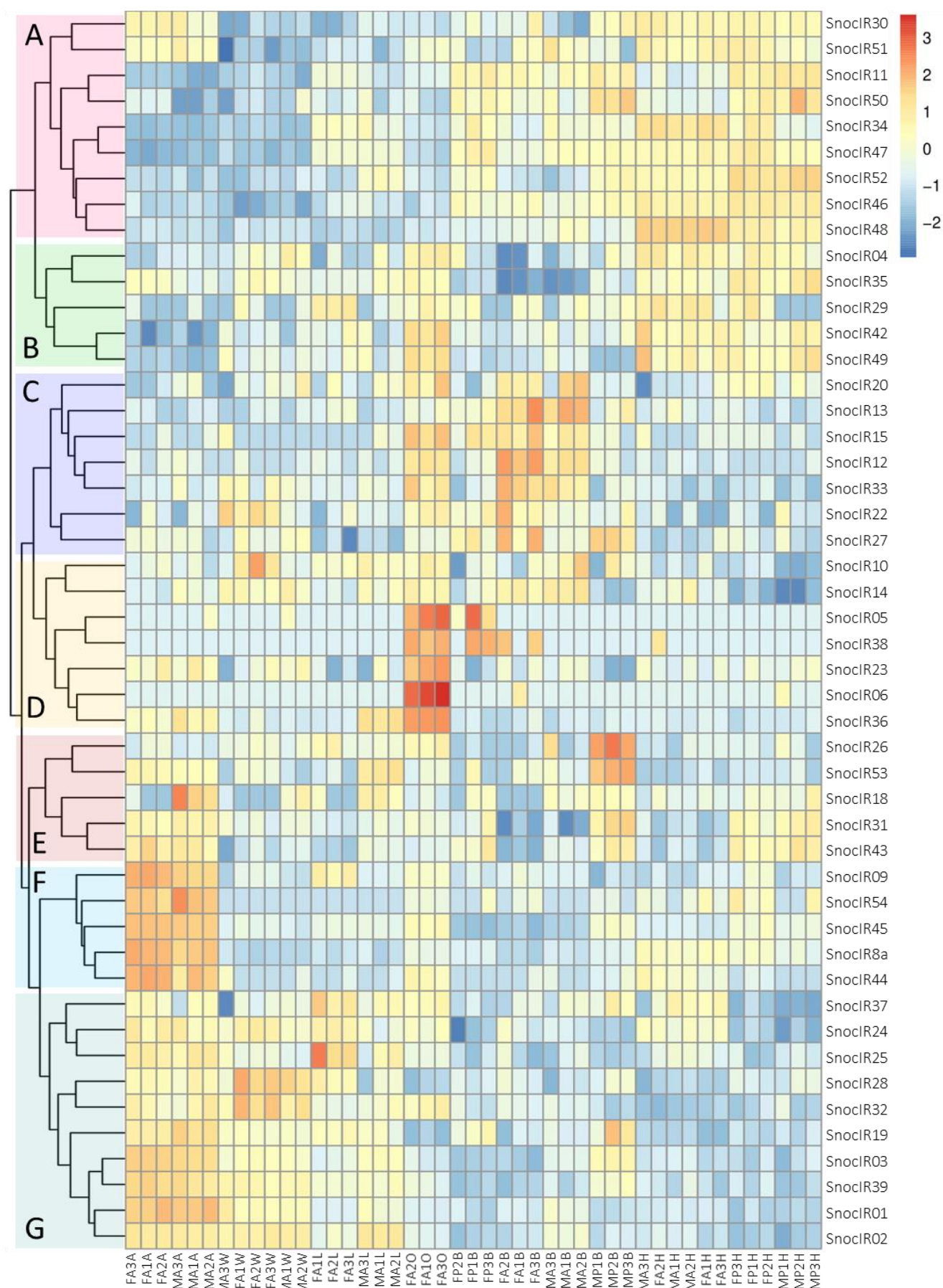


Figure 2.18. Hierarchical clustered heatmap of *S. noctilio* ionotropic receptor's (SnocIR#) gene expression across various tissue types of adult and pupa developmental stages.



Figure 2.19. Bar plots indicating the average TPM (transcripts per kilobase per million reads) per tissue type of adult female (red) and male (blue) *S. noctilio* wasps for each SnocIR gene.

2.11. Supplementary material

Supplementary figures

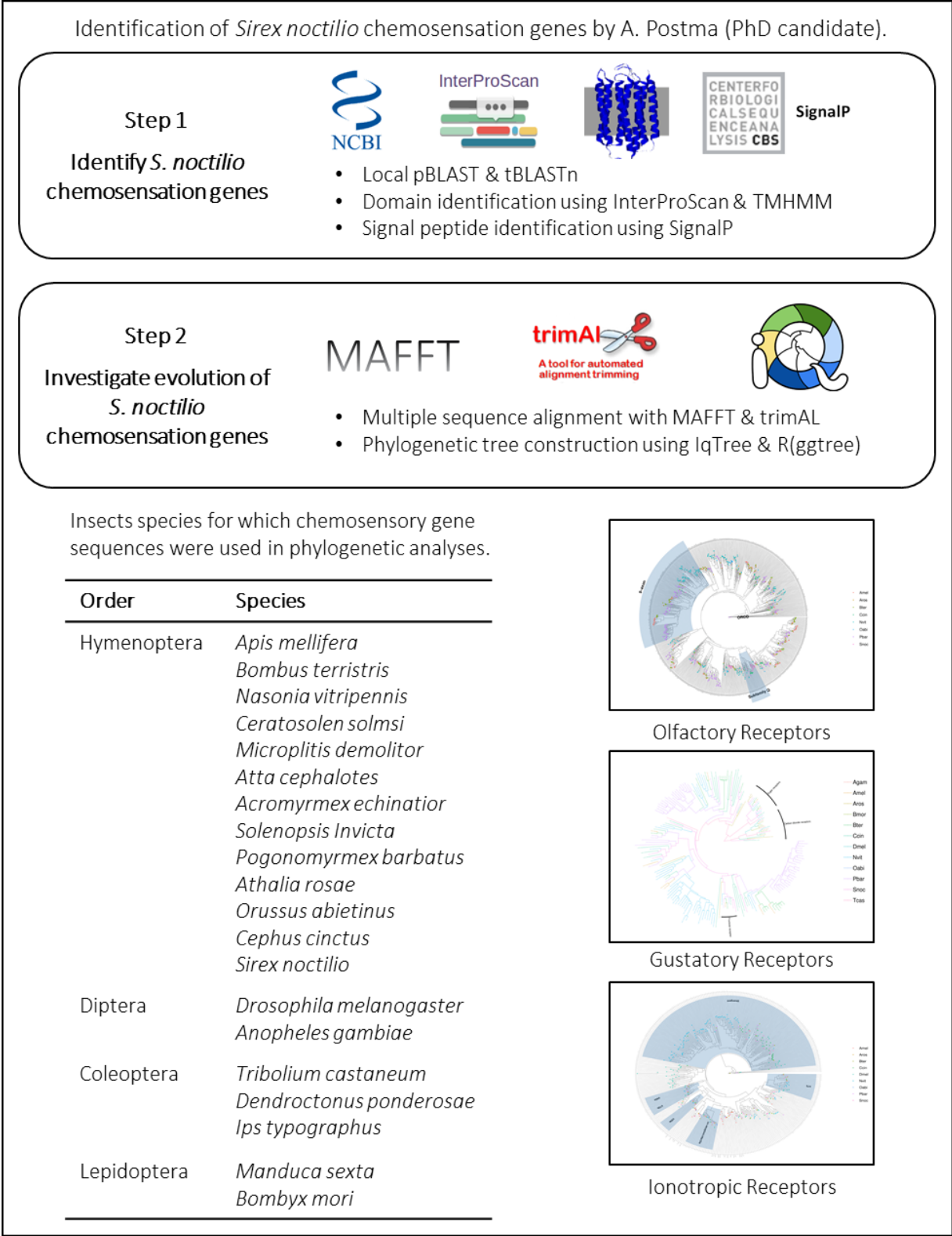


Figure S2.1. Identification and phylogenetic analysis of *S. noctilio* chemosensory genes. Analyses conducted by Ms. Alisa Postma during her PhD degree. Enlarged versions of phylogenetic trees in ensuing pages and available [online](#).

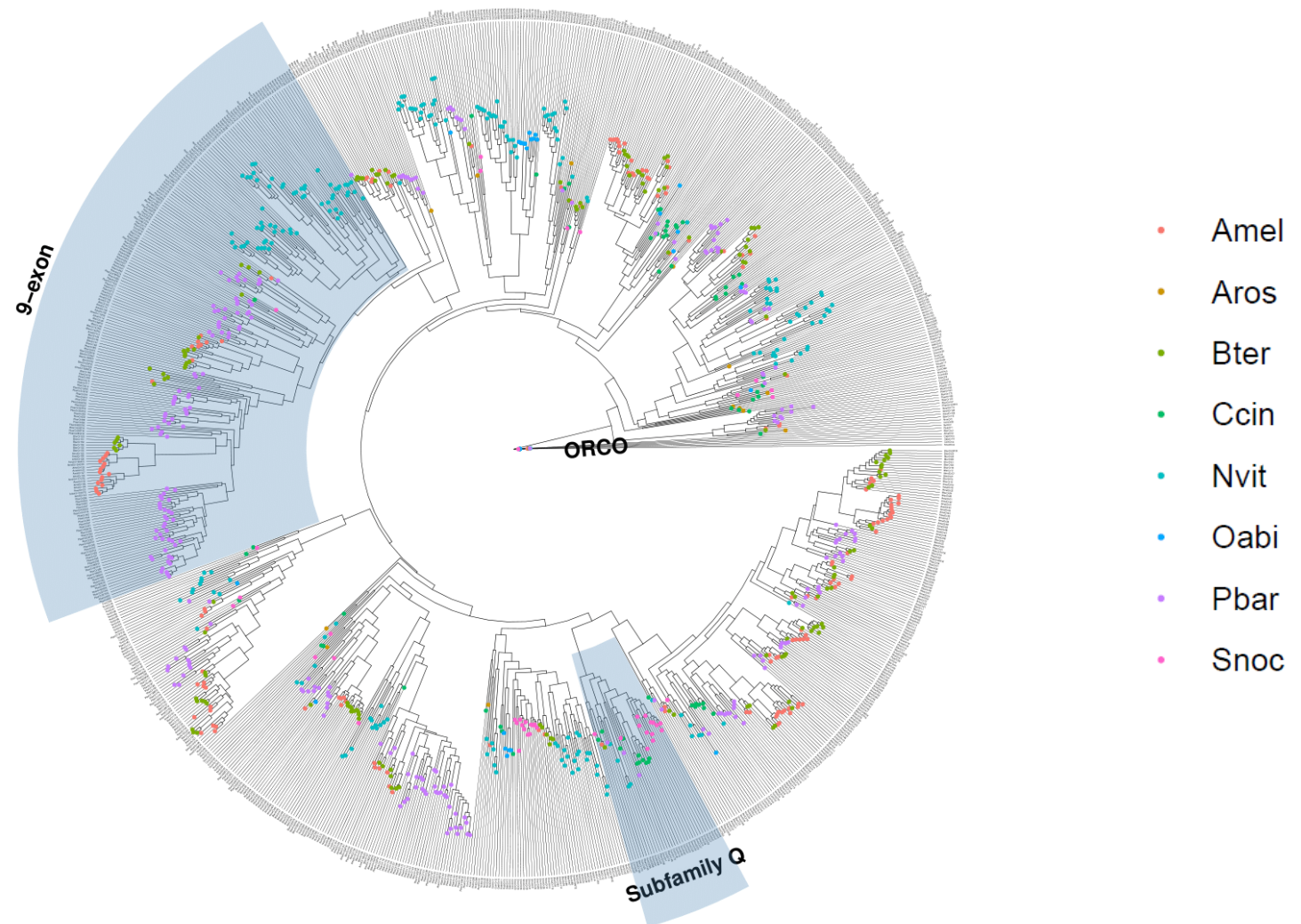


Figure S2. 2. Identification and phylogenetic analysis of *S. noctilio* olfactory receptor genes. Amel, *A. mellifera*; Aros, *A. rosea*; Bter, *B. terrestris*; Ccin, *C. cinctus*; Nvit, *N. vitripennis*; Oabi, *O. abientinus*; Pbar, *P. barbatus*; Snoc, *S. noctilio*.

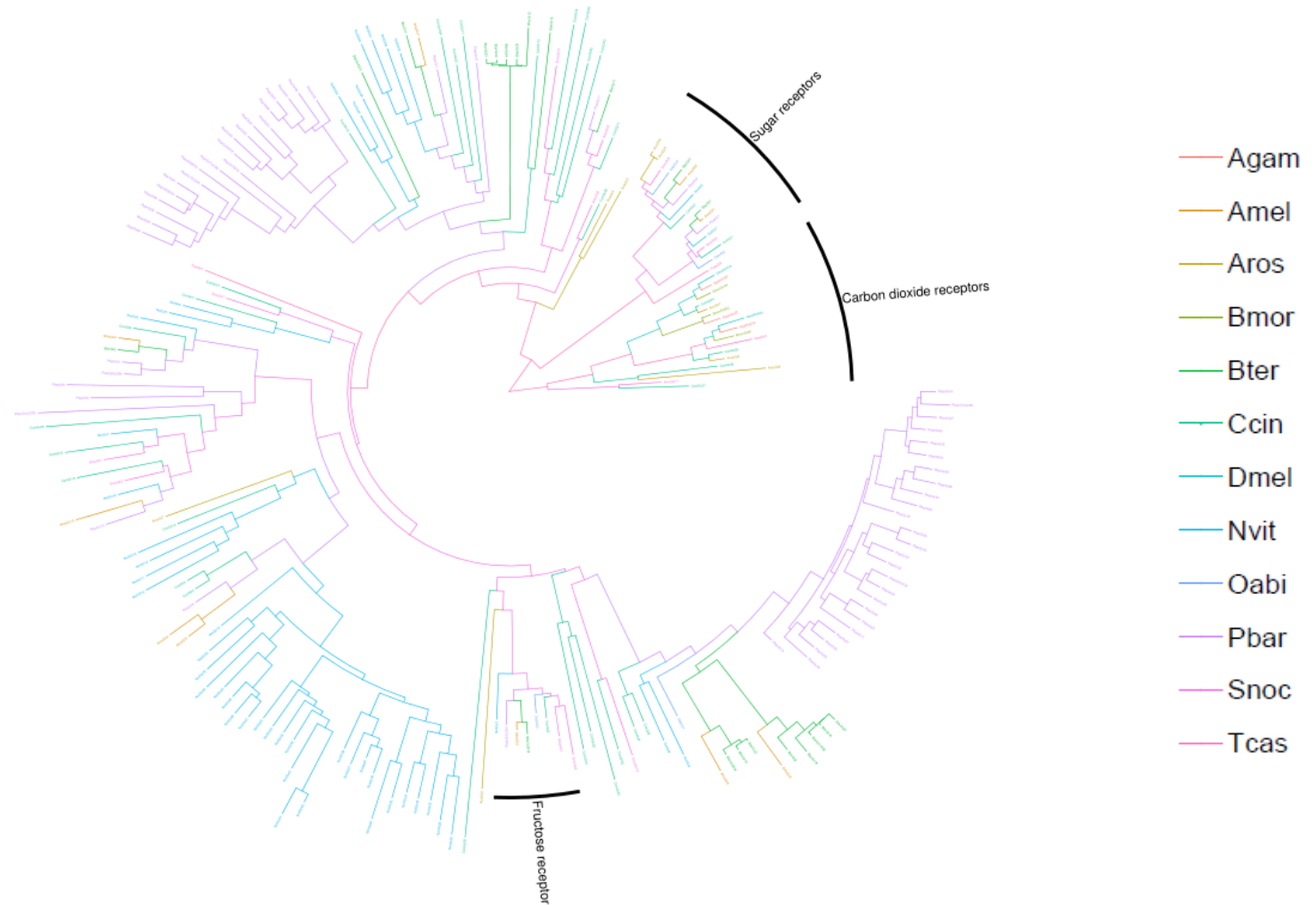


Figure S2.3. Identification and phylogenetic analysis of *S. noctilio* gustatory receptor genes. Agam, *A. gambiae*; Amel, *A. mellifera*; Aros, *A. rosea*; Bmor, *B. mori*; Bter, *B. terrestris*; Ccin, *C. cinctus*; Dmel, *D. melanogaster*; Nvit, *N. vitripennis*; Oabi, *O. abientinus*; Pbar, *P. barbatus*; Snoc, *S. noctilio*; Tcas, *Tribolium castaneum*.

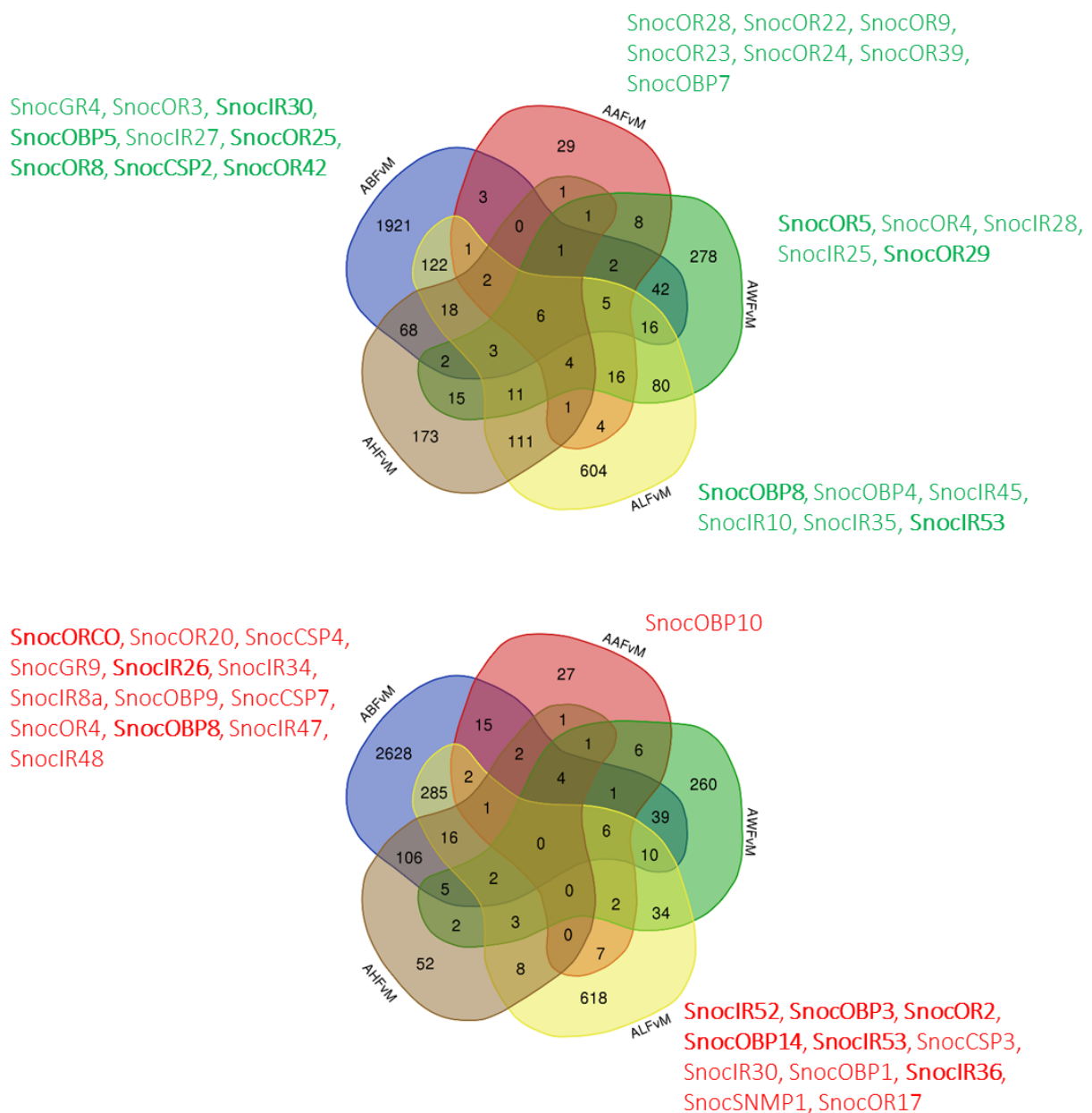


Figure S2.5. Chemosensory genes uniquely differentially expressed in olfactory and non-olfactory tissues of adult female and male *S. noctilio*. Significantly differentially expressed genes (DEGs): adjusted p-value < 0.05, $|\log_2\text{FoldChange}| > 0$. Genes indicated around the Venn diagram were differentially expressed for the specific body tissue. Genes indicated in bold had a $\log_2\text{FoldChange} > 2$. Genes indicated in green were up-regulated in female tissues (less expressed in male tissues) and genes indicated in red were down-regulated in female tissues (more expressed in male tissues). ABFvM – Adult body female vs. male; AAFvM – Adult antennae female vs. male; AWFvM – Adult wings female vs. male; ALFvM – Adult legs female vs. male; AHFvM – Adult head female vs. male. Venn diagrams of DEGs were constructed using an online Venn tool, <http://bioinformatics.psb.ugent.be/webtools/Venn/>.

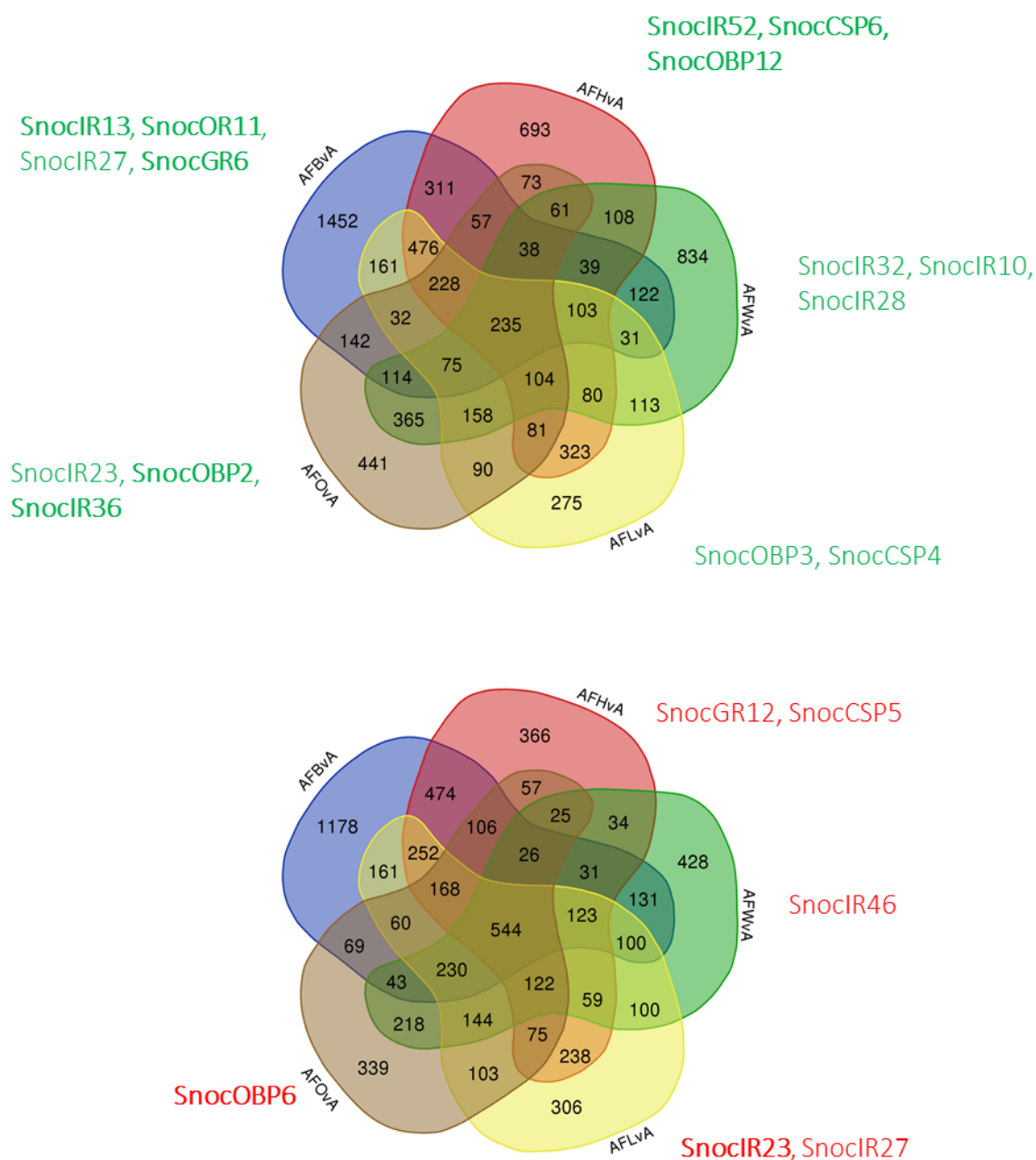


Figure S2.6. Chemosensory genes uniquely differentially expressed in olfactory and non-olfactory tissues compared to antennal tissues of adult female *S. noctilio*. Significantly differentially expressed genes (DEGs): adjusted p-value < 0.05, $|\log_2\text{FoldChange}| > 0$. Genes indicated around the venn diagram were differentially expressed for the specific body tissue. Genes indicated in bold had a $\log_2\text{FoldChange} > 2$. Genes indicated in **green** were **up-regulated** in female tissues (less expressed in male tissues) and genes indicated in **red** were **down-regulated** in female tissues (more expressed in male tissues). **AFBvA** – Adult female body vs. antennae; **AFHvA** – Adult female head vs. antennae; **AFWvA** – Adult female wings vs. antennae; **AFLvA** – Adult female legs vs. antennae; **AFOvA** – Adult female ovipositor vs. antennae. Venn diagrams of DEGs were constructed using an online Venn tool, <http://bioinformatics.psb.ugent.be/webtools/Venn/>.

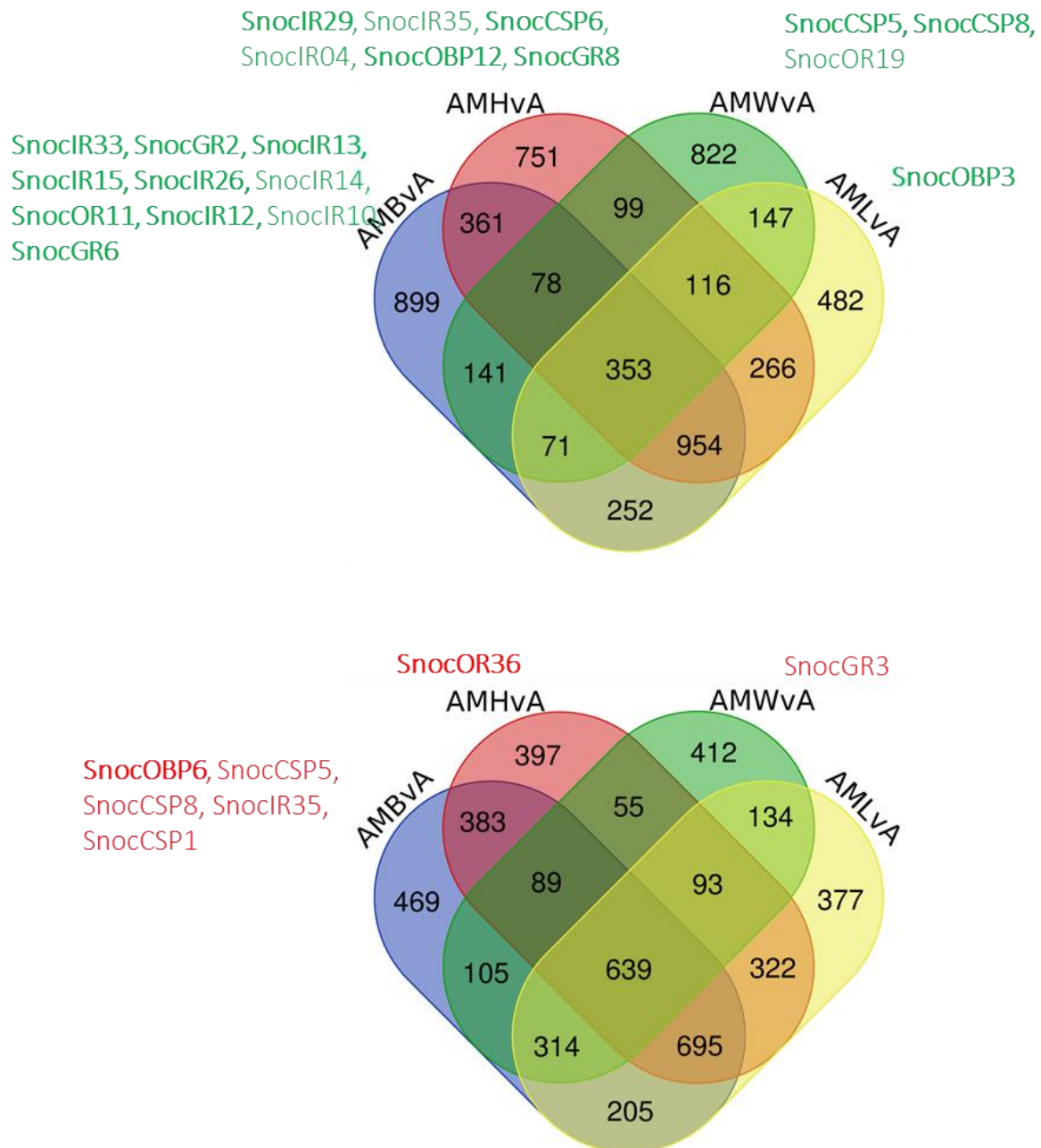


Figure S2.7. Chemosensory genes uniquely differentially expressed in olfactory and non-olfactory tissues compared to antennal tissues of adult male *S. noctilio*. Significantly differentially expressed genes (DEGs): adjusted p-value < 0.05, $|\log_2\text{FoldChange}| > 0$. Genes indicated around the venn diagram were differentially expressed for the specific body tissue. Genes indicated in bold had a $\log_2\text{FoldChange} > 2$. Genes indicated in green were up-regulated in female tissues (less expressed in male tissues) and genes indicated in red were down-regulated in female tissues (more expressed in male tissues). **AMBvA** – Adult male body vs. antennae; **AMHvA** – Adult male head vs. antennae; **AMWvA** – Adult male wings vs. antennae; **AMLvA** – Adult male legs vs. antennae. Venn diagrams of DEGs were constructed using an online Venn tool, <http://bioinformatics.psb.ugent.be/webtools/Venn/>.

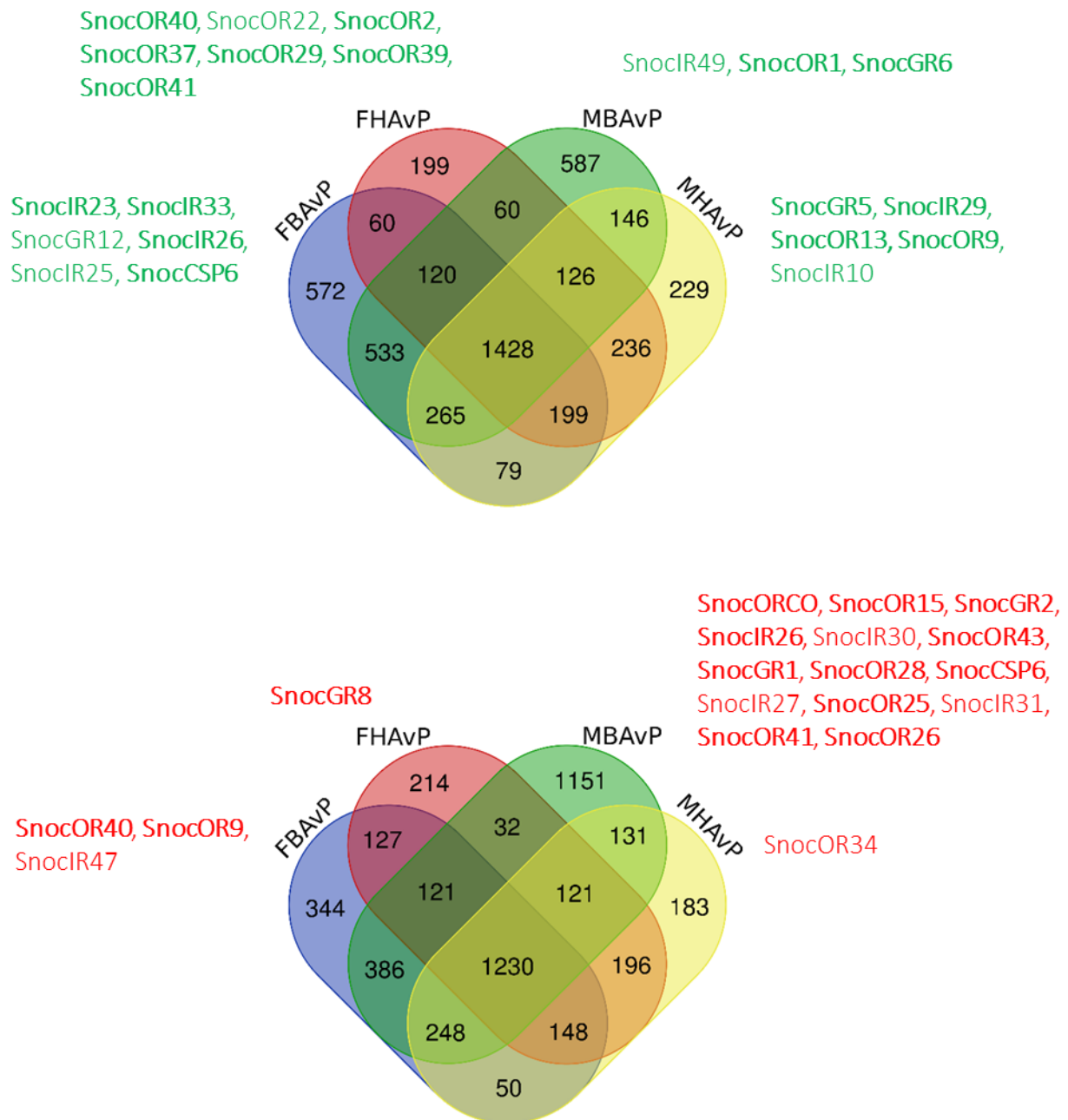


Figure S2.8. Chemosensory genes uniquely differentially expressed in olfactory and non-olfactory tissues compared between sexes of adult and pupa *S. noctilio*. Significantly differentially expressed genes (DEGs): adjusted p-value < 0.05, $|\log_2\text{FoldChange}| > 0$. Genes indicated around the venn diagram were differentially expressed for the specific body tissue. Genes indicated in bold had a $\log_2\text{FoldChange} > 2$. Genes indicated in green were up-regulated in female tissues (less expressed in male tissues) and genes indicated in red were down-regulated in female tissues (more expressed in male tissues). FBAvP – Female body adult vs. pupa; FHAVP – Female body adult vs. pupa; MBAvP – Male body adult vs. pupa; MHAvP – Male head adult vs. pupa. Venn diagrams of DEGs were constructed using an online Venn tool, <http://bioinformatics.psb.ugent.be/webtools/Venn/>.

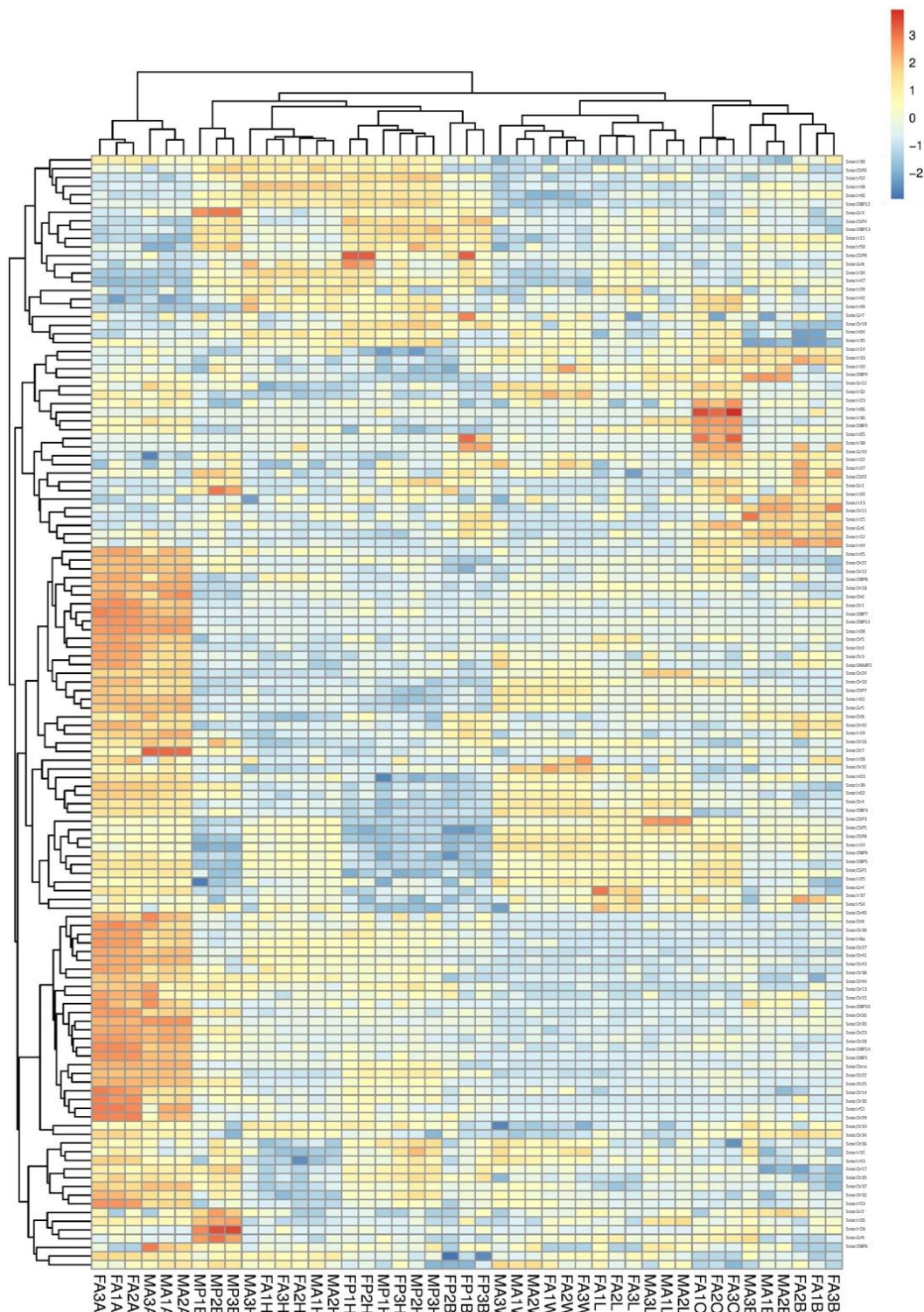


Figure S2.9. Heatmap of chemosensation gene expression in *S. noctilio*. The tissue samples for which gene expression was analysed are represented in 3 biological replicates on the x-axis. Chemosensation genes of *S. noctilio* (Snoc*) are indicated on the y-axis. Count data produced through featureCounts were normalised and used to produce this figure using the pheatmap R package (<https://CRAN.Rproject.org/package=pheatmap>). Gene expression data was hierarchically clustered using a k-means approach and count data was transformed using variance stabilizing transformation, both using the R DESeq2 package.

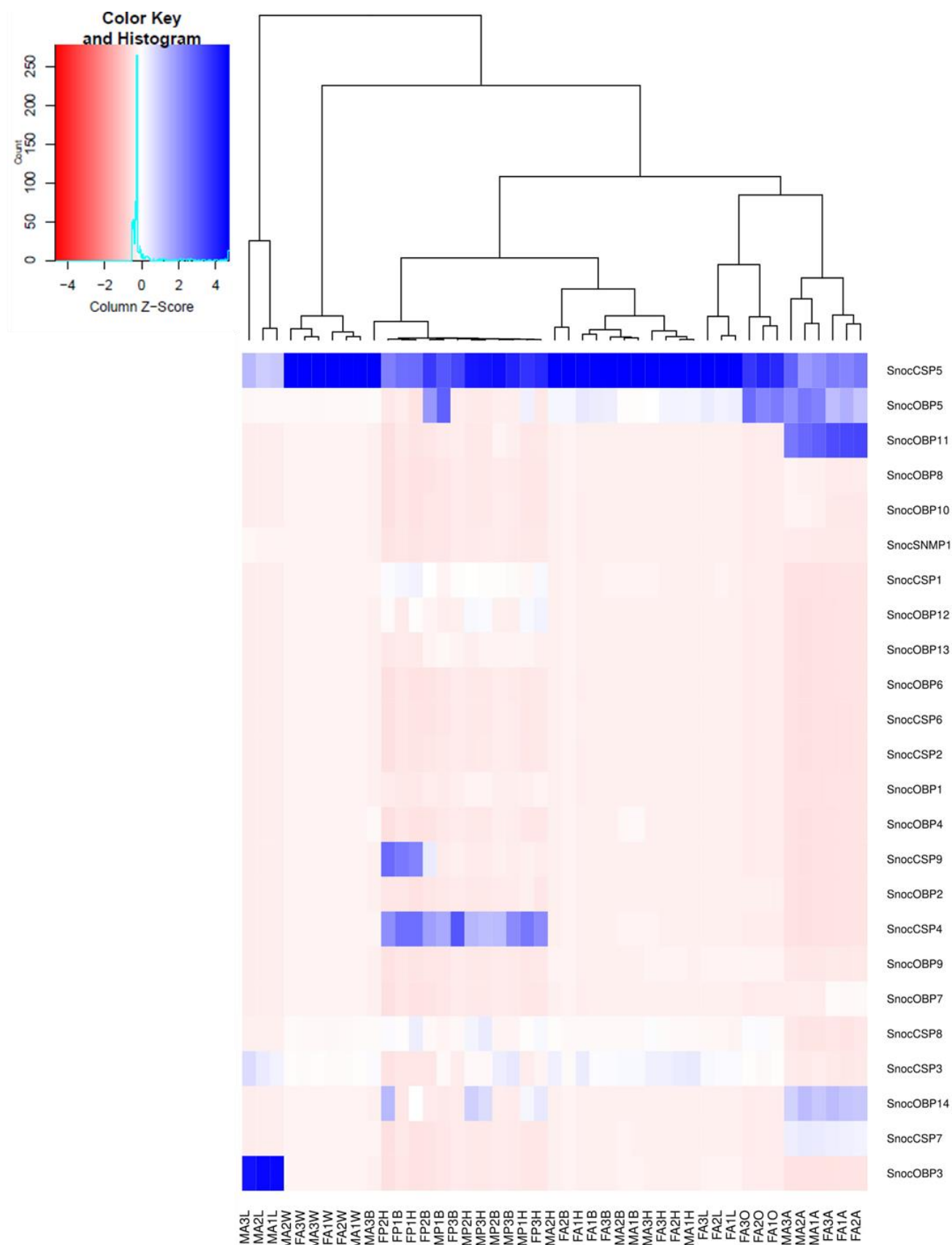


Figure S2.10. Heatmap of the expression abundances (TPM, transcripts per kilobase per million reads) of chemosensation carrier and supporting proteins (OBPs, CSPs and SNMP) of *S. noctilio*. Blue represents up-regulated genes whereas red represent down-regulated genes.

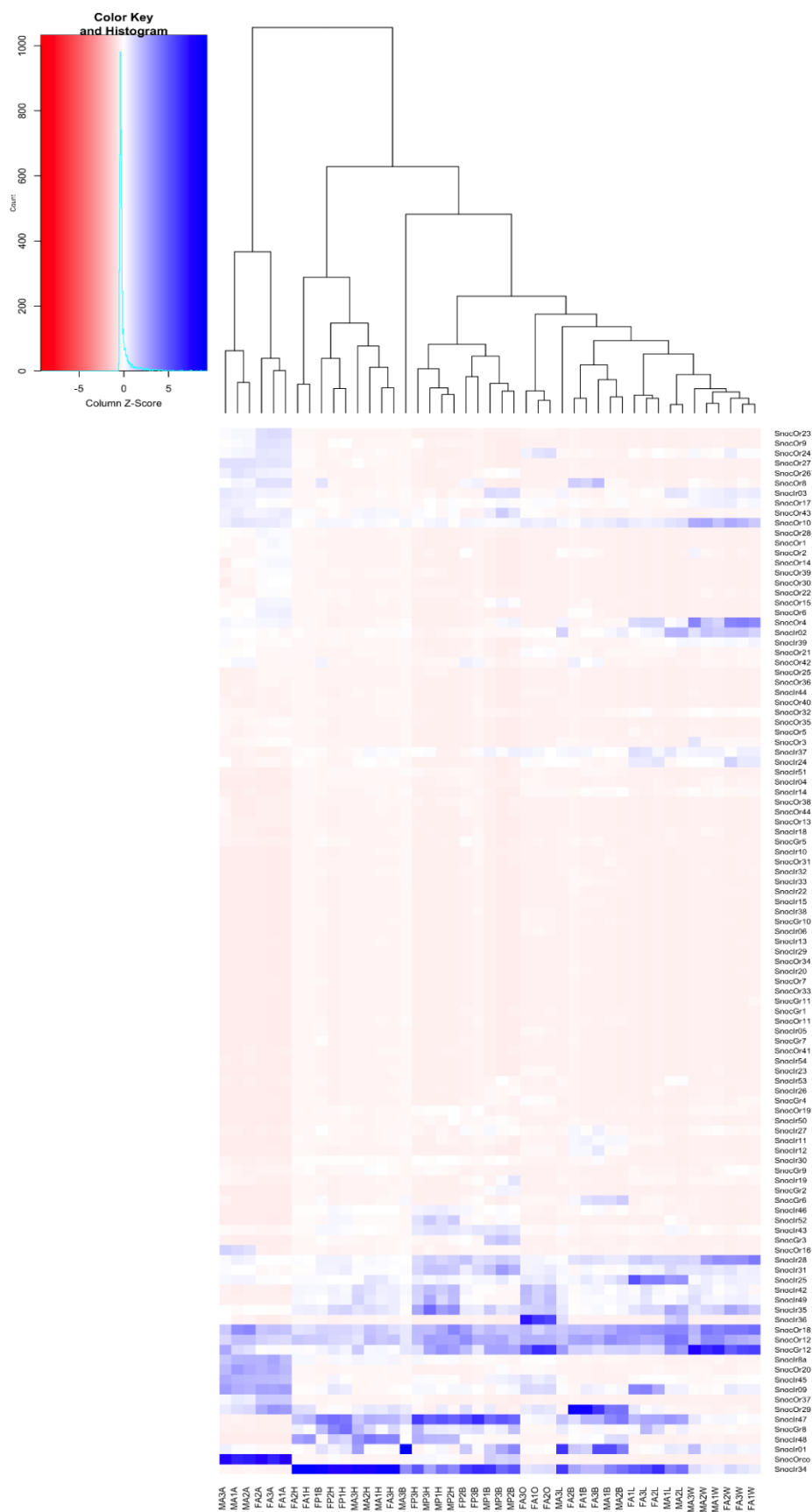


Figure S2.11. Heatmap of the expression abundances (TPM, transcripts per kilobase per million reads) of chemoreceptors proteins (ORs, GRs, and IRs) of *S. noctilio*. Blue represents up-regulated genes whereas red represent down-regulated genes.

Supplementary tables

Table S2.1. RNA data for each tissue sample. The quality and quantity of the extracted RNA, RNA library and sequenced RNA reads are indicated. Conc. – Concentration. RIN – RNA integrity number. Q20 – Phred quality score indicating a base call accuracy of 99%. Q30 – Phred quality score indicating a base call accuracy of 99.9%.

Tissue type	Sample replicate	Quality of extracted RNA			Stranded mRNA library quality				Raw RNA data				
		Conc. (ng/ul)	Total amount (ug)	RIN	Conc. (ng/ul)	Conc. (nM)	Insert size (bp)	Total Bases	Read Count	GC (%)	AT (%)	Q20 (%)	Q30 (%)
Female adult antennae	1	55.5	4.606	8.5	10.42	43.56	368	6 225 154 594	61 635 194	39.92	60.08	98.10	94.43
	2	70.283	5.833	8.9	18.80	83.36	347	6 034 971 594	59 752 194	39.75	60.26	98.15	94.43
	3	121.439	9.837	9	9.44	36.86	394	6 325 320 940	62 626 940	39.11	60.89	97.94	93.89
Male adult antennae	1	176.564	14.125	9.2	14.50	65.06	343	6 472 863 356	64 087 756	39.23	60.77	98.21	94.57
	2	328.028	26.242	8.7	15.12	68.80	338	6 668 422 788	66 023 988	39.19	60.81	98.15	94.45
	3	58.239	5.067	9.2	7.10	33.73	324	5 424 214 292	53 705 092	40.07	59.93	98.03	94.23
Female adult head	1	65.885	5.403	8.3	27.66	117.54	362	6 040 089 062	59 802 862	40.53	59.47	97.03	92.01
	2	69.12	5.53	8.5	16.39	73.10	345	6 030 754 238	59 710 438	40.58	59.43	98.21	94.64
	3	64.701	5.241	8.7	16.55	74.68	341	6 705 697 242	66 393 042	40.51	59.49	98.23	94.61
Male adult head	1	68.11	5.721	8.8	19.17	83.77	352	6 124 472 744	60 638 344	41.87	58.13	98.37	95.12
	2	134.541	10.091	9.1	32.95	143.22	354	7 805 077 798	77 277 998	41.25	58.75	98.51	95.32
	3	64.104	5.192	9.1	18.80	80.34	360	8 871 248 140	87 834 140	43.44	56.56	98.44	95.21
Female adult legs	1	92.23	6.364	8.8	11.16	52.04	330	5 187 772 080	51 364 080	42.30	57.70	97.96	94.15
	2	76.359	6.338	9.2	16.51	76.51	332	6 173 748 422	61 126 222	41.81	58.19	98.06	94.37
	3	90.233	7.399	9	12.74	56.97	344	5 297 140 536	52 446 936	42.24	57.76	97.82	93.88
Male adult legs	1	119.01	9.521	9.2	21.98	93.42	362	9 030 718 656	89 413 056	42.11	57.89	98.56	95.55
	2	193.046	13.899	9.3	31.01	129.98	367	8 115 862 676	80 355 076	41.51	58.49	98.46	95.23
	3	71.002	5.68	9.3	8.92	38.34	358	5 515 451 834	54 608 434	41.42	58.58	98.27	94.84
Female adult wings	1	56.001	4.312	8.6	5.51	23.24	365	7 430 363 354	73 567 954	41.21	58.79	98.42	95.23
	2	54.853	4.333	8.5	5.49	22.69	372	7 731 350 626	76 548 026	41.81	58.19	98.30	94.92
	3	51.651	4.132	8.5	11.54	50.45	352	7 026 221 550	69 566 550	41.90	58.10	98.47	95.22

Tissue type	Sample replicate	Quality of extracted RNA			Stranded mRNA library quality				Raw RNA data				
		Conc. (ng/ul)	Total amount (ug)	RIN	Conc. (ng/ul)	Conc. (nM)	Insert size (bp)	Total Bases	Read Count	GC (%)	AT (%)	Q20 (%)	Q30 (%)
Male adult wings	1	57.838	4.222	9.2	8.42	38.19	339	6 155 538 324	60 945 924	40.63	59.37	97.91	94.03
	2	63.506	4.953	9	10.28	46.52	340	6 218 520 510	61 569 510	40.69	59.32	97.67	93.44
	3	57.418	4.708	9.1	3.82	17.55	335	6 133 307 820	60 725 820	43.55	56.45	98.20	94.65
Female adult ovipositor	1	29.839	2.447	8.5	15.55	70.80	338	7 522 029 338	74 475 538	42.19	57.81	98.47	95.25
	2	54.41	4.462	8.9	17.97	78.99	350	8 868 659 712	87 808 512	42.40	57.60	98.43	95.14
	3	28.869	2.338	8.4	12.88	61.52	322	6 014 575 250	59 550 250	42.28	57.72	98.36	95.12
Female adult body	1	128.119	9.481	9	15.57	70.27	341	6 012 916 830	59 533 830	41.84	58.16	98.11	94.45
	2	128.279	10.006	9.1	2.93	13.46	335	5 869 219 686	58 111 086	41.38	58.62	97.96	94.31
	3	165.082	11.721	8.9	14.25	63.16	347	5 812 165 190	57 546 190	41.01	58.99	98.07	94.35
Male adult body	1	86.068	5.508	9.2	17.82	79.69	344	5 968 890 728	59 097 928	41.20	58.80	98.06	94.31
	2	79.406	6.432	9	14.55	64.69	346	6 595 699 556	65 303 956	40.56	59.44	98.08	94.31
	3	66.261	5.433	9.1	12.44	53.16	360	6 690 928 214	66 246 814	38.88	61.13	98.03	94.17
Female pupa head	1	70.494	5.287	9.1	23.98	99.97	369	7 555 538 108	74 807 308	39.30	60.70	98.46	95.19
	2	69.848	5.658	9.3	19.81	81.70	373	7 153 322 172	70 824 972	38.91	61.09	98.49	95.26
	3	68.656	5.698	8.9	11.46	48.99	360	7 169 968 790	70 989 790	41.53	58.47	98.29	94.89
Male pupa head	1	74.983	6.299	8.4	9.71	40.48	369	6 417 889 258	63 543 458	41.67	58.33	98.38	95.11
	2	74.438	5.979	8.9	11.64	48.52	369	7 081 532 786	70 114 186	41.06	58.94	98.40	95.11
	3	74.31	6.019	8	6.69	29.93	344	8 657 557 592	85 718 392	42.93	57.07	98.39	95.16
Female pupa body	1	94.527	6.522	8.2	18.69	73.73	390	8 305 985 682	82 237 482	32.79	67.22	98.52	95.20
	2	90.635	9.154	6.1	4.80	19.69	375	7 029 462 438	69 598 638	33.97	66.03	98.38	94.87
	3	167.057	13.03	8.6	17.17	74.42	355	6 311 649 580	62 491 580	35.83	64.17	98.43	95.08
Male pupa body	1	91.628	6.231	8	10.05	44.07	351	7 231 000 262	71 594 062	38.93	61.07	98.53	95.41
	2	132.753	10.753	8.4	12.52	54.40	354	7 330 262 254	72 576 854	38.63	61.37	98.45	95.15
	3	88.463	5.927	7.6	11.84	46.97	388	6 541 546 790	64 767 790	36.94	63.06	98.47	95.17

Table S2.2. Differentially expressed chemosensation genes identified in pairwise comparisons of various tissues. Genes with a negative log2FoldChange (LFC) value is up-regulated in second tissue in the pairwise comparison whereas genes with a positive LFC value were up-regulated in the first tissue in the pairwise comparison. Adjusted probability values (padj-value) < 0.05 were regarded as statistically significant. baseMean, mean of the normalized counts for the gene across all samples; lfcSE, Standard error of the log₂FoldChange; padj-value, Benjamini-Hochberg adjusted probability value. [Combined file of DESeq2 comparisons available.](#)

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Antennae Female vs Male Comparison						
SnocOR39	25.06613876	1.716076798	0.368384323	4.658387158	3.19E-06	0.000769682
SnocOR9	63.13422613	1.663944338	0.294845454	5.64344579	1.67E-08	7.11E-06
SnocOR23	68.15463492	1.572495713	0.297285951	5.289505629	1.23E-07	4.36E-05
SnocOR6	42.34619867	1.493768018	0.405479713	3.683952542	0.000229645	0.024701313
SnocOR22	33.88343062	1.486622702	0.422834251	3.515852127	0.000438345	0.03923648
SnocOR28	27.63417182	1.20157675	0.309568673	3.881454599	0.000103834	0.013561932
SnocOBP7	12118.50655	1.110416049	0.320171061	3.46819618	0.000523965	0.043834949
SnocOR24	225.7722528	0.764521072	0.189071511	4.043555095	5.26E-05	0.008319491
SnocGR12	328.4596079	-1.333341036	0.353807435	-3.768550073	0.000164199	0.019282032
SnocOBP10	4059.27834	-1.530001	0.430553318	-3.553569174	0.000380041	0.035507502
SnocOR16	101.7910646	-4.086258488	0.316432543	-12.91352164	3.78E-38	2.42E-34
SnocIR18	8.453322592	-5.677349422	1.142072788	-4.971092456	6.66E-07	0.000185257
<i>Sirex</i> Adult Body Female vs Male Comparison						
SnocOR6	42.34619867	5.201257509	1.111865654	4.677955014	2.90E-06	2.48E-05
SnocOR25	12.03122844	4.052422369	1.680480719	2.41146615	0.015888527	0.043725692
SnocOR8	112.1400021	3.286296054	0.559208224	5.876694782	4.19E-09	6.47E-08
SnocCSP2	9.393823335	2.739562007	1.077592981	2.542297561	0.011012637	0.032265215
SnocOR42	53.63464192	2.440041468	0.427418546	5.708787066	1.14E-08	1.64E-07
SnocOBP5	221649.8715	2.412087079	0.880304223	2.740060782	0.006142782	0.019955984
SnocIR30	95.5506514	2.064580829	0.380972644	5.419236422	5.99E-08	7.42E-07
SnocOR3	31.32577049	1.972167536	0.821312605	2.401238609	0.016339678	0.044785501
SnocIR27	30.26473407	1.452754935	0.41119762	3.532984782	0.000410896	0.001961364
SnocGR4	14.02173065	1.411783127	0.456804945	3.09056008	0.001997794	0.007622344
SnocCSP5	809015.4868	1.226022045	0.334297088	3.667462535	0.000244969	0.001255623
SnocSNMP1	16944.27711	1.169252161	0.432356677	2.704369386	0.006843417	0.0217848
SnocOBP11	68421.3101	1.160684679	0.227067026	5.111639064	3.19E-07	3.38E-06
SnocIR43	172.2539251	-0.700392697	0.202734703	-3.454725249	0.000550854	0.002514783
SnocOR10	213.0939545	-0.706199206	0.209812825	-3.365853378	0.000763073	0.003333965
SnocIR47	786.6561263	-0.849697368	0.185291627	-4.58572998	4.52E-06	3.69E-05
SnocIR8a	471.7037306	-0.883182389	0.339551889	-2.601023346	0.009294613	0.028116846
SnocIR34	1585.251292	-0.969617814	0.367456258	-2.638729897	0.008321725	0.025670071
SnocCSP4	2248.279673	-0.988533575	0.395136389	-2.501752817	0.012358017	0.035606194
SnocGR9	44.2004385	-1.10131309	0.409944538	-2.686492897	0.007220648	0.022741608
SnocOR16	101.7910646	-1.103620567	0.391495153	-2.818989097	0.004817515	0.016266683
SnocIR48	460.3123721	-1.108980367	0.242016603	-4.582249124	4.60E-06	3.74E-05
SnocOR4	141.2516972	-1.336475554	0.508827631	-2.626578184	0.008624818	0.02642754
SnocIR02	148.0835805	-1.383059653	0.271870202	-5.08720574	3.63E-07	3.80E-06

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
Sirex Adult Body Female vs Male Comparison						
SnocOBP9	4437.958162	-1.487396694	0.380567381	-3.908366216	9.29E-05	0.000537636
SnocOR20	183.6185733	-1.704028824	0.528912884	-3.221757069	0.001274071	0.005198137
SnocIR01	218.6742791	-1.757998678	0.465633535	-3.775498428	0.000159688	0.000864233
SnocCSP7	92114.69353	-1.942610274	0.621159965	-3.127391306	0.00176365	0.00686137
SnocIR03	85.25030268	-2.330123272	0.473265844	-4.923497656	8.50E-07	8.24E-06
SnocORCO	595.8901994	-4.017811252	1.316154447	-3.052689798	0.002268003	0.008516373
SnocIR26	11.90558972	-4.727224168	1.50120255	-3.148958259	0.001638536	0.006450405
SnocOBP8	5081.213618	-4.773950399	1.230700211	-3.87905223	0.000104864	0.000598222
SnocIR18	8.453322592	-4.93812573	1.442591032	-3.42309471	0.000619125	0.002776605
SnocOBP4	275.5610933	-8.116629517	0.486919188	-16.66935648	2.19E-62	2.23E-59
Sirex Adult Head Female vs Male Comparison						
SnocIR11	89.16480833	1.876024099	0.397578303	4.718627962	2.37E-06	0.000162765
SnocOR10	213.0939545	-0.616571533	0.205204639	-3.004666644	0.002658721	0.044035339
SnocGR12	328.4596079	-1.404708846	0.363215064	-3.867430026	0.000109988	0.004011745
Sirex Adult Legs Female vs Male Comparison						
SnocOR29	250.2982943	2.875639543	0.976029691	2.946262363	0.003216395	0.025950053
SnocOR5	18.05668037	2.776927582	0.957742651	2.899450681	0.003738171	0.0292627
SnocIR09	401.1008842	2.141445113	0.276073578	7.756791251	8.71E-15	6.13E-13
SnocIR24	89.87055686	1.662186358	0.47487589	3.500254261	0.000464815	0.005637323
SnocIR11	89.16480833	1.609356469	0.411316878	3.912692517	9.13E-05	0.001404347
SnocOR4	141.2516972	1.316436169	0.426965521	3.083237651	0.002047616	0.018205793
SnocCSP5	809015.4868	1.092819269	0.334292642	3.269049723	0.001079093	0.011007589
SnocIR28	388.8178104	0.828933514	0.290640279	2.852094406	0.00434322	0.032828917
SnocIR25	847.5756711	0.696499656	0.179697246	3.875961782	0.000106204	0.001596849
SnocOBP11	68421.3101	0.691629152	0.231977727	2.981446373	0.002868903	0.023713501
SnocIR43	172.2539251	-0.607506003	0.198021389	-3.067880729	0.002155826	0.019001018
SnocOR17	188.5602842	-0.930041833	0.290698078	-3.199339466	0.001377429	0.013367506
SnocIR30	95.5506514	-1.332827035	0.407843108	-3.267989602	0.001083143	0.011031799
SnocOBP1	495.1163185	-1.433708202	0.309985827	-4.625076627	3.74E-06	8.39E-05
SnocIR03	85.25030268	-1.531869124	0.317267365	-4.828322393	1.38E-06	3.47E-05
SnocIR02	148.0835805	-1.722908612	0.243994797	-7.061251433	1.65E-12	9.40E-11
SnocCSP3	75592.54521	-1.816912713	0.503571208	-3.608055193	0.000308501	0.0039375
SnocIR01	218.6742791	-2.075339578	0.455379199	-4.55738774	5.18E-06	0.000112468
SnocOBP4	275.5610933	-2.100808158	0.409777538	-5.126704038	2.95E-07	8.31E-06
SnocOBP14	32050.68857	-3.111897695	0.765131396	-4.067141555	4.76E-05	0.000801896
SnocOR2	37.82693197	-3.600671184	1.282437251	-2.807678257	0.004990005	0.03637866
SnocIR52	66.78474154	-3.899541594	0.638888983	-6.103629427	1.04E-09	4.19E-08
SnocIR53	24.73669766	-4.902987465	1.110063282	-4.416854015	1.00E-05	0.000201814
SnocIR36	96.31687251	-6.30210468	0.841937134	-7.485243758	7.14E-14	4.61E-12
SnocSNMP1	16944.27711	-8.1738697	0.374763948	-21.81071508	1.84E-105	2.01E-102
SnocOBP3	87804.10493	-8.451803532	0.667301329	-12.66564769	9.17E-37	2.41E-34
Sirex Adult Wings Female vs Male Comparison						
SnocIR53	24.73669766	4.678643258	1.49594673	3.127546699	0.001762718	0.030560735
SnocOBP4	275.5610933	2.662631775	0.495432477	5.374358561	7.69E-08	1.61E-05
SnocSNMP1	16944.27711	2.164827065	0.373642585	5.793844582	6.88E-09	1.83E-06

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Wings Female vs Male Comparison						
SnocIR10	13.36267031	1.964392664	0.616474035	3.186497003	0.00144007	0.026877072
SnocIR24	89.87055686	1.373408176	0.472818752	2.904724423	0.003675766	0.049803439
SnocOBP8	5081.213618	1.04864797	0.350749316	2.989736325	0.002792184	0.042225022
SnocIR09	401.1008842	1.039564401	0.290317054	3.580789991	0.000342557	0.01036051
SnocIR45	371.8211052	0.929082893	0.29013563	3.202236462	0.00136365	0.026071744
SnocIR35	457.2488906	0.66584112	0.215667885	3.087344778	0.002019532	0.033477958
<i>Sirex</i> Adult Female Body vs Antennae Comparison						
SnocCSP2	9.393823335	7.386845282	1.545154787	4.780650681	1.75E-06	9.13E-06
SnocIR12	15.80332584	6.278904143	0.988900771	6.349377335	2.16E-10	1.80E-09
SnocOR11	4.164431007	5.970504977	1.556982515	3.834664115	0.000125736	0.000494629
SnocIR13	10.18649879	5.827183283	1.135782471	5.130545179	2.89E-07	1.69E-06
SnocIR11	89.16480833	5.564803799	0.609299063	9.133123844	6.66E-20	1.21E-18
SnocIR15	2.874628063	4.817008977	1.524804537	3.159099322	0.001582575	0.005121639
SnocIR33	6.590483207	4.072730676	0.918276117	4.435191771	9.20E-06	4.32E-05
SnocGR6	67.84170803	2.781510736	0.594567582	4.678207856	2.89E-06	1.47E-05
SnocIR47	786.6561263	2.602270667	0.203068704	12.81473029	1.36E-37	6.28E-36
SnocIR22	3.128804552	2.563230578	1.069630688	2.396369706	0.016558379	0.042874375
SnocGR10	25.04714529	2.539693359	0.487341761	5.211318955	1.88E-07	1.12E-06
SnocIR34	1585.251292	2.022245972	0.371859924	5.438192828	5.38E-08	3.44E-07
SnocIR46	90.41283967	1.934681614	0.326070009	5.933331983	2.97E-09	2.19E-08
SnocIR14	39.37454891	1.565488472	0.360258662	4.345456851	1.39E-05	6.38E-05
SnocIR20	20.64701759	1.450553642	0.455961829	3.181304988	0.001466132	0.004776445
SnocIR27	30.26473407	1.401772445	0.407852623	3.436958267	0.000588286	0.002056619
SnocIR42	207.1661834	1.233549186	0.399258627	3.089599326	0.002004267	0.006356663
SnocIR48	460.3123721	1.12200951	0.25821964	4.34517494	1.39E-05	6.38E-05
SnocIR28	388.8178104	-0.768089651	0.291401651	-2.635845225	0.0083928	0.023291025
SnocIR25	847.5756711	-0.794977027	0.181515579	-4.379662793	1.19E-05	5.50E-05
SnocIR32	312.7103091	-0.799192332	0.254910699	-3.135185521	0.001717455	0.005512011
SnocOR42	53.63464192	-0.983367001	0.3704706	-2.654372575	0.007945604	0.022159341
SnocOR12	525.0787443	-1.151991324	0.215693235	-5.340878323	9.25E-08	5.76E-07
SnocCSP1	2551.539137	-1.200129747	0.330767719	-3.628315823	0.000285276	0.00104908
SnocOR31	48.78794332	-1.205817547	0.371804222	-3.243151844	0.001182152	0.003913796
SnocOR8	112.1400021	-1.428402493	0.537863013	-2.655699425	0.007914412	0.022082305
SnocIR43	172.2539251	-1.620234821	0.19604515	-8.264600365	1.40E-16	1.98E-15
SnocOR34	28.92399412	-1.649852912	0.696083166	-2.370195102	0.017778701	0.045601532
SnocOR16	101.7910646	-1.745805611	0.382320322	-4.566342695	4.96E-06	2.43E-05
SnocOR18	572.3454477	-1.919535264	0.224786923	-8.539354695	1.35E-17	2.07E-16
SnocIR31	242.9019269	-2.033238904	0.293312686	-6.931984187	4.15E-12	4.07E-11
SnocIR24	89.87055686	-2.101102868	0.480491124	-4.372823481	1.23E-05	5.67E-05
SnocOR33	14.97868901	-2.309018729	0.850232245	-2.715750601	0.006612571	0.018811974
SnocIR35	457.2488906	-2.322737985	0.228700995	-10.15622159	3.11E-24	7.31E-23
SnocOR10	213.0939545	-2.382503438	0.202581302	-11.76072725	6.22E-32	2.23E-30
SnocOR17	188.5602842	-2.457798224	0.271389688	-9.056343463	1.35E-19	2.39E-18
SnocOBP3	87804.10493	-2.523745817	0.671861353	-3.756349141	0.00017241	0.000659644
SnocOR36	66.23712062	-2.555621075	0.60984771	-4.190588951	2.78E-05	0.000121706

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Female Body vs Antennae Comparison						
SnocOBP4	275.5610933	-2.741077956	0.49615781	-5.524609105	3.30E-08	2.16E-07
SnocOR3	31.32577049	-2.795487709	0.766164328	-3.64867902	0.000263592	0.000977868
SnocGR9	44.2004385	-2.818731447	0.390363559	-7.220785305	5.17E-13	5.49E-12
SnocIR02	148.0835805	-2.898758933	0.264200948	-10.97179609	5.22E-28	1.49E-26
SnocOBP5	221649.8715	-3.177522826	0.880271752	-3.609706683	0.000306543	0.001121294
SnocIR36	96.31687251	-3.274863538	0.765331167	-4.279014992	1.88E-05	8.45E-05
SnocOR24	225.7722528	-3.319698571	0.212637458	-15.61201212	6.03E-55	6.40E-53
SnocOR35	41.65738404	-3.53286902	0.588354615	-6.004659319	1.92E-09	1.45E-08
SnocIR09	401.1008842	-3.554982847	0.274197351	-12.96505178	1.93E-38	9.41E-37
SnocOR21	47.41464246	-3.618373123	0.477344719	-7.580209809	3.45E-14	4.10E-13
SnocOR44	8.673122668	-3.649818331	1.111515389	-3.283641743	0.001024751	0.003432481
SnocOR2	37.82693197	-3.771011716	1.056378289	-3.569755034	0.000357315	0.001292743
SnocIR54	4.392650681	-3.998947592	1.466912315	-2.72609859	0.006408785	0.01828267
SnocOR6	42.34619867	-4.023268818	0.441542509	-9.111849346	8.10E-20	1.47E-18
SnocIR19	28.23047251	-4.036561565	0.765188566	-5.275250759	1.33E-07	8.09E-07
SnocOR38	9.688376947	-4.072145108	1.062861434	-3.831303853	0.000127466	0.00050101
SnocIR39	39.50566078	-4.328150889	0.438379813	-9.873061575	5.45E-23	1.19E-21
SnocOR22	33.88343062	-4.45959259	0.511736607	-8.714624928	2.92E-18	4.75E-17
SnocOR13	4.976388719	-4.587892033	1.592451407	-2.881024823	0.003963844	0.01179935
SnocOR26	59.63113286	-5.080932776	0.426316747	-11.9182106	9.51E-33	3.50E-31
SnocOR4	141.2516972	-5.140332003	0.488715083	-10.51805475	7.13E-26	1.81E-24
SnocOR37	113.2795806	-5.186149817	0.601813153	-8.617541488	6.84E-18	1.08E-16
SnocOR25	12.03122844	-5.193751059	1.20093123	-4.324769755	1.53E-05	6.96E-05
SnocOBP1	495.1163185	-5.518918013	0.273219277	-20.19959233	9.87E-91	3.16E-88
SnocIR03	85.25030268	-5.85568198	0.450739561	-12.99127587	1.37E-38	6.73E-37
SnocOR43	88.98720413	-5.879625816	0.464155489	-12.66736246	8.97E-37	4.04E-35
SnocOR15	39.2343263	-6.084727047	0.609020183	-9.991010513	1.67E-23	3.78E-22
SnocIR01	218.6742791	-6.176950352	0.452356025	-13.65506375	1.88E-42	1.11E-40
SnocOR30	16.82665887	-6.356531711	1.531258001	-4.151182691	3.31E-05	0.000142965
SnocOR5	18.05668037	-6.927656218	1.10660705	-6.260267558	3.84E-10	3.12E-09
SnocIR8a	471.7037306	-6.989065062	0.316568866	-22.0775503	5.19E-108	2.61E-105
SnocIR44	14.90359555	-7.066947578	1.241984345	-5.690045617	1.27E-08	8.71E-08
SnocOR41	5.837886768	-7.353213272	1.308201816	-5.620855424	1.90E-08	1.28E-07
SnocOR20	183.6185733	-7.467659749	0.500853128	-14.90987944	2.84E-50	2.44E-48
SnocOR39	25.06613876	-7.522685814	0.909728879	-8.26915138	1.35E-16	1.91E-15
SnocOR40	10.20681596	-7.542292118	1.499486168	-5.029917768	4.91E-07	2.78E-06
SnocOR27	83.1456525	-7.750099179	0.785075034	-9.871794221	5.52E-23	1.21E-21
SnocOR28	27.63417182	-8.287275671	1.056973488	-7.840570992	4.49E-15	5.66E-14
SnocIR45	371.8211052	-8.490764697	0.426802572	-19.89389301	4.60E-88	1.42E-85
SnocOBP10	4059.27834	-8.74812161	0.459817077	-19.02522123	1.05E-80	2.68E-78
SnocOBP9	4437.958162	-8.88028729	0.372389247	-23.84678765	1.09E-125	8.12E-123
SnocCSP7	92114.69353	-9.342409917	0.621003139	-15.04406231	3.78E-51	3.35E-49
SnocOR23	68.15463492	-9.696001512	1.054555296	-9.194398386	3.77E-20	6.95E-19
SnocOBP11	68421.3101	-9.990566179	0.220526843	-45.30317514	0	0
SnocSNMP1	16944.27711	-10.23673782	0.393968553	-25.98364198	7.58E-149	8.79E-146

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
Sirex Adult Female Body vs Antennae Comparison						
SnocOR9	63.13422613	-10.36156277	1.21278253	-8.543627991	1.30E-17	1.99E-16
SnocOR1	32.76642584	-10.45151672	2.273412134	-4.597282017	4.28E-06	2.12E-05
SnocOR14	31.67263679	-10.48407826	1.632223108	-6.423189456	1.33E-10	1.13E-09
SnocOBP14	32050.68857	-11.6076794	0.66936502	-17.34132953	2.29E-67	3.80E-65
SnocOBP7	12118.50655	-13.08085834	0.409124482	-31.97280758	2.60E-224	6.91E-221
SnocORCO	595.8901994	-14.32754674	1.242342338	-11.53268813	9.03E-31	3.05E-29
SnocOBP8	5081.213618	-15.86522007	1.207139374	-13.14282378	1.87E-39	9.49E-38
Sirex Adult Female Head vs Antennae Comparison						
SnocIR48	460.3123721	5.036222134	0.245980421	20.47407721	3.67E-93	1.07E-90
SnocIR34	1585.251292	4.950530943	0.370318375	13.36831031	9.26E-41	5.34E-39
SnocIR52	66.78474154	4.873627947	0.638932415	7.627767558	2.39E-14	3.19E-13
SnocIR11	89.16480833	4.204421311	0.613780938	6.850035655	7.38E-12	8.05E-11
SnocIR47	786.6561263	3.886123704	0.200024611	19.42822781	4.45E-84	1.05E-81
SnocIR29	2.149564268	3.586093176	1.416065154	2.532435154	0.011327332	0.031141906
SnocOBP12	299.0320935	2.980541391	0.23226513	12.83249616	1.08E-37	5.50E-36
SnocIR46	90.41283967	2.558526222	0.318256214	8.039202721	9.04E-16	1.33E-14
SnocIR42	207.1661834	2.367353939	0.393152948	6.021457944	1.73E-09	1.47E-08
SnocCSP6	7.585377378	2.204714094	0.907197503	2.430247092	0.015088532	0.039919805
SnocIR49	197.542681	2.009875743	0.368689983	5.451397744	5.00E-08	3.60E-07
SnocGR8	126.0733797	1.994381245	0.590750526	3.376012642	0.000735445	0.002734089
SnocIR04	29.51708344	1.696660295	0.452511629	3.749429154	0.000177238	0.000742039
SnocOBP13	247.4246332	1.308740874	0.289736526	4.517003397	6.27E-06	3.39E-05
SnocIR25	847.5756711	-0.584349761	0.179870158	-3.248731013	0.00115921	0.00411904
SnocOR12	525.0787443	-0.747987081	0.213534191	-3.502891404	0.000460237	0.00177946
SnocCSP1	2551.539137	-0.839895502	0.3302499	-2.543211982	0.010983857	0.030329738
SnocGR9	44.2004385	-0.918324195	0.32490012	-2.826481548	0.004706246	0.014400855
SnocCSP5	809015.4868	-1.224890823	0.334293949	-3.664113057	0.000248197	0.001011002
SnocIR24	89.87055686	-1.281399731	0.468716761	-2.733846613	0.00625992	0.018552288
SnocIR43	172.2539251	-1.383783482	0.184590309	-7.496512068	6.55E-14	8.47E-13
SnocIR28	388.8178104	-1.562994159	0.292332786	-5.34662629	8.96E-08	6.24E-07
SnocOBP4	275.5610933	-1.581490252	0.435467756	-3.631704594	0.000281555	0.001132661
SnocGR12	328.4596079	-1.607982088	0.363508186	-4.423509982	9.71E-06	5.10E-05
SnocGR6	67.84170803	-1.625345246	0.634109431	-2.563193617	0.010371419	0.028862438
SnocIR31	242.9019269	-1.639963594	0.283824101	-5.778098426	7.55E-09	5.97E-08
SnocIR32	312.7103091	-1.641303171	0.256582738	-6.396779387	1.59E-10	1.52E-09
SnocOR18	572.3454477	-1.763854125	0.222540891	-7.925977633	2.26E-15	3.23E-14
SnocOR31	48.78794332	-1.83404164	0.373257262	-4.913612742	8.94E-07	5.51E-06
SnocOR43	88.98720413	-2.121524473	0.327329337	-6.481314783	9.09E-11	8.95E-10
SnocOR41	5.837886768	-2.166179119	0.628913725	-3.444318407	0.000572501	0.0021828
SnocOR29	250.2982943	-2.246418817	0.937031943	-2.397376987	0.016512925	0.043226141
SnocOR10	213.0939545	-2.613668426	0.198476467	-13.16865658	1.33E-39	7.30E-38
SnocOR16	101.7910646	-2.704392523	0.402989326	-6.710829167	1.94E-11	2.03E-10
SnocIR02	148.0835805	-2.729480155	0.249473406	-10.94096641	7.34E-28	2.43E-26
SnocOR17	188.5602842	-2.953200527	0.2706511	-10.91146692	1.02E-27	3.33E-26
SnocIR36	96.31687251	-2.996866976	0.684440263	-4.378566163	1.19E-05	6.19E-05

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Female Head vs Antennae Comparison						
SnocOR34	28.92399412	-3.089943376	0.737933513	-4.18729238	2.82E-05	0.00013683
SnocOR21	47.41464246	-3.188022974	0.443846347	-7.182717615	6.83E-13	8.19E-12
SnocOR24	225.7722528	-3.226304881	0.203341126	-15.86646511	1.08E-56	1.15E-54
SnocIR8a	471.7037306	-3.398114091	0.259928398	-13.07326989	4.68E-39	2.50E-37
SnocOR33	14.97868901	-3.424823464	0.906208433	-3.779288891	0.000157277	0.000664954
SnocOR39	25.06613876	-3.607799004	0.398233452	-9.059507644	1.31E-19	2.54E-18
SnocOBP9	4437.958162	-3.69469776	0.342718137	-10.78057261	4.25E-27	1.34E-25
SnocOR42	53.63464192	-3.718379407	0.421668798	-8.818246505	1.16E-18	2.12E-17
SnocIR39	39.50566078	-3.759646246	0.350387519	-10.72996624	7.36E-27	2.28E-25
SnocOBP5	221649.8715	-3.773223118	0.880271875	-4.286429258	1.82E-05	9.11E-05
SnocOR38	9.688376947	-3.825284286	0.996897783	-3.837188076	0.000124451	0.000537852
SnocIR09	401.1008842	-4.03108353	0.273676354	-14.7293819	4.18E-49	3.52E-47
SnocOR22	33.88343062	-4.0922302	0.468204549	-8.740261516	2.33E-18	4.14E-17
SnocIR44	14.90359555	-4.195216419	0.774672651	-5.415469897	6.11E-08	4.36E-07
SnocOR27	83.1456525	-4.386008367	0.569466067	-7.701966136	1.34E-14	1.82E-13
SnocOR36	66.23712062	-4.448240724	0.641516097	-6.933950284	4.09E-12	4.57E-11
SnocIR03	85.25030268	-4.520378509	0.32220836	-14.02936443	1.03E-44	7.23E-43
SnocOR40	10.20681596	-4.718271585	1.024843317	-4.60389555	4.15E-06	2.30E-05
SnocOR44	8.673122668	-4.845999409	1.166019642	-4.156018675	3.24E-05	0.000155314
SnocOR9	63.13422613	-5.157715949	0.345910332	-14.91055765	2.81E-50	2.49E-48
SnocOR4	141.2516972	-5.168994457	0.468040185	-11.04391166	2.35E-28	7.98E-27
SnocIR53	24.73669766	-5.17293737	1.224871413	-4.223249328	2.41E-05	0.00011805
SnocGR5	21.81385482	-5.208910093	0.830947348	-6.268640372	3.64E-10	3.33E-09
SnocOR13	4.976388719	-5.588441698	1.680683063	-3.325101454	0.000883864	0.003222659
SnocOR26	59.63113286	-5.671966307	0.430689295	-13.16950846	1.31E-39	7.24E-38
SnocOR20	183.6185733	-5.858223073	0.400858	-14.61421019	2.28E-48	1.85E-46
SnocOR35	41.65738404	-6.172299246	0.722835437	-8.539010304	1.35E-17	2.25E-16
SnocOR3	31.32577049	-6.20177578	0.875597337	-7.082908458	1.41E-12	1.65E-11
SnocIR45	371.8211052	-6.257095934	0.26662299	-23.46795351	8.67E-122	5.50E-119
SnocOR25	12.03122844	-6.282267863	1.253809958	-5.010542327	5.43E-07	3.46E-06
SnocOR8	112.1400021	-6.332096646	0.591292346	-10.70891022	9.24E-27	2.84E-25
SnocOR37	113.2795806	-6.369441204	0.617817897	-10.30957703	6.38E-25	1.77E-23
SnocOBP1	495.1163185	-6.398560704	0.28063555	-22.80024998	4.56E-115	2.77E-112
SnocIR01	218.6742791	-6.417056931	0.441313964	-14.54079737	6.68E-48	5.22E-46
SnocOR28	27.63417182	-6.776384883	0.591748208	-11.45146668	2.31E-30	8.77E-29
SnocOR5	18.05668037	-6.990152103	1.016168845	-6.878927783	6.03E-12	6.64E-11
SnocOR23	68.15463492	-7.177042507	0.46344351	-15.4863373	4.29E-54	4.23E-52
SnocIR19	28.23047251	-7.528336007	1.313804029	-5.730181854	1.00E-08	7.83E-08
SnocOR14	31.67263679	-7.569265863	1.273968715	-5.941484884	2.82E-09	2.34E-08
SnocOR30	16.82665887	-7.619944768	1.6174601	-4.71105579	2.46E-06	1.42E-05
SnocOR15	39.2343263	-8.219976636	0.848861247	-9.683533871	3.54E-22	8.33E-21
SnocOR6	42.34619867	-8.868796975	0.92477337	-9.590238279	8.79E-22	2.00E-20
SnocOR2	37.82693197	-8.981414675	1.450220333	-6.193138013	5.90E-10	5.30E-09
SnocOBP8	5081.213618	-9.082785174	0.285999293	-31.75806862	2.46E-221	5.12E-218
SnocOBP10	4059.27834	-10.53448893	0.496675125	-21.21001918	7.72E-100	2.82E-97

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
Sirex Adult Female Head vs Antennae Comparison						
SnocCSP7	92114.69353	-10.56204859	0.621435965	-16.99619782	8.76E-65	1.14E-62
SnocOR1	32.76642584	-10.98157618	2.273412134	-4.83043792	1.36E-06	8.19E-06
SnocOBP11	68421.3101	-11.52228623	0.224070242	-51.42265275	0	0
SnocSNMP1	16944.27711	-11.62580745	0.411169354	-28.27498529	7.02E-176	7.32E-173
SnocOBP14	32050.68857	-12.23826902	0.669752658	-18.27281888	1.36E-74	2.58E-72
SnocOBP7	12118.50655	-13.02747014	0.382066174	-34.09741824	8.06E-255	2.94E-251
SnocORCO	595.8901994	-14.85760716	1.242342338	-11.95935026	5.80E-33	2.44E-31
Sirex Adult Female Legs vs Antennae Comparison						
SnocIR11	89.16480833	4.084936564	0.621423051	6.573519528	4.91E-11	5.78E-10
SnocIR29	2.149564268	3.887724982	1.431177815	2.716451402	0.006598588	0.02077929
SnocIR34	1585.251292	3.077210806	0.371046898	8.293320383	1.10E-16	2.04E-15
SnocIR47	786.6561263	2.912371896	0.202536377	14.37950028	6.96E-47	5.46E-45
SnocCSP3	75592.54521	2.071135082	0.503593538	4.112711787	3.91E-05	0.000206391
SnocOBP3	87804.10493	1.938201993	0.667843878	2.902178273	0.003705776	0.012617845
SnocGR10	25.04714529	1.817018238	0.504819293	3.599343889	0.000319021	0.001411758
SnocIR42	207.1661834	1.77865075	0.396988444	4.48035901	7.45E-06	4.50E-05
SnocGR8	126.0733797	1.76203526	0.593194094	2.970419428	0.002973934	0.010429129
SnocCSP4	2248.279673	1.4159338	0.394756534	3.586853356	0.000334692	0.001473959
SnocOBP13	247.4246332	1.335681724	0.29356289	4.549899762	5.37E-06	3.34E-05
SnocIR49	197.542681	1.217509532	0.374692536	3.249356243	0.001156665	0.004492194
SnocCSP5	809015.4868	0.790064088	0.334292258	2.363393314	0.01810844	0.049534403
SnocIR35	457.2488906	-0.646178894	0.216476659	-2.98498183	0.002835952	0.009993256
SnocIR32	312.7103091	-0.666398588	0.254818111	-2.615193184	0.0089177	0.026945345
SnocOR16	101.7910646	-0.978130802	0.360268964	-2.715001565	0.006627546	0.020847994
SnocIR31	242.9019269	-1.067940724	0.284603979	-3.752374536	0.000175168	0.000823067
SnocOR4	141.2516972	-1.110972437	0.419995253	-2.645202367	0.008164207	0.024976795
SnocOBP12	299.0320935	-1.201410509	0.291765699	-4.117723618	3.83E-05	0.00020232
SnocGR9	44.2004385	-1.23770336	0.340847851	-3.631248831	0.000282053	0.001266982
SnocOR12	525.0787443	-1.274184438	0.216467955	-5.886249706	3.95E-09	3.79E-08
SnocOR18	572.3454477	-1.34103306	0.223214026	-6.007835101	1.88E-09	1.86E-08
SnocIR27	30.26473407	-1.347443143	0.496215763	-2.715438007	0.006618817	0.020825023
SnocIR43	172.2539251	-1.372903386	0.194094818	-7.073364459	1.51E-12	2.07E-11
SnocIR02	148.0835805	-1.707656058	0.244240035	-6.991712296	2.72E-12	3.62E-11
SnocIR51	37.29977006	-1.774849868	0.60353965	-2.940734494	0.003274351	0.01132218
SnocIR09	401.1008842	-1.831916049	0.267955711	-6.836637447	8.11E-12	1.03E-10
SnocGR5	21.81385482	-1.845119675	0.500696082	-3.685109075	0.000228605	0.001049827
SnocOR10	213.0939545	-1.878498421	0.197755437	-9.499098725	2.12E-21	5.18E-20
SnocIR39	39.50566078	-1.994604679	0.298898633	-6.673180997	2.50E-11	3.02E-10
SnocOR24	225.7722528	-2.065028579	0.198316341	-10.4128009	2.17E-25	6.75E-24
SnocOR36	66.23712062	-2.264206027	0.607403888	-3.727677859	0.000193252	0.00090137
SnocIR23	6.300662129	-2.556785293	1.067980439	-2.394037569	0.016664042	0.046119118
SnocOR21	47.41464246	-2.764311271	0.450706325	-6.133287057	8.61E-10	8.83E-09
SnocOR42	53.63464192	-2.885648167	0.415107725	-6.951564595	3.61E-12	4.76E-11
SnocIR30	95.5506514	-2.974366798	0.397659892	-7.479675118	7.45E-14	1.14E-12
SnocOR17	188.5602842	-2.984499483	0.282928569	-10.54859711	5.16E-26	1.67E-24

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Female Legs vs Antennae Comparison						
SnocOBP9	4437.958162	-3.073321396	0.342741881	-8.966868559	3.05E-19	6.62E-18
SnocIR03	85.25030268	-3.506946796	0.309340353	-11.3368552	8.62E-30	3.39E-28
SnocOR5	18.05668037	-3.569133538	0.764277997	-4.669941505	3.01E-06	1.93E-05
SnocIR36	96.31687251	-3.72009372	0.852808333	-4.362168585	1.29E-05	7.45E-05
SnocOR35	41.65738404	-3.758775379	0.600907849	-6.255161067	3.97E-10	4.24E-09
SnocIR53	24.73669766	-3.834546352	1.115216288	-3.438388045	0.000585188	0.0024423
SnocOR29	250.2982943	-4.10732825	0.942961188	-4.35577657	1.33E-05	7.65E-05
SnocOR22	33.88343062	-4.427531291	0.518923637	-8.532144191	1.44E-17	2.83E-16
SnocOR43	88.98720413	-4.691168026	0.396351851	-11.8358676	2.55E-32	1.14E-30
SnocIR45	371.8211052	-4.874789608	0.251956926	-19.34771032	2.13E-83	6.62E-81
SnocOR3	31.32577049	-4.935099914	0.834444578	-5.914233305	3.33E-09	3.22E-08
SnocOR37	113.2795806	-5.453897717	0.610902855	-8.927602273	4.35E-19	9.36E-18
SnocOR20	183.6185733	-5.825928245	0.419089124	-13.90140645	6.21E-44	4.51E-42
SnocIR01	218.6742791	-5.919495758	0.447604806	-13.22482618	6.31E-40	3.87E-38
SnocOR8	112.1400021	-6.015097926	0.606124559	-9.923864396	3.28E-23	8.91E-22
SnocIR54	4.392650681	-6.175268934	1.668595816	-3.700877632	0.000214855	0.000992303
SnocOR41	5.837886768	-6.250579953	1.308201816	-4.777993638	1.77E-06	1.18E-05
SnocIR8a	471.7037306	-6.319666594	0.299410347	-21.1070414	6.85E-99	3.57E-96
SnocOBP1	495.1163185	-6.339911758	0.298574379	-21.23394442	4.64E-100	2.61E-97
SnocOR44	8.673122668	-6.677294897	1.550913913	-4.30539364	1.67E-05	9.42E-05
SnocOR26	59.63113286	-6.709798957	0.604695042	-11.09616995	1.31E-28	4.84E-27
SnocOR13	4.976388719	-6.77374683	1.780599691	-3.804194095	0.000142267	0.00067963
SnocOBP8	5081.213618	-6.788351879	0.271258981	-25.02535347	3.24E-138	5.91E-135
SnocOR2	37.82693197	-7.388328243	1.271835031	-5.809187562	6.28E-09	5.91E-08
SnocOR38	9.688376947	-7.468659048	1.480456899	-5.04483383	4.54E-07	3.32E-06
SnocSNMP1	16944.27711	-7.504099031	0.374769564	-20.02323496	3.46E-89	1.40E-86
SnocIR44	14.90359555	-7.754459881	1.372765587	-5.648786619	1.62E-08	1.44E-07
SnocOR6	42.34619867	-8.212492871	0.927035104	-8.858880136	8.08E-19	1.71E-17
SnocOR40	10.20681596	-8.363248999	1.499486168	-5.577409901	2.44E-08	2.13E-07
SnocOR15	39.2343263	-8.546062527	1.110361944	-7.696645741	1.40E-14	2.25E-13
SnocCSP7	92114.69353	-8.648595023	0.620748234	-13.93253264	4.02E-44	2.95E-42
SnocOR25	12.03122844	-8.805064827	1.596038769	-5.516823902	3.45E-08	2.94E-07
SnocOR23	68.15463492	-8.928455774	0.880796859	-10.13679338	3.79E-24	1.11E-22
SnocOR30	16.82665887	-9.395464111	1.819808978	-5.162884801	2.43E-07	1.84E-06
SnocOR39	25.06613876	-9.775237969	1.230121464	-7.94656321	1.92E-15	3.27E-14
SnocOR28	27.63417182	-9.96067211	1.215401283	-8.195377319	2.50E-16	4.51E-15
SnocOR1	32.76642584	-10.31067886	2.273412134	-4.535332026	5.75E-06	3.55E-05
SnocOR14	31.67263679	-10.34324022	1.632223108	-6.336903434	2.34E-10	2.57E-09
SnocOBP11	68421.3101	-10.8951146	0.224319939	-48.56953264	0	0
SnocOBP7	12118.50655	-11.17141761	0.3488059	-32.0276051	4.50E-225	2.19E-221
SnocOR9	63.13422613	-11.18251996	1.21278253	-9.22054836	2.96E-20	6.80E-19
SnocOR27	83.1456525	-11.18393262	1.300217818	-8.601583876	7.86E-18	1.58E-16
SnocORCO	595.8901994	-12.32562277	1.090442714	-11.30331985	1.26E-29	4.90E-28
SnocOBP10	4059.27834	-13.35551649	0.933969712	-14.2997319	2.20E-46	1.71E-44
SnocOBP14	32050.68857	-15.09050773	0.758254564	-19.90163784	3.94E-88	1.47E-85

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Female Ovipositor vs Antennae Comparison						
SnocCSP2	9.393823335	7.753386067	1.540437757	5.033235542	4.82E-07	4.46E-06
SnocIR15	2.874628063	5.224834592	1.509936206	3.46030155	0.000539571	0.002716743
SnocIR36	96.31687251	5.05871307	0.556247639	9.094354237	9.52E-20	3.50E-18
SnocOBP2	790.2717246	4.68696605	1.101231617	4.256112863	2.08E-05	0.000143711
SnocIR12	15.80332584	4.598422135	0.993124085	4.630259408	3.65E-06	2.92E-05
SnocGR10	25.04714529	3.676553097	0.471705814	7.794165321	6.48E-15	1.54E-13
SnocIR33	6.590483207	3.586266479	0.91729915	3.909593154	9.25E-05	0.000560179
SnocIR42	207.1661834	3.158834391	0.391987863	8.058500502	7.72E-16	2.07E-14
SnocIR11	89.16480833	3.086653948	0.625717695	4.932981715	8.10E-07	7.22E-06
SnocIR49	197.542681	3.003602121	0.366977107	8.184712523	2.73E-16	7.55E-15
SnocCSP8	25070.43435	2.653494909	0.37191377	7.134704672	9.70E-13	1.84E-11
SnocOR19	30.21547201	1.989455264	0.50824121	3.914391882	9.06E-05	0.000551266
SnocIR23	6.300662129	1.910640605	0.691744753	2.762060136	0.00574379	0.020981484
SnocGR12	328.4596079	1.759289059	0.353216567	4.980765972	6.33E-07	5.75E-06
SnocIR04	29.51708344	1.701077126	0.452381759	3.76026905	0.000169731	0.000962483
SnocIR20	20.64701759	1.591449258	0.443329994	3.589762208	0.00033098	0.001758526
SnocIR14	39.37454891	1.509698472	0.35439535	4.259927427	2.04E-05	0.000141624
SnocCSP3	75592.54521	1.311997937	0.503594005	2.605269172	0.009180211	0.03115277
SnocIR47	786.6561263	1.197284179	0.206315507	5.803171058	6.51E-09	7.85E-08
SnocIR34	1585.251292	1.161512328	0.372230492	3.120411556	0.001805985	0.007790192
SnocIR25	847.5756711	-0.500375269	0.179730616	-2.784029125	0.005368821	0.01978945
SnocOBP12	299.0320935	-0.932038561	0.26360295	-3.535766808	0.000406593	0.002118362
SnocIR43	172.2539251	-0.933891503	0.179939566	-5.190028652	2.10E-07	2.07E-06
SnocOR16	101.7910646	-1.106474641	0.346533868	-3.192976911	0.001408142	0.006273634
SnocOR21	47.41464246	-1.108194058	0.414946662	-2.670690377	0.007569543	0.026495262
SnocOR24	225.7722528	-1.120467671	0.189542182	-5.911442294	3.39E-09	4.23E-08
SnocIR24	89.87055686	-1.19269527	0.468245011	-2.547160654	0.010860342	0.035855754
SnocOR12	525.0787443	-1.198350629	0.214352004	-5.590573486	2.26E-08	2.55E-07
SnocOR10	213.0939545	-1.589156356	0.189410183	-8.39002598	4.86E-17	1.45E-15
SnocIR28	388.8178104	-1.609864784	0.292512435	-5.503577246	3.72E-08	4.05E-07
SnocOR17	188.5602842	-1.698396733	0.258751881	-6.563804396	5.25E-11	8.34E-10
SnocOR18	572.3454477	-1.716885541	0.222415784	-7.719261231	1.17E-14	2.71E-13
SnocOR34	28.92399412	-1.731401071	0.681745837	-2.539657709	0.011096101	0.0365143
SnocGR5	21.81385482	-1.768771941	0.466554874	-3.791133772	0.000149961	0.000857893
SnocOR33	14.97868901	-1.986880979	0.795915576	-2.496346394	0.012548	0.040597813
SnocIR30	95.5506514	-1.987727317	0.353491285	-5.623129633	1.88E-08	2.14E-07
SnocIR02	148.0835805	-2.198128135	0.241773472	-9.091684526	9.75E-20	3.58E-18
SnocIR39	39.50566078	-2.470139739	0.29205568	-8.457769912	2.73E-17	8.27E-16
SnocOR42	53.63464192	-2.506480912	0.384755251	-6.514481362	7.29E-11	1.14E-09
SnocIR09	401.1008842	-2.780553022	0.268579975	-10.35279352	4.06E-25	2.12E-23
SnocIR44	14.90359555	-2.806282325	0.732196993	-3.832687583	0.000126751	0.000740994
SnocOR31	48.78794332	-2.919168536	0.401992834	-7.261742714	3.82E-13	7.59E-12
SnocIR45	371.8211052	-2.979384917	0.231305556	-12.88073215	5.78E-38	5.88E-36
SnocGR9	44.2004385	-3.092771432	0.377627291	-8.190010371	2.61E-16	7.24E-15
SnocOR36	66.23712062	-3.216100075	0.611268001	-5.261358474	1.43E-07	1.45E-06

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Female Ovipositor vs Antennae Comparison						
SnocOR29	250.2982943	-3.316589249	0.938383364	-3.534364928	0.000408756	0.002128073
SnocIR54	4.392650681	-3.715577841	1.350137631	-2.751999318	0.005923264	0.021515654
SnocOR43	88.98720413	-3.799139391	0.346399209	-10.9675175	5.48E-28	3.51E-26
SnocOR22	33.88343062	-3.816746987	0.458472966	-8.324911762	8.44E-17	2.48E-15
SnocIR03	85.25030268	-3.929670938	0.30098978	-13.05582845	5.89E-39	6.40E-37
SnocOBP6	16.06752651	-4.010912185	1.133715608	-3.537846843	0.000403404	0.002103284
SnocOBP1	495.1163185	-4.295898	0.252289327	-17.02766445	5.12E-65	1.38E-62
SnocIR8a	471.7037306	-4.773202828	0.265921955	-17.949638	4.83E-72	1.50E-69
SnocOR35	41.65738404	-4.783992258	0.615815118	-7.768552802	7.94E-15	1.87E-13
SnocOR20	183.6185733	-4.924997236	0.384519725	-12.80817839	1.48E-37	1.47E-35
SnocOR13	4.976388719	-5.713636152	1.703922492	-3.353225385	0.000798756	0.003810104
SnocOR37	113.2795806	-5.74215332	0.601636302	-9.544226807	1.37E-21	5.66E-20
SnocOR23	68.15463492	-5.953197436	0.374172734	-15.91029194	5.38E-57	1.11E-54
SnocIR01	218.6742791	-5.9860103	0.428109027	-13.98244354	2.00E-44	2.81E-42
SnocOR41	5.837886768	-6.053182924	1.167562131	-5.18446322	2.17E-07	2.13E-06
SnocOR26	59.63113286	-6.451747623	0.490280879	-13.15928869	1.50E-39	1.70E-37
SnocSNMP1	16944.27711	-6.994131024	0.372591514	-18.77157895	1.29E-78	5.40E-76
SnocOBP8	5081.213618	-7.132547939	0.269722967	-26.44397701	4.28E-154	6.09E-151
SnocOR2	37.82693197	-7.303481623	1.180262688	-6.188013651	6.09E-10	8.37E-09
SnocOR44	8.673122668	-7.366522598	1.550913913	-4.749794645	2.04E-06	1.71E-05
SnocIR19	28.23047251	-7.546665463	1.313804029	-5.744133293	9.24E-09	1.09E-07
SnocOR3	31.32577049	-7.562853812	1.041932569	-7.258486811	3.91E-13	7.76E-12
SnocOR8	112.1400021	-8.009960968	0.697341724	-11.4864215	1.54E-30	1.10E-28
SnocOR38	9.688376947	-8.157886824	1.480456899	-5.51038455	3.58E-08	3.91E-07
SnocOR27	83.1456525	-8.471963932	0.811475687	-10.44019441	1.62E-25	8.66E-24
SnocOR1	32.76642584	-8.629952758	2.124576935	-4.061962933	4.87E-05	0.000311694
SnocOR5	18.05668037	-8.885645816	1.375903144	-6.458046013	1.06E-10	1.63E-09
SnocOR40	10.20681596	-9.052476753	1.499486168	-6.037052524	1.57E-09	2.05E-08
SnocOR4	141.2516972	-9.084437151	0.932362941	-9.74345585	1.97E-22	8.41E-21
SnocORCO	595.8901994	-9.375039986	0.48897691	-19.17276624	6.25E-82	3.42E-79
SnocOR9	63.13422613	-9.43834352	0.880437424	-10.72006171	8.19E-27	4.80E-25
SnocOR6	42.34619867	-9.479727945	1.095289715	-8.65499586	4.93E-18	1.61E-16
SnocOR25	12.03122844	-9.494292477	1.596038769	-5.948660311	2.70E-09	3.44E-08
SnocOR28	27.63417182	-9.688104811	1.215401283	-7.971116161	1.57E-15	4.03E-14
SnocCSP7	92114.69353	-9.975890967	0.621034725	-16.06333844	4.61E-58	9.80E-56
SnocOR30	16.82665887	-10.0846915	1.819808978	-5.541620918	3.00E-08	3.31E-07
SnocOR15	39.2343263	-10.1375666	1.260621432	-8.041721599	8.86E-16	2.35E-14
SnocOR39	25.06613876	-10.46446597	1.230121464	-8.506855853	1.79E-17	5.53E-16
SnocOBP11	68421.3101	-10.74998795	0.221047174	-48.63209858	0	0
SnocOR14	31.67263679	-11.03246783	1.632223108	-6.759166545	1.39E-11	2.35E-10
SnocOBP7	12118.50655	-12.00719388	0.351783428	-34.13234657	2.44E-255	1.16E-251
SnocOBP10	4059.27834	-12.6537739	0.66866261	-18.92400397	7.23E-80	3.32E-77
SnocOBP14	32050.68857	-14.77259544	0.711116244	-20.77381239	7.47E-96	5.06E-93
<i>Sirex</i> Adult Female Wings vs Antennae Comparison						
SnocIR22	3.128804552	2.582243206	1.057682767	2.441415599	0.014629808	0.046218607

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Female Wings vs Antennae Comparison						
SnocCSP8	25070.43435	2.27647645	0.371919115	6.120891226	9.31E-10	1.44E-08
SnocCSP3	75592.54521	2.098398058	0.503591073	4.166869059	3.09E-05	0.00022208
SnocGR10	25.04714529	1.864949513	0.49314107	3.78177691	0.000155713	0.000937644
SnocCSP5	809015.4868	1.845105986	0.334291536	5.519451701	3.40E-08	4.30E-07
SnocIR10	13.36267031	1.694973548	0.589717589	2.874212301	0.004050366	0.015832497
SnocOR19	30.21547201	1.352717997	0.521129375	2.595743132	0.00943866	0.032124157
SnocIR14	39.37454891	1.214087381	0.360416655	3.368566251	0.000755602	0.003737511
SnocIR42	207.1661834	1.130446376	0.397860797	2.841311294	0.004492843	0.017271234
SnocGR12	328.4596079	1.130243768	0.354102523	3.1918546	0.001413625	0.006466481
SnocIR49	197.542681	1.038104669	0.373005239	2.783083344	0.005384497	0.02011136
SnocIR28	388.8178104	1.019828742	0.287196129	3.550983587	0.000383794	0.002048552
SnocIR32	312.7103091	0.956354857	0.248853183	3.843048524	0.000121515	0.000753642
SnocIR25	847.5756711	-0.481062034	0.180048666	-2.671844473	0.00754356	0.026615416
SnocOR10	213.0939545	-0.621681539	0.185785606	-3.34623091	0.000819181	0.004018265
SnocIR31	242.9019269	-0.815473783	0.28017626	-2.910574165	0.003607653	0.014347259
SnocIR43	172.2539251	-1.093717231	0.183672813	-5.954703984	2.61E-09	3.82E-08
SnocGR9	44.2004385	-1.162125977	0.330933886	-3.511656035	0.000445324	0.002334674
SnocOR18	572.3454477	-1.166728172	0.22171621	-5.26225923	1.42E-07	1.63E-06
SnocIR39	39.50566078	-1.189324038	0.268561781	-4.42849326	9.49E-06	7.74E-05
SnocOR36	66.23712062	-1.48650999	0.596306863	-2.492860777	0.012671852	0.041031516
SnocOR24	225.7722528	-1.499032213	0.191725281	-7.818646592	5.34E-15	1.43E-13
SnocIR46	90.41283967	-1.554614587	0.420728036	-3.695058218	0.000219836	0.001266043
SnocOR17	188.5602842	-1.575534953	0.259340194	-6.075166866	1.24E-09	1.88E-08
SnocOR12	525.0787443	-1.597736602	0.215980104	-7.397610101	1.39E-13	3.30E-12
SnocGR6	67.84170803	-1.609890737	0.64000459	-2.515436237	0.011888518	0.038889645
SnocIR03	85.25030268	-1.97242789	0.27008444	-7.303004544	2.81E-13	6.53E-12
SnocOBP3	87804.10493	-2.146000942	0.670174918	-3.202150489	0.001364057	0.006276958
SnocOR16	101.7910646	-2.189774407	0.387776745	-5.646997745	1.63E-08	2.15E-07
SnocIR36	96.31687251	-2.368679985	0.654357558	-3.619855777	0.000294767	0.001632516
SnocOBP12	299.0320935	-2.391590163	0.326096724	-7.333990147	2.23E-13	5.21E-12
SnocIR30	95.5506514	-2.498345039	0.367410297	-6.79987758	1.05E-11	2.03E-10
SnocOR42	53.63464192	-2.642593741	0.392804212	-6.727508673	1.73E-11	3.24E-10
SnocOBP5	221649.8715	-2.786817671	0.880268821	-3.165871156	0.001546193	0.007001515
SnocGR5	21.81385482	-2.924672546	0.541871419	-5.397355249	6.76E-08	8.12E-07
SnocIR01	218.6742791	-3.031806738	0.395198727	-7.671600473	1.70E-14	4.40E-13
SnocOR21	47.41464246	-3.243651323	0.451150717	-7.18972885	6.49E-13	1.46E-11
SnocIR51	37.29977006	-3.277736846	0.664557032	-4.932213021	8.13E-07	8.10E-06
SnocOR3	31.32577049	-3.399642679	0.769764156	-4.41647309	1.00E-05	8.14E-05
SnocOR35	41.65738404	-3.567062565	0.579561017	-6.15476621	7.52E-10	1.17E-08
SnocIR09	401.1008842	-3.640600112	0.272652176	-13.35254375	1.14E-40	1.45E-38
SnocOR22	33.88343062	-3.719311676	0.462471526	-8.042250095	8.82E-16	2.52E-14
SnocOBP9	4437.958162	-3.932966059	0.342934297	-11.46857021	1.90E-30	1.45E-28
SnocOR5	18.05668037	-4.163318468	0.769061489	-5.413505331	6.18E-08	7.47E-07
SnocOR37	113.2795806	-4.173890175	0.58338836	-7.154565404	8.39E-13	1.86E-11
SnocSNMP1	16944.27711	-4.816763188	0.371324918	-12.97182859	1.77E-38	2.02E-36

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Female Wings vs Antennae Comparison						
SnocOR8	112.1400021	-5.048647693	0.562412468	-8.976770575	2.79E-19	1.06E-17
SnocIR45	371.8211052	-5.091795144	0.248179177	-20.51660902	1.53E-93	1.23E-90
SnocOR43	88.98720413	-5.124685447	0.394966337	-12.97499298	1.70E-38	1.95E-36
SnocOR2	37.82693197	-5.34736987	1.081966255	-4.942270468	7.72E-07	7.74E-06
SnocCSP7	92114.69353	-5.71586696	0.620288132	-9.214857846	3.12E-20	1.26E-18
SnocOBP1	495.1163185	-6.557398149	0.290616965	-22.56371421	9.85E-113	1.16E-109
SnocIR54	4.392650681	-6.637650641	1.668595816	-3.977985906	6.95E-05	0.000457342
SnocOR6	42.34619867	-6.917374904	0.606125695	-11.41244293	3.62E-30	2.75E-28
SnocIR8a	471.7037306	-6.948605184	0.304258549	-22.83783053	1.93E-115	2.69E-112
SnocOR20	183.6185733	-6.967345075	0.447903557	-15.55545824	1.46E-54	3.20E-52
SnocOR38	9.688376947	-6.969245906	1.480456899	-4.707496659	2.51E-06	2.29E-05
SnocOR29	250.2982943	-7.189330265	0.978840238	-7.344743283	2.06E-13	4.83E-12
SnocOR13	4.976388719	-7.236128444	1.780599691	-4.06387156	4.83E-05	0.000329785
SnocOR26	59.63113286	-7.355592932	0.633773031	-11.6060365	3.84E-31	3.06E-29
SnocOR39	25.06613876	-7.381813456	0.803733498	-9.184404377	4.14E-20	1.67E-18
SnocOR41	5.837886768	-7.674757115	1.308201816	-5.866646126	4.45E-09	6.31E-08
SnocOR40	10.20681596	-7.863835873	1.499486168	-5.244353728	1.57E-07	1.78E-06
SnocOR44	8.673122668	-8.101471561	1.550913913	-5.223675855	1.75E-07	1.97E-06
SnocIR44	14.90359555	-9.178636911	1.372765587	-6.686237619	2.29E-11	4.26E-10
SnocOBP8	5081.213618	-9.216548093	0.291658132	-31.60051812	3.63E-219	1.11E-215
SnocOR25	12.03122844	-9.267446581	1.596038769	-5.806529743	6.38E-09	8.82E-08
SnocOR27	83.1456525	-9.777501087	1.155183602	-8.464023438	2.58E-17	8.53E-16
SnocOR30	16.82665887	-9.857845688	1.819808978	-5.41696728	6.06E-08	7.34E-07
SnocOR23	68.15463492	-9.981619124	1.062475895	-9.394678192	5.74E-21	2.44E-19
SnocOR28	27.63417182	-10.42305411	1.215401283	-8.575812989	9.84E-18	3.34E-16
SnocOR1	32.76642584	-10.77306	2.273412134	-4.738718442	2.15E-06	1.98E-05
SnocOR14	31.67263679	-10.80562195	1.632223108	-6.620186842	3.59E-11	6.53E-10
SnocOR15	39.2343263	-10.87251586	1.260621432	-8.624727123	6.42E-18	2.21E-16
SnocOBP11	68421.3101	-11.41103679	0.22457856	-50.81089121	0	0
SnocOR9	63.13422613	-11.64490197	1.21278253	-9.601805502	7.86E-22	3.55E-20
SnocOBP7	12118.50655	-12.34349693	0.365757795	-33.74773443	1.15E-249	5.89E-246
SnocOBP10	4059.27834	-12.59818853	0.693775973	-18.15887118	1.09E-73	4.29E-71
SnocORCO	595.8901994	-13.68729533	1.242342338	-11.01732985	3.15E-28	2.17E-26
SnocOBP14	32050.68857	-15.55392287	0.758235105	-20.51332465	1.64E-93	1.25E-90
<i>Sirex</i> Adult Male Body vs Antennae Comparison						
SnocIR11	89.16480833	8.015920935	1.224369872	6.546976628	5.87E-11	5.54E-10
SnocIR13	10.18649879	6.310402611	1.281141864	4.925607997	8.41E-07	4.97E-06
SnocOR11	4.164431007	6.265167958	1.539317734	4.070094056	4.70E-05	0.000213091
SnocOBP4	275.5610933	4.7821167	0.401850261	11.90024534	1.18E-32	4.24E-31
SnocIR50	10.00132392	4.524393278	1.304144725	3.469241713	0.00052193	0.001948963
SnocGR2	9.48574097	4.499055386	1.570202219	2.865271321	0.004166521	0.012634702
SnocIR15	2.874628063	4.032552454	1.534746657	2.627503657	0.008601392	0.023969489
SnocIR12	15.80332584	3.967954892	0.907566367	4.372082347	1.23E-05	6.14E-05
SnocGR10	25.04714529	3.648574283	0.610741784	5.974004694	2.31E-09	1.87E-08
SnocIR26	11.90558972	3.181897359	1.177620635	2.70197147	0.006892968	0.019772177

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Male Body vs Antennae Comparison						
SnocIR47	786.6561263	3.115456519	0.197252965	15.79421894	3.41E-56	3.19E-54
SnocIR34	1585.251292	2.995065872	0.371047866	8.071912411	6.92E-16	9.68E-15
SnocIR48	460.3123721	2.431237884	0.254162888	9.565668331	1.11E-21	2.27E-20
SnocIR33	6.590483207	2.381019447	0.816615294	2.91571743	0.003548717	0.010977102
SnocGR6	67.84170803	2.352957858	0.587050205	4.00810329	6.12E-05	0.000271857
SnocIR49	197.542681	1.618212256	0.379082953	4.268755015	1.97E-05	9.48E-05
SnocIR46	90.41283967	1.594483076	0.334037185	4.773369996	1.81E-06	1.02E-05
SnocIR42	207.1661834	1.577212678	0.39569487	3.985931581	6.72E-05	0.000296078
SnocIR10	13.36267031	1.56696625	0.617222505	2.538738034	0.011125309	0.029953834
SnocCSP4	2248.279673	1.326418538	0.395053396	3.357567737	0.000786315	0.002844615
SnocIR14	39.37454891	1.113116408	0.335050783	3.322231928	0.000893004	0.003191984
SnocIR25	847.5756711	-0.739065083	0.180664049	-4.090825408	4.30E-05	0.000196036
SnocIR43	172.2539251	-0.811334248	0.182896	-4.43604151	9.16E-06	4.67E-05
SnocIR32	312.7103091	-0.89033253	0.253198594	-3.516340732	0.000437539	0.00165658
SnocOR31	48.78794332	-0.920261072	0.362221772	-2.540601206	0.011066206	0.029826915
SnocCSP8	25070.43435	-1.039857487	0.372018182	-2.795179208	0.005187095	0.015349903
SnocOR12	525.0787443	-1.047888725	0.215473839	-4.863183065	1.16E-06	6.68E-06
SnocGR9	44.2004385	-1.092672371	0.347036466	-3.148580846	0.001640653	0.005484365
SnocCSP1	2551.539137	-1.127195184	0.33041918	-3.411409666	0.000646279	0.002378861
SnocOR10	213.0939545	-1.304474858	0.19274113	-6.76801498	1.31E-11	1.32E-10
SnocIR02	148.0835805	-1.347612006	0.237911595	-5.664339327	1.48E-08	1.09E-07
SnocCSP5	809015.4868	-1.386567845	0.334296299	-4.147721199	3.36E-05	0.000155663
SnocIR28	388.8178104	-1.394706061	0.292640467	-4.765937113	1.88E-06	1.05E-05
SnocGR12	328.4596079	-1.59121389	0.35497125	-4.48265568	7.37E-06	3.82E-05
SnocIR35	457.2488906	-1.609151302	0.226149584	-7.115428957	1.12E-12	1.23E-11
SnocOR18	572.3454477	-1.758842142	0.223081709	-7.884295639	3.16E-15	4.26E-14
SnocIR31	242.9019269	-1.871507638	0.286018458	-6.543310702	6.02E-11	5.68E-10
SnocOBP3	87804.10493	-2.164087477	0.669819375	-3.230852315	0.001234217	0.004259238
SnocIR30	95.5506514	-2.330932614	0.376631596	-6.188892916	6.06E-10	5.19E-09
SnocOR17	188.5602842	-2.331784021	0.262499023	-8.883019795	6.51E-19	1.12E-17
SnocOR24	225.7722528	-2.390488974	0.206873344	-11.55532619	6.94E-31	2.32E-29
SnocIR24	89.87055686	-2.449393368	0.489201894	-5.006917185	5.53E-07	3.36E-06
SnocOBP6	16.06752651	-2.472594088	0.820502772	-3.013510951	0.002582437	0.008254418
SnocOBP2	790.2717246	-2.59585848	1.106193442	-2.346658714	0.018942597	0.047523469
SnocOR21	47.41464246	-2.771412037	0.440307041	-6.294271447	3.09E-10	2.73E-09
SnocIR18	8.453322592	-2.777653474	0.84119235	-3.302043192	0.000959833	0.003406439
SnocOR44	8.673122668	-2.837939106	1.090549876	-2.602301067	0.009260052	0.025595181
SnocIR39	39.50566078	-3.004640164	0.34359782	-8.744642682	2.24E-18	3.71E-17
SnocOR4	141.2516972	-3.033936455	0.440983226	-6.879936189	5.99E-12	6.20E-11
SnocOR35	41.65738404	-3.084716692	0.601475715	-5.128580614	2.92E-07	1.85E-06
SnocOR8	112.1400021	-3.177697984	0.558714718	-5.68751436	1.29E-08	9.56E-08
SnocIR03	85.25030268	-3.228097212	0.29746959	-10.85185618	1.95E-27	5.52E-26
SnocIR09	401.1008842	-3.24694209	0.275042445	-11.80524004	3.67E-32	1.30E-30
SnocOR3	31.32577049	-3.390304527	0.808593412	-4.192842133	2.75E-05	0.000129793
SnocOR22	33.88343062	-3.665425779	0.545011862	-6.725405504	1.75E-11	1.74E-10

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Male Body vs Antennae Comparison						
SnocOR15	39.2343263	-3.863926327	0.540512276	-7.148637506	8.76E-13	9.73E-12
SnocOR42	53.63464192	-3.902888211	0.417608051	-9.345816492	9.12E-21	1.74E-19
SnocIR19	28.23047251	-4.055456381	0.661273288	-6.132799339	8.63E-10	7.30E-09
SnocOR2	37.82693197	-4.068551906	1.089911381	-3.73291992	0.000189273	0.000766468
SnocOR5	18.05668037	-4.282550795	0.849993912	-5.038331141	4.70E-07	2.88E-06
SnocOR38	9.688376947	-4.283595774	1.107127419	-3.869108197	0.000109234	0.000460291
SnocOR37	113.2795806	-4.428996136	0.615582949	-7.194799895	6.26E-13	6.98E-12
SnocIR01	218.6742791	-4.496151958	0.405109296	-11.09861461	1.27E-28	3.78E-27
SnocOR16	101.7910646	-4.728443532	0.327458653	-14.43981854	2.91E-47	1.98E-45
SnocOR30	16.82665887	-4.756445113	1.532016442	-3.104695865	0.001904748	0.0062774
SnocOR41	5.837886768	-4.795093393	1.175870944	-4.077907883	4.54E-05	0.000206369
SnocOR20	183.6185733	-5.332708426	0.40438423	-13.18723142	1.04E-39	5.18E-38
SnocIR8a	471.7037306	-5.458212862	0.284576468	-19.1801272	5.42E-82	1.10E-79
SnocOR43	88.98720413	-5.683639427	0.47369382	-11.99855094	3.62E-33	1.35E-31
SnocOR27	83.1456525	-5.784473428	0.621933461	-9.300791467	1.39E-20	2.62E-19
SnocOBP1	495.1163185	-5.821851533	0.273613559	-21.27764265	1.83E-100	5.82E-98
SnocIR36	96.31687251	-5.942613379	0.843405686	-7.045972627	1.84E-12	2.00E-11
SnocOR26	59.63113286	-6.013070314	0.493958743	-12.17322378	4.32E-34	1.69E-32
SnocOR23	68.15463492	-6.068894219	0.544661276	-11.14251092	7.79E-29	2.37E-27
SnocOBP5	221649.8715	-6.07919495	0.880297442	-6.905841887	4.99E-12	5.22E-11
SnocIR44	14.90359555	-6.480184719	1.241704303	-5.218782527	1.80E-07	1.17E-06
SnocOR40	10.20681596	-6.68689825	1.502925335	-4.449255126	8.62E-06	4.43E-05
SnocOR9	63.13422613	-7.100141498	0.777756462	-9.12900355	6.91E-20	1.25E-18
SnocOR25	12.03122844	-7.115659864	1.602462467	-4.440453371	8.98E-06	4.59E-05
SnocOR14	31.67263679	-7.198009746	1.51960697	-4.736757522	2.17E-06	1.21E-05
SnocOBP9	4437.958162	-7.204242078	0.351066319	-20.52102888	1.40E-93	3.94E-91
SnocIR54	4.392650681	-7.207350434	1.665239808	-4.328115626	1.50E-05	7.40E-05
SnocIR45	371.8211052	-7.345730255	0.338873499	-21.67690978	3.39E-104	1.21E-101
SnocOR28	27.63417182	-7.348064856	1.066138793	-6.892221636	5.49E-12	5.71E-11
SnocCSP7	92114.69353	-7.407135128	0.620397899	-11.93932981	7.38E-33	2.68E-31
SnocOR6	42.34619867	-7.73075831	1.098043365	-7.040485425	1.92E-12	2.08E-11
SnocOR1	32.76642584	-8.407127771	2.274205001	-3.696732602	0.000218392	0.000872577
SnocOR39	25.06613876	-8.500269999	1.233012397	-6.893904732	5.43E-12	5.65E-11
SnocORCO	595.8901994	-9.73162555	0.587284343	-16.57055167	1.14E-61	1.27E-59
SnocOBP11	68421.3101	-10.71144603	0.223403178	-47.94670399	0	0
SnocOBP14	32050.68857	-11.07121524	0.666378691	-16.61399951	5.52E-62	6.25E-60
SnocOBP10	4059.27834	-11.27672472	0.476449955	-23.66822498	7.66E-124	3.70E-121
SnocSNMP1	16944.27711	-11.74127555	0.411445178	-28.53667068	4.11E-179	5.59E-176
SnocOBP8	5081.213618	-11.78769124	0.356459646	-33.06879576	8.35E-240	1.56E-236
SnocOBP7	12118.50655	-11.92072409	0.391939803	-30.41468105	3.51E-203	5.26E-200
<i>Sirex</i> Adult Male Head vs Antennae Comparison						
SnocIR11	89.16480833	5.175721982	1.238048703	4.180547962	2.91E-05	0.000143728
SnocIR48	460.3123721	5.174378388	0.249942867	20.70224467	3.31E-95	1.09E-92
SnocIR52	66.78474154	4.759028514	0.614155833	7.748894107	9.27E-15	1.36E-13
SnocIR34	1585.251292	4.539581531	0.370540673	12.2512368	1.65E-34	7.70E-33

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Male Head vs Antennae Comparison						
SnocIR50	10.00132392	3.960020612	1.307642938	3.028365387	0.002458806	0.008044793
SnocCSP6	7.585377378	3.805865981	1.020653851	3.728850852	0.000192355	0.000822752
SnocIR29	2.149564268	3.668727739	1.405744445	2.609811301	0.009059218	0.025457707
SnocIR49	197.542681	3.32366846	0.373562428	8.897223635	5.73E-19	1.10E-17
SnocIR47	786.6561263	3.293994105	0.196614539	16.75356321	5.33E-63	7.45E-61
SnocOBP12	299.0320935	3.147215691	0.234741246	13.4071696	5.49E-41	3.59E-39
SnocIR46	90.41283967	2.891670559	0.323245154	8.945750686	3.69E-19	7.17E-18
SnocIR42	207.1661834	2.699866561	0.392196847	6.883957847	5.82E-12	6.65E-11
SnocGR8	126.0733797	2.641044724	0.592627836	4.456497932	8.33E-06	4.51E-05
SnocCSP4	2248.279673	1.578693923	0.394683709	3.999896337	6.34E-05	0.00029604
SnocIR04	29.51708344	1.342712656	0.44003551	3.051373413	0.002277971	0.00752227
SnocOBP13	247.4246332	0.927499113	0.285418181	3.249614686	0.001155615	0.004110616
SnocIR35	457.2488906	0.685329985	0.213948905	3.203241378	0.0013589	0.004767032
SnocIR25	847.5756711	-0.55948244	0.179639429	-3.114474597	0.001842728	0.0062458
SnocIR43	172.2539251	-0.917524916	0.180092072	-5.094754614	3.49E-07	2.33E-06
SnocOR12	525.0787443	-1.014817979	0.214450992	-4.73216733	2.22E-06	1.31E-05
SnocIR31	242.9019269	-1.270171358	0.279477388	-4.54480904	5.50E-06	3.06E-05
SnocOR31	48.78794332	-1.363249972	0.362556464	-3.760103899	0.000169843	0.000733958
SnocOR43	88.98720413	-1.451619228	0.327026844	-4.438838136	9.04E-06	4.86E-05
SnocGR12	328.4596079	-1.536614278	0.353506268	-4.346780857	1.38E-05	7.19E-05
SnocIR28	388.8178104	-1.540564782	0.291535655	-5.284310023	1.26E-07	8.88E-07
SnocOR18	572.3454477	-1.564129401	0.221701762	-7.055105881	1.72E-12	2.07E-11
SnocOR10	213.0939545	-1.62526752	0.192049321	-8.462761085	2.61E-17	4.50E-16
SnocIR32	312.7103091	-1.779812149	0.255621387	-6.96268873	3.34E-12	3.92E-11
SnocIR02	148.0835805	-2.36065958	0.244388601	-9.659450427	4.48E-22	1.07E-20
SnocIR44	14.90359555	-2.376363111	0.739930495	-3.211603154	0.001319966	0.004640739
SnocGR6	67.84170803	-2.467060903	0.624384888	-3.951186122	7.78E-05	0.000356043
SnocOR36	66.23712062	-2.477911842	0.62600773	-3.958276751	7.55E-05	0.00034653
SnocOR24	225.7722528	-2.48575926	0.203040743	-12.24266233	1.84E-34	8.47E-33
SnocOR22	33.88343062	-2.594656898	0.467866978	-5.545714956	2.93E-08	2.23E-07
SnocOR17	188.5602842	-2.641745832	0.261607492	-10.09812759	5.63E-24	1.51E-22
SnocOR39	25.06613876	-2.658818611	0.4265176	-6.233784049	4.55E-10	4.35E-09
SnocIR39	39.50566078	-2.711306782	0.309828695	-8.750986664	2.11E-18	3.89E-17
SnocOR38	9.688376947	-2.765498305	0.958681871	-2.884688227	0.003918015	0.01217029
SnocIR8a	471.7037306	-2.828398783	0.259912769	-10.88210786	1.40E-27	4.53E-26
SnocOBP4	275.5610933	-2.89841556	0.445166962	-6.510850545	7.47E-11	7.69E-10
SnocOR21	47.41464246	-3.015738402	0.436586637	-6.907537123	4.93E-12	5.67E-11
SnocOR44	8.673122668	-3.070496462	1.081645134	-2.838728124	0.004529373	0.013819101
SnocOR25	12.03122844	-3.197923996	1.169403694	-2.73466213	0.006244434	0.018268849
SnocOR41	5.837886768	-3.21107417	0.775512994	-4.140580747	3.46E-05	0.000169628
SnocOBP9	4437.958162	-3.233666546	0.342567779	-9.43949416	3.75E-21	8.27E-20
SnocOR40	10.20681596	-3.366125449	1.008243025	-3.338605242	0.000842001	0.003115711
SnocOR27	83.1456525	-3.58296356	0.56301501	-6.363886385	1.97E-10	1.95E-09
SnocIR03	85.25030268	-3.717680821	0.299352892	-12.41905765	2.06E-35	1.01E-33
SnocOR42	53.63464192	-3.825384908	0.399906558	-9.565696873	1.11E-21	2.54E-20

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Male Head vs Antennae Comparison						
SnocOR35	41.65738404	-3.838925298	0.615610897	-6.235960595	4.49E-10	4.30E-09
SnocIR09	401.1008842	-4.144457763	0.278835342	-14.86345933	5.69E-50	5.23E-48
SnocGR5	21.81385482	-4.163791093	0.562207437	-7.406147306	1.30E-13	1.76E-12
SnocOR9	63.13422613	-4.172768324	0.369855092	-11.28217081	1.61E-29	5.72E-28
SnocOR13	4.976388719	-4.183347674	1.463448976	-2.858553828	0.004255769	0.013082447
SnocOBP5	221649.8715	-4.281309048	0.880273674	-4.86361137	1.15E-06	7.10E-06
SnocIR54	4.392650681	-4.529773926	1.351493247	-3.35168077	0.000803226	0.002986976
SnocOR4	141.2516972	-4.738304308	0.474717878	-9.981305803	1.84E-23	4.76E-22
SnocIR18	8.453322592	-4.751817094	0.9491202	-5.006549322	5.54E-07	3.60E-06
SnocOR37	113.2795806	-5.004127625	0.620387083	-8.066137676	7.26E-16	1.12E-14
SnocOR8	112.1400021	-5.055590537	0.595540036	-8.489085929	2.08E-17	3.63E-16
SnocOR26	59.63113286	-5.321586168	0.412084347	-12.91382748	3.76E-38	2.14E-36
SnocOR2	37.82693197	-5.387410519	1.132516251	-4.757027119	1.96E-06	1.17E-05
SnocOR20	183.6185733	-5.521636782	0.399046839	-13.83706434	1.52E-43	1.10E-41
SnocIR45	371.8211052	-5.523147879	0.254916786	-21.66647385	4.25E-104	1.78E-101
SnocOR28	27.63417182	-5.620822556	0.572364217	-9.820359817	9.20E-23	2.27E-21
SnocIR36	96.31687251	-5.695083114	0.745587366	-7.638384675	2.20E-14	3.14E-13
SnocOR3	31.32577049	-5.812397791	0.961970777	-6.04217709	1.52E-09	1.37E-08
SnocOR23	68.15463492	-6.000522542	0.485713604	-12.35403433	4.63E-35	2.21E-33
SnocOR16	101.7910646	-6.38454673	0.362145465	-17.62978513	1.46E-69	2.38E-67
SnocIR01	218.6742791	-6.428219437	0.433315575	-14.83496049	8.71E-50	7.90E-48
SnocIR53	24.73669766	-6.458866802	1.484161527	-4.351862439	1.35E-05	7.03E-05
SnocIR19	28.23047251	-6.494625297	0.868056077	-7.48180385	7.33E-14	1.02E-12
SnocOBP1	495.1163185	-6.553274461	0.280481349	-23.36438583	9.84E-121	5.39E-118
SnocOR15	39.2343263	-6.564501245	0.790121939	-8.308212845	9.72E-17	1.60E-15
SnocOR30	16.82665887	-6.572802095	1.737144562	-3.783681704	0.000154525	0.000671843
SnocOR6	42.34619867	-6.5829099	0.716196845	-9.191481286	3.87E-20	7.98E-19
SnocOR14	31.67263679	-6.599218079	1.337493336	-4.934019409	8.06E-07	5.10E-06
SnocOR1	32.76642584	-8.828053573	2.274205001	-3.881819612	0.000103678	0.000465113
SnocOR5	18.05668037	-8.863597134	1.378066273	-6.431909196	1.26E-10	1.27E-09
SnocCSP7	92114.69353	-9.181032048	0.620644589	-14.79273679	1.63E-49	1.46E-47
SnocOBP8	5081.213618	-9.848796286	0.284335241	-34.63797265	6.78E-263	3.22E-259
SnocOBP11	68421.3101	-11.57031162	0.22575852	-51.25083037	0	0
SnocOBP14	32050.68857	-11.71477585	0.667362236	-17.5538489	5.56E-69	8.89E-67
SnocOBP10	4059.27834	-12.08372699	0.48976952	-24.67227238	2.12E-134	1.59E-131
SnocSNMP1	16944.27711	-12.13714294	0.410876162	-29.53966198	8.92E-192	9.77E-189
SnocOBP7	12118.50655	-12.36675677	0.393070461	-31.46193367	2.88E-217	5.86E-214
SnocORCO	595.8901994	-12.63075132	1.096482711	-11.51933468	1.05E-30	4.00E-29
<i>Sirex</i> Adult Male Legs vs Antennae Comparison						
SnocOBP3	87804.10493	10.17099542	0.667578489	15.23565482	2.05E-52	3.12E-50
SnocIR11	89.16480833	5.322904864	1.238724375	4.297085755	1.73E-05	0.000100456
SnocIR52	66.78474154	4.230037421	0.617891077	6.845927343	7.60E-12	1.02E-10
SnocIR50	10.00132392	3.495970386	1.32865536	2.631209336	0.008508161	0.025732472
SnocCSP3	75592.54521	3.118553137	0.503577566	6.192796005	5.91E-10	6.51E-09
SnocIR34	1585.251292	2.852337007	0.371036909	7.687475115	1.50E-14	2.55E-13

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Male Legs vs Antennae Comparison						
SnocIR47	786.6561263	2.499899757	0.197935091	12.62989674	1.44E-36	1.12E-34
SnocGR10	25.04714529	1.923201741	0.639064222	3.00940293	0.002617617	0.009188409
SnocOBP4	275.5610933	1.768743568	0.403698782	4.381344826	1.18E-05	7.02E-05
SnocIR49	197.542681	1.718034926	0.377853451	4.546828723	5.45E-06	3.44E-05
SnocCSP4	2248.279673	1.607324385	0.394786135	4.07138003	4.67E-05	0.000249375
SnocOBP13	247.4246332	1.325004244	0.284773121	4.65284167	3.27E-06	2.14E-05
SnocIR42	207.1661834	1.206094341	0.396478498	3.042017028	0.002349986	0.008341222
SnocIR43	172.2539251	-0.656889506	0.179785873	-3.653732598	0.000258455	0.001176548
SnocIR28	388.8178104	-0.755826597	0.28981685	-2.60794566	0.009108741	0.027333713
SnocGR12	328.4596079	-0.836225871	0.352458559	-2.372550896	0.017665729	0.048008625
SnocIR31	242.9019269	-0.846511254	0.278692615	-3.037436973	0.002385993	0.008454639
SnocGR9	44.2004385	-0.931564213	0.340040913	-2.739565083	0.006152053	0.01938149
SnocOR12	525.0787443	-0.979085626	0.214881557	-4.55639675	5.20E-06	3.30E-05
SnocIR30	95.5506514	-1.223583121	0.351839592	-3.477673199	0.000505786	0.002147752
SnocIR39	39.50566078	-1.267256503	0.276240857	-4.587505692	4.49E-06	2.87E-05
SnocOBP12	299.0320935	-1.380569567	0.281870574	-4.897884678	9.69E-07	6.91E-06
SnocIR24	89.87055686	-1.388503845	0.474094712	-2.928747802	0.003403304	0.011546558
SnocOR31	48.78794332	-1.411242762	0.366113949	-3.854654448	0.000115893	0.000568714
SnocOR10	213.0939545	-1.412889052	0.192150654	-7.353027562	1.94E-13	2.97E-12
SnocOR24	225.7722528	-1.473954311	0.19644633	-7.503089073	6.23E-14	1.00E-12
SnocOR4	141.2516972	-1.657488612	0.424625301	-3.903414633	9.48E-05	0.000473059
SnocOR18	572.3454477	-1.66799271	0.222412915	-7.499531701	6.40E-14	1.03E-12
SnocIR03	85.25030268	-1.677616175	0.269519742	-6.224464907	4.83E-10	5.38E-09
SnocGR6	67.84170803	-1.90141056	0.616426106	-3.084571763	0.002038454	0.007337129
SnocGR5	21.81385482	-2.318338312	0.46295702	-5.007675042	5.51E-07	4.05E-06
SnocOR17	188.5602842	-2.353416894	0.261137379	-9.012179348	2.02E-19	4.79E-18
SnocOR35	41.65738404	-2.391723743	0.575993674	-4.152343771	3.29E-05	0.000180804
SnocIR19	28.23047251	-2.525145348	0.604034152	-4.18046784	2.91E-05	0.000161299
SnocIR51	37.29977006	-2.565198078	0.596220775	-4.302429879	1.69E-05	9.83E-05
SnocOR22	33.88343062	-2.70923233	0.479335314	-5.652060783	1.59E-08	1.47E-07
SnocOBP5	221649.8715	-2.862314404	0.880270021	-3.251632268	0.001147444	0.004459446
SnocOR21	47.41464246	-2.970130624	0.440380589	-6.744463087	1.54E-11	1.99E-10
SnocOBP9	4437.958162	-3.017761931	0.342576612	-8.80901331	1.26E-18	2.85E-17
SnocOR3	31.32577049	-3.042475172	0.79106432	-3.846052839	0.000120036	0.00058707
SnocIR09	401.1008842	-3.267550243	0.274042222	-11.92352851	8.92E-33	5.30E-31
SnocOR37	113.2795806	-3.773862238	0.597062035	-6.320720485	2.60E-10	2.99E-09
SnocIR01	218.6742791	-3.921356463	0.39867917	-9.835869948	7.89E-23	2.38E-21
SnocOR42	53.63464192	-4.001845214	0.413046993	-9.688595452	3.37E-22	9.75E-21
SnocOR44	8.673122668	-4.467180792	1.207996714	-3.698007402	0.000217299	0.001005178
SnocIR45	371.8211052	-4.805770138	0.247165082	-19.44356417	3.30E-84	1.27E-81
SnocOR40	10.20681596	-4.870924821	1.158626148	-4.204052213	2.62E-05	0.000146987
SnocOBP1	495.1163185	-4.879293977	0.257507296	-18.94817761	4.57E-80	1.63E-77
SnocOR43	88.98720413	-5.040499728	0.41105386	-12.26238265	1.44E-34	9.75E-33
SnocOR29	250.2982943	-5.152061122	0.970124725	-5.310720351	1.09E-07	8.95E-07
SnocOR5	18.05668037	-5.189409957	0.921512059	-5.63140754	1.79E-08	1.64E-07

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Male Legs vs Antennae Comparison						
SnocOR8	112.1400021	-5.480385454	0.625474999	-8.761957652	1.92E-18	4.30E-17
SnocOR16	101.7910646	-5.580631576	0.342298944	-16.30338529	9.34E-60	1.87E-57
SnocIR8a	471.7037306	-5.742424075	0.286134777	-20.06894837	1.38E-89	6.10E-87
SnocOR41	5.837886768	-5.909360081	1.315363434	-4.492568309	7.04E-06	4.34E-05
SnocOR1	32.76642584	-5.945120461	2.023527368	-2.937998544	0.003303386	0.011252013
SnocOR20	183.6185733	-6.200066745	0.424794752	-14.59544103	3.00E-48	3.78E-46
SnocOR23	68.15463492	-6.35607219	0.549289232	-11.57144873	5.75E-31	3.05E-29
SnocOR15	39.2343263	-6.710259342	0.853320054	-7.863707542	3.73E-15	6.70E-14
SnocOR25	12.03122844	-7.334585996	1.602462467	-4.577071942	4.72E-06	3.01E-05
SnocOR13	4.976388719	-7.387427755	1.781075747	-4.147733621	3.36E-05	0.000184082
SnocIR54	4.392650681	-7.426276543	1.665239808	-4.459583844	8.21E-06	5.01E-05
SnocIR44	14.90359555	-7.595060329	1.374628695	-5.525172256	3.29E-08	2.91E-07
SnocOR38	9.688376947	-7.68466459	1.482486087	-5.183633532	2.18E-07	1.70E-06
SnocOR26	59.63113286	-7.879413323	0.72572206	-10.85734299	1.84E-27	7.61E-26
SnocOBP8	5081.213618	-7.905377146	0.270289504	-29.247814	4.79E-188	7.77E-185
SnocOR6	42.34619867	-7.994675196	1.084665471	-7.370636764	1.70E-13	2.62E-12
SnocCSP7	92114.69353	-8.16574879	0.620477703	-13.1604226	1.48E-39	1.31E-37
SnocOR30	16.82665887	-8.170645545	1.822810812	-4.48244299	7.38E-06	4.53E-05
SnocOR39	25.06613876	-8.719196245	1.233012397	-7.071458701	1.53E-12	2.19E-11
SnocOR9	63.13422613	-9.216815394	1.213833654	-7.593145375	3.12E-14	5.13E-13
SnocOR14	31.67263679	-9.292125353	1.633692738	-5.687804774	1.29E-08	1.21E-07
SnocOR28	27.63417182	-9.419130446	1.216882373	-7.740378737	9.91E-15	1.72E-13
SnocOBP7	12118.50655	-10.18915507	0.340609996	-29.91443354	1.28E-196	2.33E-193
SnocOR27	83.1456525	-10.54021542	1.300352991	-8.105657074	5.25E-16	1.00E-14
SnocOBP11	68421.3101	-11.14693893	0.224668343	-49.61508496	0	0
SnocOBP14	32050.68857	-11.72051919	0.668594999	-17.53007308	8.45E-69	2.28E-66
SnocOBP10	4059.27834	-14.09462107	0.658319617	-21.40999707	1.08E-101	6.56E-99
SnocORCO	595.8901994	-14.26863375	1.242373254	-11.48498143	1.57E-30	7.98E-29
<i>Sirex</i> Adult Male Wings vs Antennae Comparison						
SnocCSP8	25070.43435	2.563954458	0.371902858	6.894150994	5.42E-12	1.27E-10
SnocGR10	25.04714529	2.429127498	0.637343881	3.811329441	0.000138221	0.001053181
SnocCSP5	809015.4868	2.249857336	0.334292128	6.730213337	1.69E-11	3.81E-10
SnocOR19	30.21547201	1.884154739	0.512927356	3.673336421	0.000239404	0.001730227
SnocIR49	197.542681	1.807253311	0.379297363	4.764739985	1.89E-06	2.07E-05
SnocCSP4	2248.279673	1.727521764	0.394942736	4.374106948	1.22E-05	0.000116726
SnocCSP3	75592.54521	1.514699663	0.503582301	3.007849285	0.002631036	0.013668547
SnocIR42	207.1661834	1.215150276	0.398394842	3.050115485	0.002287534	0.012132511
SnocIR25	847.5756711	-0.500893703	0.180651044	-2.772714139	0.005559093	0.02576419
SnocOR24	225.7722528	-0.706220282	0.19442223	-3.632405018	0.000280792	0.001997701
SnocIR39	39.50566078	-0.726112358	0.274338172	-2.646778436	0.008126258	0.035177895
SnocIR43	172.2539251	-1.014691203	0.187867466	-5.401101246	6.62E-08	9.28E-07
SnocOR12	525.0787443	-1.10344928	0.216319802	-5.101009112	3.38E-07	4.25E-06
SnocOR18	572.3454477	-1.418930102	0.222792599	-6.368838595	1.90E-10	3.72E-09
SnocGR9	44.2004385	-1.47996878	0.363447672	-4.072027125	4.66E-05	0.000397196
SnocOR17	188.5602842	-1.588331356	0.258660542	-6.140601669	8.22E-10	1.50E-08

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Male Wings vs Antennae Comparison						
SnocOR37	113.2795806	-1.933945612	0.581860179	-3.323729105	0.000888224	0.005455274
SnocGR3	32.05060432	-1.935529479	0.657823207	-2.942324715	0.003257581	0.016393462
SnocIR03	85.25030268	-2.047474095	0.278503695	-7.351694533	1.96E-13	5.25E-12
SnocOBP12	299.0320935	-2.190276519	0.338788611	-6.465024045	1.01E-10	2.06E-09
SnocIR30	95.5506514	-2.223304735	0.38018227	-5.847996902	4.98E-09	8.26E-08
SnocGR6	67.84170803	-2.31200905	0.639589645	-3.614831895	0.000300543	0.002124756
SnocOR22	33.88343062	-2.351739437	0.482595216	-4.873109714	1.10E-06	1.27E-05
SnocIR19	28.23047251	-2.445425999	0.610870931	-4.003179519	6.25E-05	0.000519585
SnocIR01	218.6742791	-2.462880659	0.393734601	-6.255179638	3.97E-10	7.50E-09
SnocOBP3	87804.10493	-2.58780565	0.671106379	-3.856028988	0.000115244	0.000901149
SnocIR18	8.453322592	-2.591983142	0.843064483	-3.074477925	0.002108713	0.011395396
SnocOR5	18.05668037	-3.059792853	0.785863277	-3.893543501	9.88E-05	0.000788973
SnocOBP2	790.2717246	-3.069218546	1.109371858	-2.766627371	0.005663945	0.026175353
SnocGR5	21.81385482	-3.194815031	0.535201402	-5.969369697	2.38E-09	4.13E-08
SnocOR8	112.1400021	-3.309174076	0.564886157	-5.858125638	4.68E-09	7.81E-08
SnocOR21	47.41464246	-3.340729993	0.464099829	-7.198300416	6.10E-13	1.57E-11
SnocOBP4	275.5610933	-3.367761917	0.491141797	-6.857005328	7.03E-12	1.62E-10
SnocOBP5	221649.8715	-3.503123275	0.880273087	-3.979586932	6.90E-05	0.000571016
SnocOBP9	4437.958162	-3.625357582	0.343022461	-10.56886354	4.15E-26	2.82E-24
SnocOR42	53.63464192	-3.665939199	0.41728267	-8.785265879	1.56E-18	6.62E-17
SnocIR09	401.1008842	-3.974353593	0.283949933	-13.99667031	1.63E-44	2.43E-42
SnocCSP7	92114.69353	-4.116652827	0.620259814	-6.636981365	3.20E-11	6.94E-10
SnocIR44	14.90359555	-4.196442903	0.867434613	-4.8377628	1.31E-06	1.49E-05
SnocIR51	37.29977006	-4.318385596	0.769313353	-5.613298639	1.99E-08	3.03E-07
SnocOR43	88.98720413	-5.035789187	0.43987118	-11.44832717	2.40E-30	1.91E-28
SnocIR36	96.31687251	-5.216329173	0.767618027	-6.79547508	1.08E-11	2.45E-10
SnocOR6	42.34619867	-5.337426213	0.628666102	-8.490081133	2.06E-17	7.85E-16
SnocIR45	371.8211052	-5.648087701	0.272858227	-20.69971562	3.48E-95	3.18E-92
SnocIR53	24.73669766	-5.809207405	1.484161527	-3.914134209	9.07E-05	0.000732203
SnocIR8a	471.7037306	-5.896997262	0.299964649	-19.65897406	4.84E-86	3.54E-83
SnocOR25	12.03122844	-5.925132137	1.602462467	-3.697516952	0.000217719	0.001588443
SnocOR29	250.2982943	-6.163123642	1.023941712	-6.019018045	1.75E-09	3.09E-08
SnocOR44	8.673122668	-6.184690977	1.553808762	-3.980342451	6.88E-05	0.000569527
SnocOR15	39.2343263	-6.23750351	0.854712609	-7.297778743	2.93E-13	7.70E-12
SnocOR20	183.6185733	-6.243640571	0.445949902	-14.00076678	1.54E-44	2.32E-42
SnocOR38	9.688376947	-6.275210474	1.482486087	-4.232896707	2.31E-05	0.000208287
SnocOR39	25.06613876	-6.423198986	1.084743429	-5.921399306	3.19E-09	5.46E-08
SnocOR41	5.837886768	-6.423496048	1.315363434	-4.883438204	1.04E-06	1.21E-05
SnocOR16	101.7910646	-6.502322199	0.400357027	-16.24130905	2.57E-59	7.23E-57
SnocOBP1	495.1163185	-6.551865702	0.299523653	-21.87428482	4.57E-106	5.56E-103
SnocOR1	32.76642584	-6.760812579	2.12381193	-3.18333864	0.001455872	0.008279813
SnocOR9	63.13422613	-6.884768906	0.780144623	-8.824990526	1.09E-18	4.71E-17
SnocOR26	59.63113286	-6.901973014	0.636228019	-10.8482695	2.03E-27	1.49E-25
SnocOR13	4.976388719	-6.939768836	1.781075747	-3.896391745	9.76E-05	0.000781895
SnocIR54	4.392650681	-6.978617535	1.665239808	-4.190758293	2.78E-05	0.000248401

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Adult Male Wings vs Antennae Comparison						
SnocOR23	68.15463492	-7.164744162	0.781197573	-9.17148799	4.67E-20	2.18E-18
SnocSNMP1	16944.27711	-7.316875816	0.373219306	-19.60476241	1.41E-85	9.79E-83
SnocOR40	10.20681596	-7.419960242	1.502925335	-4.937011886	7.93E-07	9.45E-06
SnocOR30	16.82665887	-7.722986662	1.822810812	-4.236855856	2.27E-05	0.000204903
SnocOR14	31.67263679	-8.844466325	1.633692738	-5.413788114	6.17E-08	8.72E-07
SnocOR28	27.63417182	-8.971471152	1.216882373	-7.372504813	1.67E-13	4.53E-12
SnocOR27	83.1456525	-9.211049387	1.162521906	-7.923334037	2.31E-15	7.40E-14
SnocOBP11	68421.3101	-10.71380289	0.224553251	-47.71163563	0	0
SnocOBP8	5081.213618	-10.96161763	0.328004186	-33.41913941	7.23E-245	3.52E-241
SnocOBP7	12118.50655	-11.18028376	0.371990899	-30.05526155	1.86E-198	6.80E-195
SnocORCO	595.8901994	-12.85917918	1.242373254	-10.35049583	4.16E-25	2.68E-23
SnocOBP14	32050.68857	-14.9830028	0.754386712	-19.8611701	8.82E-88	6.78E-85
SnocOBP10	4059.27834	-17.54869573	1.254155527	-13.99243982	1.73E-44	2.56E-42
<i>Sirex</i> Female Pupa Head vs Body Comparison						
SnocORCO	595.8901994	6.784185738	1.096296717	6.18827516	6.08E-10	1.62E-08
SnocCSP6	7.585377378	6.437625006	1.420649295	4.531466723	5.86E-06	7.97E-05
SnocOBP14	32050.68857	5.539783059	0.6750379	8.206625229	2.27E-16	1.31E-14
SnocIR45	371.8211052	5.140712955	0.463635757	11.08782677	1.44E-28	2.18E-26
SnocOR43	88.98720413	3.823849572	0.565526165	6.761578523	1.36E-11	4.58E-10
SnocOR9	63.13422613	3.702827641	0.501465649	7.384010546	1.54E-13	6.32E-12
SnocOBP2	790.2717246	3.220045566	1.155630542	2.78639708	0.005329754	0.028285638
SnocOBP6	16.06752651	3.083493869	1.126393832	2.737491791	0.006190967	0.031904876
SnocOR27	83.1456525	2.97611112	0.932605766	3.191178125	0.001416939	0.009543895
SnocSNMP1	16944.27711	2.857837447	0.399193495	7.1590281	8.13E-13	3.13E-11
SnocIR48	460.3123721	2.765034651	0.238415078	11.59756618	4.24E-31	7.45E-29
SnocOR23	68.15463492	2.553833852	0.746387489	3.421592523	0.000622555	0.004753119
SnocIR52	66.78474154	2.417421216	0.395712294	6.109037425	1.00E-09	2.62E-08
SnocGR9	44.2004385	2.327879688	0.473198736	4.919454576	8.68E-07	1.40E-05
SnocCSP3	75592.54521	2.256302338	0.513890025	4.390632681	1.13E-05	0.000141915
SnocOBP12	299.0320935	2.221315258	0.215332217	10.31575902	5.98E-25	6.75E-23
SnocIR51	37.29977006	2.141871643	0.570897991	3.751758941	0.000175598	0.001585506
SnocOR39	25.06613876	2.097578756	0.607997621	3.449978557	0.000560631	0.004345578
SnocOR28	27.63417182	1.988799798	0.766918429	2.59323511	0.009507775	0.044813375
SnocIR35	457.2488906	1.802276095	0.216425615	8.327462039	8.26E-17	4.96E-15
SnocIR49	197.542681	1.786743253	0.365576199	4.8874715	1.02E-06	1.63E-05
SnocGR8	126.0733797	1.726832674	0.580854154	2.972919556	0.002949818	0.017544884
SnocIR8a	471.7037306	1.697035511	0.280164083	6.057291482	1.38E-09	3.55E-08
SnocOBP1	495.1163185	1.381578719	0.252738032	5.466445672	4.59E-08	9.22E-07
SnocOBP9	4437.958162	1.254102542	0.424129313	2.956887214	0.003107618	0.01832272
SnocCSP8	25070.43435	1.178631969	0.373239131	3.157846728	0.001589391	0.010501781
SnocIR30	95.5506514	1.164446958	0.345617714	3.369176149	0.000753932	0.005573854
SnocIR46	90.41283967	1.054595318	0.28528557	3.696630423	0.00021848	0.001915602
SnocIR09	401.1008842	0.988871147	0.280396171	3.52669276	0.000420785	0.003396573
SnocOR24	225.7722528	0.644326579	0.230579111	2.794384005	0.005199869	0.027720306
SnocIR14	39.37454891	-1.592660452	0.407050361	-3.912686495	9.13E-05	0.0008988

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Female Pupa Head vs Body Comparison						
SnocOR42	53.63464192	-2.350088346	0.398726563	-5.893984913	3.77E-09	9.02E-08
SnocOR16	101.7910646	-2.364468264	0.461143803	-5.127398977	2.94E-07	5.14E-06
SnocGR10	25.04714529	-2.453492042	0.505902584	-4.849732182	1.24E-06	1.93E-05
SnocIR13	10.18649879	-2.881613853	1.090681279	-2.642031094	0.008241049	0.040008284
SnocOBP5	221649.8715	-2.938816906	0.881903474	-3.332356648	0.000861138	0.006255993
SnocOR8	112.1400021	-3.124761411	0.575678578	-5.427961938	5.70E-08	1.13E-06
SnocIR19	28.23047251	-3.623518712	0.784026579	-4.621678408	3.81E-06	5.44E-05
SnocGR6	67.84170803	-4.083474836	0.661155024	-6.176274379	6.56E-10	1.74E-08
SnocIR12	15.80332584	-4.378464725	1.473575963	-2.971319317	0.002965233	0.017629208
<i>Sirex</i> Male Pupa Head vs Body Comparison						
SnocOBP8	5081.213618	7.11230369	1.217436466	5.842032736	5.16E-09	6.40E-08
SnocOBP14	32050.68857	6.597660223	0.683681378	9.650197347	4.91E-22	2.02E-20
SnocOR9	63.13422613	4.007951086	0.902589832	4.440501036	8.97E-06	7.44E-05
SnocSNMP1	16944.27711	3.868924963	0.40351821	9.587981074	8.98E-22	3.60E-20
SnocOBP2	790.2717246	3.55304965	1.145613331	3.101438813	0.001925827	0.010037538
SnocIR23	6.300662129	3.224802012	1.24706604	2.585911177	0.009712196	0.040098513
SnocOR39	25.06613876	3.212927453	0.837327784	3.837120321	0.000124485	0.000858868
SnocIR49	197.542681	3.085858337	0.368253093	8.379721431	5.31E-17	1.43E-15
SnocOBP9	4437.958162	2.584536047	0.647002974	3.994627767	6.48E-05	0.000469924
SnocOBP12	299.0320935	2.329350609	0.214847468	10.84188068	2.18E-27	1.41E-25
SnocIR48	460.3123721	2.163175714	0.233705426	9.255992692	2.12E-20	7.54E-19
SnocCSP8	25070.43435	2.07643889	0.373882554	5.553719663	2.80E-08	3.23E-07
SnocOBP1	495.1163185	2.059090409	0.252554622	8.153049796	3.55E-16	8.92E-15
SnocIR52	66.78474154	2.006532079	0.385279315	5.207993262	1.91E-07	1.98E-06
SnocOR19	30.21547201	1.62080355	0.441592984	3.670356208	0.000242213	0.001586916
SnocIR35	457.2488906	1.418264691	0.212612145	6.670666389	2.55E-11	3.97E-10
SnocIR42	207.1661834	0.960885695	0.381583989	2.518149931	0.011797309	0.046801336
SnocGR9	44.2004385	-0.999634112	0.34665965	-2.883618304	0.003931349	0.018664641
SnocIR45	371.8211052	-1.003647259	0.246540701	-4.070919136	4.68E-05	0.000348619
SnocIR02	148.0835805	-1.131688253	0.283570174	-3.990857837	6.58E-05	0.000476983
SnocIR14	39.37454891	-1.218564185	0.469074606	-2.597804632	0.009382186	0.03900072
SnocOR16	101.7910646	-1.328238604	0.347011332	-3.827651959	0.000129372	0.000891314
SnocOR21	47.41464246	-1.351769681	0.445529396	-3.034075179	0.002412743	0.012243182
SnocOR43	88.98720413	-1.626882738	0.343495921	-4.736250527	2.18E-06	1.98E-05
SnocIR27	30.26473407	-1.80231061	0.404703155	-4.453413789	8.45E-06	7.04E-05
SnocOR20	183.6185733	-1.862389587	0.406952238	-4.576432838	4.73E-06	4.09E-05
SnocOR31	48.78794332	-1.989297721	0.513508232	-3.873935403	0.000107092	0.000747696
SnocGR10	25.04714529	-2.11967795	0.445422428	-4.758803811	1.95E-06	1.78E-05
SnocORCO	595.8901994	-2.125359108	0.407133563	-5.220299436	1.79E-07	1.86E-06
SnocOR26	59.63113286	-2.476256087	0.415878861	-5.954272558	2.61E-09	3.33E-08
SnocIR39	39.50566078	-2.532829183	0.376151985	-6.733526027	1.66E-11	2.64E-10
SnocIR10	13.36267031	-2.636117198	0.73508884	-3.586120554	0.000335634	0.002125778
SnocIR37	70.55714089	-2.706779626	0.522613702	-5.179312395	2.23E-07	2.29E-06
SnocOR28	27.63417182	-2.721006765	0.75926832	-3.583722242	0.000338732	0.002142614
SnocIR03	85.25030268	-3.086052314	0.319784765	-9.650404448	4.90E-22	2.02E-20

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Male Pupa Head vs Body Comparison						
SnocGR3	32.05060432	-3.224540539	0.521859393	-6.178945095	6.45E-10	8.84E-09
SnocCSP7	92114.69353	-3.269294799	0.633401724	-5.161487058	2.45E-07	2.51E-06
SnocIR13	10.18649879	-3.558895528	1.164301342	-3.056679056	0.002238038	0.011436161
SnocIR29	2.149564268	-3.803607162	1.46732603	-2.592203153	0.009536344	0.039528985
SnocIR44	14.90359555	-3.840868073	1.471656843	-2.609893802	0.009057033	0.037919022
SnocOBP6	16.06752651	-3.924433827	0.865687629	-4.533313974	5.81E-06	4.97E-05
SnocOR15	39.2343263	-4.217418235	0.63033114	-6.690797851	2.22E-11	3.48E-10
SnocIR26	11.90558972	-4.65213291	0.971199828	-4.790088278	1.67E-06	1.54E-05
SnocIR19	28.23047251	-4.781967801	0.69896979	-6.841451331	7.84E-12	1.29E-10
SnocOR4	141.2516972	-5.210226558	0.660883979	-7.883723505	3.18E-15	7.27E-14
SnocOR32	5.789361401	-5.722448217	1.418060479	-4.035404909	5.45E-05	0.000400486
SnocOBP4	275.5610933	-6.289347716	0.928279348	-6.775274846	1.24E-11	2.01E-10
SnocIR53	24.73669766	-6.402718133	1.014389713	-6.311891824	2.76E-10	3.90E-09
SnocGR2	9.48574097	-8.034716316	1.413718348	-5.683392543	1.32E-08	1.58E-07
<i>Sirex</i> Pupa Body Female vs Male Comparison						
SnocOR8	112.1400021	6.50221752	0.834844412	7.788538107	6.78E-15	2.33E-13
SnocOR6	42.34619867	4.048049121	1.357133852	2.982792828	0.002856313	0.017850731
SnocCSP9	749.0168383	3.845073578	0.652439452	5.893379942	3.78E-09	7.22E-08
SnocOBP8	5081.213618	3.812788972	1.343788047	2.837344014	0.004549057	0.026543438
SnocOBP9	4437.958162	2.854917179	0.652423952	4.375861997	1.21E-05	0.00013981
SnocOR9	63.13422613	2.506389985	0.966735565	2.592632438	0.00952445	0.047997048
SnocGR6	67.84170803	2.049004638	0.601844662	3.404540686	0.000662754	0.00515205
SnocOR42	53.63464192	1.934330436	0.388512921	4.978805927	6.40E-07	9.10E-06
SnocGR5	21.81385482	1.431144864	0.465212283	3.076326477	0.002095682	0.013719672
SnocIR14	39.37454891	1.230271432	0.389543368	3.158239962	0.001587248	0.010899454
SnocCSP8	25070.43435	1.059382591	0.374556642	2.828364183	0.004678655	0.027126165
SnocCSP1	2551.539137	0.866994328	0.331198222	2.617750553	0.008851148	0.04528268
SnocOBP11	68421.3101	-0.639088841	0.231060042	-2.765899445	0.005676604	0.03182578
SnocIR02	148.0835805	-0.832472348	0.289331929	-2.877222537	0.004011926	0.023847761
SnocIR30	95.5506514	-0.926400756	0.346440195	-2.674056787	0.007493976	0.039682465
SnocOR16	101.7910646	-0.981676557	0.350568538	-2.80024147	0.005106439	0.029257813
SnocOR17	188.5602842	-1.013135845	0.261918378	-3.868135764	0.000109671	0.001042371
SnocGR12	328.4596079	-1.07051128	0.359819821	-2.975131489	0.00292863	0.018209143
SnocIR31	242.9019269	-1.106836855	0.277168242	-3.99337546	6.51E-05	0.000654937
SnocIR37	70.55714089	-1.512752311	0.50889615	-2.972614967	0.002952746	0.018346756
SnocIR19	28.23047251	-1.740860603	0.600035802	-2.901261218	0.003716639	0.022271219
SnocOR28	27.63417182	-2.197653285	0.758252753	-2.898312304	0.003751768	0.022447566
SnocOR23	68.15463492	-2.227336372	0.754570348	-2.951794193	0.003159334	0.019420261
SnocOR26	59.63113286	-2.440369875	0.441815593	-5.523503276	3.32E-08	5.67E-07
SnocOR21	47.41464246	-2.605229033	0.511114078	-5.09715765	3.45E-07	5.10E-06
SnocIR39	39.50566078	-2.685660486	0.429171903	-6.257773328	3.91E-10	8.27E-09
SnocGR3	32.05060432	-2.70317136	0.521499957	-5.183454621	2.18E-07	3.33E-06
SnocOR20	183.6185733	-2.990760908	0.466145778	-6.415934778	1.40E-10	3.11E-09
SnocGR9	44.2004385	-3.0187532	0.465479444	-6.485255667	8.86E-11	2.00E-09
SnocOR15	39.2343263	-3.108960962	0.577979622	-5.379014833	7.49E-08	1.23E-06

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Pupa Body Female vs Male Comparison						
SnocOR32	5.789361401	-3.28591786	1.137408827	-2.888950554	0.003865298	0.023070111
SnocIR03	85.25030268	-3.97797143	0.397999686	-9.994910971	1.60E-23	1.27E-21
SnocOR4	141.2516972	-4.008129548	0.58194778	-6.887438508	5.68E-12	1.47E-10
SnocIR53	24.73669766	-4.087402035	0.926210233	-4.413039165	1.02E-05	0.000119524
SnocCSP3	75592.54521	-4.477215537	0.512743605	-8.731879818	2.50E-18	1.16E-16
SnocOR43	88.98720413	-5.081846782	0.559421699	-9.08410737	1.05E-19	5.70E-18
SnocOBP6	16.06752651	-5.098720515	1.104709754	-4.615439028	3.92E-06	4.93E-05
SnocIR45	371.8211052	-5.199952265	0.46340515	-11.22117926	3.21E-29	4.26E-27
SnocOBP4	275.5610933	-5.76782165	0.927330285	-6.219813739	4.98E-10	1.04E-08
SnocCSP6	7.585377378	-6.980221238	1.416688124	-4.927140364	8.34E-07	1.16E-05
SnocGR2	9.48574097	-7.436687075	1.391355935	-5.344920656	9.05E-08	1.46E-06
SnocIR26	11.90558972	-8.04090222	1.483199223	-5.421323107	5.92E-08	9.79E-07
SnocORCO	595.8901994	-8.64617599	1.093812032	-7.904626884	2.69E-15	9.66E-14
<i>Sirex</i> Pupa Head Female vs Male Comparison						
SnocOR14	31.67263679	5.483058474	1.660367764	3.302315663	0.000958901	0.01964741
SnocCSP9	749.0168383	4.148273139	0.65151097	6.367157776	1.93E-10	4.20E-08
SnocGR8	126.0733797	2.933543139	0.583546951	5.02709017	4.98E-07	4.52E-05
SnocOR28	27.63417182	2.512153278	0.767922535	3.271362881	0.001070305	0.021224995
SnocOR9	63.13422613	2.20126654	0.362710008	6.068943488	1.29E-09	2.22E-07
SnocCSP7	92114.69353	1.899054174	0.635561425	2.987994706	0.002808144	0.042411662
SnocIR34	1585.251292	1.847671587	0.366234593	5.045049327	4.53E-07	4.17E-05
SnocOR31	48.78794332	1.845894549	0.517683634	3.56568071	0.000362913	0.009068956
SnocGR5	21.81385482	1.581456171	0.528755099	2.990904814	0.002781522	0.042282018
SnocOBP9	4437.958162	1.524483675	0.415742119	3.666897353	0.000245511	0.006629936
SnocIR09	401.1008842	1.276218372	0.278887717	4.576101034	4.74E-06	0.000288
SnocIR8a	471.7037306	0.974381671	0.269211923	3.619385276	0.000295304	0.007673967
SnocIR45	371.8211052	0.944407949	0.246973883	3.823918289	0.000131347	0.004072466
SnocIR47	786.6561263	0.774611277	0.180753384	4.285459341	1.82E-05	0.000850405
SnocOR16	101.7910646	-2.017906217	0.458445386	-4.401628372	1.07E-05	0.000580283
SnocOBP8	5081.213618	-2.518360237	0.504859757	-4.988237238	6.09E-07	5.33E-05
<i>Sirex</i> Female Body Adult vs Pupa Comparison						
SnocOBP3	87804.10493	11.90777982	1.918089685	6.208145486	5.36E-10	8.48E-09
SnocCSP3	75592.54521	10.04313365	0.657888358	15.26571118	1.29E-52	2.83E-49
SnocOBP2	790.2717246	8.616491402	1.263171494	6.82131559	9.02E-12	1.94E-10
SnocOBP9	4437.958162	8.338931236	1.093864873	7.623365044	2.47E-14	7.92E-13
SnocOBP5	221649.8715	7.520804244	1.034128557	7.272600871	3.53E-13	9.60E-12
SnocCSP5	809015.4868	7.367929579	0.605363296	12.17108739	4.43E-34	1.39E-31
SnocIR36	96.31687251	7.292208836	1.727750582	4.220637464	2.44E-05	0.000150987
SnocOBP4	275.5610933	6.069803347	1.314460159	4.617715725	3.88E-06	2.90E-05
SnocOBP8	5081.213618	5.962196495	1.590590366	3.748417332	0.000177954	0.000885781
SnocCSP8	25070.43435	5.572490153	0.622344813	8.954023623	3.43E-19	2.13E-17
SnocOR4	141.2516972	5.361173378	1.276999451	4.198258171	2.69E-05	0.000164379
SnocIR24	89.87055686	4.808985856	0.664209545	7.24016373	4.48E-13	1.20E-11
SnocIR45	371.8211052	4.70803031	1.09194831	4.311587159	1.62E-05	0.000105405

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Female Body Adult vs Pupa Comparison						
SnocIR26	11.90558972	4.618314445	1.454522993	3.175140212	0.001497641	0.005719183
SnocIR44	14.90359555	4.507568136	1.833160142	2.458905817	0.013936117	0.038154977
SnocSNMP1	16944.27711	4.399760901	1.649715967	2.666980855	0.007653603	0.022933865
SnocCSP6	7.585377378	3.658490808	1.555320349	2.352242618	0.018660599	0.048680238
SnocCSP7	92114.69353	3.656808442	1.331940058	2.745475235	0.006042333	0.018904346
SnocOBP6	16.06752651	3.032047945	1.165423478	2.601670552	0.009277092	0.026995368
SnocIR33	6.590483207	3.012422695	1.013494719	2.972312177	0.00295566	0.010296422
SnocIR23	6.300662129	2.969537818	1.085121697	2.73659427	0.006207881	0.019327563
SnocOR43	88.98720413	2.404625857	0.71526182	3.361882027	0.000774132	0.003218582
SnocGR9	44.2004385	2.343065524	0.536058418	4.370914522	1.24E-05	8.21E-05
SnocIR03	85.25030268	2.311507898	0.872396564	2.649606835	0.008058549	0.023987765
SnocIR39	39.50566078	2.295442495	0.797689281	2.877614818	0.004006941	0.013319665
SnocOR31	48.78794332	2.209143103	0.561123267	3.937001424	8.25E-05	0.00044604
SnocIR02	148.0835805	2.129635069	0.629007791	3.385705393	0.000709956	0.002987816
SnocOR24	225.7722528	2.109862619	0.606877505	3.476587288	0.000507839	0.002223028
SnocOR21	47.41464246	2.108493152	0.764515093	2.757948367	0.005816538	0.018321379
SnocGR4	14.02173065	1.848953414	0.439337942	4.208499284	2.57E-05	0.000157733
SnocGR12	328.4596079	1.829893426	0.547868315	3.340024194	0.000837711	0.003445522
SnocIR37	70.55714089	1.496884279	0.488209285	3.066070895	0.002168919	0.007863229
SnocCSP1	2551.539137	1.196781124	0.390779547	3.062548012	0.002194613	0.007950736
SnocIR32	312.7103091	1.132577498	0.45800853	2.472830581	0.013404767	0.03695779
SnocIR25	847.5756711	0.625769134	0.250608913	2.496994721	0.012525082	0.034864968
SnocIR43	172.2539251	-0.884048706	0.275188573	-3.21251968	0.001315761	0.005113846
SnocOR19	30.21547201	-1.400723092	0.581787829	-2.407618418	0.016056954	0.043016015
SnocIR50	10.00132392	-1.734535179	0.589405363	-2.942856119	0.003251995	0.011163751
SnocGR3	32.05060432	-1.812882223	0.488853452	-3.708436986	0.000208543	0.001015278
SnocIR47	786.6561263	-1.931937661	0.723554415	-2.670065472	0.007583646	0.022755393
SnocOBP13	247.4246332	-2.226089617	0.383299334	-5.807705406	6.33E-09	8.20E-08
SnocOBP12	299.0320935	-2.807231962	0.664856405	-4.222313182	2.42E-05	0.000150111
SnocOR38	9.688376947	-3.061811084	1.226044788	-2.497307695	0.012514032	0.034853205
SnocCSP4	2248.279673	-3.252994409	0.394746249	-8.240722781	1.71E-16	7.35E-15
SnocOR9	63.13422613	-3.473440122	1.253463114	-2.771074859	0.005587158	0.017708078
SnocIR52	66.78474154	-3.476294324	1.07042171	-3.247593254	0.001163855	0.004586272
SnocOR40	10.20681596	-3.570849873	1.356307584	-2.632772916	0.008469095	0.025005783
SnocCSP9	749.0168383	-4.306620908	0.530371118	-8.120014006	4.66E-16	1.89E-14
<i>Sirex</i> Female Head Adult vs Pupa Comparison						
SnocOBP3	87804.10493	26.05358372	2.034108632	12.80835414	1.47E-37	2.15E-34
SnocOBP7	12118.50655	12.45782651	1.46041181	8.530351793	1.46E-17	1.30E-15
SnocOBP8	5081.213618	11.93983939	1.661251177	7.187257146	6.61E-13	2.90E-11
SnocCSP7	92114.69353	11.26453523	1.459579416	7.717658326	1.18E-14	6.73E-13
SnocOBP11	68421.3101	11.15793141	1.309398189	8.521419617	1.58E-17	1.39E-15
SnocOBP5	221649.8715	10.5866337	1.133707706	9.338062749	9.81E-21	1.54E-18
SnocOBP10	4059.27834	8.920539006	1.70322794	5.237431114	1.63E-07	2.31E-06
SnocOBP9	4437.958162	8.197292551	1.181037323	6.940756564	3.90E-12	1.51E-10
SnocSNMP1	16944.27711	6.877847066	1.801159738	3.818565851	0.00013423	0.000867975

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Female Head Adult vs Pupa Comparison						
SnocIR01	218.6742791	6.862818129	1.191607107	5.759296069	8.45E-09	1.63E-07
SnocCSP3	75592.54521	6.679829749	0.714188416	9.353035698	8.52E-21	1.35E-18
SnocOBP14	32050.68857	6.133305348	1.620553506	3.784697837	0.000153895	0.000977819
SnocIR44	14.90359555	6.126286351	1.731919026	3.537282204	0.000404267	0.00225725
SnocOR4	141.2516972	6.016169536	1.383701015	4.347882579	1.37E-05	0.000117096
SnocOR6	42.34619867	5.895360707	1.693394408	3.481386662	0.000498825	0.002696535
SnocCSP5	809015.4868	5.784626987	0.663109355	8.723488727	2.70E-18	2.81E-16
SnocOR20	183.6185733	5.512133239	1.015040647	5.430455675	5.62E-08	9.00E-07
SnocOR2	37.82693197	5.354816071	1.532117914	3.495041746	0.000473988	0.002580423
SnocOR23	68.15463492	5.103672533	1.325916338	3.849166336	0.000118521	0.000781978
SnocOBP4	275.5610933	4.88085576	1.256449891	3.884640202	0.000102482	0.000688286
SnocOR27	83.1456525	4.86453856	1.206689923	4.031307851	5.55E-05	0.000403326
SnocOR3	31.32577049	4.856420552	1.3485217	3.601292104	0.00031664	0.00182593
SnocOR14	31.67263679	4.833962316	1.855601657	2.605064669	0.009185692	0.031857551
SnocOR8	112.1400021	4.824397707	1.321490812	3.65072361	0.000261503	0.001545204
SnocOR26	59.63113286	4.681223112	1.085265465	4.313435985	1.61E-05	0.000135269
SnocOR5	18.05668037	4.541930526	1.728199806	2.628128131	0.008585617	0.030112562
SnocOR15	39.2343263	4.487023213	1.548754561	2.897181598	0.003765317	0.015229196
SnocOR28	27.63417182	4.269943741	1.52537018	2.799283608	0.005121613	0.019663601
SnocOR29	250.2982943	4.257320631	1.340434359	3.176075428	0.001492821	0.006983878
SnocIR24	89.87055686	3.78751272	0.635624496	5.958726806	2.54E-09	5.52E-08
SnocIR19	28.23047251	3.775834571	1.398174087	2.700546811	0.006922559	0.025231226
SnocIR03	85.25030268	3.756118052	0.916560152	4.098059516	4.17E-05	0.000315191
SnocOR40	10.20681596	3.289060517	1.293895947	2.541982239	0.011022577	0.036939341
SnocOR37	113.2795806	3.216448029	1.056258338	3.04513386	0.002325768	0.010106707
SnocOR39	25.06613876	3.073452731	0.972038164	3.16186426	0.001567626	0.007273248
SnocIR8a	471.7037306	3.024455212	0.699124774	4.326059271	1.52E-05	0.000128266
SnocIR45	371.8211052	2.957332811	1.113571161	2.655719649	0.007913938	0.0281558
SnocIR02	148.0835805	2.807082283	0.681910887	4.116494304	3.85E-05	0.000293914
SnocOR41	5.837886768	2.744449877	0.975276813	2.814021456	0.004892596	0.01888863
SnocOR16	101.7910646	2.701777037	0.916437261	2.948130933	0.003197016	0.013249967
SnocCSP8	25070.43435	2.583284681	0.681273775	3.791845181	0.000149532	0.000953952
SnocOR43	88.98720413	2.52689941	0.602260144	4.195694228	2.72E-05	0.000216695
SnocIR39	39.50566078	2.467154833	0.815878092	3.023925825	0.002495176	0.010705867
SnocOR21	47.41464246	2.434340856	0.789632602	3.082877848	0.002050093	0.009092772
SnocOR24	225.7722528	2.410946281	0.657703512	3.665703826	0.000246659	0.001473597
SnocIR09	401.1008842	2.320506078	0.775258761	2.993202005	0.00276067	0.011666725
SnocOR31	48.78794332	2.183082019	0.573126441	3.809075734	0.000139487	0.000896809
SnocOR42	53.63464192	2.160094219	0.795947791	2.713864205	0.006650342	0.024415802
SnocIR37	70.55714089	1.987232062	0.533899543	3.722108567	0.000197566	0.001212552
SnocOR22	33.88343062	1.978652479	0.763685961	2.590924252	0.009571856	0.032946409
SnocOR10	213.0939545	1.6299216	0.546933193	2.980110956	0.00288144	0.01210354
SnocGR9	44.2004385	1.437897547	0.466514321	3.082215237	0.002054662	0.009107505
SnocIR14	39.37454891	1.320909529	0.431881181	3.058502171	0.002224465	0.0097302
SnocOR12	525.0787443	1.272583708	0.262071855	4.855857977	1.20E-06	1.35E-05

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Female Head Adult vs Pupa Comparison						
SnocGR4	14.02173065	1.212144838	0.431117724	2.811633042	0.00492907	0.019004318
SnocOR18	572.3454477	1.146848678	0.392369672	2.922877993	0.003468124	0.014208214
SnocIR50	10.00132392	-1.783159297	0.633914192	-2.812934808	0.00490916	0.018937556
SnocGR3	32.05060432	-1.946244351	0.543701943	-3.579616328	0.000344099	0.001964877
SnocOBP12	299.0320935	-1.962494382	0.722589072	-2.715920373	0.006609181	0.024289115
SnocGR8	126.0733797	-2.042449383	0.713713815	-2.861720398	0.004213484	0.016748668
SnocOBP13	247.4246332	-2.435701265	0.4191607	-5.810900843	6.21E-09	1.23E-07
SnocOR19	30.21547201	-2.608554195	0.643311162	-4.054887196	5.02E-05	0.000371005
SnocIR11	89.16480833	-3.111860852	1.103057632	-2.821122633	0.00478559	0.018544163
SnocCSP4	2248.279673	-4.005612691	0.432786326	-9.255404922	2.13E-20	3.03E-18
SnocCSP9	749.0168383	-5.06423765	0.581122426	-8.71457962	2.92E-18	3.02E-16
SnocCSP2	9.393823335	-5.550938655	1.825674411	-3.04048664	0.002361962	0.010245693
<i>Sirex</i> Male Body Adult vs Pupa Comparison						
SnocOBP3	87804.10493	19.50447104	1.851480077	10.53452926	5.99E-26	5.05E-24
SnocOR1	32.76642584	17.60542815	2.713353933	6.488437771	8.67E-11	1.17E-09
SnocSNMP1	16944.27711	10.46594764	1.704566589	6.139946486	8.25E-10	9.67E-09
SnocOBP9	4437.958162	9.192482815	1.221435578	7.52596615	5.23E-14	1.11E-12
SnocOBP8	5081.213618	8.97938039	1.923736412	4.667677097	3.05E-06	1.86E-05
SnocCSP5	809015.4868	7.05943064	0.625191888	11.29162226	1.44E-29	1.73E-27
SnocCSP3	75592.54521	6.731184663	0.672587292	10.00789748	1.41E-23	8.93E-22
SnocCSP8	25070.43435	6.48938523	0.643087981	10.09097577	6.06E-24	4.02E-22
SnocCSP7	92114.69353	5.41670967	1.375293577	3.938584286	8.20E-05	0.000373669
SnocOR5	18.05668037	4.939410819	1.984369038	2.489159387	0.012804555	0.032338254
SnocOBP5	221649.8715	4.846018695	1.067942621	4.537714478	5.69E-06	3.28E-05
SnocOBP2	790.2717246	4.683427602	1.294401116	3.618219687	0.000296637	0.001178505
SnocIR36	96.31687251	4.662455889	1.717350477	2.714912274	0.006629333	0.018327674
SnocOBP4	275.5610933	4.327079835	1.04965154	4.122396502	3.75E-05	0.000184372
SnocIR01	218.6742791	4.114384887	1.115947271	3.686899009	0.000227003	0.000929896
SnocOR8	112.1400021	3.895500396	1.384147867	2.814367228	0.004887336	0.014098293
SnocOR3	31.32577049	3.076474766	1.302492735	2.361989962	0.018177134	0.043717123
SnocIR24	89.87055686	2.667518765	0.614940318	4.337849849	1.44E-05	7.71E-05
SnocGR6	67.84170803	2.321253658	0.996763307	2.32879124	0.019870128	0.047173879
SnocIR14	39.37454891	2.273804097	0.38858962	5.851427784	4.87E-09	5.02E-08
SnocIR02	148.0835805	2.245251081	0.63686022	3.525500591	0.000422683	0.001626128
SnocCSP1	2551.539137	1.791381158	0.403847183	4.43578966	9.17E-06	5.10E-05
SnocOR31	48.78794332	1.767191008	0.540418299	3.270042875	0.001075312	0.003717364
SnocOR24	225.7722528	1.679473717	0.623558805	2.693368621	0.007073402	0.019394017
SnocIR49	197.542681	1.647910154	0.651462011	2.52955679	0.011420669	0.029305762
SnocOR10	213.0939545	1.632679335	0.518058349	3.151535611	0.001624144	0.005334771
SnocIR32	312.7103091	1.163485025	0.472788167	2.460901321	0.013858848	0.034682508
SnocIR43	172.2539251	-0.704229115	0.281809313	-2.498956149	0.012455972	0.031590183
SnocIR31	242.9019269	-1.487961474	0.425767622	-3.494773669	0.000474464	0.001804528
SnocIR27	30.26473407	-1.546187089	0.492481279	-3.139585514	0.00169187	0.005532892
SnocCSP4	2248.279673	-1.937685732	0.407643482	-4.753383331	2.00E-06	1.26E-05
SnocOBP13	247.4246332	-1.96025015	0.394514312	-4.968768148	6.74E-07	4.64E-06

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Male Body Adult vs Pupa Comparison						
SnocIR30	95.5506514	-1.968712774	0.447459498	-4.399756361	1.08E-05	5.92E-05
SnocIR11	89.16480833	-2.477695949	1.037909831	-2.387197688	0.016977359	0.041191702
SnocIR50	10.00132392	-2.553418974	0.576619685	-4.42825495	9.50E-06	5.27E-05
SnocOBP12	299.0320935	-2.63073943	0.687270166	-3.827809732	0.000129289	0.000561755
SnocOR41	5.837886768	-2.898582622	1.160546357	-2.497601759	0.012503657	0.031700865
SnocIR26	11.90558972	-3.696482277	0.889640369	-4.155029838	3.25E-05	0.000162374
SnocOR15	39.2343263	-3.75935855	1.464481093	-2.567024299	0.010257542	0.02669685
SnocGR3	32.05060432	-3.826480976	0.478834371	-7.99124125	1.34E-15	3.43E-14
SnocOR43	88.98720413	-3.856919256	0.588416015	-6.55474895	5.57E-11	7.73E-10
SnocOR26	59.63113286	-3.947470097	1.034600428	-3.815453765	0.000135933	0.000587208
SnocGR1	2.728836354	-4.226295682	1.284916889	-3.289158792	0.001004873	0.00349817
SnocOR25	12.03122844	-4.227316972	1.673735294	-2.525678336	0.011547516	0.029573182
SnocOR38	9.688376947	-4.347448961	1.258739102	-3.453812593	0.000552721	0.002064608
SnocCSP6	7.585377378	-4.439013511	1.119837279	-3.963980833	7.37E-05	0.000338661
SnocOR28	27.63417182	-4.701708914	1.589205286	-2.958528363	0.003091118	0.009426647
SnocGR2	9.48574097	-6.427079116	1.190125676	-5.400336491	6.65E-08	5.55E-07
SnocORCO	595.8901994	-7.611241098	2.29109889	-3.322091914	0.000893453	0.003158302
<i>Sirex</i> Male Head Adult vs Pupa Comparison						
SnocOBP3	87804.10493	26.69929771	2.034090907	13.12591174	2.34E-39	2.85E-36
SnocCSP7	92114.69353	13.17759498	1.463163295	9.006236708	2.13E-19	2.19E-17
SnocOBP7	12118.50655	12.35386806	1.475145043	8.374680251	5.54E-17	4.21E-15
SnocOBP10	4059.27834	11.07989924	1.707446767	6.489162329	8.63E-11	2.33E-09
SnocOBP11	68421.3101	10.17410118	1.308729603	7.774028461	7.60E-15	4.24E-13
SnocOBP8	5081.213618	10.05312076	1.619515371	6.20748709	5.38E-10	1.22E-08
SnocOBP9	4437.958162	9.56269195	1.191416903	8.026318854	1.00E-15	6.40E-14
SnocOBP5	221649.8715	9.342993695	1.132917513	8.246843736	1.63E-16	1.15E-14
SnocOR14	31.67263679	8.612413201	2.177207446	3.955715482	7.63E-05	0.000504365
SnocIR44	14.90359555	8.113701278	1.925496042	4.213823919	2.51E-05	0.00019005
SnocIR01	218.6742791	7.189056522	1.19464233	6.017748026	1.77E-09	3.58E-08
SnocOR6	42.34619867	7.073969127	1.903567049	3.716164939	0.00020227	0.001177567
SnocSNMP1	16944.27711	6.848101056	1.800980329	3.80242968	0.000143284	0.000872795
SnocOBP4	275.5610933	6.460720516	1.39560175	4.629343947	3.67E-06	3.45E-05
SnocOR4	141.2516972	6.164507692	1.420664053	4.339173417	1.43E-05	0.000114675
SnocOBP14	32050.68857	5.888415165	1.620544688	3.63360246	0.000279491	0.001559363
SnocOR13	4.976388719	5.806321216	2.294954618	2.530037488	0.011405034	0.035834926
SnocCSP3	75592.54521	5.734967226	0.713503793	8.037752966	9.15E-16	5.91E-14
SnocOR28	27.63417182	5.652843026	1.639981463	3.446894464	0.00056707	0.002879927
SnocCSP5	809015.4868	5.391632565	0.663097689	8.130977768	4.26E-16	2.92E-14
SnocOR8	112.1400021	5.024895876	1.351434978	3.718192852	0.000200653	0.00117049
SnocOR27	83.1456525	4.934146469	1.210159124	4.077270808	4.56E-05	0.000321726
SnocIR24	89.87055686	4.87949641	0.689178864	7.080159688	1.44E-12	5.31E-11
SnocOR5	18.05668037	4.872983485	1.805915181	2.698345711	0.006968503	0.023759425
SnocOR20	183.6185733	4.61320416	1.008530502	4.574184072	4.78E-06	4.37E-05
SnocOR16	101.7910646	4.588893618	0.868459874	5.283944318	1.26E-07	1.70E-06
SnocOR23	68.15463492	4.5161591	1.342603124	3.363733497	0.000768958	0.003731323

Gene name	baseMean	LFC	lfcSE	Wald statistic	Wald test p-value	padj-value
<i>Sirex</i> Male Head Adult vs Pupa Comparison						
SnocOR15	39.2343263	4.467251021	1.585477743	2.817605634	0.00483832	0.017573304
SnocIR36	96.31687251	4.314943191	1.80445933	2.391266524	0.016790359	0.049099947
SnocOR26	59.63113286	4.292546043	1.0785713	3.979844487	6.90E-05	0.000460398
SnocIR29	2.149564268	4.266298979	1.456044451	2.930060944	0.003388955	0.013028472
SnocOR31	48.78794332	4.216724835	0.64133651	6.574902203	4.87E-11	1.35E-09
SnocIR19	28.23047251	4.208640825	1.359551561	3.095609572	0.001964088	0.008188934
SnocOR3	31.32577049	3.691572578	1.352316789	2.729813464	0.006337017	0.021946581
SnocIR45	371.8211052	3.538397562	1.11477738	3.174084462	0.001503099	0.006545409
SnocIR03	85.25030268	3.472028649	0.914115177	3.798239802	0.000145727	0.00088583
SnocIR8a	471.7037306	3.402936565	0.700581698	4.857301546	1.19E-06	1.27E-05
SnocOBP6	16.06752651	3.254748836	1.004240812	3.241004346	0.001191094	0.005385058
SnocCSP8	25070.43435	3.250235117	0.681269222	4.770852717	1.83E-06	1.87E-05
SnocIR39	39.50566078	3.130672158	0.835359268	3.747695486	0.000178467	0.001058405
SnocOR9	63.13422613	2.991705884	1.151296993	2.598552678	0.009361768	0.030430191
SnocIR02	148.0835805	2.942708576	0.683005689	4.30846862	1.64E-05	0.000129743
SnocIR14	39.37454891	2.88281825	0.465925811	6.187290302	6.12E-10	1.37E-08
SnocIR09	401.1008842	2.882025768	0.777265453	3.707904112	0.000208982	0.00120989
SnocGR5	21.81385482	2.605611182	0.986235968	2.641975417	0.008242404	0.027395251
SnocOR43	88.98720413	2.457851879	0.604048096	4.068967185	4.72E-05	0.000331804
SnocIR37	70.55714089	2.425772568	0.545087517	4.450244212	8.58E-06	7.30E-05
SnocOR21	47.41464246	2.305068662	0.786156976	2.932071751	0.003367089	0.012964893
SnocOR24	225.7722528	2.220310268	0.659304705	3.367654216	0.000758106	0.003682338
SnocOR10	213.0939545	2.029510354	0.548775353	3.698253473	0.000217088	0.001250376
SnocOR42	53.63464192	1.944069682	0.786825522	2.470776084	0.013482021	0.041003395
SnocIR10	13.36267031	1.892220513	0.744974588	2.539979946	0.011085883	0.035050882
SnocGR9	44.2004385	1.464344197	0.469617137	3.118166017	0.001819803	0.007686126
SnocOR18	572.3454477	1.230181817	0.392160281	3.136936292	0.001707232	0.007281798
SnocCSP1	2551.539137	1.071092832	0.42785147	2.503422118	0.012299875	0.038153914
SnocOR12	525.0787443	0.885140876	0.261834294	3.38053836	0.00072344	0.003547453
SnocOBP12	299.0320935	-1.799180064	0.722554564	-2.490026573	0.012773354	0.039255683
SnocOR34	28.92399412	-1.965685378	0.74772963	-2.628871852	0.008566864	0.028274136
SnocOR19	30.21547201	-2.539794147	0.636016992	-3.993280335	6.52E-05	0.000439483
SnocOBP13	247.4246332	-2.654461919	0.418482646	-6.34306331	2.25E-10	5.48E-09
SnocCSP4	2248.279673	-2.792123463	0.4325106	-6.455618567	1.08E-10	2.84E-09
SnocIR52	66.78474154	-2.908695589	1.145477335	-2.539286899	0.011107869	0.035097598
SnocIR50	10.00132392	-3.236892361	0.647097077	-5.002174291	5.67E-07	6.50E-06
SnocIR11	89.16480833	-5.468787799	1.117600775	-4.893328566	9.91E-07	1.08E-05
SnocCSP2	9.393823335	-6.018003351	1.79975591	-3.343788632	0.000826427	0.003961476

Table S2.3. Average TPM (transcripts per kilobase per million reads) expression abundances per tissue condition for each chemosensation gene.
TPM averages were calculated across the three biological replicates. The total number (Σ) genes with a TPM > 3 are indicated per chemosensation gene family which give an indication of which tissues are more important in chemical detection.

Gene Name	Adult female antenna	Adult male antenna	Adult female body	Adult male body	Adult female head	Adult male head	Adult female legs	Adult male legs	Adult female wings	Adult male wings	Adult female ovipositor	Pupa female body	Pupa male body	Pupa female head	Pupa male head
SnocOBP1	235.73	231.23	3.66	2.98	2.64	2.02	1.99	6.46	1.77	1.28	12	25.2	18.86	61.39	77.1
SnocOBP2	52.77	56.76	36.07	10.34	20.56	24.85	66.46	47.93	4.42	5.01	1508.23	0.78	1.49	13.26	18.86
SnocOBP3	145.39	168.08	22.21	44.09	150.92	168.34	547.94	193629.75	25.7	23.21	237.64	0	0	0	0
SnocOBP4	7.87	13.23	0.75	558.91	3.29	2.19	9.7	48.19	1.24	0.62	14.17	0.19	14.66	0	0
SnocOBP5	41072.22	57322.48	4112.67	981.42	4194.23	3902.61	12252.79	7592.24	5001.56	4128.3	63511.47	196.93	291.9	22.32	83.66
SnocOBP6	2.12	5.27	1.11	0.58	4.32	3.19	1.82	1.57	1.97	5.97	0.1	0.39	0.88	1.52	0.52
SnocOBP7	9497.92	4401.42	1	1.18	1.55	1	3.77	3.4	1.22	1.3	2.8	0.7	0.17	0.96	0.52
SnocOBP8	3596.7	5876.66	0	1.6	9.44	8.34	32.75	23.66	4.86	2.04	28.01	0.35	0	0.24	3.95
SnocOBP9	2347.2	1897.16	5.27	18.15	274.96	309.8	294.35	272.11	141.97	138.74	2334.17	3.05	0	6.93	2.82
SnocOBP10	2095.6	6005.83	2.97	1.4	0	0	0	0	0	0	0	1.31	1.82	1.4	0
SnocOBP11	92555.95	67079.54	60.25	25.14	8.22	5.15	30.35	12.83	4.28	4.49	40.66	3.99	31.19	4.65	7.45
SnocOBP12	6.41	6.58	5.45	8.43	85.79	81	2.26	1.77	0.74	0.52	3.59	43.57	35.9	198.15	197.34
SnocOBP13	4.03	5.02	4.53	8.17	13.56	12.25	10.01	12.21	4.18	4.22	5.12	44.89	55.5	55.47	75.63
SnocOBP14	37816.02	31342.86	11.15	14.67	11.06	12.05	0.67	9.14	0.24	0.14	1.11	9.14	4.14	389.2	389.3
SnocCSP1	199.12	217.77	79.59	116.32	152.15	213.08	240.8	200.52	209.83	182.81	317.86	159.04	89.7	232.54	145.74
SnocCSP2	0	0	4.78	0.78	0	0.15	0	0	0	0	6.27	2.69	4.95	2.29	9.2
SnocCSP3	2002.86	3496.82	2036.85	1631.94	4563.71	5471.85	7416.43	27170.82	6704.67	8148.43	6123.13	7.95	193.09	37.93	103.59
SnocCSP4	39.36	33.25	40.55	102.42	66.44	129.85	102.84	100.9	52.53	87.17	72.54	1057	647.08	1044.69	773.07
SnocCSP5	69148.92	56192.53	44643.5	24140.13	40642.9	48810.8	114758.3	53304.98	208864	204833	96449.69	1237.85	1380.5	1296.6	1757.65
SnocCSP6	0.66	0.19	0	0.22	3.65	5.45	0.35	0	0	0	0	0	5.61	4.08	2.71
SnocCSP7	17493.84	17481.95	16.87	86.99	15.16	31.38	41.59	53.25	287.19	779.9	18.72	4.6	0.27	0.11	0.02
SnocCSP8	1063.14	1349.82	1029.56	756.06	1479.93	2190.1	1851.33	1521.44	4368.93	6321.19	7526.07	110.43	52.51	238.67	237.8
SnocCSP9	6.69	15.32	8.62	23.02	21.2	23.06	10.39	7.84	9.35	9	10.28	459.57	25.15	780.22	42.3

Gene Name	Adult female antenna	Adult male antenna	Adult female body	Adult male body	Adult female head	Adult male head	Adult female legs	Adult male legs	Adult female wings	Adult male wings	Adult female ovipositor	Pupa female body	Pupa male body	Pupa female head	Pupa male head
SnocSNMP1	2678.73	3396.34	1.96	0.85	0.48	0.19	14.38	4185.02	79.84	15.95	23.47	1.14	0.85	15.78	21.5
SnocOR1	17.86	7.07	0	0.01	0	0	0	0	0	0	0	0.06	0	0.3	0.17
SnocOR2	16.65	6.05	1.11	0.45	0	0.1	0.06	1.07	0.13	1.21	0.04	1.29	0.06	0.14	0.5
SnocOR3	12.13	4.79	0.44	0.33	0.11	0	0.32	0.53	1.03	1.97	0	0	0.1	0.25	0.17
SnocOR4	21.68	12.89	0.45	1.7	0.84	0.57	9.72	4.02	18.86	11.16	0.03	0.28	5.08	0.13	0.07
SnocOR5	8.55	3.64	0.02	0	0.01	0	0.66	0	0.06	0.17	0	0	0	0.06	0
SnocOR6	25.73	9.25	1.41	0	0	0	0.03	0	0	0.04	0	0.17	0	0.27	0
SnocOR7	0.13	0.14	0	0	0	0	0	0.03	0	0	0	0.06	0	0	0
SnocOR8	38.55	13.51	12.67	1.61	0.43	0.4	0.32	0.18	0.65	0.88	0.08	9.18	0.13	0.94	0.25
SnocOR9	36.18	11.23	0	0	1.15	0.77	0	0	0	0.08	0	0.28	0	4.69	0.98
SnocOR10	28.72	22.11	4.5	8.51	4.26	7.04	5.44	5.79	11.04	12	7.84	6.28	5.55	6.91	5.2
SnocOR11	0	0	0.18	1.05	0	0.12	0	0	0	0	0	0.52	0.05	0	0.09
SnocOR12	47.04	40.39	20.16	22.81	40.7	26.73	19.02	20.02	12.65	15.59	23.96	27.57	22.16	22.48	25.8
SnocOR13	2.18	2.22	0	0.53	0	0	0	0	0	0	0	0	0	0.27	0
SnocOR14	19.35	5.77	0	0.06	0.05	0	0	0	0	0	0	0.13	0	0.42	0
SnocOR15	22.44	7.83	0.26	0.44	0.03	0.07	0.06	0.04	0	0	0	0.52	5.16	0.7	0.21
SnocOR16	1.5	31.18	0.34	1.15	0.21	0.24	0.65	0.43	0.15	0.15	0.35	1.17	2.33	0.14	0.96
SnocOR17	14.89	17.86	1.66	2.6	1.54	1.96	1.01	1.32	3.27	3.39	3.89	2.76	4.51	3.22	3.36
SnocOR18	63.8	64.32	15.33	20.38	24.43	26.78	22.5	17.81	21.48	17.64	18.54	22.44	19.25	23.91	25.5
SnocOR19	0.28	0.21	0.03	0.15	0.46	0.61	0.34	0.26	0.6	0.8	1.08	2.25	1.22	2.96	3.61
SnocOR20	77.03	57.11	0.18	0.58	1.48	1.16	0.83	0.61	0.52	0.37	2.13	0	3.45	0.66	0.55
SnocOR21	8.55	8.9	0.57	1.16	1.28	1.07	1.07	1.07	0.62	0.27	4.1	0.34	0.76	0.63	0.59
SnocOR22	13.42	4.27	0.04	0.13	0.28	0.36	0.14	0.13	0.32	0.21	0.14	0.61	0.68	1.65	1.13
SnocOR23	40.35	13.51	0	0	0.3	0	0	0	0	0	0.59	0	0.52	0.46	0.13
SnocOR24	32.13	14.39	0.73	0.4	2.5	2.2	1.89	1.33	2.84	1.75	9.86	0	0	1.11	0.2
SnocOR25	7.55	1.5	0.23	0	0.12	0.12	0	0	0	0	0	0.04	0.14	0.49	0.91
SnocOR26	25.44	22.06	0.2	0.22	0.5	0.55	0	0	0.08	0	0.07	0.34	4.43	0.47	0.37

Gene Name	Adult female antenna	Adult male antenna	Adult female body	Adult male body	Adult female head	Adult male head	Adult female legs	Adult male legs	Adult female wings	Adult male wings	Adult female ovipositor	Pupa female body	Pupa male body	Pupa female head	Pupa male head
SnocOR27	34.02	26.67	0.06	0.34	2.07	2.48	0	0.01	0	0	0	0.08	0.23	0.88	0.74
SnocOR28	19.05	8.29	0	0	0.15	0.15	0	0	0	0	0.05	0.15	0.86	0.56	0.06
SnocOR29	93.84	26.27	55.51	27.39	25.91	13.67	5.02	0.55	0.42	0.27	9.77	4.19	3.34	3.44	3.43
SnocOR30	15.2	3.71	0	0	0.12	0	0	0	0	0	0	0	0	0.42	0
SnocOR31	0.12	0	0	0.6	0	0.09	0.1	0.04	0.12	0	0.05	0.24	0.37	0.12	0
SnocOR32	4.93	4.88	0.24	0.9	0.2	0.44	1.75	0.67	1.44	1.44	0.17	0.14	1.34	0.46	0.23
SnocOR33	0.28	0.14	0	0.1	0	0	0	0	0	0	0	0	0	0	0
SnocOR34	0.14	0	0	0	0	0	0	0	0	0	0	0	0	0	0.03
SnocOR35	10.34	5.15	0	0	0	0	0	0	0	0	0	0.13	0.03	0.29	0.06
SnocOR36	6.48	1.71	0	0	0	0	0.05	0	0	0	0.08	0	0.04	0.45	0.03
SnocOR37	58.05	18.26	0	0	0	0	0	0.02	0.04	0	0.25	0	0.15	1.91	0.72
SnocOR38	2.42	1.89	0.05	0	0.15	0.29	0	0	0	0	0	0.46	0.6	0.73	0.93
SnocOR39	15.64	4.72	0	0	1.34	1.2	0	0	0	0.06	0	0.05	0	1.43	1.02
SnocOR40	5.01	2.42	0	0	0.26	0.22	0	0.08	0	0	0	0.27	0	0.33	0.22
SnocOR41	1.24	0.79	0	0	0.56	0.13	0	0	0	0	0	0	0.16	0.12	0.46
SnocOR42	8.75	12.51	4.03	0.73	0.68	0.62	0.73	0.36	0.83	0.61	1.45	7.03	1.72	1.11	1.84
SnocOR43	27.24	17.94	0.43	0.22	8.39	8.72	0.94	0.46	0.58	0.4	2.35	0.25	11.6	4.02	3.33
SnocOR44	2.58	1.75	0	0.08	0.11	0.13	0	0	0	0	0	0.53	0.53	0.1	0.1
SnocORCO	218.44	150.36	0	0.25	0	0	0	0	0	0	0.21	0.14	15.45	5.2	4.68
SnocGR1	0	0.05	0	0.06	0	0	0	0.02	0	0	0.24	0.2	0.24	0	0
SnocGR2	0.08	0	0	0.12	0.06	0	0	0	0.05	0	0.09	0	6.38	0.06	0
SnocGR3	0.04	0.77	0.19	0.74	0.23	0.7	0.57	0.77	0.08	0.04	0.04	2.75	16.52	2.26	1.63
SnocGR4	0.17	0.13	0.03	0.1	0	0.08	0.05	0.05	0.69	0.28	3.26	0.34	1.91	0.08	0.27
SnocGR5	2.06	2.92	0.68	0.04	0.02	0.1	0.14	0.49	0.04	0.02	0.38	2.3	0.49	0.99	0.16
SnocGR6	0.74	1.56	7.36	10.57	0.33	0.33	0.86	0.38	0.13	0.15	1.5	3.64	0.87	0.06	0.46
SnocGR7	0	0	0.1	0	0	0.03	0	0.03	0	0	0.08	1.24	0.06	0	0
SnocGR8	1.82	1.98	2.84	3.09	16.11	22.77	9.23	4.43	1.07	0.65	1.29	18.81	11.6	54.24	8.08
SnocGR9	5.43	3.5	0	0	3.47	3.92	0.73	0.55	1.55	0.32	0.04	0	1.32	2.06	2.37
SnocGR10	0	0	0.05	0.23	0.13	0.02	0.02	0.01	0.08	0	0.75	0.21	0.2	0	0.02

Gene Name	Adult female antenna	Adult male antenna	Adult female body	Adult male body	Adult female head	Adult male head	Adult female legs	Adult male legs	Adult female wings	Adult male wings	Adult female ovipositor	Pupa female body	Pupa male body	Pupa female head	Pupa male head
SnocGR11	0	0	0	0	0	0	0	0	0.27	0	0	0	0	0	0
SnocGR12	14.3	39.35	10.47	13.92	6.62	16.09	9.95	20.56	27.69	34.49	57.52	12.36	26.28	12.99	26.95
SnocIR01	9.16	14.21	22	87.35	3.07	20.41	2.26	22.75	3.5	5.39	2.78	12.32	25	9.23	3.15
SnocIR02	11.62	10.49	1.7	5.37	2.9	3.1	3.92	12.79	8.84	8.2	3.16	1.8	2.65	1.72	1.32
SnocIR03	23.91	19.83	0.26	1.84	1.38	1.91	1.65	5.51	4.48	3.44	1.72	0.45	12	1.18	1.4
SnocIR04	0.27	0.28	0.18	0.34	1.25	1.19	0.29	0.37	0.39	0.49	0.97	0.64	0.53	1.07	0.92
SnocIR05	0	0	0	0	0	0	0	0	0	0	0.94	0.71	0	0	0
SnocIR06	0	0	0	0	0	0	0	0	0	0	0.87	0	0	0	0
SnocIR8a	77.13	49.17	0.47	1.03	10.5	8.68	0.67	0.5	0.39	0.42	3.28	1.65	2.46	7.54	3.93
SnocIR09	90.63	57.08	3.83	4.17	4.5	1.99	23.42	3.9	4.1	1.42	13.36	4.7	3.98	12.02	5.1
SnocIR10	0.11	0.07	0.03	0.33	0.09	0.19	0.16	0.23	0.27	0.05	0.15	0.19	0.65	0.06	0.1
SnocIR11	0	0	3.99	3.46	1.97	0.36	1.03	0.12	0.09	0	0.6	0.48	1.29	0.83	1.04
SnocIR12	0.03	0.07	4.76	1.83	0	0.01	0	0	0	0	1.67	0.08	0.11	0	0.02
SnocIR13	0.03	0.03	0.05	0.06	0	0.03	0	0.01	0.02	0	0.01	0	0	0	0.04
SnocIR14	0.55	1.02	1.31	2.51	0.95	1.5	0.59	1.15	0.93	1.12	1.81	0.74	0.56	0.26	0.06
SnocIR15	0	0	0.19	0.01	0	0	0	0	0	0	0.33	0.17	0	0.03	0.02
SnocIR18	0	2.25	0	0.05	0.23	0.03	0	0.59	0	0.3	0.05	0.25	0.23	0.31	0.38
SnocIR19	2.52	5.06	0.17	0.38	0.02	0.06	1.26	0.81	0.82	0.69	0.01	1.66	5.88	0.13	0.14
SnocIR20	0	0	0.2	0.04	0.02	0.02	0.03	0.04	0.04	0	0	0	0	0.02	0
SnocIR22	0.03	0.02	0.16	0.08	0	0.02	0.03	0.02	0.2	0	0.17	0.13	0.08	0.02	0.1
SnocIR23	0.27	0.34	0.03	0.02	0.19	0.12	0	0	0	0.07	1.42	0.03	0.04	0.17	0.08
SnocIR24	7.23	5.6	1.34	0.96	4.18	4.16	6.56	2.06	5.76	2.04	3.43	0.05	0.28	0.19	0
SnocIR25	15.87	15.04	4.98	7.82	9.06	11.85	30.12	12.32	3.81	3.04	9.15	4.96	7.08	6.7	6.63
SnocIR26	0.13	0	0.02	0.46	0.06	0.07	0.35	0.21	0.08	0.11	0.64	0	2.59	0.05	0.23
SnocIR27	1.19	1.09	3.97	1.46	1.01	0.7	0.37	0.5	0.94	1.14	1.13	3.57	4.16	1.55	1.37
SnocIR28	15.2	15.15	8.69	6.1	6.37	6.27	11.06	6.36	18.46	13.55	5.66	12.95	14.33	12.56	14.42
SnocIR29	0	0	0	0	0	0.03	0	0	0	0	0	0.03	0.09	0.02	0
SnocIR30	3	2.27	1.94	0.53	4.12	3.72	0.23	0.26	0.26	0.15	0.71	2.08	3.65	4.35	3.76
SnocIR31	9.94	11.02	2.31	3.6	4.41	5.97	4.61	5.66	4.44	5.08	7.42	10.27	23.53	13.08	17.31

Gene Name	Adult female antenna	Adult male antenna	Adult female body	Adult male body	Adult female head	Adult male head	Adult female legs	Adult male legs	Adult female wings	Adult male wings	Adult female ovipositor	Pupa female body	Pupa male body	Pupa female head	Pupa male head
SnocIR32	0.06	0.03	0.24	0.47	0.21	0.23	0.11	0.13	0.26	0.18	0.09	0.34	0.29	0.23	0.13
SnocIR33	0	0	0.79	0.5	0	0	0	0.02	0	0	0.25	0.07	0.17	0	0
SnocIR34	4.53	4.64	17.57	44.5	204.58	140.91	38.31	32.84	5.58	4.47	11.5	85.33	49.57	101.91	32.15
SnocIR35	13.63	8.86	3	3.33	15.86	18.46	8.61	11.43	11.41	6.8	16.74	8.8	13.03	26.15	32.71
SnocIR36	1.22	5.49	0.02	0.01	0.05	0.06	0.03	10.08	0.11	0.01	62.16	0.01	0.02	0.01	0.04
SnocIR37	3.53	3.49	3.56	2.99	4.89	5.5	6.67	4.25	3.23	3.42	5.27	2.68	6.86	2.29	1.76
SnocIR38	0	0	0	0	0.1	0	0	0	0	0	0.49	0.41	0	0	0
SnocIR39	11.4	9.59	0.42	0.99	1.09	1.11	1.61	2.52	2.92	2.3	1.34	0.48	0.23	1.25	0.25
SnocIR42	1.56	1.73	3.25	5.18	12.31	17.65	5.16	3.89	2.51	3.34	18.55	5.25	3.06	11.77	17.92
SnocIR43	7.18	6.4	0.67	1.41	2.69	4.41	1.3	3.61	1.21	0.91	1.86	8.42	10.65	8.54	10.54
SnocIR44	4.89	2.74	0	0.04	0.36	0.69	0	0.01	0.02	0.09	0.74	0	0.14	0.04	0
SnocIR45	68.22	53.19	0.18	0.32	1.13	1.38	2.31	1.85	1.7	0.84	9.58	0.14	7.65	6.52	3.49
SnocIR46	0.35	0.35	2.35	1.7	4.78	5.05	0.74	0.66	0	0.06	0.6	3.5	4.65	7.23	7.28
SnocIR47	2.32	2.76	14.57	29.9	48.42	37.74	17.5	16.21	2.54	3.17	5.75	59.71	44.46	68.88	43.97
SnocIR48	0.36	0.56	2.65	8.19	75.21	64.06	0.15	0.35	0.13	0.26	0.42	2.21	2.45	26.58	20.03
SnocIR49	1.84	1.52	2.81	5.21	10.99	17.58	4.64	4.6	3.48	3.85	18.49	3.56	2.51	11.98	18.5
SnocIR50	0.17	0.02	0.46	0.46	0.31	0.26	0.17	0.06	0.05	0.15	0.11	1.16	2.89	1.31	2.43
SnocIR51	0.98	1.24	0.76	1.49	1.94	1.65	0.18	0.14	0	0	0.67	0.57	0.64	2.42	1.42
SnocIR52	0.03	0.1	0.05	0	2.82	2.83	0	1.16	0	0.03	0.13	1.83	3.59	10.33	14.08
SnocIR53	1.03	0.73	0.09	0.26	0	0.01	0.02	1.96	0.22	0	0.22	0.49	2.72	0.01	0.09
SnocIR54	0.63	0.99	0	0	0.03	0	0	0	0	0	0	0	0	0.12	0.1
Σ genes (TPM >3)	72	69	37	34	38	43	33	38	32	35	25	22	33	28	28
% genes (TPM > 3)	55.8	53.5	28.7	26.4	29.5	33.3	25.6	29.5	24.8	27.1	19.4	17.1	25.6	21.7	21.7

Supplementary files

Additional data file 1: Compilation of results and data produced in study. Combined file of additional information from analyses (e.g. Kraken) and observations

Additional data file 2: Compilation of all pairwise comparisons from DESeq2. Combined file of all differentially expressed genes identified through pairwise comparisons in DESeq2.

Additional data file 3: Results from BLAST and OrthoFinder analyses. Analyses performed with *S. noctilio* sequence data available from the study by Guo *et al.* [39].

[Additional file 4](#): **Phylogenetic trees used for interpretation purposes.** Phylogenetic trees produced by Alisa Postma the same way as previous phylogenetic trees but included *S. noctilio* datasets produced in the current study and in previous studies by Guo *et al.* [39] (antennal transcriptome) and Wang *et al.* [37] (proteome study of venom sac).

[Additional file 5](#): **Bioinformatic scripts and commands.** Command line scripts used for FastQC, MultiQC, HISAT2, featureCounts, DESeq2 and StringTie.

Addendum 1: Journey through this Masters

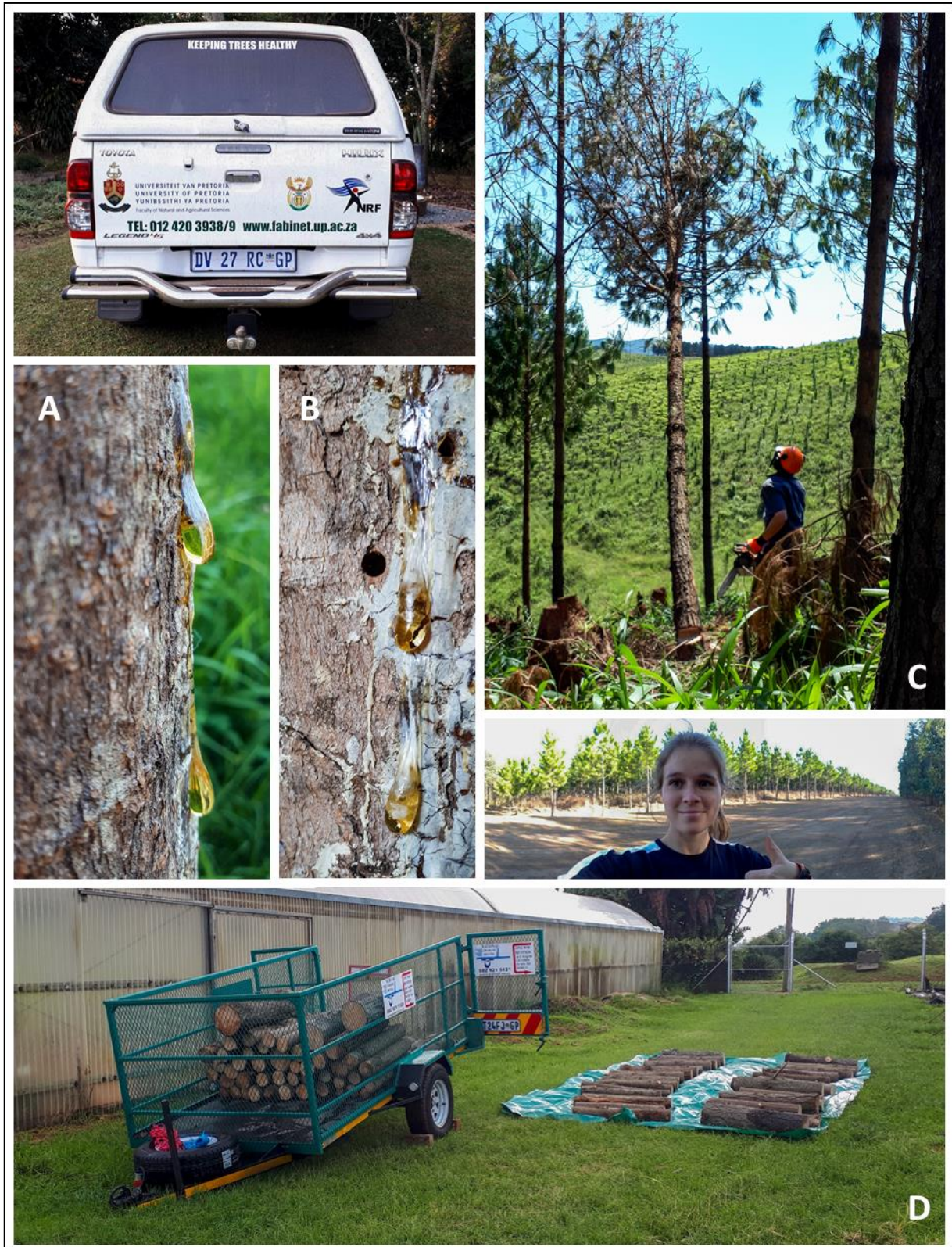


Figure A1. Several log collection trips were required to obtain enough samples during this project. Several field trips to *S. noctilio* infested pine forest plantations (A and B) were conducted in South Africa. Pine trees were felled (C) and transported back to the Biocontrol facility of the Forestry and Agricultural Biotechnology Institute (FABI) at the University of Pretoria (D).

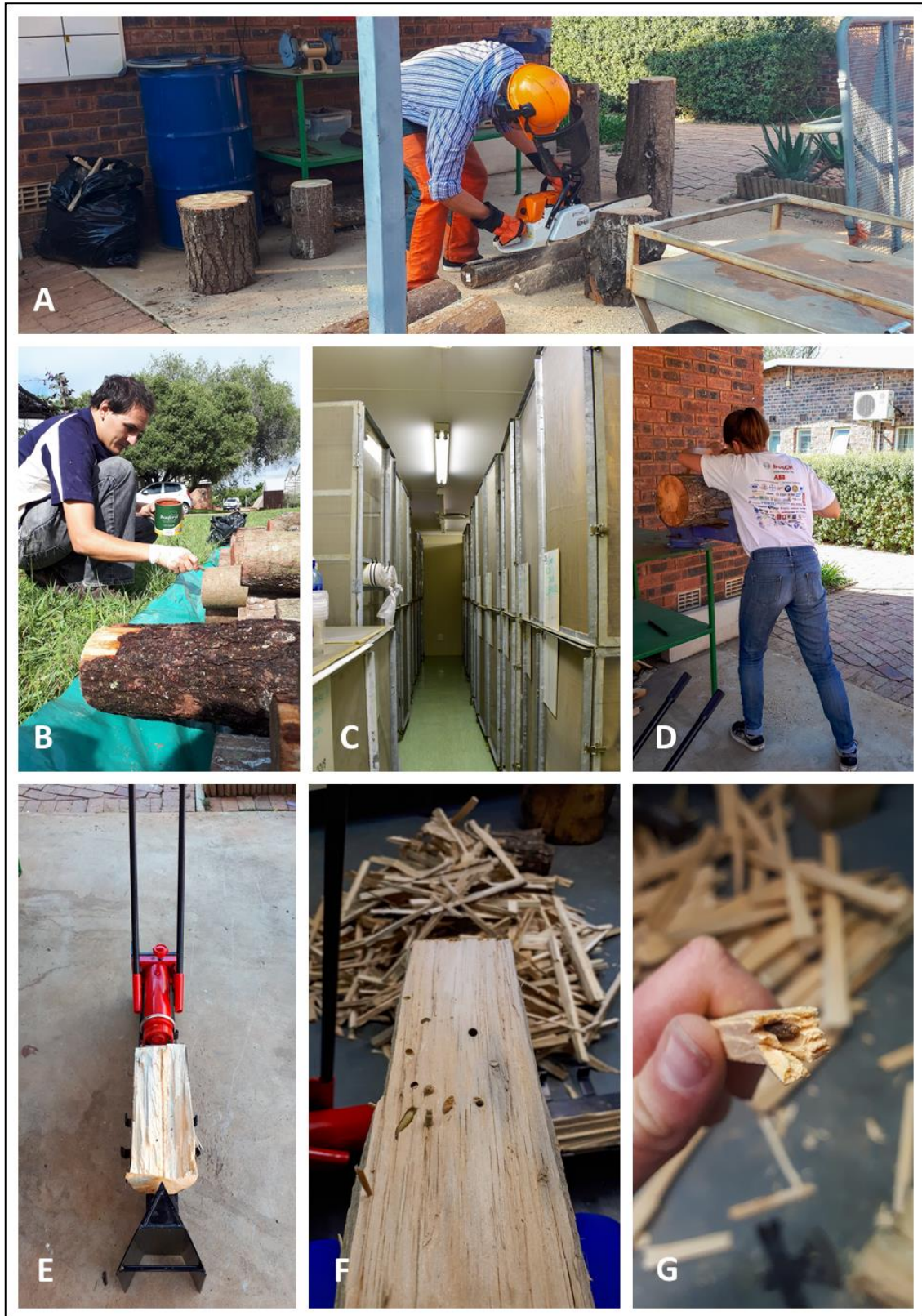


Figure A2. Sample collections are a laborious process involving sawing, splitting and hacking. Logs from plantations were cut into shorter lengths (A) and the edges sealed with roof paint to limit moisture loss (B). Logs were stored in an insectarium to await adult emergence (C). After sawing logs (D), pupa sampling was done by using a hydraulic log splitter (E). Samples can be easily located within the wood (F), but occasionally required some precision to be found (G).



Figure A3. Larvae found during sampling. Larvae were not a developmental stage investigated through transcriptome analysis but were nonetheless found during sampling. Larvae displayed variation in size which does not necessarily relate to larval instar (A). This makes age determination a difficult process. Larvae that were found were also sexed by the elongated oval shape, known as the hypopleural organ, found between the first and second abdominal segments (B). This structure houses the symbiotic fungus of *S. noctilio*. More males than females were found during the sampling process (C). Upon dissection, the endoparasitic biocontrol wasp, *Ibalia*, was also found in some larvae (D) and many larvae carried mites on them (E).



Figure A4. Pupa samples were collected from pine logs using a hydraulic log splitter and an axe. Because *S. noctilio* live a cryptic life within pine logs it is difficult to know how far they are developed and this can cause premature extraction of pupae from pine logs (A). Female pupae (B) were rarer than male pupae (A, C and D).



Figure A5. Adult *S. noctilio* wasps were collected upon emergence from pine logs. Male woodwasps (A) emerge before female (B) woodwasps. Adult wasps were dissected into separate tissues which were antennae (C), heads (D), legs (E), ovipositors for females (F), wings (G), and bodies which refers to the thoraces and abdomens (H). Trizol RNA extractions (I, J, K, and L) were pink as expected for most tissues, but head tissues produced a purple solution probably because of pigments found in the wasp heads (I and K).