Bulletin of Entomological Research

cambridge.org/ber

Molecular characterisation and expression profiles of an odorant-binding proteins gene (FoccOBP9) from *Frankliniella occidentalis*

Zhike Zhang

Ningxia Academy of Agriculture and Forestry Sciences, Institute of Plant Protection, Yinchuan, China

Research Paper

Cite this article: Zhang Z (2025). Molecular characterisation and expression profiles of an odorant-binding proteins gene (FoccOBP9) from *Frankliniella occidentalis*. *Bulletin of Entomological Research* 1–10. https://doi.org/10.1017/S0007485324000683

Received: 18 February 2024
Revised: 8 August 2024
Accepted: 28 October 2024

Keywords:
expression; *F. occidentalis*; odorant-binding proteins; sequence analysis; structure prediction

Corresponding author:
Zhike Zhang;
Email: zhangzhike98@163.com

Abstract

Insect odorant-binding proteins (OBPs) are the key proteins in insect olfactory perception and play an important role in the perception and discrimination of insects. *Frankliniella occidentalis* is a polyphagous pest and seriously harms the quality and yield of fruits, flowers and crops worldwide. Therefore, the discovery of OBPs has greatly improved the understanding of behavioural response that mediates the chemoreception of *F. occidentalis*. To identify the OBP gene of *F. occidentalis* and its sequence and expression, rapid amplification cDNA ends (RACE) and qRT-PCR reaction system were performed. The results showed that the sequence of FoccOBP9 gene was 846 bp and the reading frame was 558 bp, encoding 185 amino acid residues, a 3′ non-coding region of 195 bp and a 5′ non-coding region of 93 bp.The molecular weight of the protein was about 20.08 kDa, and the isoelectric point was 8.89. FoccOBP9 was similar to AtumGOBP and CnipOBP2 (30%), followed by BdorGOBP, DficGOBP, DsuzGOBP, AalbOBP38, CmarOBP6 and SexiOBP. Phylogenetic analysis of the FoccOBP9 demonstrated that the FoccOBP9 had a relatively close evolutionary relationship with SgreOBP1, AtumGOBP, HeleOBP3, CbowOBP17, CnipOBP2 and CpalOBP2. The prediction of secondary structure showed that FoccOBP9 protein contained 135 amino acid residues forming α-helix, 91 amino acid residues forming β-sheets and 24 amino acid residues forming β-turning. However, three-dimensional structure prediction showed that the FoccOBP9 protein skeleton was composed of six α-helices and the loops connecting these helices. Dynamic observation of the three-dimensional structure revealed that five α-helices (α1, α2, α4, α5, α6) were found in the structure. The expression profiles analysis revealed that *FoccOBP9* are highly abundant in antenna significantly, followed by the head and belly, and almost no expression in the chest and foot. Therefore, the identification and analysis of OBP may be useful for monitoring and limiting the damage of *F. occidentalis*.

Introduction

In the long-term biological evolution, insects have formed a highly sensitive, complex and unique olfactory sensing system, which enables insects to specifically identify odour substances in the environment, and thus execute corresponding behavioural responses such as foraging, avoidance and mating (Vogt *et al.*, 1999; Field *et al.*, 2000). Insects use their sensitive and selective olfactory organs to search for habitat, mates and oviposition sites and escape natural enemies (Gadenne *et al.*, 2016). Odorant-binding proteins (OBPs) are small water-soluble proteins which are involved in olfactory sensation as a main accessory proteins (Sandler *et al.*, 2000; Suh *et al.*, 2014; Wang *et al.*, 2018), and transmit the signal to elicit behavioural responses (Larter *et al.*, 2016; Silva and Antunes, 2017). Therefore, the understanding of OBPs is useful for green pest control and tools for developing pest control agents. It is of great significance to understand insect olfactory system and regulate insects through the olfactory system.

OBPs are polypeptides comprised of 100–200 amino acids which are involved in the sensitivity of the olfactory system and link external smells to olfactory receptor neurons (Maida *et al.*, 1993; Du and Chen, 2021). OBPs were first discovered in insects (Vogt and Riddiford, 1981) and vertebrates (Pelosi *et al.*, 1981, 1982). After several years, the olfactory receptors were also reported in nematodes (Troemel *et al.*, 1995) and the interaction of the olfactory receptors with OBPs was believed to response and recognise the signal transmission (Zhao *et al.*, 1998; Hallem *et al.*, 2004; Leal, 2013). Among all olfactory proteins, OBP is the most abundant, it is a kind of low molecular weight protein, exists in insect olfactory receptor lymphatic fluid, selectively binds and transports odorant molecules, activates the odorant transduction pathway (Vogt *et al.*, 1989; Tegoni *et al.*, 2000; Zhou, 2010; Jia *et al.*, 2019). OBPs are supposed to act in the first step of interaction with external odorants, binding to specific odorants and transporting them to specific membranes (Pelosi *et al.*, 2018; Ullah *et al.*, 2020). Most OBPs were mainly expressed in antennae (Niu *et al.*, 2016), taste system

Table 1. Primer sequences use for amplification of cDNA

Name	Sequence (5′-3′)	Use of primers
3′*FoccOBP9* Outer	CCCCTTCCTCCCACGACTCTGTTTT	3′-cDNA end isolation
3′*FoccOBP9* Inner	CCCCCGCCCCTTCTTCCTTCTAT	
5′*FoccOBP9* R4	TTATACTCGGAGCGGCCTGCAATCT	5′-cDNA end isolation
5′*FoccOBP9* R3	CGACCTGCTGGACCCGTCATTATACT	
5′*FoccOBP9* RT2	GCATCGGGCTCAGAATAA	
5′*FoccOBP9* RT1	TCTTCTCCGGGACATGCT	
FoccOBP9-F	ATCACCATGAAGGTCCTCGTC	Real-time quantitative PCR
FoccOBP9-R	CAGCATCGGGCTCAGAATAA	
β-actin-Fn	GGAATACACGAGACGACTTACAACT	
β-actin-Rn	TGGTAGATGGAGCCAGAGATGT	

(Shanbhag *et al*., 2001; Jeong *et al*., 2013) and larval chemosensory organs (Park *et al*., 2000; Galindo and Smith, 2001). They are the primary elements for insects to recognise and transport external information materials, and also playing a key role in the olfactory system (Hallem *et al*., 2006; Conchou *et al*., 2019).

Frankliniella occidentalis is a polyphagous pest, which has evolved resistance and sensitivity to a variety of insecticides through metabolic detoxification, causing serious harm and economic losses to the yield and quality of fruits, flowers and crops (Morse and Hoddle, 2006; Demirozer *et al*., 2012; He *et al*., 2020). As other insects, *F. occidentalis* conveys information or searches for their hosts by using colour, shape, size and volatiles of plant (Teulon *et al*., 1999; de Kogel and Koschier, 2002; Mainali and Lim, 2011). Most of current studies of insect OBPs are based on studies of species from different taxa, such as Diptera (Yasukawa *et al*., 2010; Chen *et al*., 2013), Hymenoptera (Ji *et al*., 2014), Lepidoptera (Wang *et al*., 2018), Hemiptera (Qiao *et al*., 2009; Gu *et al*., 2010) and Coleoptera (Ju *et al*., 2012). Although many researchers majored in studying OBPs in different insects, the possibility of OBPs in Thysanoptera is still an open question.

In this study, FoccOBP9 gene was cloned, expressed and identified in *F. occidentalis* firstly. In addition, we also predicted its protein structure and determined its distribution in the insect body. The characteristics of FoccOBP9 that we have identified provide a reference for the further study of olfactory mechanism and for the development of non-pesticide control measures for *F. occidentalis*.

Materials and methods

Insects

Frankliniella occidentalis was provided by the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, and reared in MLR-351H Sanyo incubator using fresh beans at temperature 26°C under a 14/10 h light/dark cycle with a relative humidity of 65%.

Total RNA extraction and reverse transcription

Total RNA was isolated from the antenna of *F. occidentalis* by the Trizol reagent RNA Isolation System (MP Biomedicals, USA). The antennae were quickly cut under dissecting microscope and placed in 1.5 ml centrifuge tubes immersed in liquid nitrogen. RNA was extracted by grinding with TRIzol reagent (synthesised by Beyotime Biotech, Shanghai, China) and dissolved in DEPC, and tested for integrity using a 1.5% agarose gel. The first strand of cDNA was synthesised with Oligo (dT) primers.

First and second instar nymphs, pupae, female and male adults at 1, 5, 10 and 15 days of plumage, as well as 1-day plumage antenna, feet, head, thorax and abdomen of *F. occidentalis* after CO_2 anaesthesia were quickly cut and placed in 1.5 ml centrifuge tubes immersed in liquid nitrogen, repeated three times.

Cloning of full-length cDNA of FoccOBP9

Bioinformatics analysis of transcriptome data and NCBI sequence alignment of *F. occidentalis* was performed to obtain sequence fragments of FoccOBP9 gene. PCR amplification was performed using the first strand of cDNA as template, and primers specific for 3′RACE and 5′RACE fragments of the target gene sequence were designed (table 1). The volume of PCR was 50 µl and contained 10× ExTaq Buffer 2.5 µl, cDNA 2 µl, $MgCl_2$ (25 mmol l^{-1}) 2 µl, 1 µl each of forward and reverse primers, TaKaRa ExTaq

Table 2. The consistency result between homologous protein and FoccOBP9

Name	Abbreviation	Register	Identify %
Aethina tumida	AtumGOBP	XP_019868892.1	34
Chrysoperla nipponensis	CnipOBP2	AKW47223.1	34
Bactrocera dorsalis	BdorGOBP	XP_011209038.1	33
Drosophila ficusphila	DficGOBP	XP_017051033.1	33
Drosophila suzukii	DsuzGOBP	XP_016941860.1	33
Aedes albopictus	AalbOBP38	AGI04321.1	33
Clunio marinus	CmarOBP6	AGH70102.1	33
Spodoptera exigua	SexiOBP	ADY17883.1	33
Heliothis virescens	HvirOBP	PCG80288.1	22

https://doi.org/10.1017/S0007485324000683 Published online by Cambridge University Press

```
AGTACGACACCCGGCTGCGCCCGGCCGCGCGCCGCCGAGGAGGACGGCCTGGACCACGCC
CTCGTCGCCAGATTGCAGGCCGCTCCGAGTATAATGACGGGTCCAGCAGGTCGGCGGCGG
                                  M  T  G  P  A  G  R  R  R
CACGCAGGGATAGGGACGCCCCCGGCTCGGTCCGGTCCGGGGTGGTGGGGAGGGGAGGGG
 H  A  G  I  G  T  P  P  A  R  S  G  P  G  W  W  G  G  E  G
GCGCGGGCCGATGATAAAAGTGGACCTCCGCGGCCGGCCAGGCAGCAGTGGTCATTGTCA
 A  R  A  D  D  K  S  G  P  P  R  P  A  R  Q  Q  W  S  L  S
AGGCGAATCGCTATCACCATGAAGGTCCTCGTCCTGTCGGCAGCGGTGCTCCTGGTGGCA
 R  R  I  A  I  T  M  K  V  L  V  L  S  A  A  V  L  L  V  A
CAGCAGGTGTGTAGCGCGCCGCCGCCCTTCGTGCACAGGTGCATGCAGGAGAACGGAGTC
 Q  Q  V  C  S  A  P  P  P  F  V  H  R  C  M  Q  E  N  G  V
ACAGGAGCGGATGCGATTAAGTTTGCTGAGACTGGGGAGGCGAGCGACGGGATGAAGTGC
 T  G  A  D  A  I  K  F  A  E  T  G  E  A  S  D  G  M  K  C
AATTTCAAGTGCATCATGATGGAAGCTGGTGTCATGACCCCAGAAGGCAAGCTTATTCTG
 N  F  K  C  I  M  M  E  A  G  V  M  T  P  E  G  K  L  I  L
AGCCCGATGCTGGAGCATGTCCCGGAGAAGATTCACCAGGCTTTCAAGGACTGCGTCGAA
 S  P  M  L  E  H  V  P  E  K  I  H  Q  A  F  K  D  C  V  E
ATAGAGCCCAGCTCCGACCTGTGCGATGTGGCTTTCCGACACAACGTGTGCCTCAGGGAA
 I  E  P  S  S  D  L  C  D  V  A  F  R  H  N  V  C  L  R  E
AAGGCCACAGATTTCTACAAGGCGATGGTGGCGAAGAAGCATCAGGCATAAGCGACAGGT
 K  A  T  D  F  Y  K  A  M  V  A  K  K  H  Q  A  *
GTGATTGGCGCCCCTCCCCTTCCTCCCACGACTCTGTTTTATACCCCCGCCCCTTCTTCC
TTCTATCTCTCTCGACAAAGTTGTCTGCCTTTCCTATCTATTAACAGAAAACGCATTTCC
TGTCTGCGAATTCGACAACGCAAATAAAGCATTTCACCTCATGCAAAAAAAAAAAAAAAA
AAAAA
```

Figure 1. Nucleotide and deduced amino acid sequence of odorant-binding protein gene of FoccOBP9. (Termination codons are indicated by an asterisk. Six conserved cysteine sites are marked with boxes.)

(5U μl^{-1}) 0.25 µl, dNTPMix (2.5 mmol l^{-1} each) 2 µl and ddH_2O 14.25 µl. PCRs were performed on a Mastercycler Gradient PCR machine (Eppendorf, USA) with the following cycling conditions: a pre-denaturation step at 95°C for 3 min, denaturation at 94°C for 30 s and a final extension at 56°C for 30 s, and 72°C for 1 min and for 10 min, then storage at 4°C with 30 cycles. PCR products were separated using a 1.5% agarose gel electrophoresis, purified with AxyPrep^{TM} DNA gel extraction kit (Sangon, Shanghai, China), and ligated into the pEASY-T1 vector. The ligation mixtures were transformed into Trans1-T1 receptor cells and the positive clones were selected by ampicillin medium isolated from them. The correct sequencing results were spliced with DNAMAN 6.0 to obtain the full-length cDNA sequence of the gene (Zhao *et al.*, 2015).

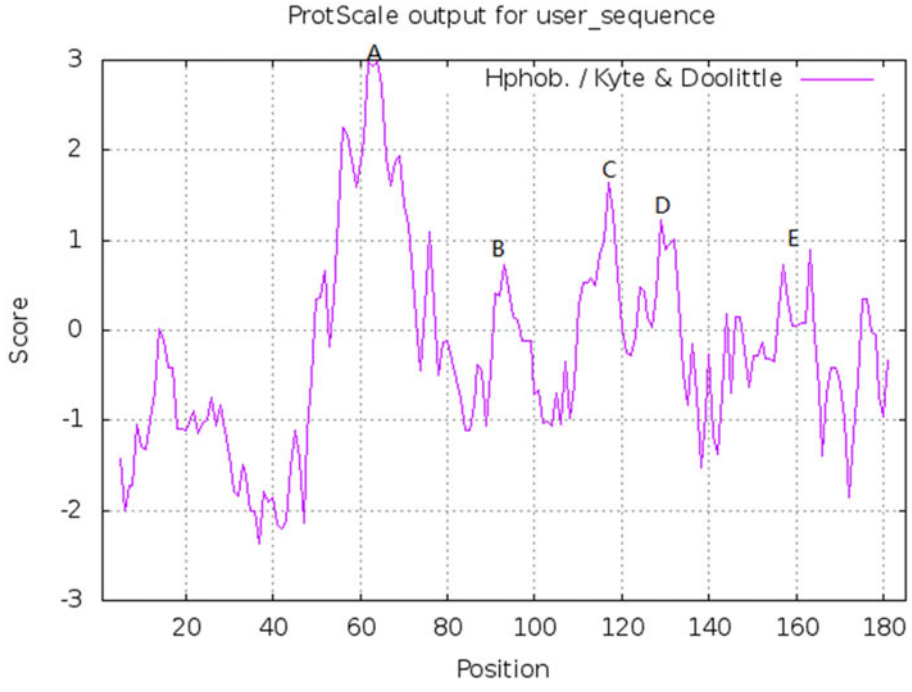

Figure 2. Predicted hydrophobicity profiles for the deduced amino acid sequences of FoccOBP9. Hydrophobicity index values are plotted against the amino acid residues using the method of Kyte and Doolittle (1982). Positive values indicate hydrophobicity and negative values indicate hydrophilicity. A, B, C, D, E: five predicted hydrophobic domains.

https://doi.org/10.1017/S0007485324000683 Published online by Cambridge University Press

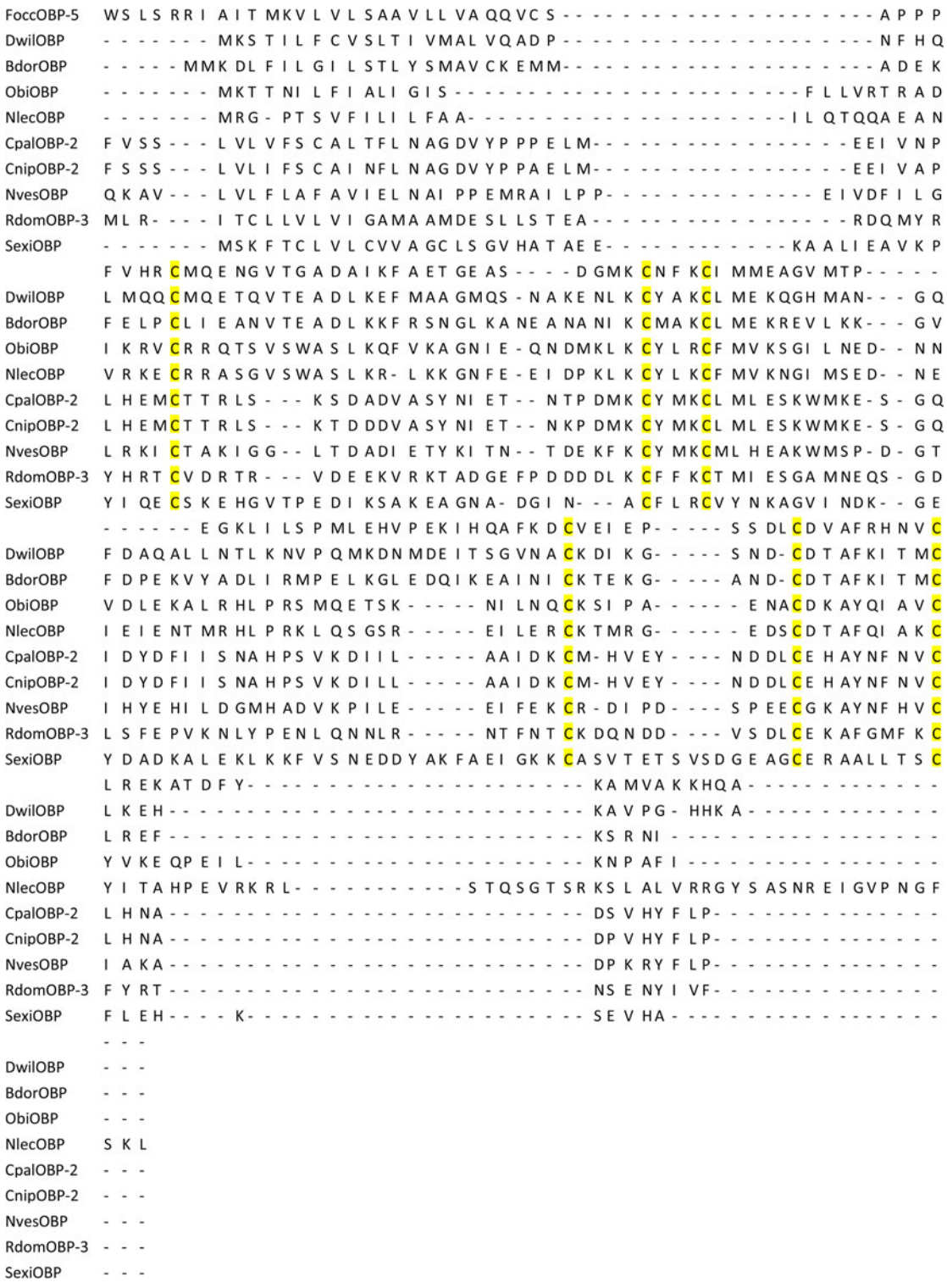

Figure 3. Alignment of FoccOBP9 with other order insect OBP. The conserved amino acids are highlighted under yellow. The other insect species are *Drosophila willistoni* (Diptera), *Bactrocera dorsalis* (Diptera), *Ooceraea biroi* (Hymenoptera), *Neodiprion lecontei* (Hymenoptera), *Chrysopa pallens* (Neuroptera), *Chrysoperla nipponensis* (Neuroptera), *Nicrophorus vespilloides* (Coleoptera), *Rhyzopertha dominica* (Coleoptera), *Spodoptera exigua* (Lepidoptera). Gene Bank accession numbers for all OBPs genes are DwilOBP, XP_002063852.1; BdorOBP, XP_011209038.1; ObiOBP, XP_011346593.1; NlecOBP, XP_015512408.1; CpalOBP2, AKW47195.1; CnipOBP2, AKW47223.1; NvesOBP, XP_017774856.1; RdomOBP3, AIX97144.1 ; SexiOBP, ADY17883.1.

Sequence analysis, phylogenetic tree construction and structure prediction

The basic physical traits of nucleotide sequences were predicted using Expasy (http://www.expasy.org). Sequence homology similarity was analysed using NCBI's BLASTx program (https://blast.ncbi.nlm.nih.gov). Signal peptides were predicted using SignaIP-5.0 Serve (https://services.healthtech.dtu.dk/services/SignalP-5.0/). Protein lipophilicity was analysed and protein sequence homology similarity was compared by the software ClustalX

https://doi.org/10.1017/S0007485324000683 Published online by Cambridge University Press

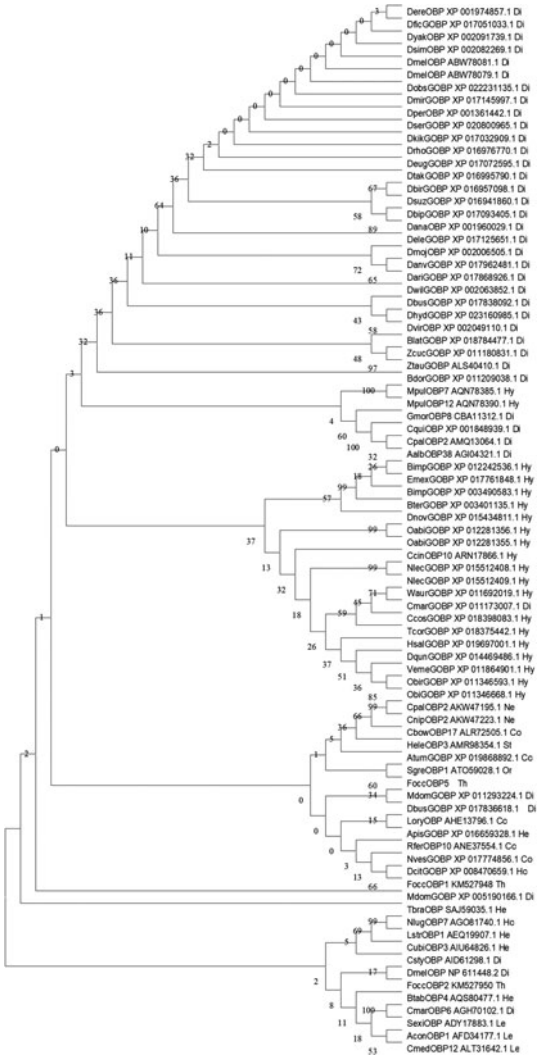

Figure 4. FoccOBP9 speculated protein phylogenetic tree based on N-J method. The length of the branch represents the genetic distance, the number on the branch is the confidence of the repeated calculation at 'Bootstrap' of 1000. The right is the abbreviation for the name of the insect species, protein name, accession number and the purpose of the insect acronym. Figure system tree insect head abbreviations were: Di (Diptera), Hy (Hymenoptera), Co (Coleoptera), Ho (Homoptera), Ne (Neuroptera), Se (Strongylida), Th (Thysanoptera), He (Hemiptera), Or (Orthoptera), Le (Lepidoptera). The species abbreviations are: Aalb (*Aedes albopictus*), Acon (*Argyresthia conjugella*), Apis (*Acyrthosiphon pisum*), Atum (*Aethina tumida*), Bdor (*Bactrocera dorsalis)*, Bimp (*Bombus impatiens*), Blat (*Bactrocera latifrons*), Btab (*Bemisia tabaci*), Bter (*Bombus terrestris*), Cbow (*Colaphellus bowringi*), Ccin (*Cephus cinctus*), Ccos (*Cyphomyrmex costatus*), Cmar (*Clunio marinus*), Cmed (*Cnaphalocrocis medinalis*), Cnip (*Chrysoperla nipponensis*), Cpal (*Chrysopa pallens*), Cpal (*Culex pipiens pallens*), Cqui (*Culex quinquefasciatus*), Csty (*Calliphora stygia)*, Cubi (*Chinavia ubica)*, Dana (*Drosophila ananassae*), Danv (*Drosophila navojoa*), Dari (*Drosophila arizonae*), Dbip (*Drosophila bipectinata*), Dbir (*Drosophila biarmipes*), Dbus (*Drosophila melanogaster*), Dcit (*Diaphorina citri*), Dele (*Drosophila elegans*), Dere (*Drosophila erecta*), Deug (*Drosophila eugracilis*), Dfic (*Drosophila ficusphila),* Dhyd (*Drosophila hydei*), Dkik (*Drosophila kikkawai*), Dmel (*Drosophila melanogaster*), Dmir (*Drosophila miranda*), Dmoj (*Drosophila mojavensis*), Dnov (*Dufourea novaeangliae)*, Dobs (*Drosophila obscura*), Dper (*Drosophila persimilis*), Dqun (*Dinoponera quadriceps*), Drho (*Drosophila rhopaloa*), Dser (*Drosophila serrata*), Dsim (*Drosophila simulans*), Dtak (*Drosophila takahashii*), Dvir (*Drosophila virilis*), Dwil (*Drosophila willistoni*), Dyak (*Drosophila yubaak*), Emex (*Eufriesea mexicana*), Focc (*Frankliniella occidentalis*), Hele (*Hylamorpha elegans*), Hsal (*Harpegnathos saltator*), Lory (*Lissorhoptrus oryzophilus*), Lstr (*Laodelphax striatella*), Mdom (*Musca domestica*), Mpul (*Meteorus pulchricornis*), Nlec (*Neodiprion lecontei*), Nlug (*Nilaparvata lugens*), Nves (*Nicrophorus vespilloides*), Oabi (*Orussus abietinus*), Obir (*Ooceraea biroi*), Rfer (*Rhynchophorus ferrugineus*), Sexi (*Spodoptera exigua*), Sgre (*Schistocerca gregaria*), Tbra (*Triatoma brasiliensis*), Tcor (*Trachymyrmex cornetzi*), Veme (*Vollenhovia emeryi*), Waur (*Wasmannia auropunctata*), Zcuc (*Zeugodacus cucurbitae*), Ztau (*Zeugodacus tau*).

1.83 (Kyte and Doolittle, 1982). The protein secondary and tertiary structures were predicted by Chou & Fasman and Swiss-PDB Viewer 4.1 (Kabsch and Sander, 1983), respectively. The phylogenetic evolutionary tree of the proteins was analysed by bootstrap 1000 replicate sampling using MEGA 6.0 neighbour-joining.

Expression of FoccOBP9

Primers specific for the target gene and the internal reference gene, β-actin, were designed in the conserved sequence region (table 1). qRT-PCR reaction system was 20 µl and consisted of: Go Taq® qPCR Master Mix (2×) 10, 0.5 µl of each forward and reverse primer, cDNA 2 µl, nuclease-free water 7 µl. The two-step PCR standard method was used, and the amplification procedure was 95°C for 2 min; 95°C for 15 s, 60°C for 1 min, 40 cycles. The PCR product melting curve measurement procedure was 95°C for 1 min, 55°C for 30 s, 95°C for 30 s and 60°C for 15 s. Ultra-pure water was used as negative control. Each reaction was performed with three biological replicates and three technical replicates were assessed for each biological replicates. To calculate the relative expression levels, the $2^{-\triangle\triangle Ct}$ relative quantification method was used to analysis the data. For tissue-specific expression pattern study, first instar nymph were used to collect samples of antenna, head (without antennae), leg and abdomen. All tissues were stored at −70°C prior to use.

Statistical analysis

The expression of OBP in different tissue was analysed by one-way analysis of variance, and the average means were separated by Tukey's honestly significance difference test. All analyses were performed using Rv.4.1.2.

Result

Sequence determination and analysis of FoccOBP9

A new gene in *F. occidentalis* was cloned. Sequence analysis revealed that the full length of this gene is 846 bp (fig. 1), with an open reading frame of 558 bp, encoding 185 amino acid residues, 195 bp in the 3′terminal non-coding region and 93 bp in the 5′ terminal non-coding region. The protein was found to have no signal peptide, and five lipophilic regions were identified in the amino acid sequence using the Expasy website (http://us.expasy.org/cgi-bin/protscale.pl) (fig. 2). This protein has six conserved cysteines and fits the model 'C_1-X_{25}-C_2-X_3-C_3-X_{33}-C_4-X_9-C_5-X_8-C_6', which is consistent with the typical OBPs 'C_1-X_{15-39}-C_2--X_3-C_3-X_{21-44}-C_4-X_{7-11}-C_5-X_8-C_6'. So a new OBP gene in *F. occidentalis* was identified and named as *FoccOBP9*.

The homologous protein of FoccOBP9 result showed that the largest number insect OBPs belonged to Diptera, accounting for 57% of the total, followed by Hymenoptera, accounting for 30%, and the smaller number of Coleoptera, Plecoptera and Lepidoptera, accounting for 7, 2 and 2% of the total, respectively. The similarity between the sequences searched and FoccOBP9 ranged from 22 to 34% (table 2), the higher similarity was 34% with *Aethina tumida* (AtumGOBP) and *Chrysoperla nipponensis* (CnipOBP2), which indicated that FoccOBP9 had higher homology with them, followed by the similarity with *Bactrocera dorsalis* (BdorGOBP), *Drosophila ficusphila* (DficGOBP), *Drosophila suzukii* (DsuzGOBP), *Aedes albopictus* (AalbOBP38), *Clunio marinus* (CmarOBP6) and *Spodoptera exigua* (SexiOBP) with 33%

https://doi.org/10.1017/S0007485324000683 Published online by Cambridge University Press

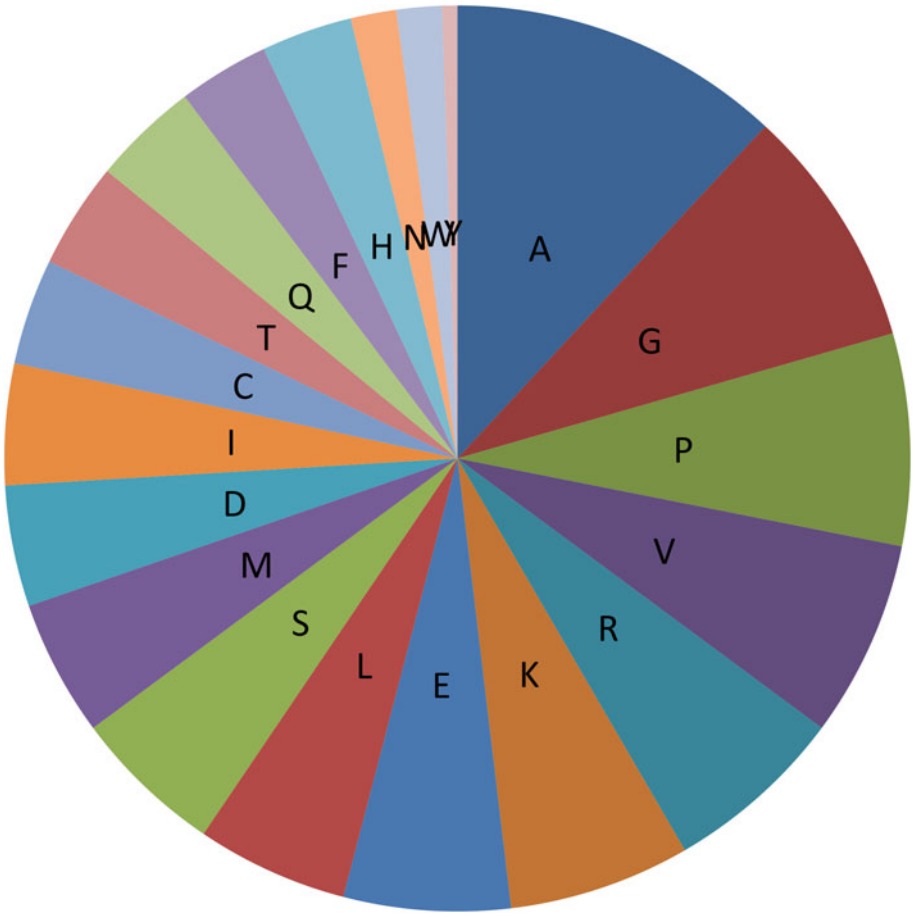

Figure 5. Amino acid composition of FoccOBP9.

similarity, and the lowest amino acid sequence homology was found with HvirOBP and FoccOBP9, only 22% similarity.

Compared with different target genes (nine insect OBPs), the sequences of FoccOBP9 were similar to DwilOBP, BdorOBP, ObiOBP, NlecOBP, CpalOBP2, CnipOBP2, NvesOBP and RdomOBP3. Although the homology of the genes was not high for SexiOBP in Lepidoptera, the six conserved cysteine sites were consistent in the location of OBPs in different insects, which indicated that the sequenced genes listed as OBP (fig. 3).

The evolutionary phylogenetic analysis (fig. 4) of the OBP amino acid sequences of 83 insects showed that FoccOBP9 had the highest identity (34%) with SgreOBP1 (*Schistucerca gregaria*), indicating FoccOBP9 may have a closer ancestor with SgreOBP1, followed by AtumGOBP (*Aethina tumida*), HeleOBP3 (*Hylamorpha elegans*), CbowOBP17 (*Colaphellus bowringi*), CnipOBP2 (*Chrysoperla nipponensis*) and CpalOBP2 (*Chrysopa pallens*), which makes it clear that the sequence belongs to the OBP (fig. 4). Among the amino acid composition of FoccOBP9, alanine (A) is the most abundant, followed by glycine (G), proline (P), valine (V), arginine (R), lysine (K) and glutamate (E), accounting for more than 50% of amount (fig. 5).

Predicted structure and analysis of FoccOBP9

The FoccOBP9 protein contained 135 amino acid residues forming α-helix, accounting for 73.0% of the overall amino acids, 91 amino acid residues forming β-sheets, accounting for 49.2%, and 24 amino acid residues forming β-angle, accounting for 13.0% (fig. 6). The Swiss model portal used 50 different templates to generate a refined model based on the best homology (fig. 7). OBP LmigOBP1 from *migratory locust* (No, ABA62340.1) was used as the best template. A total of six α-helices were predicted and the helix numbers were α1, α2, α3, α4, α5, α6, including five of the α-helices (α1, α2, α4, α5, α6) that form a binding pocket consisting mainly of hydrophobic and hydrophilic amino acid residues, while another α3 helix is at the top of the binding pocket.

Expression pattern of FoccOBP9

The expression of the FoccOBP9 in different developmental stages was examined using qRT-PCR (fig. 8). The result indicated that the expression level of FoccOBP9 in first instar nymph was significantly higher than in other developmental stages. However, it was highly expressed in 1-day-old females than in males, and although FoccOBP9 was not expressed in males at 5 days of fledging, it was higher at 10 and 15 days of fledging than in females.

In adults, FoccOBP9 was most highly expressed in the antennae, significantly lower in the head and abdomen, and showed no gene expression in the thorax and legs (fig. 9).

Discussion

OBPs play an important role in insect olfactory perception at different stages and may have additional functions (Fan *et al.*, 2011; Brito *et al.*, 2016; Rihani *et al.*, 2021). In our study, we cloned and identified an OBP gene of *F. occidentalis*, FoccOBP9. The result provides a basis for further investigation of the function of FoccOBP9 in the olfaction of *F. occidentalis*, especially in the

https://doi.org/10.1017/S0007485324000683 Published online by Cambridge University Press

```
                *         *         *         *         *         *
Query 1    MTGPAGRRRHAGIGTPPARSGPGWWGGEGARADDKSGPPRPARQQWSLSRRIAITMKVLVLSAAVLLVAQ 70
Helix 1                                HH          HHHHHHHHHHHHHHHHHHHHHHHHHHHHHH 70
Sheet 1                                               EEEE     EEEEEEEEEEEEEEEEEE 70
Turns 1      T   TT           T T    TT     T     T   T     T                    T 70
Struc 1    CCTCCCTTCCCCCCCCCCCTCTCCCCTTCHHCCTCCCCCTCHHTEEEHHHHHEHEEHEEEEHHHEEEEEEE 70

                *         *         *         *         *         *
Query 71   QVCSAPPPFVHRCMQENGVTGADAIKFAETGEASDGMKCNFKCIMMEAGVMTPEGKLILSPMLEHVPEKI 140
Helix 71   HHHH        HHHHHHH   HHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHH 140
Sheet 71   EE       EEEEEEEEEE      EE           EEEEEEEEEEEEEEE      EEEEEEEE    E 140
Turns 71         T         TT                 T                  TT            T   140
Struc 71   EEHHCCTCEEEEHHHTTEECCHHHHHHHHHHHHHHTHHEEEEEEHHHHHEEHHHHHHEHHHHHHHHHHH 140

                *         *         *         *
Query 141  HQAFKDCVEIEPSSDLCDVAFRHNVCLREKATDFYKAMVAKKHQA 185
Helix 141  HHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHHH  185
Sheet 141  EEEEEEEEE       EEEEEEEEEEE      EEEEEEEE       185
Turns 141   T          T T         T     T                 185
Struc 141  HHHHEHEHHHHTHTHEEHEHEEEEEHHHHHHEEEHHHHHHHHHHC 185
```

Figure 6. Predicted secondary structure of FoccOBP9.

olfaction of host plants, and for efficient screening of *F. occidentalis*, attractants or trophozoites.

Based on previous studies, we found that the OBP FoccOBP1 showed 37% similarity to AlinOBP5 (*Adelphocoris lineolatus*), AlucOBP8 (*Apolygus lucorum*) and LlinOBP2 (*Lygus lineolaris*) (Zhang *et al.*, 2016). FoccOBP3 showed 36% similarity to DallGOBP (*Diachasma alloeum*), TcasPBP and TcasOBP07 (*Tribolium castaneum*) (Zhang *et al.*, 2021). However, FoccOBP9 shared 34% similarity to Diptera and Hymenoptera, especially AtumGOBP (*A. tumida*) and CnipOBP2 (*C. nipponens*), followed by *B. dorsalis*, *D. ficusphila*, *D. suzukii*, *A. albopictus* and *S. exigua* (33%), and shared lower homology consistency with other insects, this may be related to the fact that OBPs come from different orders of insects.

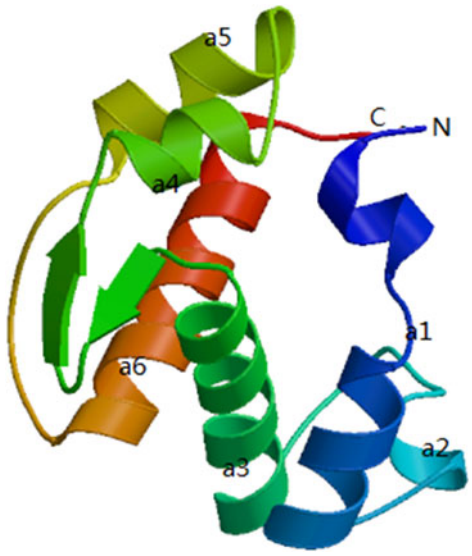

Figure 7. Predicted three-dimensional model of FoccOBP9. 3D structure of the FoccOBP9 from *F. occidentalis*. Six α-helices are represented in different colours such as N-terminus, α1: blue, α2: dark blue, α3: green, α4: sea green, α5: dark green, α6: brown and C-terminus.

Interestingly, FoccOBP9 was not in the same branch with FoccOBP1 and FoccOBP2 by phylogenetic analysis. Hence, we hypothesised that FoccOBP9 in *F. occidentalis* might have different functions. The adaptation and evolution of FoccOBP9 to different types of environmental chemical stimuli may lead to its differentiation, and it performs the same or some different functions.

Generally speaking, the expression of OBPs can reflect their role in insect life activities (Chang *et al.*, 2015; Li *et al.*, 2016b) and gene expression profiling of insects is an important way to reflect their gene functions (Xue *et al.*, 2016). Some researchers reported that OBPs are expressed in different developmental stages of insects, for example, HaxyOBP6 of *Harmonia axyridis* is expressed primarily in the adult stage (Han *et al.*, 2019), and OBPs of *Braconidae* are expressed primarily at specific developmental stages (Zhang *et al.*, 2009). Our results showed that FoccOBP9 was expressed primarily in the first instar nymph stage. The reason may be that the first instar nymph of

https://doi.org/10.1017/S0007485324000683 Published online by Cambridge University Press

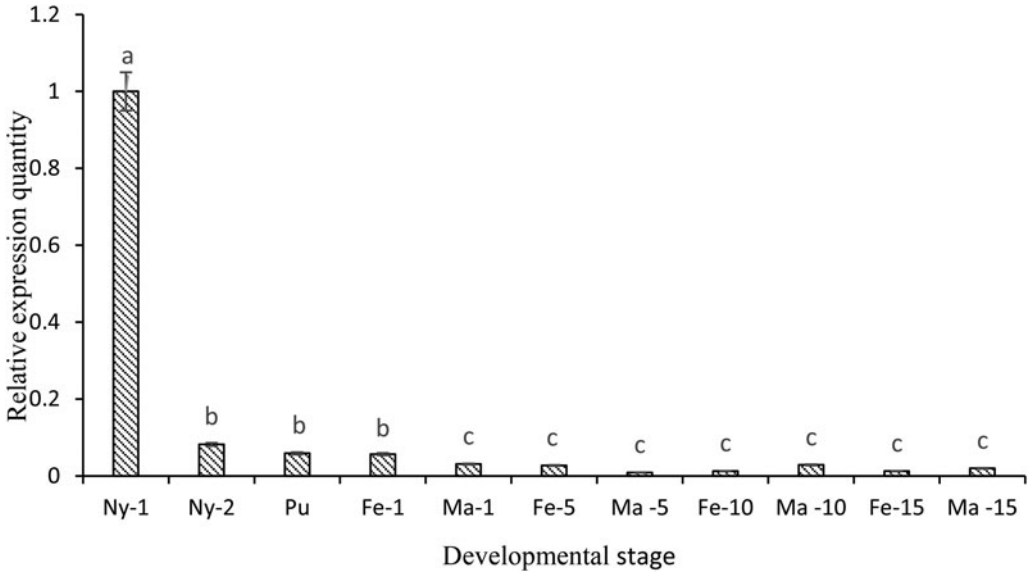

Figure 8. The relative expression level of FoccOBP9 in *F. occidentalis* different developmental stages. Ny-1: the first instar nymph; Ny-2: the second instar nymph; Pu: pupae; Fe-1, Fe-5, Fe-10, Fe-15 means 1-, 5-, 10-, 15-day-old adult female; Ma-1, Ma-5, Ma-10, Ma-15 means 1-, 5-, 10-, 15-day-old adult male.

F. occidentalis is short and has an urgent need to feed to replenish its nutrients and FoccOBP9 plays a role in this process.

In addition, the expression of OBPs was also related to the male and female sex of insects, and OBP genes were commonly biased to be expressed in both male and female adults, which may be related to the respective roles assumed by male and female adults in life (Qin *et al.*, 2016). Our results showed that the expression of FoccOBP9 was higher in females than in males at day 1 of plumage and higher in males than in females at day 10 of plumage. This result implied that FoccOBP9 has difference in the recognition of external odour between male and females in adults and performs different functions in females and adults.

OBPs are not only expressed in the lymph of olfactory sensilla on the antenna but also found elsewhere. High and specific antennal expression of OBPs suggests an olfactory role of recognizing specific information such as SinfGOBP (*Sesamia inferens*) (Zhang *et al.*, 2014), EoblOBP9 and EoblOBP11 (*Ectropis obliqua*) (Ma *et al.*, 2016; Li *et al.*, 2018), CcOBP5 (*Chouioia cunea*) (Pan *et al.*, 2020), AcerOBP14 (*Apis cerana*) (Du *et al.*, 2021), AipsPBPl-3 (*Agrotis ipsilon*) (Gu *et al.*, 2014) and CpunOBP4 (*Dichocrocis punctiferalis*) (Jia *et al.*, 2016). Of course, some OBPs are also expressed in other tissues, such as GmolOBP3 (*Grapholita molesta*) (Li *et al.*, 2016a), AzanOBP4 (*Agrilus zanthoxylumi*) (Guo *et al.*, 2021), PxylOBP2 (*Plutella xylostella*) (Cai *et al.*, 2021), CforOBP8 (*Cylas formicarius*) (Hua *et al.*, 2021), OBP10 and OBP14 (*Apis mellifera ligustica*) (Zhao *et al.*, 2015). However, FoccOBP9 gene was the most highly expressed in the antenna of *F. occidentalis*, and scarcely expressed in the head and abdomen. OBP distribution pattern can provide key clues to control pest; we hypothesised that FoccOBP9 mainly

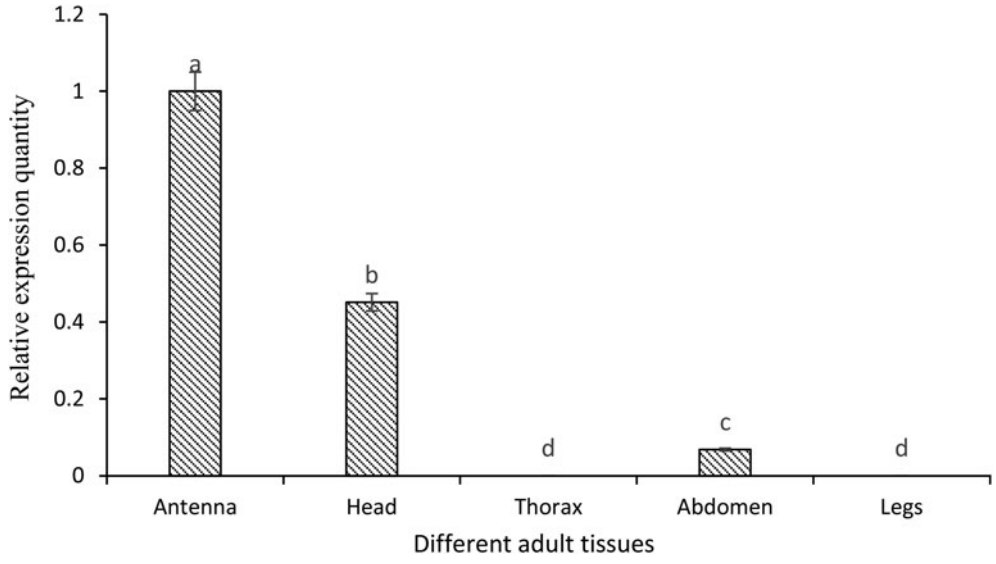

Figure 9. The relative expression level of FoccOBP9 in different adult tissues of *F. occidentalis*.

https://doi.org/10.1017/S0007485324000683 Published online by Cambridge University Press

exercises olfactory-related functions and is involved in odour binding and transport, but it may also be involved in other non-olfactory physiological functions, such as taste and touch. Based on previous study, OBP genes are mainly distributed in sensilla basiconica, a previous study in this laboratory found that multiple sensilla basiconica are distributed on the antenna of *F. occidentalis* (Zhang and Lei, 2022), so FoccOBP9 gene is highly expressed in the antenna, it is supposed that this gene may play an important role in host localisation and foraging of first instar nymph. This study may lay the foundation for the follow-up study of FoccOBP9 and further investigation of the olfactory mechanism in *F. occidentalis*.

Conclusions

In summary, we identified an OBP gene (FoccOBP9), and determined the relative expression level of FoccOBP9 in *F. occidentalis* at different developmental stages and in different adult tissues, which revealed that FoccOBP9 may play a prominent role in the olfactory chemoreception of *F. occidentalis*. These results can provide insight into the mechanism of olfactory communication of *F. occidentalis*, and provide scientific basis for further research and development of physical and chemical inducers for *F. occidentalis*.

Acknowledgments. We thank Professor Zhongren Lei (Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, China) for providing the test insect.

Author contributions. Zhike Zhang conceived and designed the experiments, performed the experiments, analysed the data and wrote the paper.

Financial support. This research was funded in part by the Special Project of the National Natural Science Foundation of China (grant number 32460673) and the Natural Science Foundation of Ningxia (grant number 2022AAC02053).

Competing interests. None.

References

Brito NF, Moreira MF and Melo AC (2016) A look inside odorant-binding proteins in insect chemoreception. *Journal of Insect Physiology* **95**, 51–65.

Cai LJ, Zheng LS, Huang YP, Xu W and You MS (2021) Identification and characterization of odorant binding proteins in the diamondback moth, *Plutella xylostella*. *Insect Science* **28**, 987–1004.

Chang H, Liu Y, Yang T, Pelosi P, Dong S and Wang G (2015) Pheromone binding proteins enhance the sensitivity of olfactory receptors to sex pheromones in *Chilo suppressalis*. *Scientific Reports* **5**, 1–12.

Chen L, Li H, Zhou Y, Zhao L, Zhang L, Ni C and Shang H (2013) cDNA cloning, tissue expression and ligand binding characteristics of odorant-binding protein 2 from the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *Acta Entomologica Sinica* **56**, 612–621.

Conchou L, Lucas P, Meslin C, Proffit M, Staudt M and Renou M (2019) Insect odorscapes: from plant volatiles to natural olfactory scenes. *Frontiers in Physiology* **972**, 1–20.

de Kogel WJ and Koschier EH (2002) Thrips responses to plant odours, *in* Proceedings Thrips and Tospoviruses: Proceedings of the 7th International Symposium on Thysanoptera, Reggio Calabria, Italy, 2–7 July 20012002, pp. 189–190.

Demirozer O, Tyler-Julian K, Funderburk J, Leppla N and Reitz S (2012) *Frankliniella occidentalis* (Pergande) integrated pest management programs for fruiting vegetables in Florida. *Pest Management Science* **68**, 1537–1545.

Du Y and Chen J (2021) The odorant binding protein, SiOBP5, mediates alarm pheromone olfactory recognition in the red imported fire ant, *Solenopsis invicta*. *Biomolecules* **11**, 1595.

Du Y, Xu K, Zhao H, Jiang Y and Li H (2021) Identification and functional characterization of AcerOBP15 from *Apis cerana cerana* (Hymenoptera: Apidae). *Apidologie* **52**, 668–683.

Fan J, Francis F, Liu Y, Chen J and Cheng D (2011) An overview of odorant-binding protein functions in insect peripheral olfactory reception. *Genetics and Molecular Research* **10**, 3056–3069.

Field L, Pickett J and Wadhams L (2000) Molecular studies in insect olfaction. *Insect Molecular Biology* **9**, 545–551.

Gadenne C, Barrozo R and Anton S (2016) Plasticity in insect olfaction: to smell or not to smell?.

Galindo K and Smith DP (2001) A large family of divergent Drosophila odorant-binding proteins expressed in gustatory and olfactory sensilla. *Genetics* **159**, 1059–1072.

Gu S, Sun Y, Ren L, Zhang X, Zhang Y, Wu K and Guo Y (2010) Cloning, expression and binding specificity analysis of odorant binding protein 3 of the lucerne plant bug, *Adelphocoris lineolatus* (Goeze). *Chinese Science Bulletin* **55**, 3911–3921.

Gu S-H, Sun L, Yang R-N, Wu K-M, Guo Y-Y, Li X-C, Zhou J-J and Zhang Y-J (2014) Molecular characterization and differential expression of olfactory genes in the antennae of the black cutworm moth *Agrotis ipsilon*. *PLoS ONE* **9**, e103420.

Guo L, Chen D, Gao X, Jia R, Zhang Z, Xie S, Lv S and Chen Z (2021) Cloning of odorant binding protein gene AzanOBP4 in *Agrilus zanthoxylumi* and its molecular docking with host volatiles. *Journal of Agricultural Biotechnology* **29**, 1364–1377.

Hallem EA, Nicole Fox A, Zwiebel LJ and Carlson JR (2004) Mosquito receptor for human-sweat odorant. *Nature* **427**, 212–213.

Hallem EA, Dahanukar A and Carlson JR (2006) Insect odor and taste receptors. *Annual Review of Entomology* **51**, 113–135.

Han S, Liang C, Li X, Han H, Zhao F and He Y (2019) Cloning and expression profiling of the odorant binding protein genes HaxyOBP1 and HaxyOBP6 in *Harmonia axyridis* (Coleoptera: Coccinellidae). *Acta Entomologica Sinica* **62**, 284–293.

He Z, Guo JF, Reitz SR, Lei ZR and Wu SY (2020) A global invasion by the thrip, *Frankliniella occidentalis*: current virus vector status and its management. *Insect Science* **27**, 626–645.

Hua J, Pan C, Huang Y, Li Y, Li H, Wu C, Chen T, Ma D and Li Z (2021) Functional characteristic analysis of three odorant-binding proteins from the sweet potato weevil (*Cylas formicarius*) in the perception of sex pheromones and host plant volatiles. *Pest Management Science* **77**, 300–312.

Jeong YT, Shim J, Oh SR, Yoon HI, Kim CH, Moon SJ and Montell C (2013) An odorant-binding protein required for suppression of sweet taste by bitter chemicals. *Neuron* **79**, 725–737.

Ji T, Shen F, Liang Q, Wu L, Liu Z and Luo Y (2014) Cloning, prokaryotic expression and tissue expression profiling of an OBP3 gene in the Chinese honeybee, *Apis cerana cerana* (Hymenoptera: Apidae). *Acta Entomologica Sinica* **57**, 897–904.

Jia X-J, Wang H-X, Yan Z-G, Zhang M-Z, Wei C-H, Qin X-C, Ji W-R, Falabella P and Du Y-L (2016) Antennal transcriptome and differential expression of olfactory genes in the yellow peach moth, *Conogethes punctiferalis* (Lepidoptera: Crambidae). *Scientific Reports* **6**, 1–16.

Jia X, Gao B, Ma J, Li X, Chen S and Wang R (2019) Gene expression profiling and ligand binding characterization of the odorant binding protein CforOBP8 in *Cylas formicarius* (Coleoptera: Brentidae). *Acta Entomologica Sinica* **62**, 275–283.

Ju Q, Qu M-J, Wang Y, Jiang X-J, Li X, Dong S-L and Han Z-J (2012) Molecular and biochemical characterization of two odorant-binding proteins from dark black chafer, *Holotrichia parallela*. *Genome* **55**, 537–546.

Kabsch W and Sander C (1983) How good are predictions of protein secondary structure? *FEBS Letters* **155**, 179–182.

Kyte J and Doolittle RF (1982) A simple method for displaying the hydropathic character of a protein. *Journal of Molecular Biology* **157**, 105–132.

Larter NK, Sun JS and Carlson JR (2016) Organization and function of Drosophila odorant binding proteins. *elife* **5**, e20242.

Leal WS (2013) Odorant reception in insects: roles of receptors, binding proteins, and degrading enzymes. *Annual Review of Entomology* **58**, 373–391.

https://doi.org/10.1017/S0007485324000683 Published online by Cambridge University Press

Li G, Chen X, Li B, Zhang G, Li Y and Wu J (2016a) Binding properties of general odorant binding proteins from the oriental fruit moth, *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae). *PLoS ONE* **11**, e0155096.

Li H-L, Ni C-X, Tan J, Zhang L-Y and Hu F-L (2016b) Chemosensory proteins of the eastern honeybee, *Apis cerana*: identification, tissue distribution and olfactory related functional characterization: comparative biochemistry and physiology part B. *Biochemistry and Molecular Biology* **194**, 11–19.

Li Z-Q, Cai X-M, Luo Z-X, Bian L, Xin Z-J, Chu B, Liu Y and Chen Z-M (2018) Comparison of olfactory genes in two ectropis species: emphasis on candidates involved in the detection of type-II sex pheromones. *Frontiers in Physiology* **9**, 1602.

Ma L, Li Z-Q, Bian L, Cai X-M, Luo Z-X, Zhang Y-J and Chen Z-M (2016) Identification and comparative study of chemosensory genes related to host selection by legs transcriptome analysis in the tea geometrid *Ectropis obliqua*. *PLoS ONE* **11**, e0149591.

Maida R, Steinbrecht A, Ziegelberger G and Pelosi P (1993) The pheromone binding protein of *Bombyx mori*: purification, characterization and immunocytochemical localization. *Insect Biochemistry and Molecular Biology* **23**, 243–253.

Mainali BP and Lim UT (2011) Behavioral response of western flower thrips to visual and olfactory cues. *Journal of Insect Behavior* **24**, 436–446.

Morse JG and Hoddle MS (2006) Invasion biology of thrips. *Annual Review of Entomology* **51**, 67–89.

Niu D-J, Liu Y, Dong X-T and Dong S-L (2016) Transcriptome based identification and tissue expression profiles of chemosensory genes in *Blattella germanica* (Blattaria: Blattidae): comparative biochemistry and physiology part D. *Genomics and Proteomics* **18**, 30–43.

Pan L, Xiang W, Sun Z, Yang Y, Han J, Wang Y, Yan C and Li M (2020) CcOBP2 plays a crucial role in 3-carene olfactory response of the parasitoid wasp *Chouioia cunea*. *Insect Biochemistry and Molecular Biology* **117**, 103286.

Park S-K, Shanbhag S, Wang Q, Hasan G, Steinbrecht R and Pikielny C (2000) Expression patterns of two putative odorant-binding proteins in the olfactory organs of Drosophila melanogaster have different implications for their functions. *Cell and Tissue Research* **300**, 181–192.

Pelosi P, Pisanelli AM, Baldaccini NE and Gagliardo A (1981) Binding of [3H]-2-isobutyl-3-methoxypyrazine to cow olfactory mucosa. *Chemical Senses* **6**, 77–85.

Pelosi P, Baldaccini NE and Pisanelli AM (1982) Identification of a specific olfactory receptor for 2-isobutyl-3-methoxypyrazine. *Biochemical Journal* **201**, 245.

Pelosi P, Iovinella I, Zhu J, Wang G and Dani FR (2018) Beyond chemoreception: diverse tasks of soluble olfactory proteins in insects. *Biological Reviews* **93**, 184–200.

Qiao H, Tuccori E, He X, Gazzano A, Field L, Zhou J-J and Pelosi P (2009) Discrimination of alarm pheromone (E)-β-farnesene by aphid odorant-binding proteins. *Insect Biochemistry and Molecular Biology* **39**, 414–419.

Qin JM, Cai LJ, Zheng LS, Cheng XJ and You MS (2016) Identification and ligand binding characteristics of antennal binding protein PxylOBP31 in the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Acta Entomologica Sinica* **59**, 812–822.

Rihani K, Ferveur J-F and Briand L (2021) The 40-year mystery of insect odorant-binding proteins. *Biomolecules* **11**, 509.

Sandler BH, Nikonova L, Leal WS and Clardy J (2000) Sexual attraction in the silkworm moth: structure of the pheromone-binding-protein–bombykol complex. *Chemistry & Biology* **7**, 143–151.

Shanbhag S, Park S-K, Pikielny C and Steinbrecht RA (2001) Gustatory organs of Drosophila melanogaster: fine structure and expression of the putative odorant-binding protein PBPRP2. *Cell and Tissue Research* **304**, 423–437.

Silva L and Antunes A (2017) Vomeronasal receptors in vertebrates and the evolution of pheromone detection. *Annual Review of Animal Biosciences* **5**, 353–370.

Suh E, Bohbot JD and Zwiebel LJ (2014) Peripheral olfactory signaling in insects. *Current Opinion in Insect Science* **6**, 86–92.

Tegoni M, Pelosi P, Vincent F, Spinelli S, Campanacci V, Grolli S, Ramoni R and Cambillau C (2000) Mammalian odorant binding proteins. *Biochimica et Biophysica Acta (BBA)-Protein Structure and Molecular Enzymology* **1482**, 229–240.

Teulon DA, Hollister B, Butler RC and Cameron EA (1999) Colour and odour responses of flying western flower thrips: wind tunnel and greenhouse experiments. *Entomologia Experimentalis et Applicata* **93**, 9–19.

Troemel ER, Chou JH, Dwyer ND, Colbert HA and Bargmann CI (1995) Divergent seven transmembrane receptors are candidate chemosensory receptors in *C. elegans*. *Cell* **83**, 207–218.

Ullah RMK, Quershi SR, Adeel MM, Abdelnabby H, Waris MI, Duan S-G and Wang M-Q (2020) An odorant binding protein (SaveOBP9) involved in chemoreception of the wheat aphid *Sitobion avenae*. *International Journal of Molecular Sciences* **21**, 8331.

Vogt RG and Riddiford LM (1981) Pheromone binding and inactivation by moth antennae. *Nature* **293**, 161–163.

Vogt R, Kohne A, Dubnau J and Prestwich G (1989) Expression of pheromone binding proteins during antennal development in the gypsy moth *Lymantria dispar*. *Journal of Neuroscience* **9**, 3332–3346.

Vogt R, Callahan F, Rogers M and Dickens J (1999) Odorant binding protein diversity and distribution among the insect orders, as indicated by LAP, an OBP-related protein of the true bug *Lygus lineolaris* (Hemiptera, Heteroptera). *Chemical Senses* **24**, 481–495.

Wang Q, Shang Y, Hilton DS, Inthavong K, Zhang D and Elgar MA (2018) Antennal scales improve signal detection efficiency in moths. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20172832.

Xue W, Fan J, Zhang Y, Xu Q, Han Z, Sun J and Chen J (2016) Identification and expression analysis of candidate odorant-binding protein and chemosensory protein genes by antennal transcriptome of *Sitobion avenae*. *PLoS ONE* **11**, e0161839.

Yasukawa J, Tomioka S, Aigaki T and Matsuo T (2010) Evolution of expression patterns of two odorant-binding protein genes, Obp57d and Obp57e, in Drosophila. *Gene* **467**, 25–34.

Zhang ZK and Lei ZR (2022) Sensilla of the western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera, Thripidae). *Revista Brasileira de Entomologia* **66**, e20220023.

Zhang S, Zhang Y-J, Su H-H, Gao X-W and Guo Y-Y (2009) Identification and expression pattern of putative odorant-binding proteins and chemosensory proteins in antennae of the Microplitis mediator (Hymenoptera: Braconidae). *Chemical Senses* **34**, 503–512.

Zhang Y-N, Ye Z-F, Yang K and Dong S-L (2014) Antenna-predominant and male-biased CSP19 of *Sesamia inferens* is able to bind the female sex pheromones and host plant volatiles. *Gene* **536**, 279–286.

Zhang Z, Wu S and Lei Z (2016) Cloning, sequence analysis and expression profile of an odorant binding protein gene in western flower thrips (*Frankliniella occidentalis*). *Scientia Agricultura Sinica* **49**, 1106–1116.

Zhang Z, Hu H and Ma R (2021) Cloning, sequence analysis and expression characteristics of FoccOBP3 in western flower thrips *Frankliniella occidentalis*. *Chinese Journal of Biological Control* **37**, 495–507.

Zhao H, Ivic L, Otaki JM, Hashimoto M, Mikoshiba K and Firestein S (1998) Functional expression of a mammalian odorant receptor. *Science* **279**, 237–242.

Zhao H, Zeng X, Liang Q, Zhang X, Huang W, Chen H and Luo Y (2015) Study of the obp5 gene in *Apis mellifera ligustica* and *Apis cerana cerana*. *Genetics and Molecular Research: GMR* **14**, 6482–6494.

Zhou J-J (2010) Odorant-binding proteins in insects. *Vitamins & Hormones* **83**, 241–272.

https://doi.org/10.1017/S0007485324000683 Published online by Cambridge University Press