Journal of Asia-Pacific Entomology 20 (2017) 720–727

Contents lists available at ScienceDirect

Journal of Asia-Pacific Entomology

journal homepage: www.elsevier.com/locate/jape

De novo transcriptomic analysis to reveal insecticide action and detoxification-related genes of the predatory bug, *Cyrtorhinus lividipennis*

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ARTICLE INFO

Keywords:
Cyrtorhinus lividipennis
Transcriptome
Detoxification enemy
Target action
Insecticide selectivity
Rice planthoppers

ABSTRACT

The mirid bug, *Cyrtorhinus lividipennis* Reuter, an important predatory natural enemy of rice planthoppers, is widely distributed in rice fields. However, genetic information on *C. lividipennis* is lacking. Especially, limited data about mechanisms of insecticide selectivity between this piercing-sucking predator (*C. lividipennis*) and piercing-sucking preys (rice planthoppers), inhibits development of selective insecticides and the integration of chemical and biological control systems to control insect pests of rice. Hence, we performed *de novo* assembly of a transcriptome from adult and nymph whole bodies of *C. lividipennis*. A total of > 29 million of reads were generated, and 34,752 transcripts matched known proteins. Then, the genes related to insecticide action and detoxification were manually identified, including 26 carboxylesterases (containing 2 acetylcholinesterases), 57 cytochrome P450s, 19 glutathione S-transferases, 15 nicotinic acetylcholine receptors, 3 GABA-gated ion channels, and 1 glutamate receptor. Comparisons of sequence differences in these genes between *C. lividipennis* and rice planthoppers, revealed that quite a lot of diversity was found among genes related to insecticide action and detoxification, while a few of these genes share much higher identities between this predator and prey. The present study provides useful information for our understanding of insecticide selectivity between rice planthoppers and the predator mirid bug.

Introduction

Several sap-sucking insect pests of rice cause serious rice crop losses by sucking plant sap and transmitting virus diseases, which consist mainly of brown planthopper, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae), white-backed planthopper, *Sogatella furcifera* (Horváth) (Hemiptera: Delphacidae), small brown planthopper, *Laodelphax striatellus*, (Fallén) (Hemiptera: Delphacidae) and rice green leafhopper, *Nephotettix cincticeps* Distant (Hemiptera: Euscelidae) in rice-growing countries and regions in Asia. Chemical control is still a major method for the control of these pest populations (Lou et al., 2013). However, due to misuse or overuse of chemical insecticides, many issues concerning insecticide resistance, ecological and environmental problems have been raised. In addition, broad-spectrum and non-selective pesticides are high risk to beneficial species (Tanaka et al., 2000). Indiscriminately killing a wide range of natural enemies by extensive and intensive use of insecticides, is one of main reasons for causing pest outbreaks (Way and Heong, 1994).

The mirid bug, *Cyrtorhinus lividipennis* Reuter (Hemiptera: Miridae), the piercing-sucking predator in rice fields in Asia, preys mainly on eggs or young nymphs of rice planthoppers and leafhoppers by piercing and sucking out their juices (Cook and Perfect, 1985; Lou et al., 2013). It is widely distributed in rice fields and is an important factor in population regulating the planthopper (Heong et al., 1990; Lou et al., 2013).

As the piercing-sucking insects in rice fields, like rice planthoppers, *C. lividipennis* showed similar or even higher sensitivity to many insecticides, such as deltamethrin, imidacloprid, fipronil, pymetrozine and chlorantraniliprole (Jiang et al., 2015; Preetha et al., 2010; Tanaka et al., 2000; Yang et al., 2012). However, some insecticides like endosulfan, chlorpyrifos, acephate, methyl parathion, and buprofezin were relatively safe to *C. lividipennis* (Hegde and Nidagundi, 2009; Preetha et al., 2010). Few studies were reported to evaluate insecticide selectivity between *C. lividipennis* and rice planthoppers on the molecular level. Guo et al. (2015) reported that key amino acid differences of nAChR α8 subunits between *C. lividipennis* and *N. lugens* might contribute to higher sensitivity to neonicotinoids for *C. lividipennis*. Jiang et al. (2015) found that *C. lividipennis* RDL expressed *in vivo* was more sensitive to fipronil than *N. lugens* RDL, which suggesting the target sensitivity was one of the major factors contributing to higher sensitivity to fipronil for *C. lividipennis* than *N. lugens*.

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http://dx.doi.org/10.1016/j.aspen.2017.04.010
Received 21 January 2017; Received in revised form 4 April 2017; Accepted 10 April 2017
Available online 25 April 2017

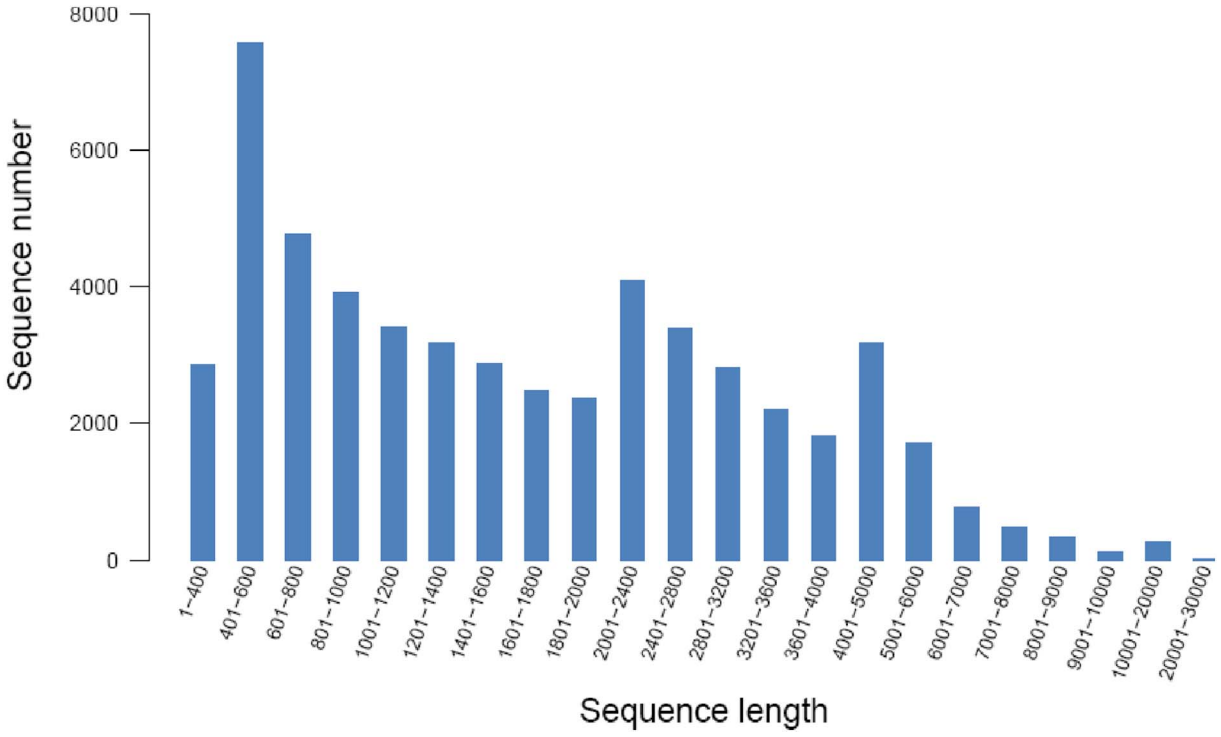

Fig. 1. Length distribution of *C. lividipennis* transcriptome sequences.

However, as an important predatory enemy of rice insect pests and a promising biocontrol agent against sap-sucking rice insect pests, genetic information on *C. lividipennis* is mostly lacking. Prior to the present study, only 13 amino acid sequences of *C. lividipennis* were found in the NCBI (National Center for Biotechnology Information) database, including two variants of GABA-gated chloride channel subunit, nAChR α8 subunit and two AChE genes.

In the present study, based on Illumina high-throughput sequencing technologies, we generated > 29 million raw reads for *de novo* assembly and annotation, without a genome reference sequence. Then, genes related to insecticide action and detoxification were manually identified, and comparisons of these sequences between the piercing-sucking predator (*C. lividipennis*) and the piercing-sucking prey (rice planthoppers) were analyzed. Genetic information supplied in the present study can aid in the in-depth investigation of insecticide selectivity between *C. lividipennis* and rice planthoppers, which might be helpful for a better balance between chemical and biological control methods.

Materials and methods

Sample preparation

N. lugens adults were collected in paddy fields in Huazhong Agricultural University, Wuhan, China, and were reared continuously on rice seedlings of the TN1 variety in the laboratory without exposure to insecticides at 26 ± 1 °C and a 16:8 h (light:dark) photoperiod.

The *C. lividipennis* individuals were collected from paddy fields in Xiaogan and reared with eggs of *N. lugens* infested on TN1. The colony was maintained for more than twenty generations before its use in the present study. The insects were cultured at 28 ± 1 °C, RH 70 ± 5% and a 16:8 h (light:dark) photoperiod.

RNA extraction of whole body

Total RNA of 50 females and 100 nymphs were isolated by TRIzol Reagent (Invitrogen, USA), respectively, according to the manufacturer's instructions. Adults and nymphs of *C. lividipennis* were starved for at least 6 h prior to extraction of RNAs. Sequencing was performed by the Nation Key Laboratory of Crop Genetic Improvement, Nation Center of Plant Gene Research (Wuhan, China), using Illumina HiSeq 2000 (Illumina, San Diego, CA, USA).

Data analysis of transcriptome data

Before assembly, raw reads were first trimmed to remove low-quality reads. The Trinity software (http://trinityrnaseq.sourceforge.net/) was used to *de novo* assemble clean reads, and to predict ORFs from the reconstructed transcripts. All assembled sequences were annotated against NCBI NR, Swiss-prot, COG and KEGG databases with an E-value cutoff of 10^{-5}. Blast2GO program (Conesa et al., 2005) was used to assign GO terms from the Blastp against the NR database.

Sequences of genes related to insecticide action and detoxification were identified using the tBLASTn with NR database with an E-value of $< 10^{-5}$. All identified sequences found in the same BLAST hit or with high homology, were eliminated selectively as different parts of the same gene, after determined by alignment results. Protein sequences of other species were downloaded from the NCBI database and used as references for sequence alignment and phylogenetic analysis. ClustalX software (Thompson et al., 2002) was used to perform a multiple sequence alignment, using the slow-accurate mode with a gap-opening penalty of 10 and a gap-extension penalty of 0.1 and applying the default Gonnet protein weight matrix. Alignments were displayed and edited using GeneDoc (Nicholas et al., 1997). Overall sequence identities and similarities were also calculated using GeneDoc. Phylogenetic trees were constructed with MEGA 6.06 software (Tamura et al., 2013), using the neighbor-joining method and a bootstrap analysis with 1000 replicates (Saitou and Nei, 1987).

Results and discussion

Analysis of Illumina sequencing results

Basic information on the transcriptome of adult and nymph whole bodies of *C. lividipennis* are summarized in Table S1. In total, 34,752

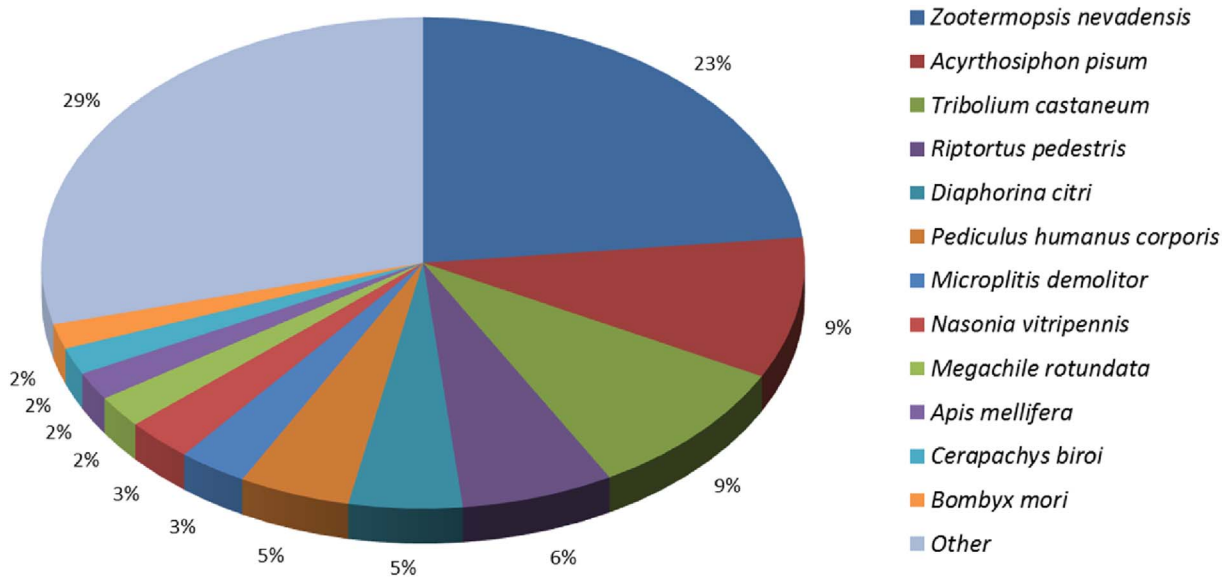

Fig. 2. Species distribution of the BLAST hits for the transcripts against NCBI NR protein database. Species distribution is shown as the percentage of total homologous sequences with an E-value of at least 10^{-5}.

transcripts (63.57% of all distinct sequences) matched known proteins, after annotated with NR, Swiss-prot, GO, COG and KEGG databases (Table S2). Sequence length distribution and species distribution of transcripts that hit in the NCBI NR protein database are shown in Figs. 1–2. The transcriptomic data were submitted to the Sequence Read Archive (SRA) database under the accession number SRX2245109 and SRX2246897.

Identification of genes related to insecticide action and detoxification

As showed in Table 1, we identified a number of transcripts of genes related to insecticide action and detoxification in the *C. lividipennis* transcriptome, including three major insecticide detoxification enzyme families (carboxylesterase, cytochrome P450 and glutathione S-transferase), and insecticide targets (acetylcholinesterase, nicotinic acetylcholine receptor, GABA-gated ion channel, and glutamate receptor).

Table 1
Information for annotated transcripts and validated genes associated with insecticide action and detoxification in the *C. lividipennis* transcriptome.

Insecticide metabolism and targets	Annotated isogene number	Validated gene number
Carboxylesterase	61	26
Dietary detoxification		2
Pheromone/hormone degradation		10
Neurodevelopment		14
Clade H - glutactin		2
Clade J - acetylcholinesterase		2
Clade K - gliotactin		1
Clade L - neuroligin		7
Clade M - neurotactin		1
Unknown function		1
Cytochrome P450	158	57
CYP2		5
CYP3		27
CYP4		21
Mitochondrial CYP		4
Glutathione S-transferase	24	18
Delta		5
Omega		1
Sigma		8
Theta		1
Zeta		1
Microsomal		2
Delta		6
Nicotinic acetylcholine receptor	20	15
GABA-gated ion channel	22	3
Glutamate receptor	11	1

(1) Carboxylesterase (COE)

A total of 61 carboxylesterase-like transcripts were identified, after annotating the transcriptome (Table S3). After removing redundancy, 26 unique putative carboxylesterase-like genes or gene fragments were obtained (Table S4). Insect COEs have been divided into three functional classes: dietary detoxification, hormone and pheromone degradation, and neurodevelopment, that in turn are divided into smaller, more specific clades (Tsubota and Shiotsuki, 2010b). Numbers of *C. lividipennis* COEs in the three classes are 2, 10 and 14, respectively (Table S4; Fig. 3). In both dietary detoxification and pheromone/hormone degradation classes, different gene contents due to species-specific expansions can be observed (Meng et al., 2015). Therefore, it is difficult to infer functional roles for genes of the dietary detoxification and pheromone/hormone degradation classes.

COEs in the dietary detoxification class are involved in the detoxification of a broad range of substrates including xenobiotics in the diet and insecticides (Tsubota and Shiotsuki, 2010a). Catalytic COEs have some common characteristics, such as conserved catalytic triad S200, E327 and H440, numbered according to *Torpedo californica* AChE (De Carvalho et al., 2006). The catalytic triad of COE amino acid sequences was predicted by blastp searching NCBI conserved domain database (CDD) (Table S4). Based on the phylogenetic analysis, it is possible that three genes (Cl-COE1 and Cl-COE2), having GESAG consensus sequences, belong to detoxification/dietary class (Fig. 3).

Ten genes may belong to pheromone/hormone degradation class (Fig. 3). Two genes (Cl-COE11 and Cl-COE12) can be found clustering together with *Rhodnius prolixus* JHE genes, with the motifs, GESAG and GNSAG, respectively. Eight genes were clustered in the beta esterase clade (Clade G, classified in Yu et al. (2009)).

Eleven genes were located in the phylogenetic tree of neurodevelopmental class (Fig. 3). The neurodevelopmental class includes the catalytic enzymes AChE (clade J) and non-catalytic COEs (Table S4, clades H and clades K–M).

Acetylcholinesterases (AChEs) were the only enzymes that perform a catalytic function in the neurodevelopmental class. AChE has a well-known and conserved function on the central nervous system of all

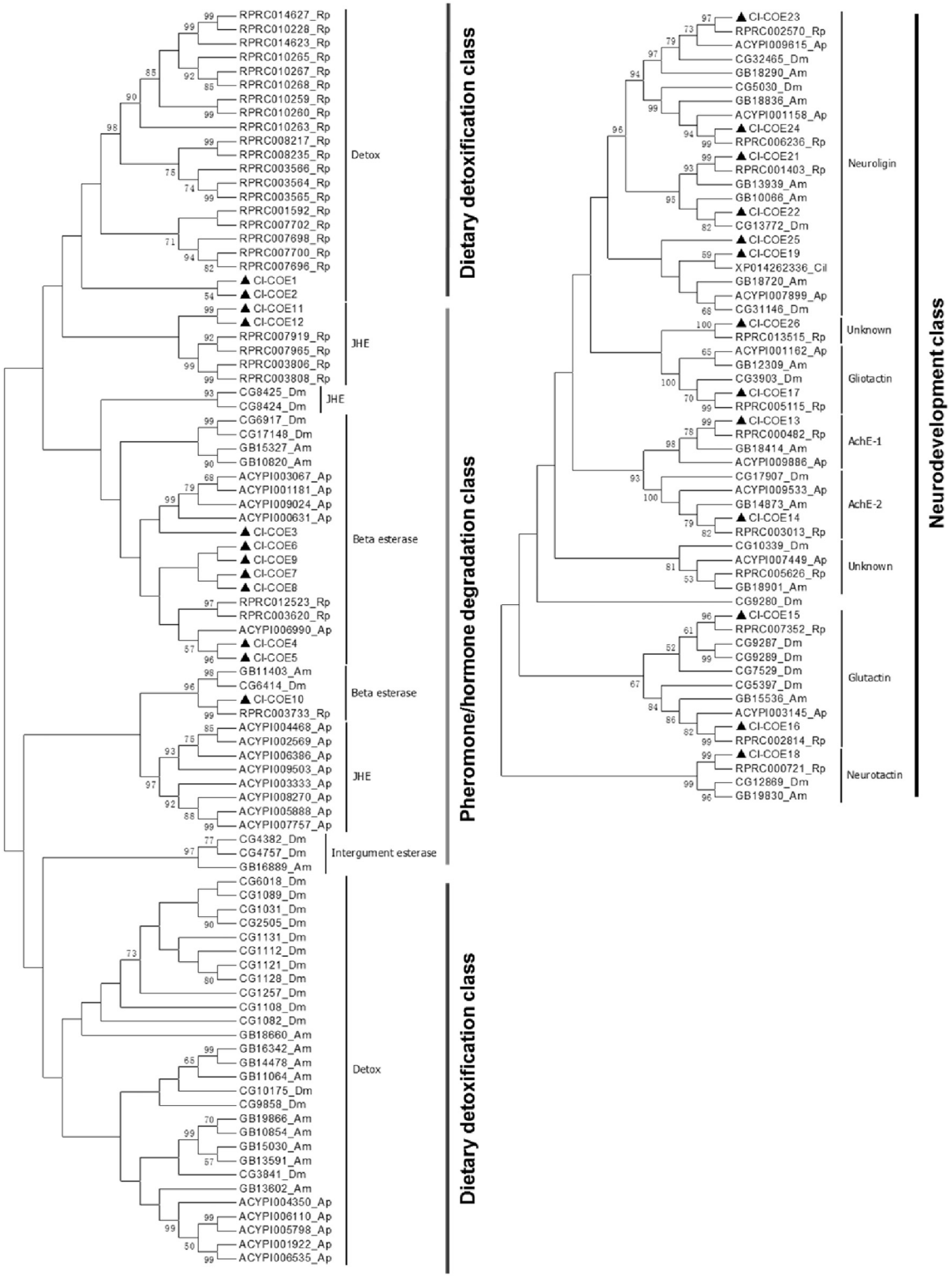

Fig. 3. Neighbor-joining phylogenetic tree of *C. lividipennis* COEs. Numbers above the branches indicate phylogenies from amino acid sequences and only values above 50% are shown. Cl: *C. lividipennis*; Dm: *Drosophila melanogaster*; Am: *Apis mellifera*; Ap: *Acyrthosiphon pisum*; Rp: *Rhodnius prolixus*; Nl: *N. lugens*; Cil: *Cimex lectularius*.

insects and is the target of organophosphorus and carbamate insecticides. Several studies showed that the mutation of insect AChE-1 gene (*ace1*) was responsible for insecticide resistance (Jiang et al., 2009; Khajehali et al., 2010; Liebman et al., 2015; Nabeshima et al., 2003; Wu et al., 2015). As usual for most insects, two AChE genes were found in *C. lividipennis* (AchE-1: Cl-COE13, AchE-2: Cl-COE14). On the phylogenetic tree, AchE clade can be obviously divided into AchE-1 and AchE-2 subclades (Fig. 3). Both AchEs have a complete catalytic triad (GESAG-E-H) (Table S4).

The non-catalytic members of the neurodevelopmental COE class include gliotactin, neuroligin and neurotactin, which are noncatalytic but have a variety of functions essential to development and neurogenesis (Oakeshott et al., 2005). In *C. lividipennis*, 7 genes were identified as putative neuroligins. In the phylogenetic tree, six genes (Cl-COE19, Cl-

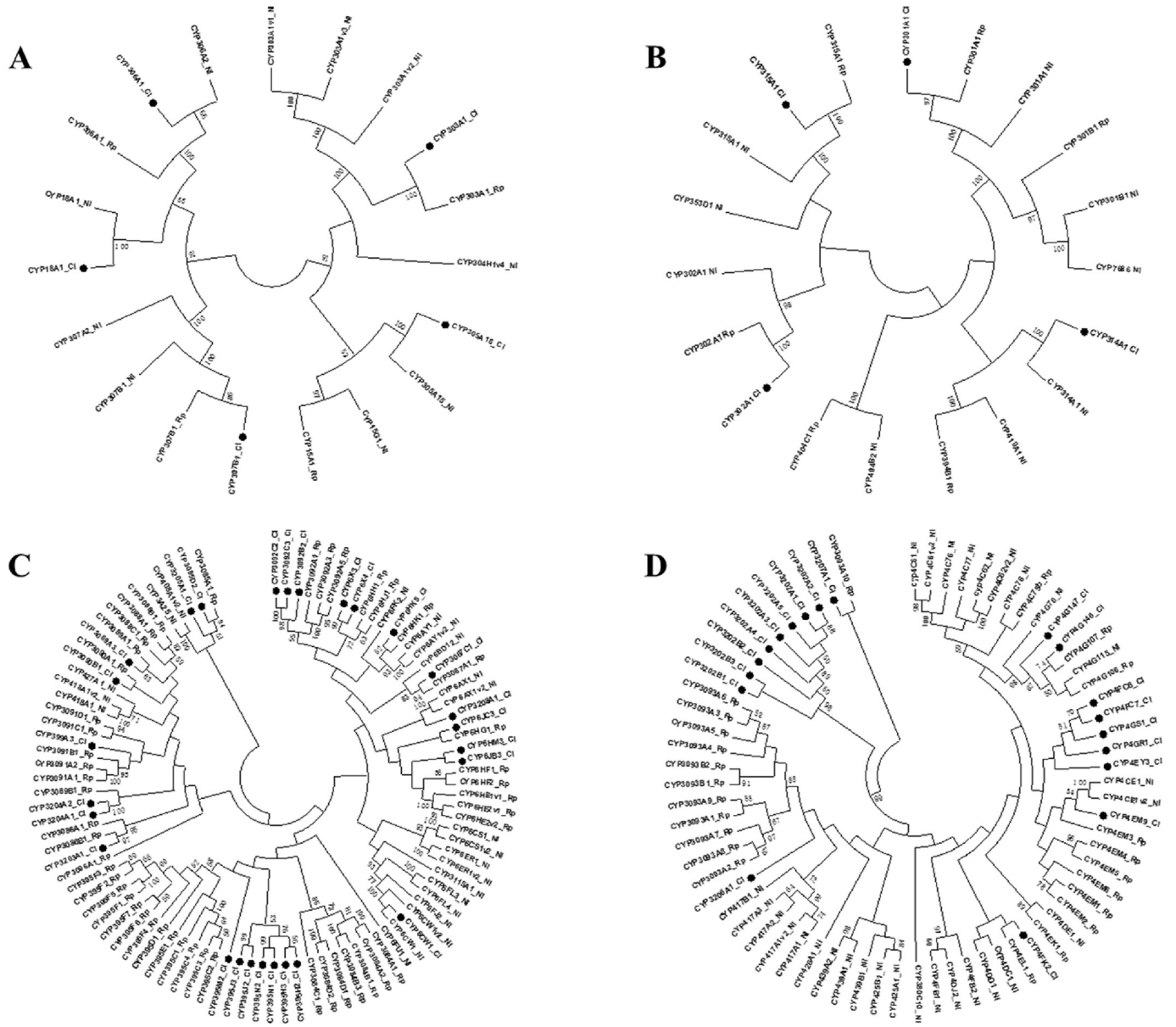

Fig. 4. Neighbor-joining phylogenetic trees of the four cytochrome P450 clans. A) CYP2, B) mitochondrial, C) CYP3, and D) CYP4. The trees were created with cut-off value of 50%. Cl: *C. lividipennis*; Rp: *R. prolixus*; Nl: *N. lugens*.

COE21–25) located in the neuroligin clade (Clade L) (Table S4, Fig. 3). One transcript (Cl-COE20) has a sequence (211 amine acids) that is too short to be included in the phylogenetic tree, though annotated to neuroligin-1 in *Tribolium castaneum* (XP_008194212.1). Moreover, two glutactin genes (Clade H) were found in *C. lividipennis* (Cl-COE15 and Cl-COE16), while one gene was found in *C. lividipennis* for neurotactin (Clade M) (Cl-COE18) and one for gliotactin (Clade K) (Cl-COE17) (Table S4, Fig. 3). Another unknown *C. lividipennis* gene (Cl-COE26), was found belonging to a sister clade to the neurotactin clade, which similar to one *R. prolixus* gene (RPRC013515), with the identity percentage of 59% when calculated after cutting the gap.

(2) Cytochrome P450 monooxygenase (P450)

P450s have functions in xenobiotic metabolism and detoxification (Li et al., 2006). A special nomenclature was established for cytochrome P450 (CYP) genes, one of the largest superfamilies in nature (Nelson, 1998). The insect P450 superfamily includes four clans: CYP2, CYP3, CYP4 and the mitochondrial CYP clan (Feyereisen, 2011). Based on the *C. lividipennis* transcriptome, 158 transcripts were annotated as P450 genes (Table S3). After removing redundancy, 57 unique putative P450 genes or gene fragments were found. The genes were further classified into 25 families and 43 subfamilies (Table S5). Seven new families were found, including 4 belonging to the CYP3 clan (CYP3203, CYP3204, CYP3205, and CYP3208), and 3 belonging to the CYP4 clan (CYP3202, CYP3206, and CYP3207).

The *C. lividipennis* CYP2 clan contains five members, each belonging to CYP18, CYP303, CYP305, CYP306, and CYP307 families (Fig. 4A). The *C. lividipennis* CYP3 clade (27 genes) is the largest clade, including 7 CYP6, 7 CYP395, one CYP399, one CYP3085, one CYP3087, one CYP3089, one CYP3090, three CYP3092B2, and 5 members of the new families described above (CYP3203, CYP3204, CYP3205, and CYP3208) (Fig. 4C). The *C. lividipennis* CYP4 clan contains 21 members, including 11 belonging to the CYP4 family and 10 from new families (CYP3202, CYP3206, and CYP3207) (Fig. 4D). Eight CYP3202 were located in one clade, clustering together with the new family (CYP3093) in *R. prolixus*, showing a similar gene expansion ("bloom") (Schama et al., 2016). The *C. lividipennis* mitochondrial P450 family

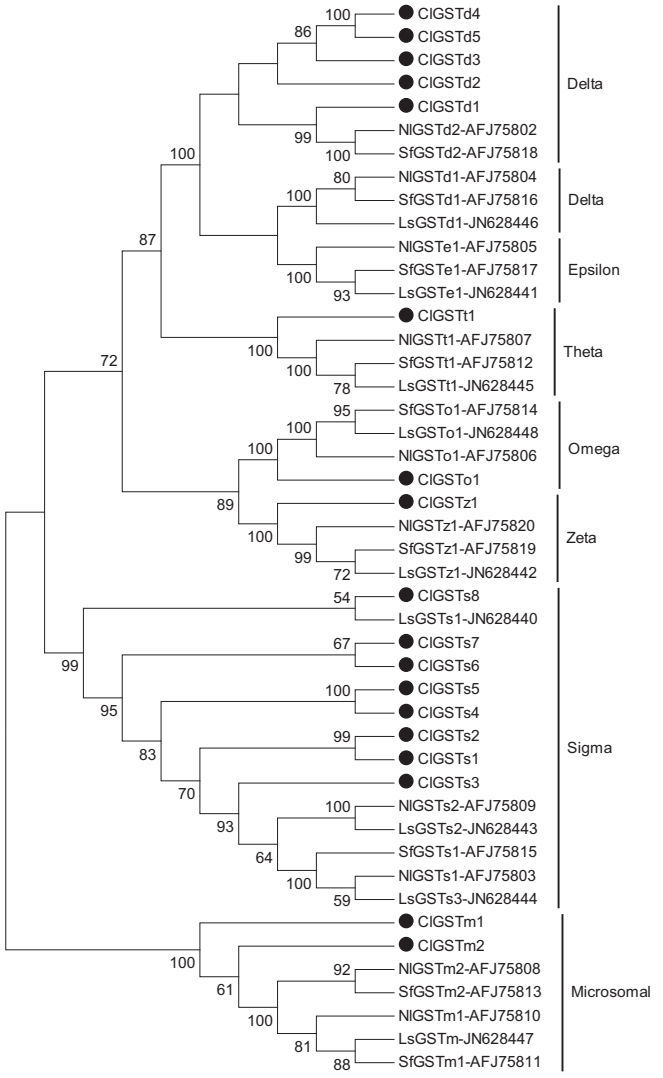

Fig. 5. Neighbor-joining phylogenetic tree of *C. lividipennis* GSTs. Numbers above the branches indicate phylogenies from amino acid sequences and only values above 50% are shown. Cl: *C. lividipennis*; Nl: *N. lugens*; Sf: *S. furcifera*; Ls: *L. striatellus*.

includes CYP301A1, CYP302A1, CYP314A1, and CYP315A1 (Fig. 4B).

(3) Glutathione S-transferase (GST)

GST, one superfamily of multifunctional detoxification enzymes, has many specific genes involved with insecticide resistance (Enayati et al., 2005; Li et al., 2006). Insect GSTs can be grouped into seven classes named delta, epsilon, omega, sigma, theta, zeta, and microsomal (Friedman, 2011). In *C. lividipennis*, 24 transcripts were annotated as GST genes, and after removing redundancy, 18 unique putative GST genes or gene fragments were found (Table S3). A neighbor-joining phylogenetic analysis of GSTs in *C. lividipennis* and three rice planthoppers (reported by Zhou et al. (2012) and Zhou et al. (2013)), showed that *C. lividipennis* GSTs belong to six classes: delta (5/19), omega (1/19), sigma (8/19), theta (1/19), zeta (1/19), and microsomal (2/19) (Table 1; Fig. 5). No epsilon GST gene was found from *C. lividipennis*.

(4) Nicotinic acetylcholine receptor (nAChR)

nAChRs are ligand-gated ion channels in insect nervous systems that mediate fast cholinergic synaptic transmission, and are targets of the neonicotinoid insecticides (Kjones and Bsattelle, 2010). In studies of insect nAChRs, no > 16 nAChR subunits were found in insects (Dermauw et al., 2012; Jones et al., 2010; Jones and Sattelle, 2007; Shao et al., 2007). In the *C. lividipennis* transcriptome, 20 transcripts were annotated as nAChR genes (Table S3). After removing redundancy, 15 nAChR unigenes were identified, including 9 alpha subunits (α1, α2, α3, α4, α5, α6, α7, α8 and α9) and three beta subunits (β1, β2 and β3) (Fig. S1). Two variants were found for α8 subunit, Clα8-v1 and Clα8-v2. Another sequence of *C. lividipennis* nAChR α8 subunit was found from the NCBI database (AIG92772.1) (Guo et al., 2015), with 90% and 91% similarity to Clα8-v1 and Clα8-v2 in the present study. Another two transcripts (comp253701_c0_seq1 and comp20079_c0_seq1), were not shown in the tree due to their short sequences, were also annotated as nAChR subunits (α6 or α7), by BLAST searching with the nAChR subunits of other insects.

(5) Ionotropic γ-aminobutyric acid receptor (GABA)

Insect GABA receptor is a ligand-gated chloride channel and an important target for insecticides including fipronil and cyclodienes (Zheng et al., 2003). Insect GABA receptors have three subunits: Rdl (resistance to dieldrin), Lcch3 (ligand-gated chloride channel homolog 3), and Grd (GABA and glycine-like receptor of *Drosophila*) (Buckingham et al., 2005). In the *C. lividipennis* transcriptome, only each of three GABA subunits was identified using phylogenetic analysis

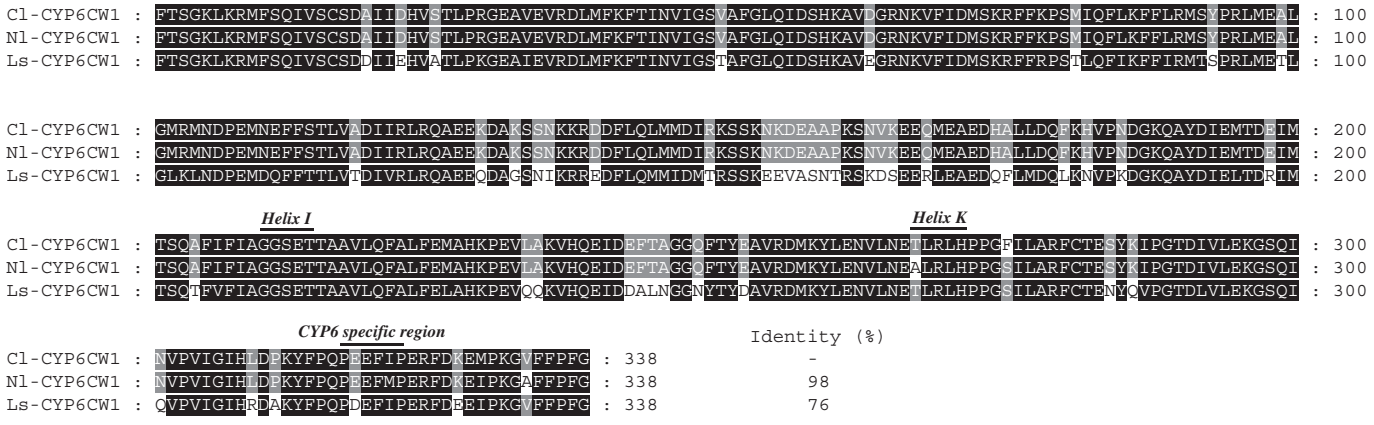

Fig. 6. An alignment of the predicted amino acid sequence of Cl-CYP6CW1 with CYP6CW1 of rice planthoppers, after cut the gap of two terminates. Nl-CYP6CW1 (*N. lugens*, CAZ65617); Ls-CYP6CW1 (*L. striatella*, AGN52753). Shading indicates identity across all four sequences (Back shading: 100%; Grey shading: 80%).

(Fig. S2). Two partial transcripts of Grd subunit (ClGrd-p1–p2) were found.

(6) Glutamate-gated chloride channel (GluCl)

GluCl is a member of the cysteine loop superfamily of ligand-gated ion channel. The insecticides acting on GluCls are avermectin, ivermectin, fipronil, *etc*. As with *D. melanogaster*, *A. mellifera* and *T. castaneum* (Jones and Sattelle, 2007), *C. lividipennis* has one GluCl (ClGluCl) (Fig. S2). Besides for nAChR and GluCl, other cys-loop LGIC channels were also found in *C. lividipennis*, such as one histamine-gated chloride channel (ClHisCl), three transcripts of one pH-sensitive chloride channel gene (ClpHCl-v1–v3) and two transcripts clustered in the Insect Group 1 of cysLGIC subunits group (ClClgc-v1–v2) (Fig. S2).

Comparison between C. lividipennis and rice planthoppers

COE

Searching the NCBI database, three *N. lugens* COE genes, three *S. furcifera* COE genes and 31 COE genes of *L. striatella* were found. A comparison of sequence identities between 26 *C. lividipennis* COEs and 37 COEs of rice planthoppers indicates most family members were highly diverse (Table S6). Only for AChEs, identities of > 50% were found between *C. lividipennis* and rice planthoppers, the identities of 53–58% were found between Cl-AChE1 and AChE1 of rice planthoppers (Fig. S3), and 62–63% identities were found between Cl-AChE2 and AChE2 of rice planthoppers (Fig. S4). Whether two AChE genes from *C. lividipennis* exhibited different or similar sensitivities to insecticides need be further determined.

P450

An alignment of 57 *C. lividipennis* P450 sequences and 70 *N. lugens* P450 sequences (Lao et al., 2015), revealed that only a few of members share > 50% identity (CYP301A1: 62%; CYP303A1: 61%; CYP314A1: 56%; CYP6CW1: 62%, *etc*.) (Table S7). For example, after being cut the gap of two terminate sequences, Cl-CYP6CW1 shares 98% identity to Nl-CYP6CW1, and has 76% identity with *L. striatellus* CYP6CW1 (Fig. 6). Ls-CYP6CW1 was highly overexpressed in the resistance strain of *L. striatellus* to buprofezin (Zhang et al., 2012). However, two important resistant genes to imidacloprid in *N. lugens*, CYP6AY1 and CYP6ER1 (Bao et al., 2016; Bass et al., 2011), were not found in *C. lividipennis* transcriptome in the present study.

GST

An alignment between 18 *C. lividipennis* GST sequences and 11 *N. lugens* GSTs, 9 *S. furcifera* GSTs (Zhou et al., 2013), and 9 *L. striatellus* GSTs (Zhou et al., 2012), revealed that several GST members share > 50% identities between *C. lividipennis* and rice planthoppers (Table S8). Among all GSTs, the highest level of identities (89–90%) were also found among members of the zeta subclass (ClGSTz1, NlGSTz1, LsGSTz1 and SfGSTz1) (Table S8).

NAChR

Eight nAChR subunits of *N. lugens* were found from the NCBI database. After aligning nAChR subunit sequences of *C. lividipennis* and *N. lugens*, it was found that only 4 of 8 proteins of *N. lugens* nAChR subunits have > 50% identities to *C. lividipennis* nAChR subunits (Table S9). The highest identity (90%) was found between *C. lividipennis* β1 and *N. lugens* β1 (ACJ07013, reported by Yao et al. (2009)), high identity (77%) for Clα8 and Nlα8 (ACK75719), 63% for Clα1 and Nlα1 (AAQ75737), and 52% for Clα7 and Nlα6 (ACL14949). It was reported that key amino acid differences between Clα8 and Nlα8 might cause neonicotinoid insecticides having much more toxic to *C. lividipennis* than to *N. lugens* (Guo et al., 2015).

Rdl

Searching from NCBI, each Rdl subunit of three rice planthoppers was found, and another two *C. lividipennis* Rdl subunit transcript variants were also found (AHW29555 and AHW29556). *C. lividipennis* Rdl found in the present study is highly identical (98%) with Cl-RDL-In (AHW29556) reported by Jiang et al. (2015). After aligning with rice planthoppers, high identities (88%) were also found between *C. lividipennis* Rdl and *N. lugens* Rdl or *S. furcifera* Rdl (Fig. S5). It was found that among four transmembrane regions (TM1–4), two regions (TM1 and TM3) were 100% identical among RDLs from *C. lividipennis* and three rice planthoppers. In TM2 or TM4, there was only one amino acid difference among RDLs for *C. lividipennis* and three rice planthoppers. The difference amino acid in TM2 is just one of the mutation sites (A2′N) in SF-Rdl, which was suggested to be a heterozygous mutation that conferred fipronil resistance to *S. furcifera* (Nakao et al., 2012; Nakao et al., 2010).

GluCl

After searching NCBI, two *L. striatellus* GluCl subunit transcript variants (AFI09244 and AEE39458) were found, which share high identities (83–84%) to *C. lividipennis* GluCl (Fig. S6).

Conclusions

The transcriptome provided significant genetic information on the natural enemy, *C. lividipennis*. Genes related to insecticide action and detoxification were manually identified, including 26 COEs (containing 2 AChEs), 57 P450s, 18 GSTs, 15 nAChRs, 3 GABA receptors, and 1 GluCl. The differences in these genes between *C. lividipennis* and rice planthoppers were analyzed, which provide useful information for our understanding of insecticide selectivity between targeted insect pests and this natural enemy.

This natural enemy and its preys have similar feeding behavior, by piercing and sucking juices from insects or plants. Therefore, it seems that it is difficult to develop highly selective insecticides against rice planthoppers with safety to *C. lividipennis*. However, this study showed that much diversity was found among genes related to insecticide action and detoxification, though a few genes share much higher identities between this predator and prey, which showed consistency with the bioassay results or field efficacies that *C. lividipennis* was more sensitive or insensitive to some insecticides than rice planthoppers (Jiang et al., 2015; Preetha et al., 2010; Tanaka et al., 2000; Yang et al., 2012). Of course, the roles of these target genes and detoxifying enzymes in insecticide selectivity and resistance require further research in the future.

Acknowledgements

We acknowledge Dr. Taiyu Chen for transcriptomic sequencing at Nation Key Laboratory of Crop Genetic Improvement, Nation Center of Plant Gene Research (WuHan, China), and Ye Tao and Liang Zeng for transcriptomic analysis at Shanghai BIOZERON Biotechnology Co., Ltd. The study was sponsored by Special Fund for Agro-scientific Research in the Public Interest of China (201403030).

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.aspen.2017.04.010.

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