ABSTRACT

ADEDIPE, FOLUKEMI EBUNOLUWA. Use of Transcriptome Sequencing and RNA Interference for Target-site Screening in Two Agricultural Pests: Western Corn Rootworm and Kudzu Bug. (Under the direction of Dr. Marcé Lorenzen).

The western corn rootworm, *Diabrotica virgifera virgifera*, and the kudzu bug, *Megacopta cribraria* are both agricultural pests in the United States. Currently, control of these species is achieved through the use of genetically engineered (GE) crops and foliar and in-furrow insecticides. However, an increase in public concern about the safety of insecticides, along with the evolution of resistance to insecticides and to GE crops, has resulted in a need to find alternative control methods. In this dissertation I report on the use of transcriptome sequencing and RNA interference (RNAi) for target-site screening in these two agricultural pests. In my study, I assembled Illumina sequencing reads to create combined transcriptome assemblies for each species, and then generated searchable databases for each. I then surveyed the respective databases for potential target genes and tested these via RNAi to assess loss-of-function phenotypes. These data represent a valuable resource that will aid future research on functional genomics in these economically-important species and could provide insight for new pest management methods.

Use of Transcriptome Sequencing and RNA Interference for Target-site Screening in Two Agricultural Pests; Western Corn Rootworm, and Kudzu Bug

by
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BIOGRAPHY

I have many memories of farmers while I was in high school, which have served as the motivation that drives my career goals today. Growing up in Nigeria, I saw how farmers labored and suffered, only to get little income from their produce, due to poor farming methods, a lack of proper storage facilities, and the lack of appropriate pest control. Because farmers do not have suitable storage and pest control methods, they need to sell produce quickly at low prices during the harvest season, only to suffer from a lack of food and income during the dry season.

I have long desired to help farmers increase productivity within a system that is environmentally friendly and sustainable. I knew that achieving this goal would require skills and knowledge I lacked; so, I undertook undergraduate studies in Post-Harvest (Storage) Technology from Federal University of Technology in Akure, Nigeria, and graduate studies (Master's degree) in Integrated Pest Management from West Virginia University (WVU). However, I realized that to accomplish my goals, I needed further education, which is why I came to NC State in Fall 2013 to pursue a Ph.D. in Molecular Entomology under the supervision of Dr. Marcé Lorenzen.

My research focuses on finding alternatives to traditional pesticides. I have been using a combination of transcriptomics and RNA interference, a highly-effective species-specific gene-silencing mechanism, to gain insight into gene function in the western corn rootworm and the kudzu bug. I hope that my research will help establish new target sites for insect control. In my free time, I enjoy cooking for my family and watching movies.

ACKNOWLEDGEMENTS

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I have always valued the contribution of my parents. They made enormous sacrifices to give me the best education and have always given me their unconditional love and support. My deepest thanks go to my husband Dr. Oluwatosin Adedipe and my children Iseoluwa, Ewaoluwa, and Oluwadarasimi, who have always had faith in me, loved me, and who have supported me throughout my years of study. They have made huge sacrifices by allowing me to pursue my

dream and study full-time, for that, and for everything else, I will always be grateful. I dedicate this work to them.

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CHAPTER 1

Introduction and Literature Review of Western Corn Rootworm, *Diabrotica virgifera virgifera*, and Kudzu Bug, *Megacopta cribraria*

Pest status of western corn rootworm

The western corn rootworm, *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae), is one of the most economically important agricultural pests in the United States (US). These beetles reproduce in corn (*Zea mays* L.), the most widely-planted field crop in the US, generating about $46 billion dollars annually (USDA-ERS 2018), with overall losses due to rootworm damage and control that are estimated around $1 billion per year in the US alone (Gray et al., 2009). *D. virgifera virgifera* are reported to have originated in Guatemala, Central America (Melhus et al., 1954) where they have been a problem for over 5,000 years (Melhus et al., 1954; Gray et al., 2009). The first report of *D. virgifera virgifera* as a pest of corn in the US was in 1940 (Wangila et al., 2015). However, their appearance was first reported in Kansas, USA in 1868 (Chiang 1973), and they are currently found in all corn-growing states throughout the US (Krysan and Miller 1986). They are highly successful at invading new corn-growing regions and are currently spreading through Europe (Baufeld and Enzian 2001), having already invaded at least 22 European countries (EPPO 2011; Lemic et al., 2015).

D. virgifera virgifera are problematic because the larvae feed on corn roots, subsequently reducing the plant’s ability to take up water and nutrients (Hou et al., 1997; Riedell 1999; Riedell 1993; Dunn and Frommelt 1998). This can directly lower yields and, depending on the level of root damage, can cause plants to fall over (lodge) in strong winds or heavy rain, which results in mechanical harvest losses. Although adult feeding mainly occurs on corn silks and is generally considered to cause only minor damage to the grain, the bigger problem is that adults can potentially transmit and spread maize chlorotic mottle virus (Jensen 1985) and corn stalk rot fungi (Gilbertson et al., 1986). Despite the fact that more insecticides are used in the US to manage *Diabrotica spp* than any other single pest (EPA 2005), their biology, ecology and behavior have been largely understudied. This is in large part due to the complexities associated with rearing and studying these soil dwelling insects for which no long-term artificial diet exists.

Rootworm Biology

D. virgifera virgifera are univoltine and overwinter as eggs in the soil, with the eggs typically hatching in late spring (Pruess et al. 1968; Gray et al. 2009). Depending on temperature they generally complete the rest of their life cycle within 4-6 weeks in the field (Jackson and Elliot 1988, Woodson and Jackson 1996). The larvae are the most economically damaging stage (Branson and Krysan 1981; Oyediran et al. 2004) with first-instar larvae feeding on root hairs (Chiang 1973), and second- and third-instar larvae tunneling into the vascular cylinder of the root. These feeding activities can result in pruned root systems (Figure 1), which in turn reduces the host plant’s ability to obtain nutrients from the soil which reduces yields and increases the odds of plant lodging (Branson and Krysan 1981; Riedell 1993). Pupation occurs in the soil with males emerging several days earlier than females (Jackson and Elliott 1988). Thirteen days after females enclose, they become sexually mature and start to lay eggs, and can continue to lay eggs for a couple of months (Branson and Johnson 1973; Hill 1975). Studies have shown that female *D. virgifera virgifera* live longer than males (Ball and Hill 1952; Branson and Johnson 1973, Hill 1975), and that in the laboratory their mean fecundity is about 1000 eggs (Hill 1975), depending on the available nutrition. Adults mainly feed on the vegetative and reproductive tissues and appear to mate in the field they emerge from (Nowatzki et al. 2002). However, when food becomes scarce, adults will move to nearby corn fields (Ball and Hill 1952; Levine and Oloumi-Sadeghi 1996).

Rootworm Management

Sampling and monitoring: There are several methods by which the number of *Diabrotica spp* eggs, larvae and adults can be estimated. For eggs, the most common method is soil sampling. Eggs are extracted from the soil sample by washing, sieving, and floating the eggs (Chandler et al., 1966). Larval sampling is generally carried out through plant-area soil sampling, using soil cubes and soil cores (Fisher and Bergman 1986). Techniques for separating larvae from the soil or plant roots is similar to that of eggs because the process also uses water to float the larvae by first mixing the soil or roots with water (Fisher and Bergman 1986) and gathering them using a Berlese-type funnel (Fromm et al., 1998). However, sampling soil for eggs and larvae is extremely labor intensive and to date no meaningful egg and larval thresholds have been set. Sampling for pupae is also difficult because they are inconspicuous in earthen cells, they are very fragile, and the pupal stage is relatively short (Chiang 1973). Therefore, the most frequently used monitoring method is based on the number of adults present. This can be done by counting how many adult beetles are on representative corn plants, caught on yellow sticky traps (Hein and Tollefson 1985a, Kuhar and Youngman 1998), or captured in emergence traps (Hein and Tollefson 1985b).

Synthetic insecticidal control: Insecticides such as cyclodienes (Ball and Weekman 1962), organophosphates (Meinke et al., 1998), and carbamates (Meinke et al., 1998), are recommended for *D. virgifera virgifera* control (Gassmann and Weber 2012). These chemicals can be applied to the soil at planting to prevent larvae from feeding on corn roots or can be applied aerially to reduce the adult population before oviposition takes place (Meinke et al., 1998). However, *D. virgifera virgifera* have evolved resistance to many of these chemicals. For example, Ball and Weekman (1962) documented resistance to cyclodiene in *D. virgifera virgifera* larvae as far back as 1959. Interestingly, this resistance persisted, even years later after the insecticides were no longer in use (Parimi et al., 2006; Meinke et al., 1998). The genetic basis of resistance to cyclodienes such as aldrin, is most likely a mutation in a subunit of the gamma-aminobutyric acid receptor (Wang et al., 2013).

Crop rotation and resistance: To lessen selective pressure on resistance genes in *D. virgifera virgifera* populations, alternative management strategies such as crop rotation were implemented. Since 1912, farmers have found that rotating corn with soybeans is an effective method of *D. virgifera virgifera* control. When overwintering eggs hatch in soybeans fields, neonates die of starvation unless they are able to locate a suitable host shortly after hatching (Gillette, 1912). Surprisingly, *D. virgifera virgifera* have developed resistance to crop rotation, an unusual trait that was documented in East-central Illinois as early as 1987 (Levine et al., 2002; Knolhoff et al., 2006). This is one of the reasons that *D. virgifera virgifera* are thought to be highly adaptive, allowing them to overcome different pest-control methods through a variety of resistance mechanisms more rapidly than other pest species.

Bt corn and resistance: *Bacillus thuringiensis (Bt)* Berliner is a gram positive, soil dwelling bacterium which produces spores that contain crystal (cry) proteins. These cry proteins are toxic to some insect species and have been used as bioinsecticides since the late 1950s, but, their high cost and variable efficacy once limited their use to a small niche market (Cannon 1993). However, everything changed when genetically engineered (GE) corn (aka *Bt* corn) expressing one or more cry proteins was approved (EPA, 2003). Importantly, due to their specificity, each cry protein (aka *Bt* toxin) only affects a few target species. For example, Cry3Bb1, mCry3A and Cry34/35Ab1 are only effective for control of coleopterans such as *D. virgifera virgifera*, but not lepidopterans. Studies have shown that adoption of *Bt* corn has significantly reduced crop damage, and increased yields (Tabashnik et al., 2008).

Originally many thought that as long as *Bt* corn produced a high enough dose of Bt toxin to kill most of the rootworms that feed on it, resistance would never develop (James, 2009). However, this is not the case, some populations have developed resistance to one, or more *Bt* toxins. For example, field populations of *D. virgifera virgifera* resistant to Cry3Bb1 and mCry3A have been discovered in Iowa (Gassmann et al 2011; Monsanto 2011). This might be due to the continual usage of Bt corn, causing a high selective pressure (Tabashnik et al., 2008), and moreso, low levels of *Bt* expression can also cause a similar effect (Diverly et al., 2016; Tabashnik et al. 2013). To slow resistance development to *Bt*, a refuge strategy has been implemented (Gould, 1998). This method involves growing some non-*Bt* corn in, or near the field having Bt corn to enable survival of non-resistant (aka susceptible) beetles. Since only a few resistant individuals are expected to emerge from a *Bt* field, the refuge helps maintain a high percentage of susceptible alleles in the population, thus delaying widespread resistance (Gould, 1998). Yet, the basic biological question of what makes them so adaptive remains unanswered. To date, *Bt* corn and crop rotation are the major control methods for this pest; however, new methods are being developed.

One promising new pest control method is based on RNA interference (RNAi), a naturally occurring phenomena that can silence genes. RNAi was first used in the laboratory for understanding gene function, but was quickly coopted as a potential means of crop protection (Baum et al., 2007). Since RNAi has been shown to work exceptionally well in *D. virgifera virgifera* (Baum et al., 2007; Alves et al., 2010), I wanted to look at the impact of RNAi on other target genes. However, a major requirement for RNAi is prior knowledge of each target gene's sequence. Since the sequence of the *D. virgifera virgifera* genome is not yet publically available I utilized Next Generation Sequencing (NGS) technology to obtain transcriptomic data for several *D. virgifera virgifera* life stages. The data were then surveyed for members of the ABC superfamily of genes and a subset of these were tested via RNAi.

Pest Status of Kudzu Bug

The kudzu bug, *Megacopta cribraria*, (Hemiptera: Plataspidae), a native of Asia and Australia, was first discovered in northern Georgia during the fall of 2009, and until that time *M. cribraria* had not been seen in the United States (Suiter et al., 2010). However, since then they have been reported in thirteen additional states: Alabama, Arkansas, Delaware, Florida, Georgia, Kentucky, Louisiana, Maryland, Mississippi, North Carolina, South Carolina, Tennessee, Virginia, and the District of Columbia (Figure 2), (www.kudzubug.org 2015; Gardner et al., 2013). Their rapid spread has been attributed to being strong fliers (Suiter et al., 2010).

While not a major pest in its home range, *M. cribraria* is a pest of soybeans (*Glycine max* L. Merrill); the second most planted field crop in the US, generating about $42 billion dollars annually (USDA-ERS 2018). The primary host plants that support *M. cribraria* reproduction and nymphal development are the invasive kudzu plant, *Puereria montana* (Loureiro) Merrill variety *lobata* (Willdenow), and soybean (Suiter et al. 2010, Zhang et al. 2012). There has been speculation that *M. cribraria* was deliberately brought to the US to control the kudzu plant, and *M. cribraria* has been shown to reduce kudzu biomass by as much as 33% (Zhang et al., 2012); however, there is no evidence that they can be used as a biocontrol to reduce the distribution of this invasive weed in the United States. In fact, the presence of vast acres of kudzu in US has helped the *M. cribraria* population to grow and expand (Blaustein 2001). Moreover, (Blount et al., 2015) described *M. cribraria* as a potential pest of several agronomically important legume crops, including soybean. *M. cribraria* have indeed been shown to be a serious pest in soybeans, with densities up to 50 or more adults per plant (Suiter et al., 2010), and if untreated, infestations could potentially devastate soybean production, causing yield losses as high as 60% (Seiter et al., 2013). The sustainability of this crop is not only of economic importance but is also vital to overall food security (USDA-ERS 2016).

Apart from being an agricultural pest, *M. cribraria* is also a nuisance pest. The problem stems from *M. cribraria* forming overwintering aggregations both in and around homes (Suiter et al., 2010). In the fall, they congregate on outside walls, where they defecate, leaving brown spots and are an annoyance to residents (Dhammi et al., 2016; Eger et al., 2010). Similar to stink bugs, when disturbed *M. cribraria* produces a defensive chemical which can be harmful to skin and eyes (Ruberson et al., 2013).

Kudzu Bug Biology

M. cribraria undergo one to three generations per year in China and Japan (Dhammi et al., 2016; Eger et al., 2010). Similarly, in the US, Zhang et al. (2012) reported that in Georgia, *M. cribraria* undergo two and maybe a third generation on kudzu. The authors further reported a significant variation between years. The adults have been found overwintering in leaf litter and under tree bark near kudzu patches and soybean fields, as well as in and around urban structures (Lahiri et al., 2015; Halbert & Eger 2010). Adults are not active until temperatures warm in the spring (Zhang et al., 2012; Reisig et al., 2012), at which time they disperse to kudzu, where they come together, feed, mate and lay eggs (Zhang et al., 2012; Reisig et al., 2012). Adults will also converge on volunteer or early-planted soybeans when available (Del Pozo-Valdivia and Reisig

2013). While they usually complete their first generation on kudzu (Del Pozo-Valdivia and Reisig 2013, Seiter et al., 2013), the second generation can develop on either kudzu or soybeans (Zhang et al., 2012, Seiter et al., 2013a).

M. cribraria nymphs and adults feed by piercing the plant's epidermis and sucking sap from the phloem ((Tayutivutikul and Yano 1990, Thippeswamy and Rajagopal 2005, Suiter et al., 2010), these feeding activities deprive the host of water and nutrients required for growth (Stubbins et al., 2017), reducing the number of pods per plant and number of beans per pod (Seiter et al., 2013; Waldvogel and Alder, 2011). Since *M. cribraria* do not overwinter in soybean fields it is not surprising that they infest the field by first occupying the edges, and later move into the field (Seiter et al., 2013).

Although studies have reported *M. cribraria* on a variety of host plants from several legume crops such as pigeon pea (*Cajanus cajan* L.), black eye pea (*Vigna sinensis* L.), lima bean (*Phaseolus lunatas* L.), pinto bean (*Phaseolus vulgaris* L.) (Medal et al., 2013), wisteria (*Wisteria sinensis* Sims) (Ruberson et al., 2013), white sweet clover (*Melilotus alba* Medikus), white clover (*Trifolium repens* L.), red clover (*Trifolium pretense* L.), alfalfa (*Medicago sativa* L.), perennial peanut (*Arachis glabrata* Benth), and American joint vetch (*Aeschynomene Americana* L.) (Medal et al., 2016), Eger et al., (2010) indicated that many of these are likely incidental occurrences. Therefore, to date the primary host plants for *M. cribraria* reproduction and nymphal development in the US are thought to be the invasive kudzu plant, and soybeans (Suiter et al., 2010, Zhang et al., 2012).

Interestingly, *M. cribraria* deposits a bacterical capsule containing *Candidatus Ishikawaella capsulata* along with their eggs (Jenkins et al., 2010; Brown et al., 2014). Moreover, it has been shown that *M. cribraria* relies on these endosymbiotic bacteria for proper development (Fukatsu and Hosokawa 2002; Hosokawa et al., 2006). Specifically, nymphs reared in the absence of this bacterium were shown to develop slower, have smaller body sizes and have higher death rates (Jenkins et al., 2010; Brown et al., 2014). Research over the past several decades has demonstrated that many of the phenotypic properties displayed by insects are due to inputs they receive from their associated symbionts (Fukatsu and Hosokawa 2002; Hosokawa et al., 2006; Seiter et al., 2015).

Kudzu Bug Management

Chemical control: In the US, insecticides are used to control *M. cribraria* (Seiter et al., 2014; Brown et al., 2015), In China, 85% of the *M. cribraria* populations found in soybean fields are controlled with the use of pyrethroids such as cypermethrin, deltamethrin, sumicidin and organophosphate insecticides (Zhang et al., 2012). However, insecticidal sprays alone may not be sufficiently effective to stop yield loss in soybeans when *M. cribraria* population sizes are high. It is not surprising that research has shown that yield loss from *M. cribraria* feeding is directly linked to the number of nymphs and adults per plant (Seiter, et al., 2013). Therefore, the economic threshold for insecticide application in soybean fields has been set at five adults per plant, or a single nymph per sweep (Stubbins et al., 2015; Dhammi et al., 2016). Moreso, a recent study reported that applying insecticide immediately after detecting the presence of one nymph per sweep was enough to keep the population below the economic threshold (Seiter et al., 2015). However, there are drawbacks to insecticidal sprays, including potential hazards to humans and the environment. For example, increased use of insecticides could have a negative impact on pollinators and other beneficial insects (Vanbergen et al., 2013). Therefore, finding alternative methods for managing this agricultural pest are needed.

Biological control: Given the fact that *M. cribraria* is exotic to the US, there is very little information about what natural enemies may impact it in the US. Several biological control agents such as adult parasitoids have been identified that appear to reduce the populations of *M. cribraria*. Specifically, two egg parasitoids, *Paratelenomus saccharalis* (Dodd) (Hymenoptera: Platygastridae), and *Ooencyrtus nezarae* (Hymenoptera: Encyrtidae), have been shown to be effective in parasitizing *M. cribraria* eggs in the US (Ruberson et al., 2013; Ademokoya et al., 2017). For example, study showed up to 40% parasitism in *M. cribraria* adults, eggs and in Soybean (Knight et al., 2017). Some even speculate that these parasitoids may have contributed to the sudden decrease in *M. cribraria* populations over the past few years (Ademokoya et al., 2017). Interestingly, many other insect species have been found to feed on *M. cribraria* including, the big-eyed bugs (*Geocoris punctipes*), the insidious flower bug (*Orius insidiosus*), the spined soldier bug (*Podisus maculientris*), the lady beetle (*Hippodamia convergens*), the assassin bug (*Zelus renardii*), the striped lynx spider (*Oxyopes salticus*) and the green lynx spider (*Peucetia viridians*) (Greenstone et al., 2014). Other natural enemies include the entomopathogenic fungus, *Beauveria bassiana* (Hypocreales: Clavicipitaceae), and two native dipteran species *Strongygaster triangulifera* and *Phasia robertsonii* (Golec et al., 2013, Ruberson et al., 2012). The fungus has been reported to infect both *M. cribraria* nymphs and adults (Golec et al., 2013, Ruberson et al., 2012); while the dipteran species have only been reported to parasitized *M. cribraria* adults. However, despite the current reduction in *M. cribraria* population size and the availability of both chemical and biological control methods, it is wise to investigate alternate control strategies since resistance is inevitable.

The ability of insects to evolve resistance to insecticides, including *Bt*, demonstrates a continuing need to understand pest biology, not only on the organismal level, but also at the molecular level.

My research focuses on the use of RNAi, a sequence-specific technique, (Fire et al., 1998) used for assessing gene function in arthropods due to its power, speed, and relative ease of use to knock-down transcript levels of essential genes in *M. cribraria*. Results from these studies are expected to provide insights into the role of potential target genes in *M. cribraria* and may help establish new target sites for insect control.

The objectives of my Ph.D. research were to obtain genetic (transcriptomic) data for *D. virgifera virgifera* and *M. cribraria*, establish custom databases, and survey these for target genes which I then characterized via RNAi to determine their potential for use in new control methods. This dissertation is composed of two manuscripts, chapters 3 and 4, each is written in the format of the journal to which it will be submitted.

Figure 1: Corn root damaged by the western corn rootworm, *Diabrotica virgifera virgifera.* The primary damage done by *Dvv* feeding on corn roots reduces corn plants structural support and makes it more susceptible to lodging. Undamaged corn roots (left) and damaged corn roots (right). Figure adapted from Jim Kalisch, University of Nebraska-Lincoln.

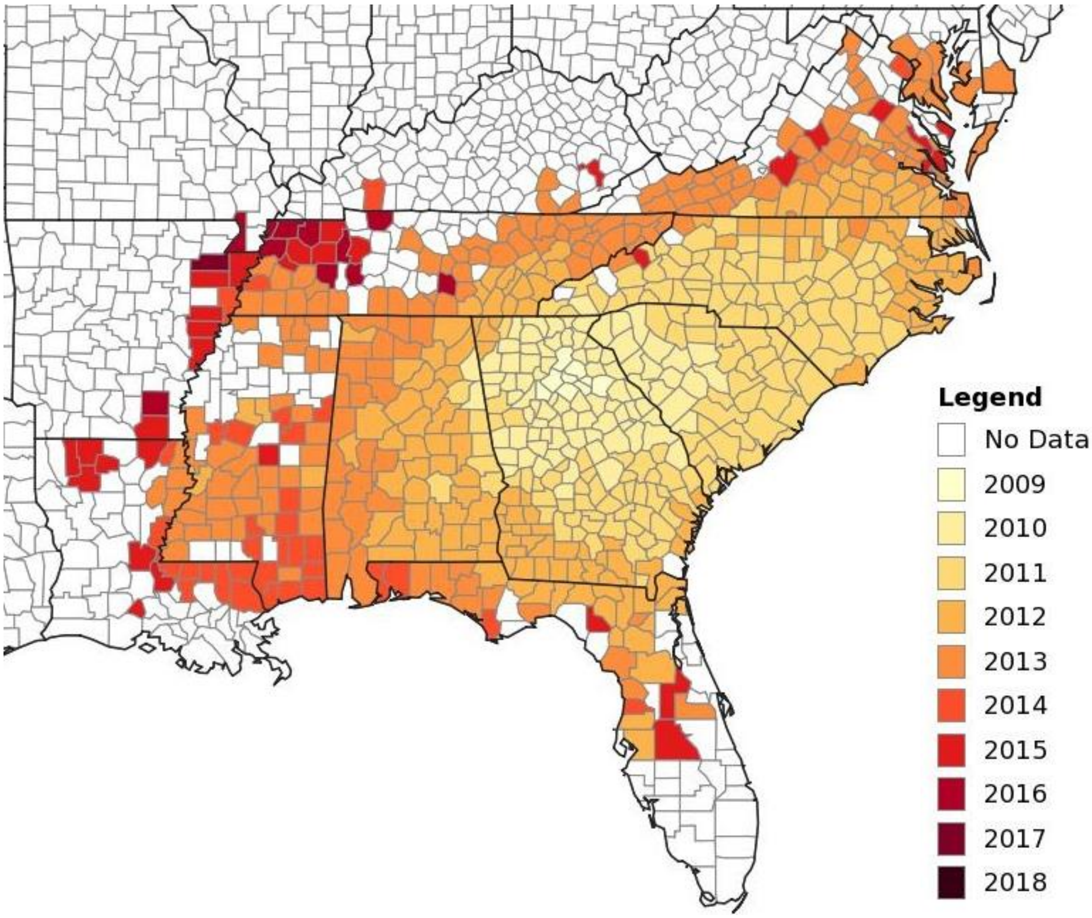

Figure 2: Distribution of the kudzu bug, *Megacopta cribraria* in the southeast U.S from 2009-2018. Map is adapted from University of Georgia (available at https://www.kudzubug.org/distribution-map/)

Figure 3: **Soybean stems damaged by *M. cribraria***. The primary damage is when nymph and adults feed on stems and petioles. Damaged stems exhibit brown lesions and often develop sooty mold. Figure adapted from https://soybeans.ces.ncsu.edu

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CHAPTER 2

Use of RNA Interference in Agriculture

INTRODUCTION

As the global population increases, the demand for food also increases. Insect damage is one of the major problems faced globally and can substantial reduce both pre- and post-harvest production if left untreated (Oerke, 2006; Fox and Fimeche, 2013). While insect pests are controlled through various methods, including insecticide applications, heavy or improper use can lead to major problems. One obvious issue is the evolution of insecticide resistance. For example, over 100 insect species are now known to be resistant to one or more insecticides (Elzen and Hardee, 2003). Another issue is the impact insecticides have on human health, and beneficial insects, including predators, parasitoids, and pollinators (Vanbergen et al., 2013). Due to indirect effects on human health and the environment it is impossible to know the total economic impact these control measures have. However, unlike conventional insecticides, new technologies based on RNA interference (RNAi) appear to be species-specific. In fact, RNAi can be designed to target a single pest species, while sparing beneficial ones. This is due to RNAi's sequence-dependent mode of action (Zhang et al., 2015; Chen et al., 2015). As long as the DNA sequence of the target gene is unique (significantly different from that found in beneficial species) the double-stranded RNA (dsRNA) should only impact the pest it was designed to target. However, RNAi-based insecticides can also be designed to target a broad range of insects, either by choosing more conserved sequences (Powell et al., 2016; Baum et al., 2007), or by deploying multiple dsRNAs at once. The active ingredient is RNA, therefore, is organic, biodegradable, and could be more economical than traditional insecticides if produced by microorganisms (e.g., yeasts). Clearly, there is a need for alternative management strategies that are sustainable and environmentally friendly for controlling agricultural pests, and RNAi may be such an approach.

RNAi is a natural process cells use to control gene expression. It is thought to have evolved from an early defense mechanism against viruses, where double-stranded RNA (dsRNA) were recognized as foreign to the cell and destroyed along with mRNA, and other single-stranded RNAs. Such destruction leads to the post-transcriptional inhibition of gene expression and protein synthesis. The power of this technology lies in its molecular mechanism, specifically, its ability to destroy only transcripts from those genes it is designed to target. The introduction of dsRNA that match part of a target gene’s sequence into the cell will trigger an RNAi response causing the destruction of the homologous mRNA and a loss-of-function phenotype (Castel and Martienssen 2013; Ketting, 2011). This review provides background on naturally occurring RNAi, how it was discovered, and the potential RNAi holds for use in pest control with a focus on the use of RNAi in agriculture.

The reason researchers are fascinated by the potential use of RNAi for insect control, is the fact that it is species-specific (Baum et al., 2007; Whyard et al., 2009; Bellés, 2010; Terenius et. al., 2011), can be delivered by a variety of methods (Baum et al., 2007; Scott et al., 2013; Terenius et al., 2011), and can possibly serve as an eco-friendly pest management tool that can be modified for use in a wide range of insect pests (Borovsky, 2005; Gordon and Waterhouse, 2007; Price and Gatehouse, 2008). Unlike conventional pesticides, RNAi appears to have minimal off-target effects (Birmingham et. al., 2006).

RNAi DISCOVERY

Prior to its discovery (Fire et al., 1998), researchers observed and reported that RNA inhibited protein expression in plants and fungi (Napoli et al. 1990; Romano and Macino 1992). Napoli et al., (1990) wanted to deepen the pigment in petunia petals by introducing a transgene, *chalcone synthase* (*CHS*) known to have an important role in floral pigmentation. However, rather than finding petunias with darker color, they found plants with white flowers or ones having patterns of white on a wild-type pigmented background- phenotypes not seen in the control plants. This result was unexpected, so they termed this phenomenon co-suppression as the transgene introduced created a block in anthocyanin biosynthesis. Romano and Macino (1992) discovered a similar thing in a fungus, *Neurospora crassa*, a process they called quelling. In this case, the transformation was carried out with constructs of the *albino* gene (*Al-3*) known to be involved in the carotenoid biosynthetic pathway. In this study, exogenous sequences were introduced into ectopic locations, about 36% of *N. crassa* transformants showed an albino phenotype. A few years later, Guo and Kemphues (1995) reported mRNA silencing by sense and antisense RNA in the roundworm, *Caenorhabditis elegans*. They observed in their studies that the introduction of a *proteinase-activated receptor* gene (*par-1*) known to play an important role in germline development resulted in degradation of the *par-1* message. While all of these processes resulted in gene silencing, their mechanism was not fully understood. It wasn't until Fire and Mello's landmark publication (1998) describing the effect of injecting dsRNA into *C. elegans* that the cause of this phenomenon was fully recognized. Fire and Mello were later awarded the Nobel Prize in Medicine for this discovery.

Since then three classes of noncoding (nc) RNAs have been identified and reported to be involved in post-transcriptional regulation of gene transcripts (Koch and Kogel 2014; Mercer, 2009). MicroRNAs (miRNAs) are known to interfere with mRNA translation (Cartel and Sontheimer, 2009; Yeo and Chong, 2011), and PIWI-interacting RNAs (piRNAs) known as endogenous small noncoding RNAs act as guardians in the genome, by protecting it from invasive transposable elements in the germline (Siomi et al., 2011; Thomson and Lin, 2009).

Moreso, long noncoding RNAs (lncRNA) (Mercer et al., 2009) have been identified, but their specific function is still unknown (Kaikkonen et al., 2011).

Since its discovery in 1998, RNAi has played an essential role in functional genetics studies. It has been used in many model systems including *Drosophila melanogaster* (Roignant et al., 2003; Bischoff et al., 2006; Miller et al., 2008), *Tribolium castaneum* (Tomoyasu and Denell, 2004; Fujita et al., 2006; Arakane et al., 2008; Konopova and Jindra, 2008; Minakuchi et al., 2009; Parthasarathy and Palli, 2009) and *Bombyx mori* (Quan et al., 2002; Ohnishi et al., 2006; Hossain et al., 2008) to study loss-of-function phenotypes for a wide-array of genes. Such functional genomic studies provide researchers with a greater understanding of the genes involved in biological phenomena like physiology, embryology, reproduction and behavior in both model and non-model insects (Bellés, 2010).

In addition to the benefit of using RNAi as a tool for assessing a gene's role in biological processes, there are also many other applications for RNAi including medical therapy for viral infection (Shankar et al., 2005), and genetic diseases (Shankar et al., 2005); however, discussion of RNAi technology in medical field is beyond the scope of this review. Here I will focus on the use of RNAi in agriculture, and specifically on its use in pest management (Baum et al., 2007; Mao et al., 2007).

RNAi MECHANISMS

Since the discovery of RNAi, significant efforts have been made to describe the molecular mechanisms of RNAi (Aravin, et al., 2007). Studies performed on several model insects, including *D. melanogaster, T. castaneum* and the silkworm, *Bombyx mori* whose genomes have been sequenced revealed that the RNAi pathway is composed of two phases, the initiator phase, and the effector phase, and together they result in post-transcriptional gene silencing (PTGS) Vaucheret et al., 2001; Vaucheret and Fagard, 2001; Castel and Martienssen, 2013). The initial step starts with the introduction of long dsRNA into a cell. These long dsRNA molecules are cut into small interfering RNAs (siRNA) by an enzyme called Dicer (Shreve et al., 2013; Swevers et al., 2013; Hammond et al., 2000). Dicer encodes a multidomain protein containing an ATP-dependent RNA helicase, PAZ domain, two tandem RNase III domains, and a dsRNA-binding domain (Bernstein et al., 2001; Knight and Bass 2001). The 21- to 25-bp products of Dicer activity are referred to as short interfering RNAs (siRNAs) (Hamilton and Balcombe, 1999). They are thought to serve as "guides" to bring nuclease machinery to the target mRNA; each siRNA associates with a protein complex called RNA-induced silencing complex (RISC), which then binds to one of the strands in the RNA fragments, allowing it to search for similar or identical mRNA (Hamilton and Balcombe, 1999). For this to occur, the unincorporated sequence must be cleaved from the siRNA duplex by the RNase H activity of an Argonaute (Ago) protein (Matranga et al., 2005; Rand et al., 2005). If the incorporated sequence is the antisense strand, then it guides RISC to its homologous target mRNA where the activity of the Ago protein causes the destruction of the target mRNA (Hammond et al. 2001; Song et al., 2004).

In addition to the mechanism described above, RNAi components have also been shown to play a role in two other processes; (1) post-transcriptional silencing (PTGS) through the action of microRNAs (miRNAs) (Ouellet et al., 2006), and transcriptional gene silencing (TGS) by chromatin modification (Niwa and Slack 2007). Regardless of whether PTGS or TGS, gene silencing by RNAi pathway involves the production of small RNAs utilizes Ago family members (Zamore 2009). The main components of RNAi are well conserved across phyla, however, the mechanism and systemic spread of silencing are highly diverged and gene regulation is mediated by a variety of RNA-based products (siRNAs, miRNA) (Shreve et al., 2013; Swevers et al., 2013). RNAi is also likely to have significant implications for the biological role of heterochromatin and genome maintenance (Lippman and Martienssen 2004). Finally, miRNAs play important roles in development and fundamental cellular processes, influencing the expression of an estimated 30 percent of all protein coding genes (Ouellet et al., 2006).

SYSTEMIC RNAi

In some genetic model organisms, the application of RNAi as a tool is less problematic, because the cells have the ability to up-take dsRNA from the extracellular environment and in some cases spread the dsRNA (or its signals) to neighboring cells (Yu et al., 2012; Voinnet and Baulcombe 1997, Fire et al., 1998). This process is referred to as systemic RNAi (Huvenne and Smagghe, 2010; Whangbo and Hunter, 2008). The phenomenon that the RNAi effect could be seen throughout the organism regardless of the site of injection was first discovered in *C. elegans* (Fire et al., 1998). Later, it was also discovered that a systemic RNAi response could be triggered when *C. elegans* were soaked in a solution of dsRNA (Tabara et al., 1998) or fed transgenic *Escherichia coli* expressing dsRNA (Timmons and Fire 1998).

Studies on the systemic RNAi mechanism in insects are very important as they broaden our knowledge on RNAi for pest control. In *C. elegans*, two types of dsRNA uptake mechanisms have been identified and studied (Whangbo and Hunter, 2008). The first is mediated by a transmembrane protein called SID-1 (systemic-interference-defective). It is believed to act as a passive dsRNA channel that shows a preference for long dsRNA molecules (Hunter et al., 2006). In *C. elegans*, Sid-1 is essential for systemic RNAi and plays a role in dsRNA uptake and subsequent spreading of the RNAi signal in both somatic and germ-line cells (Winston et al., 2002). The second method uses a protein known as SID-2, which is mainly found in the intestinal tissue of the roundworm and facilitates environmental RNAi; it may induce receptor-mediated endocytosis of dsRNAs, delivering them to the cytoplasm where they trigger RNAi pathway (Whangbo and Hunter, 2008).

Several other genes such as *RNA spreading defective* (*Rsd-2, Rsd-3, and Rsd-6*) are also known to play a role in the systemic spread of dsRNA in *C. elegans*, which was previously attributed to endocytosis, suggesting that transport of dsRNA in *C. elegans* could also use a Sid-1-independent mechanism. However, in insects, Sid-1-like (sil) proteins vary in copy number and sequence conservation across orders (Gu, et.al., 2012). For example, Diptera do not possess *sil* genes, while *T. castaneum* and *B. mori* each have three sil homologues (Tomoyasu et al., 2008). The *T. castaneum sil* genes share more identity with *C. elegans TAG-130* gene, which is not required for systemic RNAi compared to SID-1 (Tomoyasu et al., 2008). However, the relationship between *sid-1* and *sil* genes is unknown, as is the relationship between *sil* genes and systemic RNAi (Tomoyasu et al., 2008). This is partially due to the lack of one-to-one orthology between *sid-1* and *sil* genes. However, the conclusion so far is that the *sil* genes are functional *sid-1* orthologs.

Hence, flour beetles and honeybees have systemic RNAi, while dipterans, which lack *sil* genes have poor systemic RNAi. The existence of a Sid-2-mediated mechanism is also questionable, as *sid-2* orthologs have not been found in any animal genomes other than *C. elegans*, but this may be due to the rapid evolution of *sid-2* homologs. Furthermore, the presence of *Rsd* homologs does not seem to determine whether systemic RNAi occurs in insects; it is possible that the expression level and tissue specificity of these genes are responsible for the RNAi efficiency and the dsRNA uptake from the cell (Tomoyasu et al., 2008). While systemic RNAi has been documented in several insects (Bucher et al., 2002; Tomoyasu and Denell 2004), it is assumed that all animals with systemic RNAi response use the mechanism described in *C. elegans*. However, it is clear that the systemic RNAi response is not universal, as the leading insect model, *Drosophila melanogaster*, lacks a systemic RNAi response (Roignant et al., 2003).

METHODS OF dsRNA DELIVERY TO INSECTS

Several methods have been employed to deliver dsRNAs to insects, these include microinjection, feeding, and soaking (Scott et al., 2013; Yu et al., 2012). Determining which method to use one must consider the end goal (e.g. pest control), the insect species and/or life stage, as well as when and where the target gene is expressed. Almost all entomological RNAi experiments rely on extracellular dsRNA, whereby the dsRNAs are delivered to the hemolymph or midgut so that the cells can take up the dsRNAs (Yu et al., 2012). However, the delivery of dsRNA into individual cells of a multicellular organism has been problematic, because some species lack systemic RNAi, therefore posing challenges for the use of RNAi as a pest control tool (Zotti and Smagghe 2015).

Microinjection was the first method used for dsRNA delivery in both *C. elegans* (Fire et al., 1998) and *D. melanogaster* (Kennerdell and Carthew, 1998). In insects, this method delivers dsRNAs corresponding to the target gene directly into the hemolymph or embryo, and has advantages over other methods. In some organisms, it is possible to deliver dsRNA directly by injecting dsRNA into any stage (Kennerdell and Carthew 1998; Brown et al., 1999), unlike oral RNAi where dsRNA can only be administered to larvae, nymphs and adults.

Secondly, oral RNAi enables delivery of dsRNAs in a high-throughput manner, while avoiding the mechanical damage caused by microinjection (Scott et al., 2013). In addition, RNAi delivered by feeding is of particular interest for insect control in agriculture as they can act as a species-specific insecticide (Baum et al., 2007). The first study on oral RNAi in an insect was demonstrated in a lepidopteran, the light brown apple moth, *Epiphyas postvittana*, with temporary knockdown of a gut gene, *Carboxylesterase 1* (*EposCXE1*) and a pheromone binding protein gene (*EposPBP1*) by feeding larvae *EposCXE1 and EposPBP1* dsRNA (Turner et al., 2006). Since then, several studies have reported a knockdown through oral RNAi in Lepidoptera (Bautista et al., 2009; Mao et al., 2007; Whyard et al., 2009), Coleoptera (Baum et al., 2007; Whyard et al., 2009), Diptera (Walshe et al., 2009; Whyard et al., 2009), Hemiptera (Price & Gatehouse, 2008), and Isoptera (Zhou et al., 2008), suggesting that knockdown of specific targets may be feasible in some insects.

Feeding insects genetically modified bacteria (microbe-based RNAi) that express dsRNA targeting host genes has been documented in various species to be effective (Taracena et al., 2015). While it requires several steps, it has been shown to be very effective in insects that exhibit a robust RNAi response (Zhu et al., 2011). In insects, Murphy et al., (2016) were the first group that proved yeast can be genetically modified to deliver dsRNA to an insect pest through feeding. Because yeast is naturally growing on the surface of fruit crops and are known to be attractive to Drosophila species, this group took advantage of the microbe's relationship with Drosophila to create a yeast-based biopesticide. The yeast expressed dsRNA targeting *y-Tubulin*, required for nuclear division and microtubule assembly, and was fed to *Drosophila suzukii*. The authors found a reduction in population size, as well as in reproductive fitness. dsRNA has also been delivered to larval mosquitos through ingestion using nanoparticles that is composed of chitosan (Zhang et al., 2010). Zhu et al., (2011) reported that bacteria expressing dsRNA fed to insects induce RNAi effect (Tian et al., 2009). Delivering dsRNAs in bacteria and yeast will likely increase the environmental stability of the dsRNAs, while lowering the overall production cost. While dsRNA synthesis in vitro could be expensive, dsRNA synthesis and delivery via bacteria and yeast are more practical for field applications (Zhu et al., 2011). Some crops have been genetically modified to express dsRNA targeting a vital gene within a given pest species (Baum et al., 2007; San Miguel and Scott 2015). Baum (2007) was the first study to demonstrate the potential for RNAi in insect control via feeding dsRNAs expressed in planta that targeted essential insect genes.

RNAi by soaking is mainly conducted in cell lines. However, it has been suggested to be valuable as a high-throughput tool for large-scale gene expression studies in *C. elegans* (Maeda et al., 2001). While all of these methods have been successful, they all have certain disadvantages. Microbe-based RNAi methods of dsRNA delivery and chemically modified siRNAs do not provide continuous expression, so silencing is only for a short period. However, transgenic approaches could allow for continuous expression, and therefore silencing can be sustained.

IDENTIFICATION OF TARGET GENES

Since RNAi is species specific, appropriate target genes must be identified for each new species to be controlled by this strategy. One way to identify potential target genes is through homology to ones used in previous studies (She et al., 2009; Lorenzen et al., 2002). For the purpose of pest control, scientists have been using RNAi to target vital genes such as *Vacuolar-type H+ -ATPase* (*V*-ATPase) in a variety of pest species, including the western corn rootworm, *Diabrotica virgifera virgifera* and the Colorado potato beetle, *Leptinotarsa decemlineata* (Baum et al., 2007; Mao et al., 2015). Not only is *V*-ATPase necessary for survival, performing a wide range of functions including the transport of protons across membranes, but it is also highly conserved, making it relatively easy to identify in genomic or transcriptomic sequence data. As mentioned earlier, the successful use of RNAi for pest control rests on the ability of ingested dsRNAs to trigger gene knock down. Since V-ATPase plays an essential role in the insect midgut, keeping an alkaline environment in the lumen (Wieczorek et. al., 2009), dsRNAs don't have to travel far to cause serious disruption of essential functions.

Another common target is a gene that encodes a vacuolar-sorting protein (*Snf7*) (Rusten 2008) Snf7 is a component of the ESCRT-III complex (endosomal sorting complex required for transport), and like V-ATPase, is highly conserved due to its conserved function (i.e. required for sorting of cell membrane receptors (Rusten 2008). As a result of their involvement in biological processes, Bolognesi et al., (2012) characterized the ortholog of WCR larvae *DvvSnf7* gene, which lead to a significant high mortality in targeted species even at low concentration. And as mentioned earlier, Murphy and colleagues (2016), successfully knockdown *y-Tubulin* when fed genetically modified yeast that express dsRNA targeting *y-Tubulin* to *Drosophila suzukii.* Their RNAi analysis showed a reduction in population size as well as reproductive fitness in adults. A result that is not surprising since *y-Tubulin* is responsible for nuclear division and microtubule assembly. All of the above-mentioned genes will function well as targets for RNAi-based control (Baum et al., 2007).

An added advantage of using highly conserved genes is that they can be easily recognized in database searches. BLAST analysis of NCBI and other genomic and transcriptomic databases can reveal potential target genes for a wide number of species; however, if the target species lacks genomic and transcriptomic data, these sequences can be easily obtained by extracting RNA and performing RNA-Seq. This type of next generation sequencing is a rapid method of obtaining a wealth of genetic data and allows identification of novel transcripts; especially in non-model insects that lack a sequenced genome (Wang et. al., 2011). Homologous genes can be quickly identified based on identity to known targets (e.g. V-ATPase), and offers an easy way to select candidate genes for RNAi analysis. In addition, publically available sequence data, such as that found at NCBI can be used to determine if a particular target sequence is unique, not expected to harm other species.

FACTORS AFFECTING THE EFFICIENCY OF RNAi IN INSECT CONTROL

According to the review literature, there are several factors known to influence the silencing effect and efficiency of RNAi as a control tactic. As detailed below, some factors known to have a sizable impact on the efficiency of RNAi are: dsRNA concentration, sequence composition, length of sequence, life stage and in the case of protein-coding genes – rate of target proteins' turnover rate.

For each RNAi target, the optimal dsRNA concentration has to be determined (Meyering-Vos and Muller, 2007; Shakesby et al., 2009). For example, exceeding the optimal dsRNA concentration does not result in more silencing; however, it can decrease the exposure time required to get a phenotype (Bolognesi et. al., 2012, Saleh et. al., 2006), suggesting a relationship between dsRNA concentration and exposure time.

The dsRNA sequence of a particular gene could possibly silence a gene in a non-target species. Such off target effects can be minimized through database search as mentioned above; however, in the absence of genomic resources, lab experiments would be required to determine off-target effects. Studies have reported an off-target silencing in the triatomid bug *R. prolixus,* when two homologous *nitroporin* genes were silenced (Araujo et al., 2006). In addition, dsRNA targeting *V-ATPase* in the Colorado potato beetle *(Leptinotarsa decemlineata*) also silenced the orthologous gene in *D. virgifera virgifera* (Baum et al., 2007). Although this result implies that

RNAi could be used to control two or even more coleopteran pests, it could also affect non-target insects leading to a biosafety issue.

The length of the dsRNA fragments plays an essential role and determines the efficiency of uptake and gene silencing in organisms (Mao et al., 2007). The length of the dsRNA is directly involved in the success of gene silencing, and frequently ranges between 300 and 520bp. In most experiments, insects are fed long dsRNAs (Huvenne and Smagghe 2010). While RNAi can be triggered by a dsRNA as short as 50 nt in length, some experiments have shown that long dsRNAs are more efficiently taken up compared to siRNAs (Saleh et al. 2006, Bolognesi et. al., 2012). This could be due to the fact that a long dsRNA with the highest match of mRNA can be processed into siRNA. Therefore, giving a higher identity of siRNAs to cause specific silencing of the target gene (Auer and Frederick 2009). Studies have reported silencing of genes in varieties of insects by incorporating siRNA into diet instead of dsRNA (Kumar et al., 2009, Upadhyay et al., 2011).

The silencing effect of RNAi targeting *aquaporin* (*AQP2*) in aphid (*Acyrthosiphon pisum* pea) persists for five days and is then reduced (Shakesby et al., 2009). A similar effect was reported by Turner et al., (2006), where a transient effect of dsRNA against the pheromone binding protein in the light brown apple moth (*Epiphyas postvittana*) was thought to be correlated with the turnover rate of the target protein.

Early stage juvenile insects show more silencing effects than later stages (Araujo et al., 2006); however, older stages are easier to handle. For instance, no silencing effect was observed after treating 4th instar nymphs of *Rhodnius prolixus* with *nitropin* dsRNA compared to 42% silencing when using 2nd instar larvae (Araujo et al., 2006). Also, in the case of the fall armyworm (*Spodoptera frugiperda*), a stronger silencing effect was observed in 5th instar larvae when treated with allatoregulating genes (*AT 2*) compared to adult moths (Griebler et al., 2008).

PROSPECTS OF RNAi IN INSECT CONTROL

After a decade of using RNAi as a method to study the function of various genes, there is now significant growth in the use of RNAi for the control of insect pests (Baum et al., 2007; Mao et al., 2007). To date, RNAi has been used in more than 30 species, from eight insect orders (see Table 1). Most of the published studies on RNAi have focused on injection of dsRNA, with few published reports looking at the effectiveness of feeding dsRNA. However, successful feeding of dsRNA has been documented in several insect species including, *Diabrotica virgifera virgifera* (Chitvan et al., 2015; Baum et al., 2007), *Leptinotarsa decemlineata* (Zhu et al., 2010), *Epiphyas postvittana* (Turner et al. 2006*), Aedes aegypti* (Singh et al. 2013), *Helicoverpa armigera* (Mao et al., 2007) and *Drosophila suzukii* (Murphy et al., 2016). Although, Murphy et al., (2016) reported that ingestion of yeast expressing dsRNA targeting *D. suzukii yTub23C* during the larval stage decreased survival to adulthood, a closely related species, *Drosophila melanogaster*, lacks a systemic RNAi response (Roignant et al., 2003). This might explain why Murphy et al (2016) found so much variation in their results. While both injection and feeding have been documented in a variety of insects, there is evidence that in some species, RNAi is not very efficient. Allen and Walker (2011) demonstrated that repeated delivery of dsRNA corresponding to tarnished plant bug, *Lygus lineolaris*, *Inhibitor of Apoptosis* (*IAP*) was not successful. Their further analysis revealed that the dsRNA had been degraded prior to contact with *Lygus lineolaris* cells. So, while this technology has proved promising in some insect species, others have less successful stories.

In 2007, two studies reported the concept of plants expressing dsRNA from hairpin vectors that targeted economically important agricultural pests (see Table 2), the cotton bollworm, *Helicoverpa armigera* (Mao et al., 2007), and western corn rootworm, *D. virgifera virgifera* (Baum et al., 2007). Baum et al., (2007) demonstrated that silencing of a *V-ATPase* gene in the midgut cells of the western corn rootworm protected the plant and led to larval stunted growth and mortality. This was the first study to show that RNAi can be an effective insect control method. Similar results were obtained when the *cytochrome P450 monooxygenase (CYP6AE14)* gene, known to help insects detoxify plant secondary metabolites, was silenced in midgut cells of the cotton bollworm. In this case, the insect's ability to detoxify these compounds was drastically reduced (Mao et al., 2007). Cotton plants engineered to produce dsRNAs targeting *CYP6AE14* were fed to larvae, and successfully decreased endogenous *CYP6AE14* mRNA levels in the insects, and resulted in stunted larval growth due to the presence of gossypol in cotton plants (Mao et al., 2007). Mao et al. (2013), show that co-expressing *CYP6AE14* dsRNA with a plant cysteine protease, and enzyme that damages the insect's peritrophic matrix- a barrier which prevents large molecules from getting into the midgut cells, could protect the plant from bollworms. A similar approach has been exploited in plants, with the aim of developing plants that are more resistant to nematodes. Engineered plants producing dsRNA targeting genes in the root knot nematode have been reported (Yadav et al., 2006; Huang et al., 2006). Arabidopsis expressing a dsRNA targeting *CYP9A14*, when silenced, reduced larval resistance to deltamethrin, a pyrethroid insecticide that can protect cotton from insect attack (Tao et al., 2012). In a related study, injection of dsRNAs targeting *CYP6B7* into the midgut of resistant cotton bollworm larvae restored susceptibility to the pyrethroid insecticide deltamethrin (Tang et al., 2012). These studies suggest that targeting detoxification genes such as those in the cytochrome

P450 family could serve as an effective method to increase the lifespan of insecticide chemistries that are at, or near the end of their effectiveness due to resistance development.

CONCLUSIONS AND FUTURE PERSPECTIVES

RNAi has potential for becoming a successful approach for insect pest management. However, several issues need to be addressed before this technology can be used in the field. Although RNAi is known for its specificity (Bellés, 2010), studies have shown that off-target gene silencing can occur (Xu et al., 2006). The specific case of a single dsRNA causing knock down of a specific target in two pest species, such as *Diabrotica virgifera* and *Leptinotarsa decemlineata* (Baum et al., 2007) is not a problem; however, if a pest-specific target triggers RNAi in a non-target species, this will likely have a negative effect on RNAi as a pest control method. Moreover, RNAi targeting a particular insect pest could have an adverse impact on beneficial organisms. Therefore, species-specific biology such as genes involved in mate recognition might be good targets for pest management, since this would reduce the possibility of silencing genes in a non-target species. Extensive studies are needed to completely understand the factors behind off-target silencing and to prevent potential hazards to the environment.

Similar to insecticides and *Bt* plants, there is also some possibility that some insects may evolve resistance to a particular dsRNA sequence due to mutations in the target gene. In addition, resistance due to a mutation in Dicer or another part of the RNAi pathway could be a huge hindrance for RNAi as a pest management tool (Carthew and Sontheimer 2009). Even creating another dsRNA targeting a different portion of the same gene or a new target gene might not overcome this resistance barrier. Therefore research into RNAi resistance should be investigated before this technology is accepted on a large scale.

To further our understanding of the dsRNA uptake and processing mechanisms in insects, RNAi pathways in different insect species and orders need to be identified and their roles studied. Differences, such as what makes *Tribolium castaneum* have strong systemic RNAi, when *Drosophila* appears deficient in systemic RNAi needs to be understood (Roignant et al., 2003). Likewise we need to understand why *Drosophila*, which is not responsive to environmental dsRNA when unpackaged, has significant gene knockdown and high mortality when fed dsRNAs in transfection solution (Whyard et al. 2009), or in the case of *D. suzukii*, is responsive to dsRNA when expressed in yeast (Murphy et al., 2016). Taken together this suggests that the presence of a robust systemic RNAi response may not be a precondition for RNAi-mediated insect control. Therefore, a better understanding of how dsRNA gets into midgut cells might increase our ability to improve oral RNAi in other insect species. Despite various setbacks associated with this technology, perhaps in the future, RNAi will be a widely-accepted tool for used in integrated pest management.

Table 1: Overview of oral and injection-based RNAi against a number of target genes in several species

ORDER	SPECIES	TARGET GENE	STAGE	REFERENCES
Coleoptera	*Aethina tumida*	*Vacuolar ATPase A*[1]	Larvae	Powell et al., 2016
Coleoptera	*Tribolium castaneum*	*Distal-less*[1]	Adult	Bucher et al., 2002
Coleoptera	*Leptinotarsa decimlineata*	*Vacuolar ATPase E*[2]	Larvae	Zhu et al., 2010
Coleoptera	*Diabrotica virgifera virgifera*	*Hunchback*[1, 2], *brahma* [1, 2]	Larvae	Chitvan et al., 2015
Coleoptera	*Diabrotica undecimpunctata*	*Subunits of vacuolar ATPase*[2]	Larvae	Baum et al., 2007
Coleoptera	*Harmonia axyridis*	*Distal-less* [1]	Larvae	Niimi et al., 2005
Coleoptera	*Protaetia brevitarsis*	*Pbtf* [1]	Larvae	Kim et al., 2008
Diptera	*Drosophila suzukii*	*Y-Tubulin* [2]	Adult	Murphy et al. 2016
Diptera	*Anopheles gambiae*	*Defensin* [1]	Adult	Blandin et al. 2002
Diptera	*Aedes aegypti*	*Chitin*[1]	Adult	Kato et al. 2006
Diptera	*Culex pipiens*	*Foxo*[1]	Adult	Sim & Denlinger 2008
Diptera	*Drosophila melanogaster*	*Beltless* [1]	Adult	Dzitoyeva et al., 2003
Diptera	*Sarcophaga peregrina*	*P120-catenin* [1]	Larvae	Nashikawa & Natori 2001
Diptera	*Lutzomyia longipalpis*	*Xanthine dehydrogenase*[1]	Adult	Sant' Anna et al., 2008
Diptera	*Glossina morsitans*	*Transferrin* [1, 2]	Adult	Lehane et al., 2008
Lepidoptera	*Spodoptera litura*	*Aminopeptidase* [1]	Larvae	Rajagopal et al. 2002
Lepidoptera	*Epiphyas postvittana*	*Carboxylesterase 1*[2]	Larvae	Turner et al. 2006
Lepidoptera	*Manduca sexta*	*Vacuolar ATPase E*[1]	Larvae	Whyard et al., 2009
Lepidoptera	*Hyalophora cecropia*	Peptidoglycan recognition protein [1]	Pupae	Bettencourt et al. 2002
Lepidoptera	*Bombyx mori*	Creb binding protein [1]	Larvae	Tabunoki et al., 2004
Lepidoptera	*Helicoverpa armigera*	*Cytochrome P450* [2]	Larvae	Mao et al., 2007
Hemiptera	*Oncopeltus fasciatus*	*Hunchback* [1]	Adult	Liu and Kaufman 2004
Hemiptera	*Rhodnius prolixus*	*Nitrophorin 2* [1, 2]	Nymphs	Araujo et al., 2006
Hemiptera	*Bemisia tabaci*	*Chickadee* [1]	Adult	Ghanim et al., 2007
Hemiptera	*Acyrthosiphon pisum*	*Ap-crt* [1] *& Ap-cath-L* [1]	Nymphs	Jaubert et al., 2007
Orthoptera	*Locusta migratoria*	*Hunchback* [1]	Nymphs	He et al., 2006
Orthoptera	*Gryllus bimaculatus*	*Sulfakinin* [1,2]	Nymphs	Meyering & Muller 2007
Hymenoptera	*Apis mellifera*	*Vitellogenin* [1,2]	Workers	Amdam et al., 2003
Hymenoptera	*Nascoonia vitripennis*	*Epoxide hydrolase* [1]	Pupae	Abdel-latief et al., 2008
Isoptera	*Reticulitermes flavipes*	*Cellulase hexamerin* [1,2]	Workers	Zhou et al., 2006
Blattodea	*Blatella germanica*	*BgEcR-A* [1]	Larvae	Cruz et al., 2006
Blattodea	*Periplaneta americana*	*Engrailed* [1]	Larvae	Marie et al., 2000

[1]dsRNA delivered by injection. [2]dsRNA delivered by feeding

Table 2.O verview of the published studies on the use of plant-based RNAi against different insect pests

ORDER	SPECIES	TARGET GENE	STAGE	REMARKS	REFERENCES
Coleoptera	*Diabrotica virgifera virgifera*	*Vacuolar ATPase*	Larvae	Mortality	Baum et al. 2007
Coleoptera	*Leptinotarsa decemlineata*	*Vacuolar ATPase A & E*	Larvae	Mortality	Zhu et al. 2011
Coleoptera	*Diabrotica undecimpunctata howardii*	*Vacuolar ATPase*	Larvae	Mortality	Baum et al., 2007
Lepidoptera	*Helicoverpa armigera*	*HaEcR*	Larvae	Molting defect	Zhang et al. 2015
Lepidoptera	*Helicoverpa armigera*	*HR3*	Larvae	Deformities	Xiong et. al. 2013
Lepidoptera	*Helicoverpa armigera*	*HaAK*	Larvae	Deformities	Liu et al. 2015
Lepidoptera	*Helicoverpa armigera*	*CYP6AE14*	Larvae	Reduced growth	Mao et al. 2011
Hemiptera	*Myzus persicae*	*MpC001, Rack1*	Nymphs	Progeny reduced	Pitino et al. 2011
Hemiptera	*Bemisia tabaci*	*Hacuolar ATPase*	Adults	Mortality	Thakur et. al. 2014
Hemiptera	*Myzus persicae*	*Serine protease*	Adults	Progeny reduced	Bhatia et al. 2012
Hemiptera	*Myzus persicae*	*Hunchback*	Nymphs	Inhibited reproduction	Mao et. al. 2014

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CHAPTER 3

Insights into the *Diabrotica virgifera virgifera* ATP-binding Cassette Transporter Gene Family Through Transcriptomics

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ABSTRACT

The western corn rootworm, *Diabrotica virgifera virgifera*, is a pervasive pest of cultivated maize in North America and Europe, which has evolved to survive exposure to multiple insecticidal agents. Members of the ATP-binding cassette (ABC) transporter family play diverse cellular roles in arthropods, including xenobiotic detoxification. In this study, 65 putative *D. virgifera virgifera* ABC transporters, belonging to subfamilies A to H (*Dvv*ABC-A to *Dvv*ABC-H), were identified within transcriptome assemblies from the combined sequencing reads from Illumina libraries prepared from four RNA samples (embryos, larvae, adult male, and adult female). Eight *D. virgifera virgifera* ABC genes, with direct orthology to *Tribolium castaneum* gene models and known to have obvious knockdown phenotypes, were tested for functional conservation using RNA interference, which resulted in phenotypes similar to those seen in *T. castaneum*. Interestingly, depletion of *DvvABCB_19147* and *DvvABCG_3712* transcripts in adult females produced detrimental reproductive and developmental phenotypes (egg-laying and -hatching defects), demonstrating their potential as insect birth control targets. This study provides insights into the developmental and physiological roles of *D. virgifera virgifera* ABC transporters and suggests candidate target sites for the development of novel insect control tactics.

Keywords: ATP-binding cassette (ABC) transporter, phylogenetic, transcriptome, RNA interference (RNAi), corn rootworm

INTRODUCTION

The western corn rootworm, *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae), is a major pest of maize in North America (Levine and Oloumi-Sadeghi, 1991; Levine et al., 2002). It is considered a notorious pest due to its ability to overcome various management methods. Costs from managing this pest, as well as from crop losses due to the damage it causes are estimated to be over one billion dollars annually in North America (Marra et al., 2012). Common management practices include the use of insecticides, crop rotation, and transgenic maize expressing crystal proteins from the soil bacterium *Bacillus thuringiensis* (*Bt*). Unfortunately, *D. virgifera virgifera* has evolved resistance to crop rotation (Gray et al., 2009; Krysan, 1986; Sammons et al. 1997), to many chemical insecticides (Meinke et al., 1998; Miller et al. 2009), and to a number of *Bt* proteins (Gassmann *et al*., 2011; Narva *et al*., 2013). However, recent studies have shown that *D. virgifera virgifera* is highly sensitive to a new management tool, RNA interference (RNAi), which could be used as an alternative technology to protect corn from rootworm damage (Baum *et al*., 2007; Rangasamy and Siegfried, 2012; Li *et al*., 2015). Nonetheless, the ability of this insect to adapt to control methods demonstrates a fundamental need for a greater understanding of *D. virgifera virgifera* biology and molecular genetics.

Unfortunately, the genetic resources available for *D. virgifera virgifera* are limited, so progress toward understanding multigenic traits, like those that contribute to resistance evolution, will require the development of fundamental genetic and genomic tools for this species. Complicating the development of these tools is the fact that *D. virgifera virgifera* has a large genome, about 2.58 GB (Coates et al., 2012; Sappington et al., 2009), which is ten times bigger than in species like *Drosophila melanogaster* and *Tribolium castaneum*, which are rich with genetic resources. However, focusing on the transcriptome could provide valuable information, even in the absence of a completed genome assembly. Indeed, RNA-Seq has become a quick, cost effective method for obtaining a wealth of genetic data in non-model insects that lack a sequenced genome (Wang et al., 2011).

ATP-binding cassette (ABC) transporters comprise one of the largest protein families; and are present in all organisms from prokaryotes to eukaryotes (Higgins, 1992). Functional studies on ABC-family genes of several arthropod species have relied on genomic data, including *T. castaneum* (Broehan et al., 2013*), Bombyx mori (*Liu et al., 2011), *D. melanogaster (*Dean et al., 2001), *Bemisia tabaci* (Tian et al., 2017), *Daphnia pulex* (Sturm et al., 2009), and *Tetranychus urticae* (Dermauw et al., 2014); however, a significant proportion of the reported ABC transporters in each of these species could have been discovered in the transcriptomic data alone.

ABC-family proteins are structurally characterized by two domains: the highly conserved nucleotide-binding domain (NBD) and the variable transmembrane domain (TMD) (George and Jones, 2012). The NBD binds and hydrolyzes ATP to provide the energy required for driving a substrate across a cellular membrane, while the TMD creates the channel through which the substrate is transported (Rees et al., 2009). Each NBD possesses several highly-conserved, characteristic motifs including; Walker A, Walker B, Q-loop, D-loop, H-loop, and the ABC signature motif, while each TMD is made up of five to six transmembrane α-helices, and dictate substrate specificity (Rees et al., 2009). To function as transporters, ABC proteins require two NBDs and two TMDs to work together. Some ABC transporters, called full-transporters (FT) contain all the necessary domains (2 TMDs and 2 NBDs), in a single protein. Half-transporters (HT), on the other hand, only have a single TMD and a single NBD, so must work as pairs, either as homodimers or heterodimers, with another half transporter molecule to form a functional unit (Higgins, 1992; Dean et al., 2001; Rees et al., 2009). Because of its conserved nature, the sequence of the NBD has been used to classify this superfamily into eight subfamilies designated A to H (ABCA to ABCH) (Dean and Annilo, 2005).

Among insects, ABC transporters have been implicated in diverse functions such as, development (Broehan et al., 2013), transportation of eye pigments (Ewart et al., 1994; Mackenzie et al., 1999; Liu et al., 2014; Mackenzie et al., 2000), and resistance to insecticides (Aurade et al., 2010; Buss and Callaghan, 2008). Interestingly, based on transcriptomic data, Bretschneider et al., (2016) suggested that ABC transporters are involved in the degradation of plant secondary metabolites in the cotton bollworm, *Helicoverpa armigera*. And Broehan et al., (2013) reported the effects of RNAi knock-down of several ABC transporters in the red flour beetle, *T. castaneum*, which included growth arrest, eye pigmentation defects, abnormal cuticle formation, egg-laying and egg-hatching defects, and mortality.

As mentioned above, there are many transcriptomic and functional genomic studies on ABC genes of several arthropod species, but, none in *D. virgifera virgifera*. Characterizing the ABC genes in *D. virgifera virgifera* is particularly important since members of the ABC family have been implicated in the mode of action and resistance to *Bt* toxins in Lepidoptera (Guo et al., 2015). As a first step toward understanding the function of these transporters in this species, we mined the transcriptome data (RNA-Seq) for ABC transporter genes and characterized several via RNAi. Specifically, eight ABC transporters were identified as putative orthologs to those previously reported to have a defining RNAi phenotype in the model coleopteran species, *T. castaneum* (Broehan et al., 2013; *DvvABCA_18330*, *DvvABCB_19147*, *DvvABCE_2830*, *DvvABCF_2701*, *DvvABCG_3712*, *DvvABCG_49457*, *DvvABCG_13829* and *DvvABCH_18290*). Subsequent RNAi-mediated knockdown demonstrated conservation of function with *T. castaneum*, as well as established potential new insecticidal targets for the control of this devastating agricultural pest.

MATERIALS AND METHODS

Insect rearing

All *D. virgifera virgifera* used in this study were obtained from a laboratory-established colony at North Carolina State University (see Chu et al., 2017). Eggs deposited in an oviposition chamber (agar plate with cheese cloth) were collected weekly, pipetted into soil-filled containers, and kept at 26°C. Experimental larvae were reared on roots of germinated corn seeds in 16-oz containers, while adults were maintained in a 30cm^3 BugDorm (MegaView Science, Taiwan) at 26°C, 70% relative humidity with an L14:D10 photoperiod and fed an artificial diet as needed. All injected beetles were kept and reared in a container containing corn seedling under similar conditions to allow further observation.

RNA isolation and Illumina sequencing

In an effort to identify as many *D. virgifera virgifera* ABC transporters as possible, we isolated RNA from four samples. Specifically, four distinct sets of insects were collected by separating three life stages (embryos, larvae, and adults) and then separating adults by sex. Total RNA was isolated using the RNeasy Mini Kit (Qiagen, Hilden, Germany) and treated with DNase I (Qiagen) according to the manufacturer’s instructions. The RNA was submitted to the Genomic Sciences Laboratory (North Carolina State University, NC USA) for quality assessment, poly(A) selection, fragmentation, size selection (600- to 700-bp) and Illumina TruSeq library preparation and sequencing (Illumina MiSeq sequencer, 2 x 300-bp).

Transcriptome assembly and annotation

Raw reads (all life stages) underwent an initial quality assessment using FastQC (Andrews, 2010), and were trimmed based on quality sores, and any remaining Illumina adapter sequences removed. Trimmed reads were *de novo* assembled into contigs using SeqMan NGen (DNASTAR, Inc; Madison, Wisconsin, USA) to generate a combined assembly and the relative completeness evaluated by comparison with the universal single copy orthologs from Arthropoda obtained from OrthoDB v 9 using BUSCO v 3 (Waterhouse et al., 2012). SeqMan NGen (DNASTAR) assemblies were evaluated for total number and median length (N50) of contigs. The derived transcript sequences from SeqMan NGen (DNASTAR) were imported into Blast2GO v 4.0 (Conesa et al., 2005; Götz et al., 2008) and annotations acquired with BLASTx comparisons to the non-redundant (nr) arthropod-specific database at the National Center of Biotechnology Information (NCBI). The combined graphs were created at level 2 for Biological Process (BP), Cellular Component (CC), and Molecular Function (MF) categories from Blast2GO.

Bioinformatics analysis of the *D. virgifera virgifera* ABC transporter superfamily

A searchable database was created from the combined *D. virgifera virgifera* assembly and the database searched using BlastStation software (TM Software Inc.; Arcadia, CA, USA). The deduced amino-acid sequence of each *T. castaneum* ABC transporter was used as query to identify the corresponding *D. virgifera virgifera* genes (Broehan et al., 2013). Homologous sequences were selected based on their sequence identity and E-values ($<10^{-6}$). Each of the selected *D. virgifera virgifera* sequences were then compared (BLASTx) to the complete nr database at NCBI (http://blast.ncbi.nlm.nih.gov/), retaining only those matching ABC transporters. This process was repeated until no new ABC transcripts were found in the *D. virgifera virgifera* database. The number and positions of transmembrane domains were assessed with NCBI's Conserved Domain Search Service. Finally, each putative *D. virgifera virgifera* ABC gene was assigned to a subfamily (A-H) based on BLASTx analyses, as well as phylogenetic inferences.

To ensure all potential ABC transporters were identified we generated a second set of assemblies, one was produced using Trinity (Grabherr et al., 2011) and another using SOAPdenovo (Xie et al., 2014). Independent databases were then generated from each (Trinity and SOAPdenovo) and all ABC-related sequences identified. The complexity of each ABC gene set was reduced by clustering allelic variants (sequence), and a non-redundant, comprehensive file of *D. virgifera virgifera* ABC contigs generated. The assembly of origin is denoted by D (DNAStar), T (Trinity), and S (SOAPdenovo).

Phylogenetic trees were constructed using the NBD, the most conserved region among all ABC transporters, corresponding to the *D. virgifera virgifera* ABC. Sequence alignments were performed with ClustalW using MEGA 7 (Tamura et al. 2013),) and subjected to phylogenetic analysis with 1000 bootstrap replications. The phylogenetic trees were constructed using the Neighbor-joining method, but the Best Model was determined for each tree by the program. Subfamily-specific clustering was then compared with that of previous phylogenetic analyses of ABC transporters from *T. castaneum, B. mori* and *D. melanogaster*. To help determine orthology, an unrooted phylogenetic tree showing the phylogenetic relationships of the selected *D. virgifera virgifera* genes and the full set of *T. castaneum* ABC transporters was constructed. The deduced amino-acid sequence of each *T. castaneum* ABC gene was obtained from NCBI, and aligned to the full-length of the *D. virgifera virgifera* deduced amino-acid sequence when possible (note that some *D. virgifera virgifera* contigs failed to represent full-length transcripts). We used *ABCD2* from *T. castaneum* and *Anoplophora glabripennis* as the outgroup. Sequence alignments were performed as described above.

Gene expression analyses by RT-PCR

Relative levels of gene expression were determined for each of the selected ABC genes (*DvvABCA_18330, DvvABCB_19147, DvvABCE_2830, DvvABCF_2701, DvvABCG_3712, DvvABCG_49457, DvvABCG_13829* and *DvvABCH_18290*), by semi-quantitative RT-PCR to ensure injection of dsRNAs would be performed before peak expression occurred. RNA was extracted from each developmental stage, with adults separated by sex and total RNA reverse transcribed into cDNA using the Superscript™ III First-Strand Synthesis System (Invitrogen) along with an anchored poly(T) primer. Each cDNA pool represents a specific developmental stage, or sex. These pools were then individually used as template for PCRs using each of eight pairs of gene-specific primers. PCR expression profiling was performed by using each of the 4 prepared cDNA pools, Master Mix and the gene-specific primer set designed to amplify the *D. virgifera virgifera* ABC transcript of interest. The highly-conserved housekeeping gene, *DvvRPS6*, was used to assess template quality and quantity. The PCRs were performed in a T100 Thermal Cycler (Bio-Rad) with the following cycling conditions: (95°C for 3 min), 25× (95°C for 30s, 58°C for 30s, 72°C for 10s), (4min incubation at 72°C). Amplification products from each of the different life stages and sexes were then visualized and compared using gel electrophoresis.

Primer design and *in vitro* dsRNA synthesis

Primer sets used to generate dsRNA were designed (Table 1) to regions encoding the gene-specific TMD domains, and not in regions encoding the conserved NBD domains, to avoid potential off-target effects. Primers were designed using Vector NTI Advance (VNTI) software (Invitrogen), for all ABC genes whose orthologs are known to produce obvious RNAi phenotypes in *T. castaneum* (Broehan et al., 2013). Partial cDNAs were amplified for the selected genes (*DvvABCA_18330, DvvABCB_19147, DvvABCE_2830, DvvABCF_2701*, *DvvABCG_3712*, *DvvABCG_49457*, *DvvABCG_13829* and *DvvABCH_18290*), as previously described. Fully-nested PCR was performed with an initial denaturation of (95°C for 3 min), 35× (95°C for 30s, 58°C for 30s, 72°C for 10s), (4min incubation at 72°C). The PCR products were purified using the QIAquick PCR Purification Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions, then ligated into the pGEM-T vector (Promega), and the resulting plasmids were used to transform competent *E. coli* cells. All positive clones were cultured in a selective LB medium. The recombinant plasmid DNAs were isolated using the Plasmid Mini Kit (Qiagen), and the inserts sequenced and confirmed by BLAST analysis (http://blast. ncbi.nlm.nih.gov). Each ABC-containing plasmid was individually used as template in PCR reactions containing the following primers; T7 as a forward primer (due to location in pGEM), and a pGEM-specific reverse primer that was tailed with T7. This enabled all PCRs to be performed with the same set of primers. PCR was performed with an initial denaturation of (95°C for 3 min), 35× (95°C for 30s, 58°C for 30s, 72°C for 10s), (4min incubation at 72°C). The PCR products were confirmed by agarose gel electrophoresis, purified, and ~1µg of each was used as template for dsRNA synthesis using the MEGAscript T7 *in vitro* Transcription Kit

(Ambion). Each of the synthesized dsRNAs were purified using the MEGAclear Kit (Ambion) and concentration determined using a Nanodrop 1000 (Thermo Scientific, Waltham, MA, USA).

RNAi bioassay

RNAi assays were conducted by individually injecting dsRNA corresponding to each of the 10 specific *D. virgifera virgifera* ABC genes into the hemocoel of 3rd-instar larvae, pre-pupae and/or newly-eclosed female adults. Before microinjection, experimental insects were anesthetized on ice for 30 min, then injected with a gene-specific dsRNA at a concentration of 1-2µg/µl. For each treatment, the entire process was replicated three times, as three independent biological replicates, with at least 20 individuals in each replicate. Following injection, larvae and pre-pupae were allowed to recover at room temperature for one hour, and then moved to germinated corn for further monitoring and phenotypic analysis. Phenotypes were observed daily using a stereomicroscope, and transcript levels assessed after 5 days by RT-PCR using RNA isolated from pools of injected individuals (one individual per replicate, for a total of three individuals per RT-PCR).

Treated females were kept in an oviposition chamber (agar plate with cheese cloth) and maintained on an artificial diet. Two days post-injection, females were mated to untreated males, and generally started to lay eggs ~10 days later. To determine egg viability, eggs were harvested from the oviposition chamber and placed on moistened filter paper in Petri dishes and held at 26°C, 70% relative humidity with an L14:D10 photoperiod. Females were allowed to lay eggs over a two-week period, and eggs were counted every other day to assess the rate of egg laying. Hatch rate counts were made every other day, beginning ten days after the first egg lay (22 days post injection) and continuing for four weeks until no further hatching was observed.

RESULTS

Transcriptome sequencing, assembly, and annotation

Illumina (MiSeq) sequencing generated 22,296,672 raw sequence reads across four libraries. Of these, 13,070,671 assembled in a single-combined transcriptome producing 25,296 contigs with an average length of 2,463 bp. BLAST-based annotation was performed with Blast2GO (Conesa et al., 2005) using BLASTx against the arthropod-specific section of NCBI's non-redundant (nr) protein database. Among the 25,296 contigs derived from the *D. virgifera virgifera* transcriptome, BLASTx analysis revealed over 18,343 contigs that shared significant identity (*E*-values < 10^{-6}) with known arthropod proteins, and a subset of these received GO mapping and annotation terms (Figure 1). Sequences lacking significant identity to known arthropod proteins likely represent poorly conserved and/or novel sequences, as well as non-coding RNAs. The distribution of top BLAST hits by species showed that *T. castaneum* was the most frequent, representing 65% of the matches (Figure 2). The primary reason for this is the extensive genomic/transcriptomic data available for *T. castaneum.* BLAST-based annotation was performed using BLASTx in Blast2GO against the NCBI nr database. Among ontologies acquired by GO mapping at level 2, a majority of the associated GO terms were assigned to cell structural component, metabolic process, and catalytic activity respectively for GO Cellular Component (C), Biological Process (P) and Molecular Function (Figure 3). The SeqMan NGen assembly showed a high degree of completeness based on a BUSCO score of 955, or 98.6% of the 1,066 arthropod reference set (v. 9.0) being represented.

Annotation and phylogeny of ABC transporter genes

Because of the prominent role ABC transporters play in resistance to insecticides, we used our database of *D. virgifera virgifera* transcriptome contigs to identify the ABC genes for this species. To do this, we used the BLAST function of BlastStation to search the *D. virgifera virgifera* transcriptome database with each of the predicted protein sequences of the 74 known *T. castaneum* ABC genes (Broehan et al., 2013; Grubbs et al., 2015). Our analysis identified 65 putative *D. virgifera virgifera* ABC genes. To determine the evolutionary relationships of the *D. virgifera virgifera* ABC genes, phylogenetic analysis was carried out based on ClustalW multiple sequence alignment of amino-acid sequences of the identified NBDs. We found that the sequences formed clades according to the eight known ABC transporter subfamilies (A to H) (Figure 4; Table 2). The most similar sequences from BLASTx analyses were putative transporters from *T. castaneum* and *A. glabripennis.* Although these results suggest that *D. virgifera virgifera* shared a lineage with both *T. castaneum* and *A. glabripennis*, it is important to note that these species have extensive publicly available genomic data (Broehan et al., 2013; McKenna et al., 2016). In addition, an unrooted tree constructed using only the eight genes selected for RNAi analysis reveals that these genes are more evolutionarily conserved and clearly group into clusters with *T. castaneum* (Figure 5). Moreso, the phylogenetic tree reveals the differences between each of the selected genes and their outgroup, indicating that the *D. virgifera virgifera* genes selected for RNAi analysis are indeed orthologous to the intended *T. castaneum* genes.

Each *D. virgifera virgifera* ABC gene was named based on subfamily as well as *D. virgifera virgifera* contig (Table 2 – list of ABCs). Broehan et al., (2013) identified 73 ABC transporters in *T. castaneum*, and a 74th ABC transporter was reported by Grubbs et al. in 2015, but our study only identified 65 ABC transporters in *D. virgifera virgifera*. However, since our survey is only based on low-coverage transcriptomic data, it is entirely possible that the *D. virgifera virgifera* genome harbors additional ABC genes, which are either transcribed at relatively low levels, or are expressed at time points not covered by our RNA-Seq libraries. The ABCA subfamily is comprised of full-transporters that are among the well-characterized ABCs; the *D. virgifera virgifera* ABCA subfamily contains four members. The ABCB subfamily contains seven members, which includes two types of proteins: full transporters and half transporters with a TMD-NBD arrangement. As expected, the ABCC subfamily proteins are always full transporters, and 32 were identified in *D. virgifera virgifera*. The ABCD, ABCE and ABCF subfamilies each contained only a small number of ABC members, with clear orthologous relationships to *T. castaneum*. The ABCD subfamily contained two ABC proteins, which were TMD-NBD half transporters. Only one ABCE and three ABCF genes were identified, and each had two NBD motifs with no TMDs, suggesting they are unlikely to function as transmembrane transporters. The *D. virgifera virgifera* ABCG group is the second largest subfamily, with 12 members, most of which were half transporters with only a single NBD. The *D. virgifera virgifera* ABCH subfamily contains four members with a reverse domain organization similar to the ABCG subfamily.

Gene expression across developmental stages

Broehan et al., (2013) published a comprehensive analysis of the ABC genes of *T. castaneum*, in which they tested the developmental function of each of the 73 genes they identified using RNAi. However, only ten of these genes produced obvious phenotypes. Because *D. virgifera virgifera* is a difficult species to rear (Chu et al., 2014), we chose to focus our functional analysis of *D. virgifera virgifera* ABC genes to those orthologous to the ten TcABC genes that gave observable phenotypes: *DvvABCA_18330, DvvABCB_19147, DvvABCE_2830, DvvABCF_2701, DvvABCG_3712, DvvABCG_49457, DvvABCG_13829* and *DvvABCH_18290* (Table 2). Interestingly our initial survey (DNASTAR assembly) failed to find an ortholog of *T. castaneum scarlet*, so while *TcABCG-9A* and *TcABCG-9B* represent two separate, but related eye-color genes in *T. castaneum* (*white* and *scarlet*, respectively) we only identified the *white* ortholog in the initial *D. virgifera virgifera* transcriptome assembly. Therefore, our analysis is of eight *D. virgifera virgifera* genes. We used RT-PCR to examine the developmental expression profiles of these eight *D. virgifera virgifera* ABC genes, not surprisingly, all of the transcripts were expressed in all of the examined developmental stages, except for ABCG group which exhibit stage-specific transcription in eggs, and adult (Figure 6). The low expression of *white* transcripts in *D. virgifera virgifera* stages is similar to what (Bohen et al., 2013) reported for *white*, in *T. castaneum*. While *white* expression peaks during the larval and pupal stages due to its role in the transport of pigments (Sullivan et al., 1980), its expression level remains relatively low.

RNAi bioassays

Insects were microinjected with dsRNAs at the growth stages specified in Table 3, and five days post injection, RNA was isolated from both the experimental and control groups. Transcript levels were then assessed via semi-quantitative RT-PCR and treated samples compared to the control group. As seen in Figure 7, the level of each target transcript was significantly reduced at 5 days post-injection when compared to buffer-injected controls. Moreover, each dsRNA treatment resulted in defined phenotypes among each specific dsRNA treated cohort (Table 4; Figure 8). Specifically, knockdown of *DvvABCA_18330* led to mortality among approximately 60% of the treated pre-pupae compared to 5% for the buffer treated control. In addition, the adults that survived pre-pupal injection and successfully eclosed showed defects in wing and elytra development (Figure 8A), while buffer-injected controls did not. Importantly, these results are similar to those reported for the *T. castaneum* orthologs (Broehan et al., 2013). Subfamily A transporters have been implicated in lipid transport in mammals, which can impact cell physiology (Quazi and Molday, 2011), so it is conceivable that *DvvABCA_18330* also plays a role in lipid transport like its orthologs, *TcABCA-9A/9B*, in *T. castaneum* (Broehan et al., 2013).

In insects, ABCB genes have been implicated in insecticide resistance (Labbe et al., 2011), while in humans, subfamily B genes are known to be mitochondrial transporters with roles in iron metabolism and transportation of Fe/S protein precursors (Pondarré et al., 2006; Krishnamurthy et al., 2006). Injection of *DvvABCB_19147* dsRNA into larvae resulted in 100% mortality, and injections into pre-pupae led to defects in their development, which occurred during the pupal-adult molt and ultimately resulted in mortality. Injection of *DvvABCB_19147* dsRNA into pre-pupae caused severe abnormalities, leaving individuals partially trapped in their pupal cuticle (Figure 8B). To evaluate the effects of *DvvABCB_19147* RNAi on female fecundity, dsRNA was injected into newly-eclosed adult females. Once they recovered, these females were mated with un-injected males. Interestingly, drastic reduction in egg laying was observed compared to untreated females (Figure 9). Injection of this dsRNA also affected ovary development, causing the ovaries to be underdeveloped and resulting in the failure to produce eggs (Figure 8J).

RNAi knockdown of *DvvABCE_2830* and *DvvABCF_2701* (the ortholog of *TcABCE1* and *TcABCF1*; Broehan et al., 2013) resulted in the deaths of all injected subjects. Prior to death, it was noted that body mass was reduced in the treated individuals and was significantly less than the body mass of larvae treated with buffer alone (Figure 8G, 8H). Injection of *DvvABCE_2830* and *DvvABCF_2701* dsRNA separately into pre-pupae both caused 100% mortality with no adult eclosion (results not shown).

Injection of dsRNA targeting *DvvABCG_3712, DvvABCG_49457,* and *DvvABCG*_13829 resulted in phenotypes similar to those seen in *Tribolium* (Broehan et al 2013) when performing RNAi with dsRNAs targeting the corresponding *T. castaneum* orthologs. Specifically, injection of dsRNA targeting *DvvABCG_13829*, which are most closely related to eye-color genes, gave a white-eye phenotype (Figure 8E). While injection of *DvvABCG_3712* dsRNA into pre-pupae caused developmental defects and resulted in 80% mortality (Figure 8C). Adult females treated with *DvvABCG_3712* dsRNA produced fewer eggs than females injected with buffer (Figure 10), and the eggs were not viable and failed to hatch (Figure 11), even after an additional four weeks of observation (Figure 8I). Injection of *DvvABCG_49457* dsRNA into larvae and pre-pupae resulted in molting defects in both stages, where about 80% of injected larvae died during molt, and development of the surviving pupae was arrested at the pupal stage (Figure 8D).

Injection of dsRNA specific for *DvvABCH_18290* into young larvae and pre-pupae arrested their development as they were preparing to molt and resulted in 100% mortality (Figure 8F), and injected larvae appeared to desiccate prior to death (personal observation). In other species, orthologs of *DvvABCH_18290* are known to transport cuticular lipids that are deposited in the outer epicuticle layer to form a waterproof barrier (Guo et al., 2015; Broehan et al., 2013). Therefore, desiccation is not an unexpected loss-of-function phenotype for these genes.

DISCUSSION

D. virgifera virgifera is a serious agricultural pest, and since its genome sequence is not yet publically available, the transcriptomic data presented here is a particularly valuable genetic resource. Moreover, due to the importance of ABC transporters in resistance development, the 65 ABC transporter genes we identified are expected to be useful in downstream studies. For example, in recent years ABC transporters have become a major focus for research in arthropods because of their roles in xenobiotic transport and insecticide resistance (Lage et al., 2003; Tian et al., 2017; Labbe et al., 2011; Merzendorfer et al., 2014; Dermauw et al., 2014). In particular, ABC transporters have been implicated as targets for *Bt* toxins (Heckel, 2015). Gahan et al., (2010), reported *Bt* resistance to have been genetically linked to *HvABCC2* in *Heliothis virescens* and *HaABCC2* in the cotton bollworm, *Helicoverpa armigera* (Xiao et al., 2014). Recently, Tay et al., (2015), demonstrated that a member of subfamily A, *HaABCA2*, is involved in *Bt* mode of action in *H. armigera*, Thus, highlighting the importance of studying this protein superfamily in *D. virgifera virgifera*.

Here we used RNAi to determine if eight *D. virgifera virgifera* genes, each a putative one-to-one ortholog of a *Tribolium* ABC transporter with a documented RNAi phenotype, served a similar function in *D. virgifera virgifera*. Interestingly, our RNAi results do indeed demonstrate that these eight genes play similar roles in both species. While some loss-of-function phenotypes included a visible developmental defect such as loss of eye pigmentation, others simply caused growth arrest, and/or death. However, one of our most interesting findings was of two ABC transporters whose loss-of-function phenotype results in females that either fail to lay eggs, or whose eggs never hatch. These genes are exciting new targets for RNAi-based management of this pest.

Given the species specificity of RNAi technology, ABC transporters could be ideal targets due to the fact that they may have less sequence conservation than some of the vital genes currently being tested. RNAi against several of our targeted *DvvABC* genes resulted in lethality. For example, targeting genes necessary for survival may also be useful in pest control. *DvvABCA_18330* knockdown gave the same phenotype as seen in *T. castaneum* (Broehan et al., 2013), and resulted in significant rates of death during the pupal-to-adult molt. Severe phenotypes were also seen with RNAi of *DvvABCE_2830* and *DvvABCF_2701*. ABCE and ABCF subfamilies are highly conserved across all phyla; they lack TMDs and therefore do not function as transporters. Instead, ABCE proteins play a role in ribosome recycling and regulation of protein translation (Barthelme et al., 2011), whereas ABCFs play a role in translation (Paytubi et al., 2009). Because of their role in translation and ribosome biosynthesis, ABCE and ABCF proteins are essential for all life stages (Barthelme et al. 2011). These genes are highly conserved across taxa in both sequence and RNAi phenotype (Broehan et al., 2013). Given their likely role in basic cell function, the lethal phenotype from RNAi is not surprising. Targeting *DvvABCG_49457* and *DvvABCH_18290* both caused molting defects that resulted in mortality. This result was consistent with RNAi knock-down of *TcABCG8* in *T. castaneum*, but Broehan et al., (2013) also reported that injected individuals prematurely developed compound eyes during the larval stage; we did not observe an eye phenotype in *D. virgifera virgifera*. This could be because most of the injected *D. virgifera virgifera* larvae failed to develop into the next stage and eventually died, so they may not have had the opportunity to develop compound eyes.

The ABCG proteins are half-transporters that form the second largest ABC subfamily (19 members) in *D. virgifera virgifera* (Table 2). In insects, some of the first ABCGs to be characterized were pigment transporters (*brown*, *scarlet* and *white* genes) in *D. melanogaster* (Sullivan et al., 1974; Mackenzie et al., 1999). Mutants of *white* are characterized by white eyes (i.e. complete loss of eye pigmentation), *brown* mutants by dark brown eyes (i.e. loss of red pigments), and *scarlet* mutants by bright red eyes (i.e. loss of brown pigments) (Mackenzie et al., 1999). Studies have revealed that some ABCG proteins perform a physiological role due to their ability to transport lipids, sterols, and drugs (Tarr et al. 2009). RNAi targetting *DvvABCG_13829* gave white eye-color phenotypes, this is consistent with Broehan et al., (2013). Our findings support that *DvvABCG_13829* is part of the ommochrome pathway, and is likely acting as a heterodimer to import ommochrome pigments into the eyes. The *white* gene is necessary to transport both pigment types in *D. melanogaster*, thus loss of this gene's function results in loss of all visible eye pigments. Not surprisingly, loss of *white* function in *D. virgifera virgifera* results in white eyes, just as it does in *D. melanogaster* and *T. castaneum* (Grubbs et al., 2015). A more interesting result would be RNAi targeting the *ABCG-9A* transcript (*scarlet*) since loss of *scarlet* function in *T. castaneum* results in a white-eyed phenotype, rather than the red-eyed phenotype seen in flies (Lorenzen et al., 2002; Broehan et al., 2013; Grubbs et al., 2015). While the same is likely true in *D. virgifera virgifera*, this hypothesis hasn't yet been confirmed.

In *D. melanogaster* a third ABCG transporter, Brown, is required for proper pigmentation of the eye. In flies, Brown dimerizes with White and transports pteridine-based pigments into the eye. Although a *brown* gene has been found in the *T. castaneum* genome, its function is not known (Grubbs et al., 2015). While our initial survey of the *D. virgifera virgifera* transcriptome failed to idenitify *scarlet* and *brown*, a later assembly revealed a *scarlet* ortholog. In summary, this study provides the first insights into the biology of ABC transporters in *D. virgifera virgifera* and provides a much-needed resource for comparative genomics/transcriptomics with other species and will also greatly aid annotation of the *D. virgifera virgifera* genome when the sequence becomes available.

Table 1: Primer sequences used for dsRNA synthesis and RT-PCR analysis

Gene	Sequences	Purpose
DvvABCA_18330 -F	TAATACGACTCACTATAGGGGAGATGGTGTGACCTGGAGC	dsRNA synthesis
DvvABCA_18330 -R	TAATACGACTCACTATAGGGACGGTGAGCTCGTCGAAAAT	dsRNA synthesis
DvvABCA_18330 -F3	GCATGAGGTTGGATGTCATC	RT-PCR
DvvABCA_18330 -R3	GTCCAGCGGTACTTAAGAGAG	RT-PCR
DvvABCB_19147-F	TAATACGACTCACTATAGGGGGATGCGTTGGTGTGTATGC	dsRNA synthesis
DvvABCB_19147-R	TAATACGACTCACTATAGGGAGGATTCGCCCTTTCGATGG	dsRNA synthesis
DvvABCB_19147-F3	TGGTCGGCAAATGGTAGGAG	RT-PCR
DvvABCB_19147-R3	CACCGTAATGGAGGTTATGCC	RT-PCR
DvvABCE_2830-F	TAATACGACTCACTATAGGGCCTGGGCAACCTTCAACTCA	dsRNA synthesis
DvvABCE_2830-R	TAATACGACTCACTATAGGGTTCCTGGACGGTTTTGTCCC	dsRNA synthesis
DvvABCE_2830-F3	ACACGATCGGCCAAGTAGGTC	RT-PCR
DvvABCE_2830-R3	GGATCCTCCAGATTGGACAGA	RT-PCR
DvvABCF_2701-F	TAATACGACTCACTATAGGGGCCGCTGCTAATAGTGGAGA	dsRNA synthesis
DvvABCF_2701-R	TAATACGACTCACTATAGGGCTGGTCGTGGGAAACGATCA	dsRNA synthesis
DvvABCF_2701-F3	CAGGTACGTGATGAATCTCCAG	RT-PCR
DvvABCF_2701-R3	TGCCAAGGCCACTCTTGCTT	RT-PCR
DvvABCG_3712-F	TAATACGACTCACTATAGGGACGGTATGTCCGCCAATGTT	dsRNA synthesis
DvvABCG_3712-R	TAATACGACTCACTATAGGGGCTCTCCACATGCTACCTCC	dsRNA synthesis
DvvABCG_3712-F3	GCACGTCAGCTTCGGTCTAT	RT-PCR
DvvABCG_3712-R3	GGGGAAAGACAGTCGTCCTG	RT-PCR
DvvABCG_49457-F	TAATACGACTCACTATAGGGTGCTCTCGAAGGAACACTGG	dsRNA synthesis
DvvABCG_49457-R	TAATACGACTCACTATAGGGAAGCCATACAGCGTTGTCGA	dsRNA synthesis
DvvABCG_49457-F3	CGTAGGCAGTATCGAGATGACG	RT-PCR
DvvABCG_49457-R3	CAACCAACAGCACGATCTGTC	RT-PCR
DvvABCG_13829-F	TAATACGACTCACTATAGGGCGACCTCTGGCTTGGATTCT	dsRNA synthesis
DvvABCG_13829-R	TAATACGACTCACTATAGGGCCATTCACCAACCTAGCTCC	dsRNA synthesis
DvvABCG_13829-F3	CGTTCGCCTCAGAAATGCTG	RT-PCR
DvvABCG_13829-R3	CCATCAGCATCCTCTCTGGTT	RT-PCR
DvvABCH_18290-F	TAATACGACTCACTATAGGGGTGTTACACCGGCTACCCAA	dsRNA synthesis
DvvABCH_18290-R	TAATACGACTCACTATAGGGCCCGTTCTAACCGCCTCTTT	dsRNA synthesis
DvvABCH_18290-F3	CCCCATTTTACGGTACTTGCTAGG	RT-PCR
DvvABCH_18290-R3	AGCGGTAAGCTCCTGGCAGAA	RT-PCR
DvvRPS6-F	TTGAAGAAGAAGAGGTGC	RT-PCR
DvvRPS6-R	ACCTACGCCTCTTCAACATC	RT-PCR

Underlined sequence corresponds to T7 promoter

Table 2: Classification of *D. virgifera virgifera* ATP binding cassette (ABC) transporters

	***D. v. virgifera* transcript**			**Nearest *T. castaneum* ortholog**		
Subfamily	**Gene ID**	**Size (AA)**	**Contig Name**	**Accession**	**E-value**	**Identity(%)**
DvvABC-A	TBD	1644	*18330*	XP_008199153.1	0.0	60
DvvABC-A	TBD	1708	*50718*	KXZ75645.1	0.0	58
DvvABC-A	TBD	1757	*49125*	XP_008195104.1	0.0	42
DvvABC-A	TBD	1641	*266167*	XP_008195056.1	0.0	53
DvvABC-B	TBD	1247	*21313*	XP_967244.3	0.0	60
DvvABC-B	TBD	1257	*17742*	XP_008191266.1	0.0	63
DvvABC-B	TBD	667	*19147*	XP_015834348.1	0.0	71
DvvABC-B	TBD	716	*39715*	XP_001813375.1	0.0	75
DvvABC-B	TBD	834	*9796*	XP_008194672.1	0.0	76
DvvABC-B	TBD	657	*13664*	XP_008190820.1	0.0	60
DvvABC-B	TBD	682	*17837*	XP_972133.2	0.0	69
DvvABC-C	TBD	1268	*41801*	XP_969849.1	0.0	37
DvvABC-C	TBD	1257	*44708*	XP_015836131.1	0.0	44
DvvABC-C	TBD	1252	*48952*	XP_971802.2	0.0	48
DvvABC-C	TBD	1285	*17573*	XP_015836083.1	0.0	44
DvvABC-C	TBD	1556	*51687*	XP_008197283.1	0.0	73
DvvABC-C	TBD	1297	*21020*	EFA03948.2	0.0	52
DvvABC-C	TBD	1234	*222633*	XP_971802.2	0.0	46
DvvABC-C	TBD	1343	*18126*	EFA04472.2	0.0	57
DvvABC-C	TBD	1374	*49513*	XP_008193834.1	0.0	44
DvvABC-C	TBD	1343	*14070*	XP_008194093.1	0.0	51
DvvABC-C	TBD	1350	*22628*	XP_008193834.1	0.0	56
DvvABC-C	TBD	1345	*20002*	EFA04472.2	0.0	58
DvvABC-C	TBD	1364	*7536*	XP_008193834.1	0.0	61
DvvABC-C	TBD	1377	*47333*	XP_008193834.1	0.0	59
DvvABC-C	TBD	753	*49618*	XP_015835265.1	0.0	76
DvvABC-C	TBD	1535	*45163*	XP_008192060.1	0.0	61
DvvABC-C	TBD	1082	*43960*	XP_973693.2	0.0	48
DvvABC-C	TBD	1224	*48940*	XP_015836125.1	0.0	42
DvvABC-C	TBD	1165	*217405*	XP_015835266.1	0.0	50
DvvABC-C	TBD	871	*10132*	XP_008200429.1	0.0	55
DvvABC-C	TBD	1258	*48300*	XP_971632.1	0.0	44
DvvABC-C	TBD	1324	*47673*	XP_969781.1	0.0	72
DvvABC-C	TBD	1258	*5345*	XP_015836093.1	0.0	40
DvvABC-C	TBD	1331	*22413*	XP_969781.1	0.0	55
DvvABC-C	TBD	1260	*18709*	XP_008193834.1	0.0	53
DvvABC-C	TBD	1329	*21941*	XP_969849.1	0.0	48
DvvABC-C	TBD	1324	*15305*	XP_969781.1	0.0	64
DvvABC-C	TBD	1320	*12562*	XP_972534.1	0.0	49
DvvABC-C	TBD	1307	*10642*	XP_008195764.1	0.0	60
DvvABC-C	TBD	1308	*41602*	XP_008193119.1	0.0	50
DvvABC-C	TBD	1318	*12703*	KYB27686.1	0.0	54
DvvABC-C	TBD	1310	*14968*	EFA03655.1	0.0	49
DvvABC-D	TBD	755	*11014*	XP_971218.1	0.0	77
DvvABC-D	TBD	658	*11628*	XP_015838765.1	0.0	78
DvvABC-E	TBD	609	*2830*	XP_968009.1	0.0	92
DvvABC-F	TBD	922	*2701*	XP_971562.1	0.0	90
DvvABC-F	TBD	624	*802*	XP_966990.1	0.0	89
DvvABC-F	TBD	711	*9935*	XP_972814.1	0.0	84

Table 2. Continued

D. v. virgifera transcript				Nearest *T. castaneum* ortholog		
Subfamily	**Gene ID**	**Size (AA)**	**Contig**	**Accession**	**E-value**	**Identity (%)**
DvvABC-G	TBD	660	9811	XP_008192053.1	0.0	69
DvvABC-G	TBD	668	3712	XP_001813184.1	0.0	77
DvvABC-G	TBD	720	14042	XP_973458.1	0.0	76
DvvABC-G	TBD	652	10897	XP_008192849.1	0.0	63
DvvABC-G	TBD	641	22358	XP_015834971.1	0.0	63
DvvABC-G	TBD	604	23081	XP_971735.1	0.0	54
DvvABC-G	TBD	638	13051	XP_015834339.1	0.0	60
DvvABC-G	TBD	622	38769	XP_973526.1	0.0	54
DvvABC-G	TBD	658	13829	NP_001034521.1	0.0	59
DvvABC-G	TBD	941	49457	XP_968472.1	0.0	73
DvvABC-G	TBD	643	36869	XP_968555.2	0.0	71
DvvABC-G	TBD	651	79525	NP_001306193.1	0.0	61
DvvABC-H	TBD	714	20789	XP_015839275.1	0.0	43
DvvABC-H	TBD	704	18290	XP_008198313.1	0.0	84
DvvABC-H	TBD	796	5118	XP_973444.1	0.0	43
DvvABC-H	TBD	763	11818	XP_967359.1	0.0	72

Table 3: Results of RNAi of select ABC transporters

DvvABCA_18330	Pre-pupal	60%	Deformed wings & elytra	8A
DvvABCB_19147	Larval	100%	Lethal	NS
	Pre-pupal	100%	Defect in pupal-adult molt	8B
	Eclosed females	0%	Malformed ovaries; low egg lay	8J
DvvABCE_2830	Larval	100%	Lethal	8G
DvvABCF_2701	Larval	100%	Lethal	8H
DvvABCG_3712	Pre-pupal	80%	Lethal; pupal developmental arrest	8C
	Eclosed females	0%	Prevented embryonic development	8I
DvvABCG_13829	Pre-pupal	0%	Pigmentation defect; white eyes	8E
DvvABCG_49457	Larval	100%	Lethal at molting	NS
	Pre-pupal	80%	Lethal pupal developmental arrest	8D
DvvABCH_18290	Larval	100%	Lethal at molting	NS
	Pre-pupal		Lethal at adult-pupal transition	8F

NS = image not shown

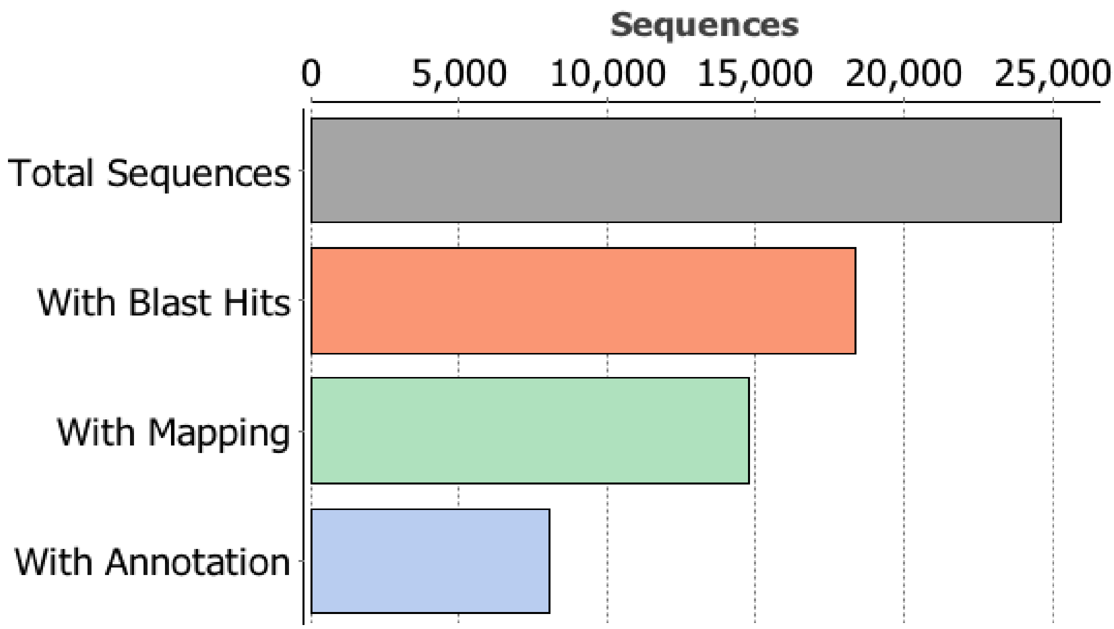

Figure 1: Blast2GO annotation results for the combined *D. virgifera virgifera* transcriptome. Among the 25,296 contigs used for the BLASTx search against the NCBI nr protein database, BLASTx analysis revealed over 18,343 contigs shared significant identity with known arthropod proteins.

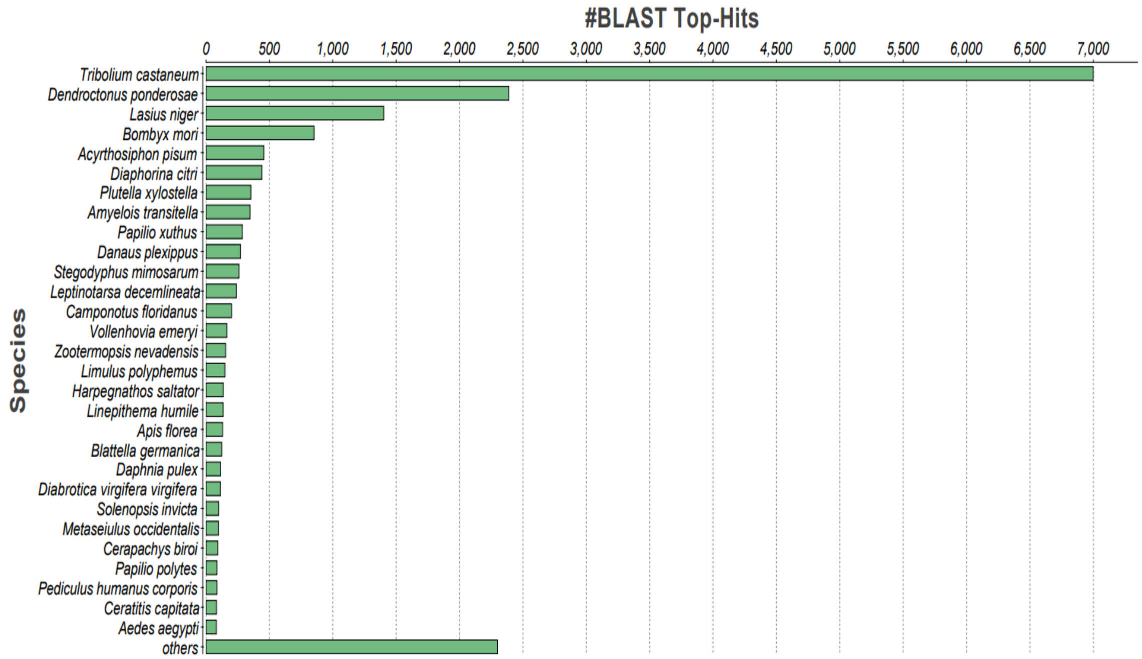

Figure 2: Top-Hits species distribution from Blast2GO. The most represented species in the top scoring BLASTx-matches the *D. virgifera virgifera* contigs when compared to an arthropod-specific database.

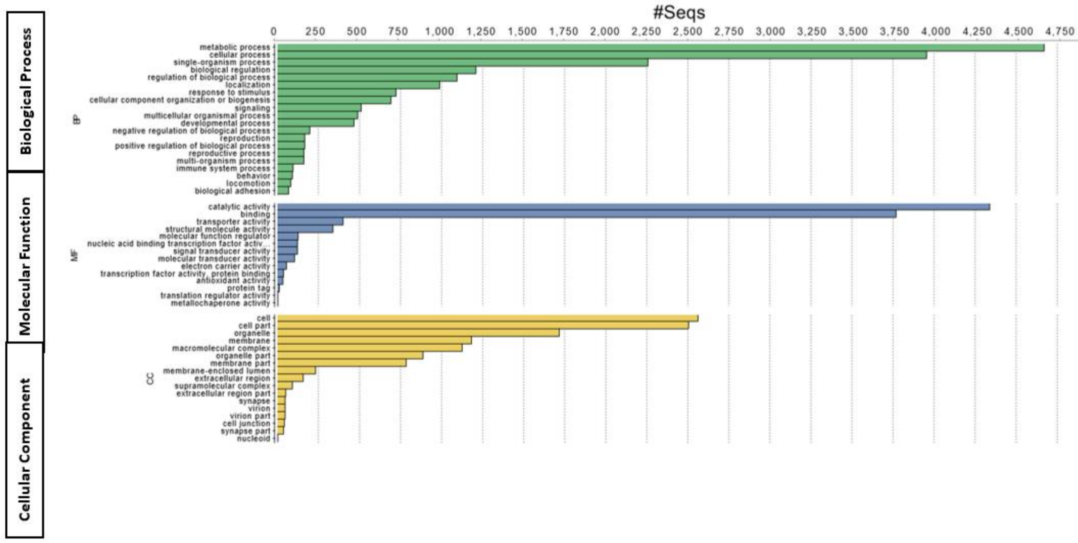

Figure 3: Gene ontology classification of the *D. virgifera virgifera* transcriptome.

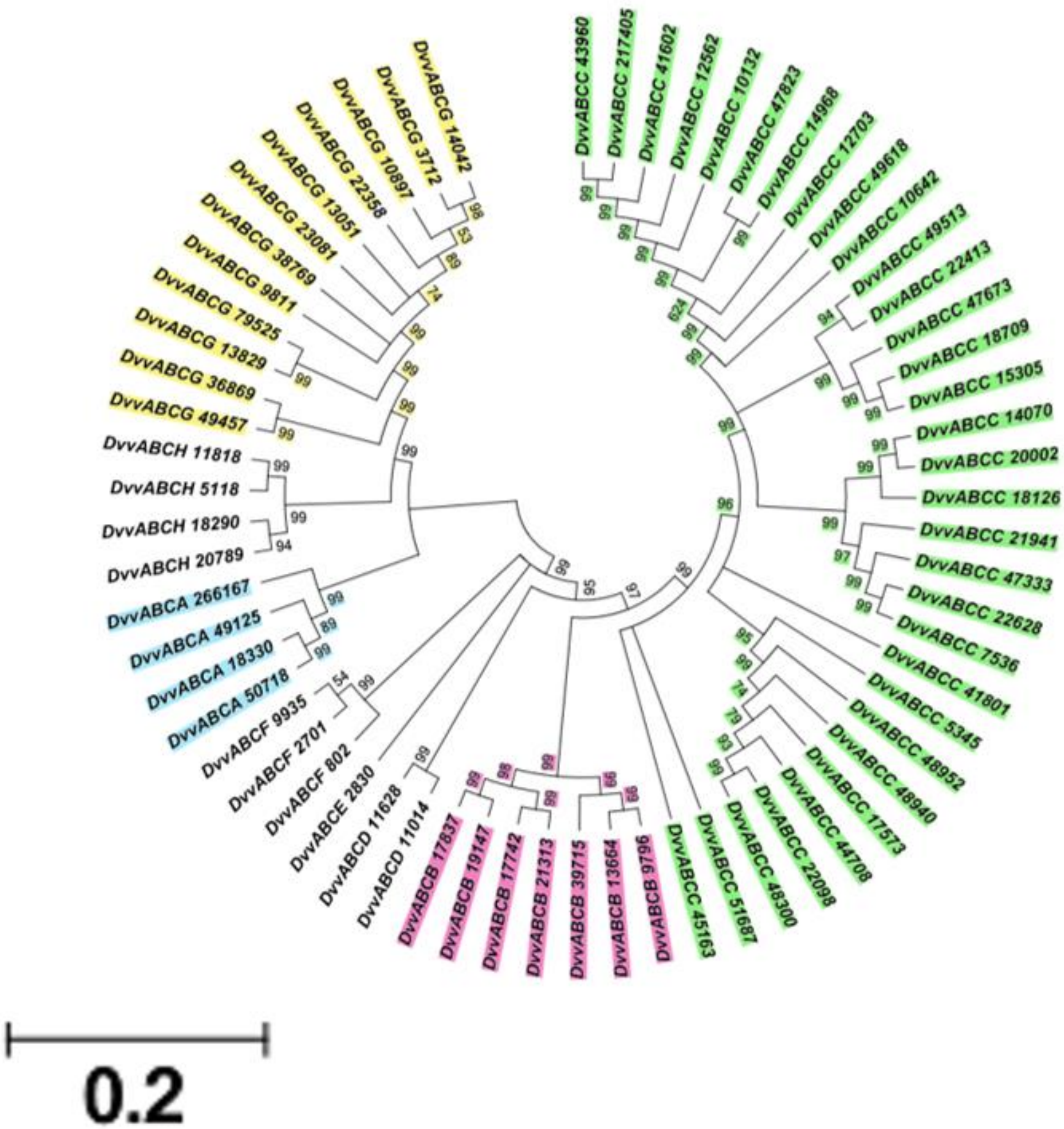

Figure 4: Phylogeny of ABC transporters in *D. virgifera virgifera*. The scale bar indicates an evolutionary distance of 0.5 amino acid substitutions per site. Bootstrap values are given in percentages at the internodes.

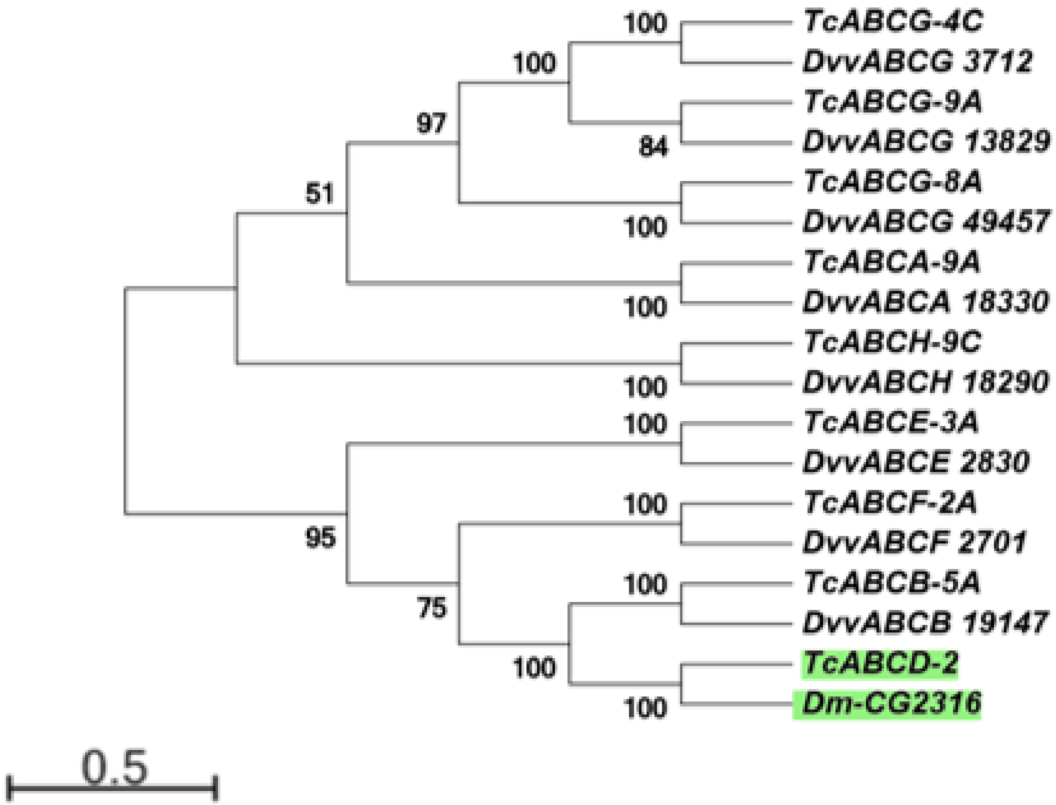

Figure 5: Phylogenetic relationships of select *D. virgifera virgifera* ABC transporters targeted with RNAi to their *T. castaneum* orthologs. The scale bar indicates an evolutionary distance of 0.5 amino acid substitutions per site. Bootstrap values are given in percentages at the internodes. *T. castaneum* and *Drosophila melanogaster* were used as an outgroup.

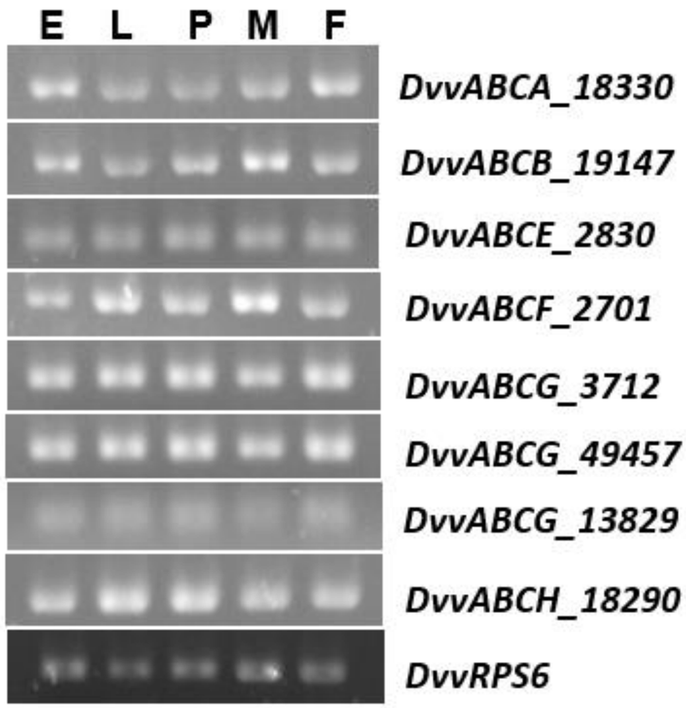

Figure 6: Developmental expression profile of select *D. virgifera virgifera* ABC transcripts. RT-PCR results from RNA isolated from E (eggs); L (larvae); P (pupae); M (Male); F (female). *RPS6* was used as a positive control.

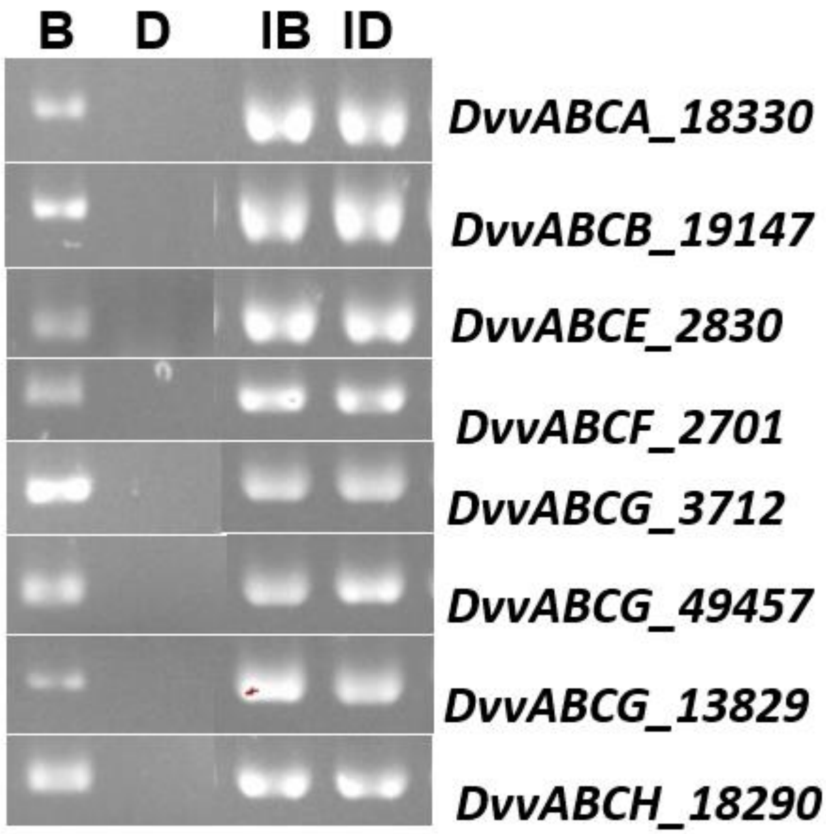

Figure 7: RNAi gene knockdown confirmed by RT-PCR. Target RNA levels were evaluated five days after injection. Gene names given next to gel samples. The lanes are as follows: RNA from pools of buffer injected (B) individuals, dsRNA injected (D) individuals, and the highly-conserved housekeeping gene, *DvvRPS6*, was used to assess template quality in buffer injected (IB) as well as dsRNA injected (ID) individuals.

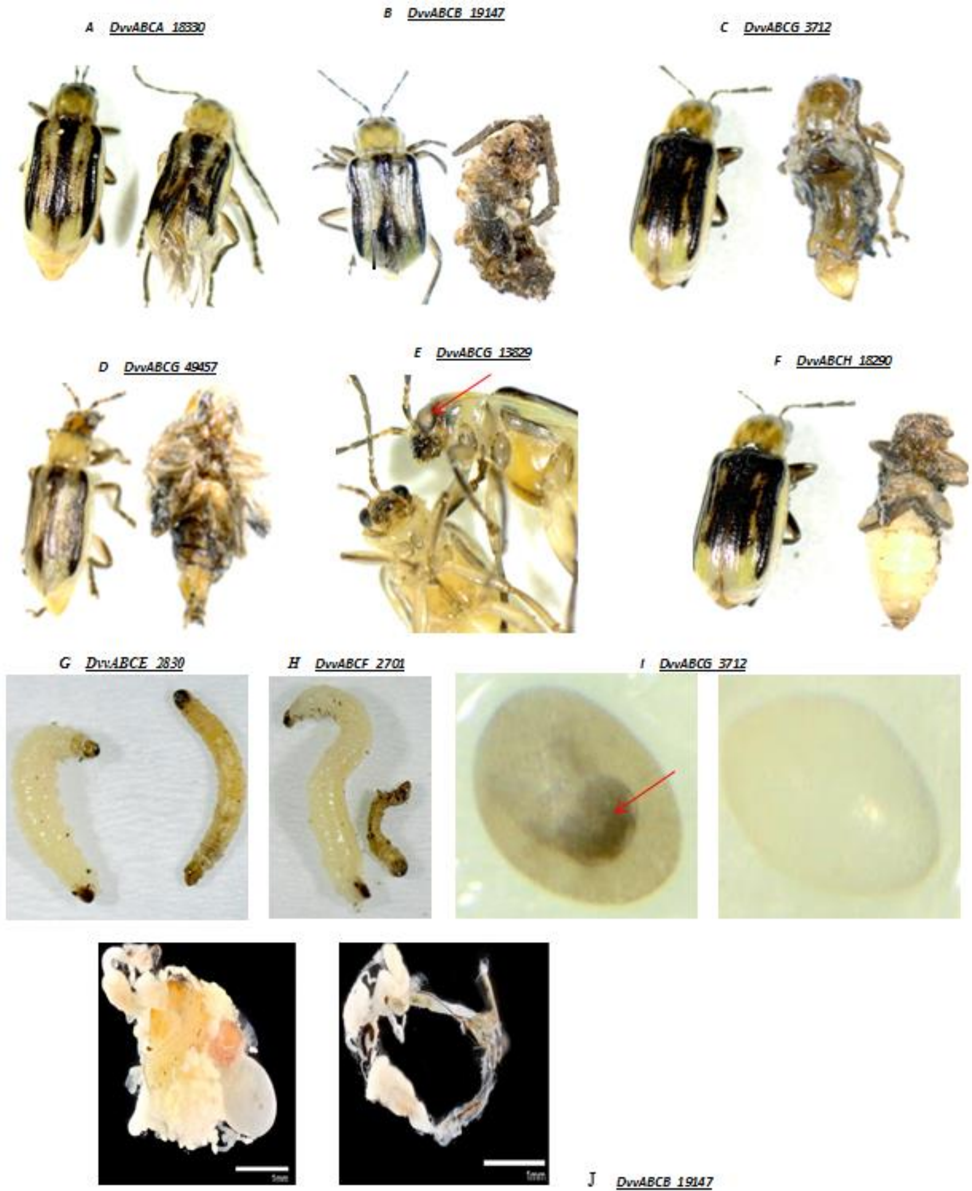

Figure 8: Developmental effects of ABC transporter knockdown by RNAi. Buffer-injected control (right) of comparable stage individuals are shown next to experimentals in each image. (A) *DvvABCA-18330* – pre-pupal injection caused defects in adult wing development. (B) *DvvABCB-19147* –pre-pupal injection caused molting defects during eclosion. (C, D&F) *DvvABCG-3712, DvvABCG-49457* and *DvvABCH-18290* – larval and pre-pupal injections caused severe molting defects during eclosion (individuals injected as pre-pupae shown). (E) *DvvABCG-13829* – pre-pupal injections caused loss of eye pigment (arrow). (G-H) *DvvABCE-2830* and *DvvABCF-2701* – larval injection caused reduction in body mass and death before molting. (I) *DvvABCG-3712* – injections into adult females prevented embryonic development in oviposited eggs (arrow indicates developed embryo). (J) *DvvABCB-19147* – injections into adult females caused disruption of ovary development.

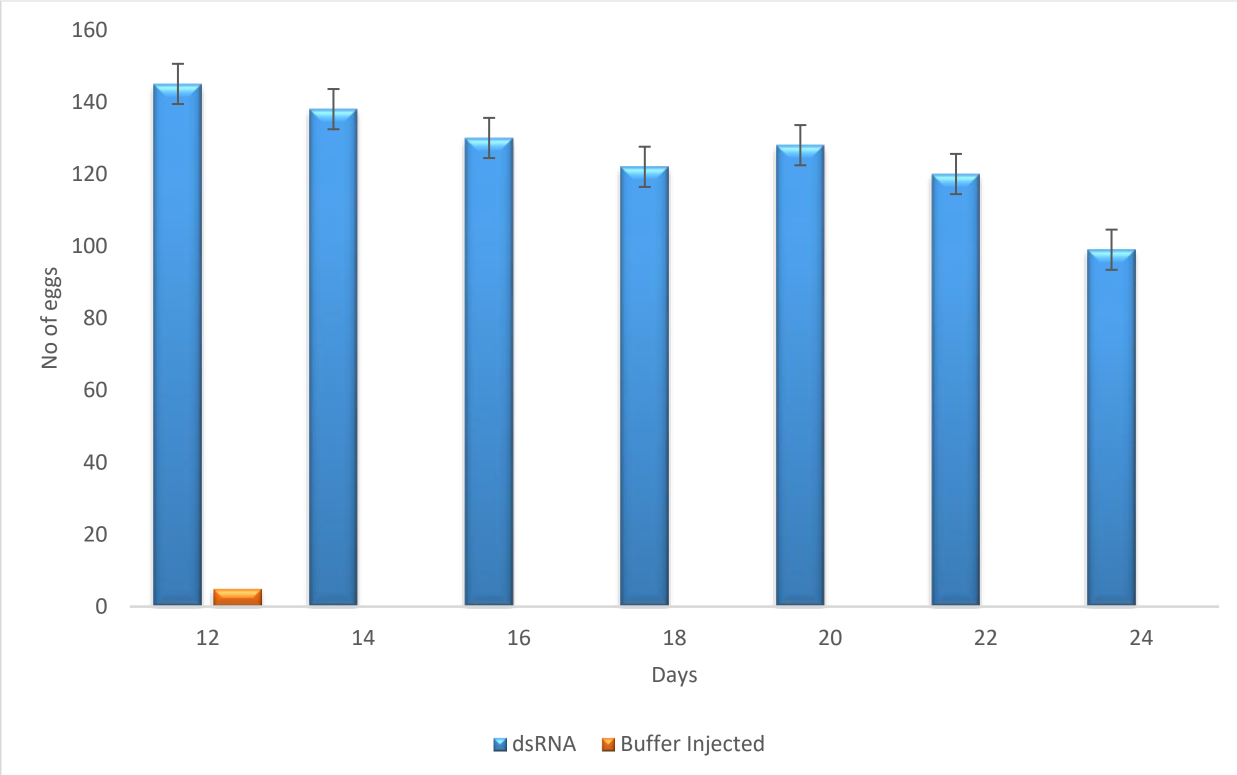

Figure 9: Effects of *DvvABCB_19147* RNAi on oviposition. Females injected with *DvvABCB_19147* dsRNA failed to lay eggs, while buffer-injected females lay near-normal numbers. The eggs laid within a period of two weeks were counted every other day.

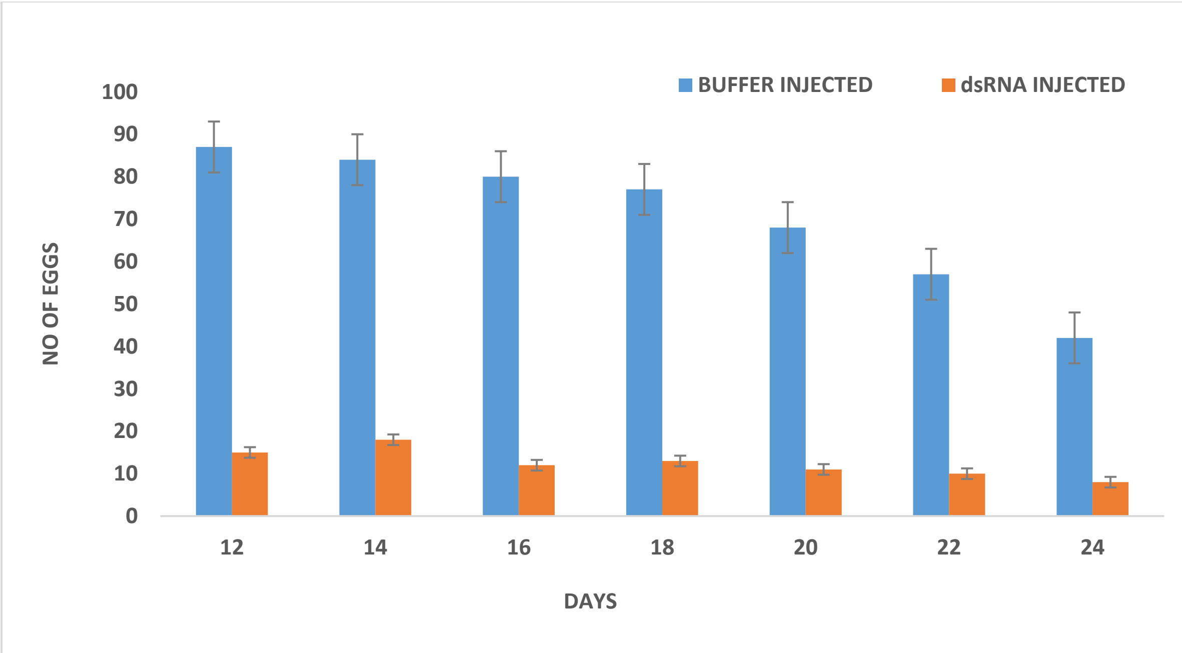

Figure 10: Effects of *DvvABCG_3712*RNAi on egg laying. Females injected with *DvvABCG_3712* dsRNA failed to lay eggs, while buffer-injected females lay near-normal numbers. The eggs laid within a period of two weeks were counted every other day.

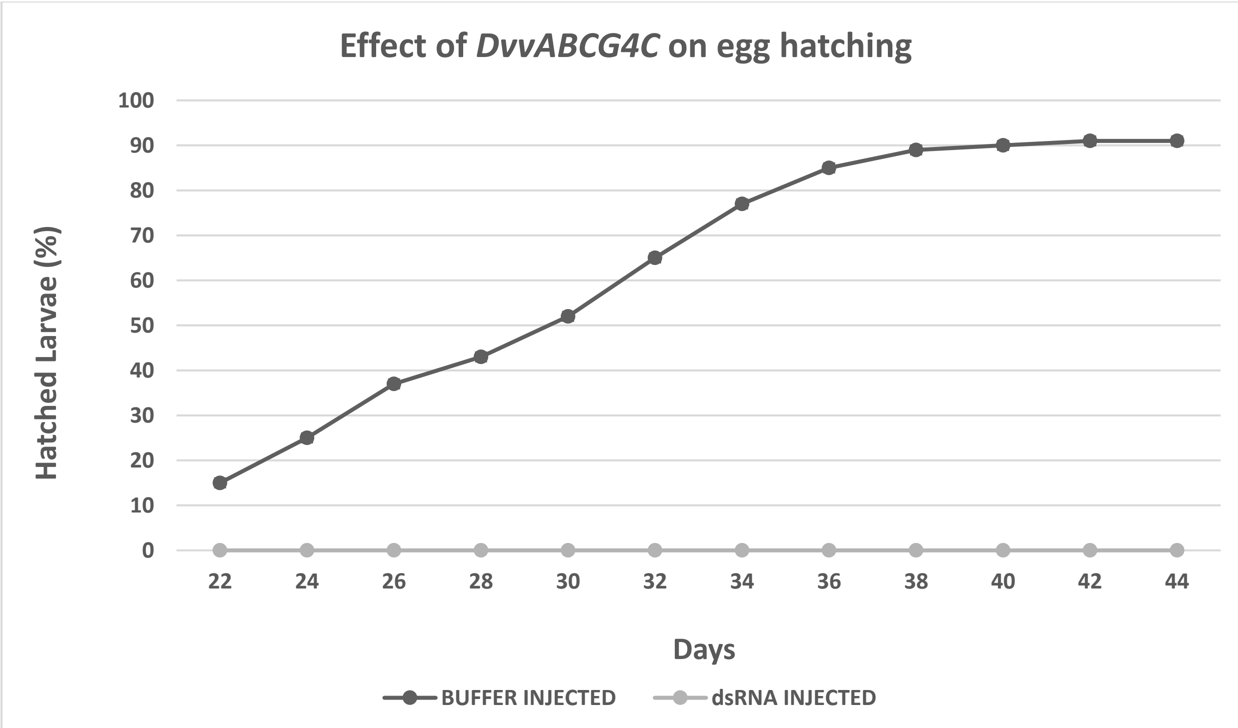

Figure 11: Effect of *DvvABCG_3712* RNAi on egg hatching. Eggs laid by females treated with *DvvABCG-4C* dsRNA failed to hatch, while those laid by buffer-injected females hatched successfully.

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CHAPTER 4

Transcriptome Analysis and Systemic RNAi Response in the Kudzu Bug, *Megacopta cribraria*

ABSTRACT

The kudzu bug, *Megacopta cribraria* (Hemiptera: Plataspidae), a native of Asia, arrived in the southeastern United States in 2009 and has rapidly become an economically important pest of soybeans, *Glycine max* (L.) Merrill. While pyrethroid-based insecticides are effective against kudzu bugs, increased use could lead to resistance, and cause additional harm to non-target species such as pollinators. Here we investigate the potential of RNA interference (RNAi) as a possible control strategy for *M. cribraria*. Since limited genetic data was available for this species, we first isolated and sequenced RNA from four groups of individuals; mixed-staged embryos, mixed-staged nymphs, adult females and adult males. The combined *M. cribraria* transcriptome assembly consists of 12,857 contigs, 11,224 of which had at least one significant match in NCBI's non-redundant protein database. Importantly, we were able to identify orthologs of many of the RNAi pathway genes, including *Dicer2* and *Argonaute-2*, however, no transcript sharing significant homology with the *systemic RNA interference deficient-1* (*sid-1*) gene was found. Although sid-1 plays a key role in double-strand RNA (dsRNA) uptake in *Caenorhabditis elegans*, it is unclear what role *sid-1* like genes play in insects. To assess RNAi functionality in *M. cribraria* we next surveyed the transcriptome for potential RNAi target genes and tested one of these, *catalase*, via microinjection of target-specific dsRNA into forth-instar nymphs. The resultant phenotypes (mortality and inhibition of nymphal growth) and RT-PCR results indicate that we achieved gene-specific knockdown of *catalase*, demonstrating that the RNAi pathway is functional in *M. cribraria*, and can induce a systemic response. This is the first published transcriptomic data from this species; these findings represent a valuable resource to aid future research on functional genomics in this economically important species and could provide insight into new pest control methods.

INTRODUCTION

The kudzu bug, *Megacopta cribraria* Fabricius (Hemiptera: Plataspidae), is endemic to Asia, but was discovered in Georgia, USA during the fall of 2009 (Suiter et al., 2010). *M. cribraria* has since been reported in twelve additional states (Alabama, Arkansas, Delaware, Florida, Kentucky, Louisiana, Maryland, Mississippi, North Carolina, South Carolina, Tennessee, Virginia), as well as the District of Columbia (www.kudzubug.org 2018; Gardner et al., 2013). This rapid spread was attributed to it being a strong flyer (Suiter et al., 2010). While not a major pest in its home range, *M. cribraria* is a pest in southern regions of the U.S. Its pest status is in large part due to its impact on soybeans (*Glycine max* L. Merrill); the second most planted field crop in the U.S. generating about $42 billion dollars annually (USDA-ERS 2018). If untreated, *M. cribraria* infestations can devastate soybean production, causing yield losses of up to 60% (Seiter et al., 2013). The sustainability of this crop is not only of economic importance but is also vital to overall food security (USDA-ERS 2016). In addition, *M. cribraria* is also a threat to other legume crops and various fruit trees (Eger et al., 2010, Ruberson et al. 2013, Seiter et al., 2013).

The primary reproductive hosts of *M. cribraria* in the United States are the invasive kudzu plant, *Puereria montana* (Loureiro) Merrill variety *lobata* (Willdenow), and soybeans; the insects can complete two generations per year in the southeastern U.S. (Suiter et al., 2010, Zhang et al., 2012). The first generation is typically completed on kudzu, or early-planted soybeans (Del Pozo-Valdivia and Reisig 2013, Seiter et al., 2013), while the second generation can develop on kudzu or soybeans (Zhang et al., 2012, Seiter et al., 2013a). Interestingly, *M. cribraria* development may also occur on secondary hosts such as lima bean (*Phaseolus lunatus* L. [Fabales: Fabaceae]) and pigeon pea (*Cajanus cajan* L. [Fabales: Fabaceae]) (Zhang et al., 2012, Medal et al., 2013, Ruberson et al., 2013, Seiter et al., 2013, Blount et al., 2015). Apart from being an agricultural pest, *M. cribraria* is also a nuisance pest. The problem stems from the insects forming overwintering aggregations both in and around homes (Suiter et al., 2010).

M. cribraria nymphs and adults feed by piercing the plant's epidermis and sucking sap from the phloem (Tayutivutikul and Yano 1990, Thippeswamy and Rajagopal 2005, Suiter et al., 2010). These feeding activities deprive the host of water and nutrients required for growth (Stubbins et al., 2017), and therefore weakens and stunts the plant, reducing the number of pods per plant and number of seeds per pod (Seiter et al. 2013; Waldvogel and Alder, 2011). Although insecticide applications have been an effective method for reducing pest pressure from *M. cribraria* in soybean fields (Miao et al., 2016; Seiter et al., 2015), continuous usage will likely hasten resistance development, and result in increased negative pressure on beneficial species, such as pollinators and parasitoids (Gay 2012; Ademokoya et al., 2017). Also, control of this species may be more challenging than control of leaf-feeding insects because unlike leaf feeders that ingest topical insecticides along with leaf tissue, this mode of feeding could greatly reduce the amount of topical insecticide *M. cribraria* ingests (Stubbins et al., 2017).

Biological control methods are also available. Specifically, two egg parasitoids, *Paratelenomus saccharalis* (Dodd) (Hymenoptera: Platygastridae), and *Ooencyrtus nezarae* (Hymenoptera: Encyrtidae), have been shown to be effective in parasitizing *M. cribraria* eggs in the U.S. (Ruberson et al., 2013; Ademokoya et al., 2017). Some speculate that these parasitoids have contributed to the sudden decrease in *M. cribraria* populations over the past few years (Ademokoya et al., 2017). However, despite the current reduction in *M. cribraria* population size and the availability of both chemical and biological control methods, it is wise to investigate alternate control strategies since resistance is inevitable.

One promising alternative to chemical-based control is RNA interference (RNAi). RNAi is a naturally occurring phenomenon that results in gene-specific silencing (Price and Gatehouse 2008; Smagghe et al., 2010). When a double-stranded RNA (dsRNA) is introduced into the cell, its recognized by an enzyme called Dicer and processed into small interfering RNAs (siRNAs). After processing, one strand of the siRNA is assembled into an RNA-induced silencing complex (RISC) in conjunction with the Argonaute multidomain protein, which is responsible for recognition and degradation of mRNA transcripts that are homologous to the dsRNA (Hannon 2002; Kim et al., 2009). This technique has been shown to be an effective control method for some agricultural pests (Baum et al., 2007; Yu et al., 2013), including some hemipterans (Price and Gatehouse 2008; Smagghe et al., 2010). Moreso, RNAi has proven to be an effective tool for studying gene function in some hemipterans. For example, Futahashi et al., (2010) investigated the biological role of *laccase2* in three hemipteran, *Riptortus pedestris* (Alydidae), *Nysius plebeius* (Lygaeidae) and *M. punctatissima* (Plataspidae). In this study, when *laccase2*-specific dsRNA was injected into last-instar nymphs, their cuticular pigmentation after adult molting was impacted. The results highlight the conserved biological role of *laccase2*, as well as the efficacy of RNAi in these species.

Interestingly, *M. cribraria* and *M. punctatissima* are considered by some to be distinct species (Hosakawa et al., 2014; McPherson 1941), while others suggest that they are conspecific (i.e. belong to same species) and consider them to be synonymous with one another (Eger et al., 2010). Since their identity in the U.S. is still unclear (Dhammi et al., 2016) I sought to perform RNA-Seq on individuals from the U.S. population and compare available sequence data to ascertain if there are significant differences and perhaps help address this controversy. In the process I also surveyed the transcriptomic data for key genes involved in the RNAi pathway and tested RNAi functionality by microinjecting dsRNA targeting *catalase* (*cat*), a highly-conserved gene known to be vital in other organisms (eg. *Drosophila melanogaster*). Our results both confirm the functionality and utility of RNAi in this species as well as demonstrate that *cat* expression is required for *M. cribraria* survival. Also, this study shows that the *M. punctatissima laccase-2* gene sequence is 99% identical to our *M. cribraria laccase-2* sequence.

MATERIALS AND METHODS

Insect collection and rearing

M. cribraria adults were collected from a patch of wild kudzu, *Puereria montana* (Loureiro) Merrill variety *lobata* (Willdenow), growing on the North Carolina State University campus in Raleigh, NC. Adults were maintained in the lab on soybean, *Glycine max L*. Merrill, under a controlled environment of 28^{0}C, 60% relative humidity (RH) and 14:10 light: dark (L:D) cycle in 60-cm^3 cages (BugDorm, MegaView Science, Taichung, Taiwan). The soybean plants used as host were grown and maintained under standard greenhouse conditions in a greenhouse at NCSU.

RNA isolation and Illumina sequencing

Total RNA was isolated from four separate flash-frozen (liquid nitrogen) *M. cribraria* samples (mixed-stage embryos, mixed-stage nymphs, adult males and adult females), using the RNeasy Mini Kit (Qiagen, Valencia, CA, USA) and treated with DNase I (Qiagen) according to the manufacturer’s instructions. The RNA was submitted to the Genomic Sciences Laboratory (North Carolina State University, NC USA) for quality assessment, 2x poly(A) selection, fragmentation, size selection (600- to 700-bp) and separate Illumina TruSeq libraries were then generated and sequenced on an Illumina MiSeq sequencer (2 x 300-bp).

Transcriptome assembly and annotation

Raw reads underwent an initial quality assessment using FastQC (Andrews, 2010), and were trimmed based on quality scores, and all remaining Illumina adapter sequences removed. Trimmed reads (all life stages) were *de novo* assembled into contigs using SeqMan NGen (DNASTAR, Inc; Madison, Wisconsin, USA) to generate a combined assembly. This dataset was annotated using Blast2GO software (4.0) (Conesa et al., 2005; Götz et al., 2008) with BLASTx comparisons to the non-redundant (nr) arthropod-specific database at the National Center of Biotechnology Information (http://blast.ncbi.nlm.nih.gov/). The combined graphs were created at level 2 for Biological Process (BP), Cellular Component (CC), and Molecular Function (MF) categories from Blast2GO.

RNAi pathway and *Catalase* sequence identification

A searchable database was generated from the *M. cribraria* combined assembly and the database searched (tBLASTn) using BlastStation software (TM Software Inc. Arcadia, CA, USA). The deduced amino-acid sequence of each *Cylas puncticollis*, the African sweetpotato weevil *core* RNAi gene (Prentice et al., 2015) was used as bait to identify the corresponding *M. cribraria* RNAi gene. Putative orthologs were identified via initial BLAST searches based on sequence identity (E-values less than 10^{-6}) and homology was determined via reciprocal BLAST comparison (BLASTx) to all known arthropod proteins in the nr database at NCBI. Only sequences having high-scoring hits to core RNAi genes were retained.

Phylogenetic trees were constructed using the putative *M. cribraria* (*Mc*) orthologs of *Dcr-2*, and *Ago-2*, along with aligned orthologous proteins from other species, the following species were selected: *Halyomorpha halys* (*Hh*), *Acyrthosiphon pisum* (*Ap*), *Aphis glycines* (*Ay*), *Tribolium* *castaneum* (*Tc*), and *Bemisia tabaci* (*Bt*). Sequence alignments were performed with ClustalW using MEGA 7 (Tamura et al., 2013), and subjected to phylogenetic analysis using maximum likelihood tree search and 1000 bootstrap replications in Mega 7. An optimal model of sequence evolution was determined for each data set by likelihood ratio tests and AIC within the Mega 7 program.

The *M. cribraria* transcriptomic database was queried with the deduced amino-acid sequence of the *T. castaneum catalase* (*Tccat*) gene. The top hit was assessed as described above for the core RNAi genes. A phylogenetic tree was constructed using cat proteins from the following species: *T. castaneum* (*Tc*), *H. halys* (*Hh*), *D. melanogaster* (*Dm*), *Bombyx mori* (*Bm*), *A. pisum* (*Ap*), *B. tabaci (Bt) Helicoverpa armigera (Ha),* and *Spodoptera litura (Sl).* Sequence alignments were performed as outlined above and subjected to phylogenetic analysis with 1000 bootstrap replications.

Primer design and *in vitro* dsRNA synthesis

Primers used to generate *Mccat*-specific dsRNA **(**Table 1) were designed using Vector NTI Advance (VNTI) software (Invitrogen), and PCR performed using 100ng of *M. cribraria* cDNA as template. The *Mccat* gene was amplified from developmental stage-specific cDNA template using cycling conditions of 95°C for 3 min, 40 cycles of 95°C for 30s, 58°C for 30s, and 72°C for 10s, and finally 4 min at 72°C. The PCR product was purified using a QIAquick PCR Purification Kit (Qiagen) according to the manufacturer’s instructions, then ligated into the pGEM-T vector (Promega, Madison, WI, USA), with the resulting plasmids used to transform chemically competent *E. coli* (Top10; Invitrogen). Recombinant clones were selected on LB agar containing ampicillin as described by the manufacturer. Plasmid DNA was isolated using a

Plasmid Mini Kit (Qiagen), and the insert sequenced at the Genomic Sciences Laboratory (NCSU), and confirmed by BLAST analysis (http://blast. ncbi.nlm.nih.gov). The cloned *Mccat* gene fragment was used as template in PCR reactions containing the following primers; T7 as a forward primer (due to location in pGEM), and a pGEM-specific reverse primer that was tailed with T7. PCR was performed with an initial denaturation of 95°C for 3 min, the 40 cycles of 95°C for 30s, 58°C for 30s, and 72°C for 10s, then 4 min at 72°C). The PCR products were confirmed via agarose gel electrophoresis and purified as described above and quantified on a Nanodrop 1000 spectrophotometer (Thermo Scientific, Waltham, MA, USA) and ~1.0 µg was used as template for dsRNA synthesis using the MEGAscript T7 *in vitro* Transcription Kit (Ambion, Foster City, CA, USA). Synthesized dsRNAs were purified using the MEGAclear Kit (Ambion) and concentration determined using a Nanodrop 1000 spectrophotometer (Thermo Scientific).

RNAi bioassay

Insects were anesthetized on ice for 30 min before microinjecting *Mccat*–specific dsRNA (concentration = 1 µg/µl) into the hemocoel of fourth-instar nymphs. This process was replicated three times, with at least 30 individuals per replicate. The same procedure was also conducted for control injections (buffer alone). Following injection, nymphs were allowed to recover at room temperature, before returning to soybean plants where they were held for monitoring phenotypes and downstream molecular analysis. Phenotypes were observed daily using a stereomicroscope, and transcript levels were assessed by RT-PCR using total RNA pooled from three injected individuals (one per replicate) at day 1 through day 5 time points. The earliest time point was 24-hours post injection, and the latest was five days post injection. The *M. cribraria ribosomal* *protein 6* (*McRSP6*) gene was used as an internal standard to estimate the relative expression of mRNA. The sequence of the *McRSP6* primers is given in Table 1.

RESULTS AND DISCUSSION

Transcriptome sequencing, assembly, and annotation

To generate a fairly representative combined transcriptome for *M. cribraria*, four separate samples of RNA (mixed-staged embryos, mixed-staged nymphs, adult females and adult males) were each sequenced using the Illumina (MiSeq™ 2000) platform. A total of 23,983,499 raw sequence reads of ~300 bp in length were obtained across the four libraries. Of these, 9,875,298 assembled into a single-combined transcriptome producing 12,857 contigs with an average length of 2008 bp and an average GC content of 48%. BLAST-based annotation was performed with Blast2GO (Conesa et al., 2005) using BLASTx against the arthropod-specific section of NCBI's non-redundant (nr) protein database. Among the 12,857 contigs derived from the *M. cribraria* transcriptome, BLASTx analysis revealed that 11,224 of these shared significant identity (*E*-values < 10^{-6}) with known arthropod proteins, and a subset of these received GO mapping and annotation terms (Figure 1). Sequences lacking significant identity to known arthropod proteins likely represent poorly conserved or novel sequences, as well as non-coding RNAs. The distribution of top BLAST hits by species showed that the brown marmorated stink bug, *Halyomorpha halys* was the most frequent, representing (>9000) of the matches (Figure 2).

Blast2GO also grouped annotated contigs into three broad Gene Ontology (GO) categories based on predicted function: Biological Processes, Molecular Function and Cellular Component (Fig. 3). The most dominant terms for Biological Process were cellular, metabolic and single organism processes, while the most frequent for Molecular Function were binding, catalytic and transporter activity. Lastly, the most frequent terms for Cellular Component were cell, organelle, and membrane (Fig. 3). As expected, GO analysis of the *M. cribraria* combined transcriptome indicates that the majority of biological processes, molecular functions, and cellular components are similar to those found in other published transcriptomes (Kaur et al., 2017; Sparks et al., 2014; Zhang et al., 2013). The SeqMan NGen assembly was assessed for its degree of completeness using BUSCO, and received a score of 2006, or 75% of the 2,675 genes in the arthropod reference set v. 9.0 were represented as either single copy or duplicated, thus indicating that a reasonable proportion of genes in the arthropod reference were represented within *M. cribraria* transcriptomic data.

Identification of RNAi-related genes

A searchable database was created, and the combined transcriptome was queried for the presence of core RNAi pathway genes (Prentice et al., 2015). BLAST analysis revealed 31 putative homologs in the *M. cribraria* transcriptome database **(**see Table 2, Appendix C). To confirm their identity the putative *M. cribraria* homologs were compared (BLASTp) to known arthropod proteins in the NCBI database. Twenty-nine of these shared the greatest identity to sequences from *H. halys*, while 2 shared more identity to *Operophtera brumata* and *Locusta migratoria* (Table 2). Although we could not identify orthologs for all 47 known RNAi pathway genes, there are many reasons this could occur.

Although our RNA-Seq analysis only identified 31 of 47 RNAi pathway genes, the remaining 16 genes could have been missed due to the fact that our survey is based on low-coverage transcriptomic data. It is entirely possible that these genes are in the *M. cribraria* genome, but are either transcribed at relatively low levels, or are expressed at time points not covered by our

RNA-Seq libraries. While these sequences were not present in our transcriptome dataset, many of these will likely be detected when the *M. cribraria* genome is sequenced.

Chief among the sequences we failed to identify is what is thought to be the insect version of the *systemic RNA interference deficient-1* (*sid-1*) gene. While *C. elegans* possesses *sid-1*, a gene that encodes a pivotal protein involved in dsRNA uptake, insects do not appear to have a clearly assignable one-to-one ortholog of *sid-1*, but rather have a gene known as *sid-1-like*. Previous analysis of several insect genomes and transcriptomes shows that the number of *sid-1-like* genes varies among insect species (Price and Gatehouse, 2008). For example, dipterans like *D. melanogaster* lack *sid-1-like* genes, while some hemipterans, hymenopterans, orthopterans and phthirapterans have been reported to have a single *sid-1-like* gene (Tomoyasu et al., 2008). Among lepidopterans the number of *sid-1-like* genes are even more diverse, with *Spodoptera exigua* having only one and *B. mori* having three copies (Price and Gatehouse, 2008). Interestingly, Sparks et al (2014), reported that the *H. halys* transcriptome lacks *sid-1-like* genes. It was first thought that the presence or absence of these genes explained the robust and systemic RNAi response in *T. castaneum* and the lack of systemic RNAi in *D. melanogaster*, respectively. However, there are reports that suggest the *sid-1-like* genes found in *T. castaneum* may not be critical for the systemic RNAi response observed in these beetles, but this was based on RNAi-mediated knockout of the *sid-1-like* genes and then assessing the impact via RNAi (Gourley et al., 2003). Since this did not affect the systemic RNAi response the authors concluded that the *sid-1-like* genes found in *T. castaneum* are not responsible for the movement of dsRNA across cell membranes (Gourley et al., 2003). This conclusion would be stronger if knockout was through CRISPR/Cas9 rather than RNAi, since the effect of CRISPR/Cas9 is permanent, and RNAi is not. Another gene, *FBX011*, is thought to be involved in dsRNA uptake in some species

(Sabin et al., 2009) and a *FBX11* ortholog was found in *M. cribraria* transcriptome. The core components of the RNAi machinery are proteins that, together with the small RNA fragments, are involved in gene silencing. Besides these core genes, many different factors have been identified that play a role in the efficiency of RNAi. Since the discovery of RNAi, significant efforts have been made to describe the molecular mechanisms of RNAi (Aravin, et al., 2007). Studies performed on several model insects, including *D. melanogaster*, *T. castaneum* and the silkworm, *Bombyx mori*, have revealed that the RNAi pathway is composed of two phases, the initiator phase, and the effector phase, and together they result in post-transcriptional gene silencing (PTGS) Vaucheret et al., 2001; Vaucheret and Fagard, 2001; Castel and Martienssen, 2013). The main components of RNAi are well conserved across phyla; however, the mechanism and systemic spread of silencing are highly diverged and gene regulation is mediated by a variety of RNA-based products (siRNAs, miRNA) (Shreve et al., 2013; Swevers et al., 2013). While systemic RNAi has been documented in several insects (Bucher et al. 2002; Tomoyasu and Denell 2004); it is assumed that all animals with systemic RNAi response use the mechanism described in *C. elegans*. Nevertheless, it seems clear that the systemic RNAi response is not universal, as the leading insect model, *D. melanogaster*, lacks a systemic RNAi response (Roignant et al., 2003). Therefore, more comprehensive searches for the proteins involved in the systemic RNAi mechanism in insects continues to be critically important for broadening our knowledge of RNAi and its possible applications in pest control.

In this study, we found putative orthologs for 31 RNAi pathway genes in the *M. cribraria* transcriptome. Our results, together with previous studies, highlight the conserved biological role of the RNAi pathway among hemipterans species (Upadhyay et al., 2013; Bansal and Andy, 3013; Clauvis et al., 2016). Phylogenetic analyses (Figure 4A, B) revealed the relationship of the major RNAi genes in *M. cribraria* to those found in other insect species. For example, phylogenetic analysis shows that *McDcr-2* and *McAgo-2* are grouped into clusters along with orthologs from other hemipterans as expected (Figure 4A & B), indicating that RNAi core genes are evolutionarily conserved within sampled Hemiptera (Figure 4). As expected, we did not find a *sid-2* ortholog, which to date appears to only be present in nematodes. Phylogenetic analyses of the *catalase* (*cat*) gene shows a similar relationship among sampled species. *Mccat* joins a cluster with the two sampled hemipterans indicating that these genes are evolutionarily conserved in the order, well separated from sequences present in Diptera and Lepidoptera (Figure 5).

Transcripts encoding sid-1 or sid-1-like, which are thought to be involved in dsRNA uptake were not found in the *M. cribraria* transcriptome. While these have been reported in other insect systems (excluding *Drosophila*), hemipterans, *A. pisum* and *H. halys*, have been shown to possess systemic RNAi, but no *sid-1-like* gene has been found in their genomes/transcriptomes (Mogilicherla et al., 2018; Lu et al., 2017; Sparks et al., 2014; Mutti et al., 2006). This suggests that sid-1-like may not be necessary for systemic RNAi and that these species may have other pathways for dsRNA uptake. Additionally, some recent studies have shown that the delivery of dsRNA either by microinjection or by feeding leads to gene knockdown. Injection of dsRNA targeting the homeotic gene *sex combs reduced* (*Scr*), which is responsible for determining segmental identity in early embryos, into *H. halys* females resulted in a range of defects in offspring, and death was observed prior to hatching (Lu et al., 2017). In addition, Mogilicherla et al., (2018) demonstrated that they could induce mortality in *H. halys* by injectiong or feeding nymphs dsRNAs targeting genes known to cause mortality in other insects. Thus the lack of an apparent *sid-1* ortholog in the *H. halys* transcriptome had no negative impact on RNAi silencing in their bioassays. Similarly, while transcripts encoding *sid-1* were not found in this study, gene knockdown via RNAi was confirmed in *M. cribraria.* While this implies that *sid-1* may not be necessary for this process in *M. cribraria,* with additional mechanisms and gene interactions remaining to be described in Hemiptera, it is also possible that a *sid-1* ortholog simply has not yet been found or recognized in Hemiptera.

RNAi Bioassay

To determine if the RNAi pathway is functional and capable of inducing a systemic RNAi response in *M. cribraria* as it does in *M. punctatissima* (Futahashi et al., 2010), we injected dsRNAs targeting the *M. cribraria catalase* (*Mccat*) gene into fourth-instar nymphs and assessed knockdown both phenotypically and molecularly at several time points. The dsRNA-treated individuals showed a significant decrease in transcript accumulation, while no change is seen in the buffer-injected controls (Figure 6). The decrease can be detected 3 days post injection and lasted through day 5 (Figure 6). The housekeeping gene *RPS6* maintained its expression level independent of the treatment (Figure 6). Moreover, knockdown of *Mccat* led to mortality among treated nymphs relative to buffer injected controls, with nymphal mortality being significantly higher in treated individuals compared to those injected with buffer alone. By day 5, mortality had reached an average of 75% in treated nymphs compared to 5% for buffer treated controls (Figure 7). In addition, nearly all dsRNA-treated individuals displayed a reduction in body size, and none survived to adulthood (data not shown); this is likely due to a reduction in *cat* expression since it is required for survival. The control group, however, showed no signs of growth inhibition. Taken together, injection of dsRNAs targeting *Mccat* confirms the functionality and utility of RNAi in this species and shows that *cat* expression is required for survival in *M. cribraria*.

Since RNAi successfully reduced *cat* expression and resulted in significant mortality, we believe *cat* could be an excellent target for controlling *M. cribraria*. Moreover, *cat* is known to be an important antioxidant enzyme, like superoxide dismutase which helps defend against oxidative stress (Li et al., 2005). Moreover, the efficacy of *cat* gene silencing has been observed and reported in several species, including the palm weevil (*Rhynchophorus ferrugineus*) (Al-ayedh et al. 2016), the sand fly (*Lutzomyia longipalpis*) (Diaz-Albiter et al., 2011), the tobacco cutworm (*S. litura*), (Haiming et al., 2013), the fruit fly (*D. melanogaster*) (Mackay et al., 1989), and the kissing bug (*R. prolixus*) (Paes et al., 2001), and in each case the authors found a significant reduction in growth and an increase in mortality. Therefore, targeting the *cat* gene has great potential for insect control due to its essential role in homeostasis.

It should be noted that *M. cribraria* and the closely related species *M. punctatissima* are morphologically indistinguishable and this has led to controversy over which species is found in the U.S., or whether both species are present (Eger et al., 2010). Interestingly, Jenkins & Eaton (2011) conducted a molecular analysis confirming that genes sampled from primary and secondary endosymbionts of these species are highly similar, suggesting a shared origin and identity. Also, Hosakawa et al., (2014) reported that *M. cribraria* populations found in the U.S. are related to *M. punctatissima* populations found in the Kyushu region of Japan, and that the two species share many features, so they cannot be morphologically distinguished from one another. Comparison of the *M. punctatissima laccase-2* gene and the *laccase-2* sequence found in our *M. cribraria* transcriptome database shows that these sequences share 99% identity, with only four nucleotide differences (Figure 8). While this high similarity in a single gene is not sufficient evidence to confirm species identity, it does support the idea, as proposed by Dhammi et al., (2016), that the two forms are better considered a single species. More extensive population genetic sampling will be required to more fully resolve the species boundaries within this group.

This study presents transcriptomic data generated from various *M. cribraria* developmental stages. These datasets represent a valuable genetic resource for screening potential genes for the development of biotechnological tools for insect control. Through transcriptomic analysis I identified 31 RNAi pathway genes and performed RNAi bioassays to demonstrate RNAi efficiency in *M. cribraria*. My RNA-Seq data will enable others to perform a wide range of functional genomic studies on this pest and offers insights into stage-specific expression. My work also characterized the *cat* gene and demonstrated its possible use for biological control of *M. cribraria*, and *RP6S* for use as a control gene when performing RT-PCR. In addition, since no transcriptomic or genomic data was available for this species, my RNA-Seq data provides a valuable resource for comparative genomics/transcriptomics with other hemipteran species and will also greatly aid annotation of the *M. cribraria* genome when the sequence becomes available. Given the fact that insecticide resistance is likely to evolve in major crop pests, RNAi offers a completely new mode of action, making it a promising approach for controlling *M. cribraria*. Although *in planta* RNAi (dsRNA delivered by the plant) would be the best option for RNAi-based control (Baum, et al., 2007; Mao, et al., 2007), my tests or oral RNAi in *M. cribaria* failed to demonstrate target gene knock down. This could be due to not having a high enough titer of dsRNA, or it could be due to nucleases in the insect gut, or some other potential factor, thus leaving additional research to be performed by others.

Table 1: Primer sequences used for dsRNA synthesis and RT-PCR analysis

Gene	Primer sequences	Purpose
MccatF	TAATACGACTCACTATAGGGCCTCGCCACATCTCCGATAG	dsRNA synthesis
MccatR	TAATACGACTCACTATAGGGGGGTCTCTAGCTGTGTCAGC	dsRNA synthesis
McRSP6F	ATGGCAATGCGATGCCTCTT	RT-PCR
McRSP6R	ACCTACGCCTCTTCAACATC	RT-PCR

Underlined sequence corresponds to T7 promoter

Table 2: Overview of RNAi genes identified in the transcriptome of *M. cribraria.*

RNAi core genes	Contig	Size (AA)	ComparIson to *Cylas brunneus*	First hit Blastp
miRNA				
Dcr-1	11725	1090	E= 0.0; bits = 748	*AVK59457.1 Nezara viridula*
Ago-1	7709	901	E= 0.0; bits = 1664	*XP_024214308.1 H. halys*
Loquacious	1167	384	E = 1E-98; bits = 351	*AVK59462.1 Nezara viridula*
Expotin-5	8269	1889	E= 0.0; bits = 722	*XP_014241155.1 Cimex lectularius*
SiRNA				
Dcr-2	7670	1603	E = 9E-175; bits =610	*XP_014275310.1 H. halys*
Ago-2	7506	1234	E= 0.0; bits = 741	*AVK59467.1 Nezara viridula*
piRNA				
Ago-3	1655	483	E = 6E-118; bits = 422	*XP_014276831.1 H. halys*
Aubergine/piwi	241	791	E = 3E-172; bits = 601	*AGJ83331.1 Oncopeltus fasciatus*
Antiviral				
Ars2	4509	757	E = 8E-106; bits = 381	*Hh(XP_014277996.1)*
Egghead	3764	457	E= 0.0; bits = 632	*Hh(XP_014283435.1)*
Nucleases				
dsRNAse	3484	409	E = 2E-38; bits = 156	*Hh(XP_014282547.1)*
Exsome	2692	809	E = 2E-144; bits = 509	*Hh(XP_014279792.1)*
Poly(A) polymerase	7462	601	E= 0.0; bits = 713	*Hh(XP_014282208.1)*
dsRNA uptake				
SID1-related	No Hit			
FBX011	3711	871	E= 0.0; bits = 1395	*Hh(XP_014287303.1)*
Hermansky(CG4966)	5140	405	E = 1E-61; bits = 235	*Hh(XP_014288755.1*
RISC				
Tudor-SN	2299	907	E=8.00E-05; bit= 43.9	*(BAW35372.1) Locusta migratoria]*
Vasa intronic gene	2606	395	E =8E-28; bits = 123	*XP_014276922.1 H. halys*
FXMRI	1649	563	E = 1E-166; bits = 583	*XP_014287676.1 H. halys*
P68 RNA helicase	211	533	E =2E-179; bits = 625	*XP_014287495.1 H. halys*
Translin factor X	5300	282	E =1.00E-13; bits = 178	*XP_024218689.1 H. halys*
Armitage	5309	797	E =1E-170; bits = 597	*Hh(XP_014289817.1)*
Homeless(spindle-E)	4827	1771	E= 0.0; bits = 639	*Hh(XP_014286769.1)*
Maelstrom	9069	477	E = 5E-40; bits = 162	*Hh(XP_014290039.1)*
RNA helicase Belle	3595	678	E= 0.0; bits = 692	*Hh(XP_014279436.1)*
PRP16, mut6 homolog	10285	1203	E =0.0; bits = 1561	*Hh(XP_014279344.1)*
Gawky	602	1452	E = 3E-51; bits 201	*Hh(XP_014288686.1)*
Staufen	522	734	E = 4E-141; 385	*Hh(XP_014282520.1)*
Clip1	10636	425	E = 9E-163;569	*Hh(XP_014270973.1)*
Elp-1	10864	630	E= 4.00E-15; bits =80.9	*Hh(XP_014290480.1)*
GLD-1 homolog	3261	342	E =8E-121; bits = 469	*Hh(XP_014271454.1*
ACO-1 homolog	3707	893	E= 0.0; bits = 1368	*Hh(XP_014275296.1)*

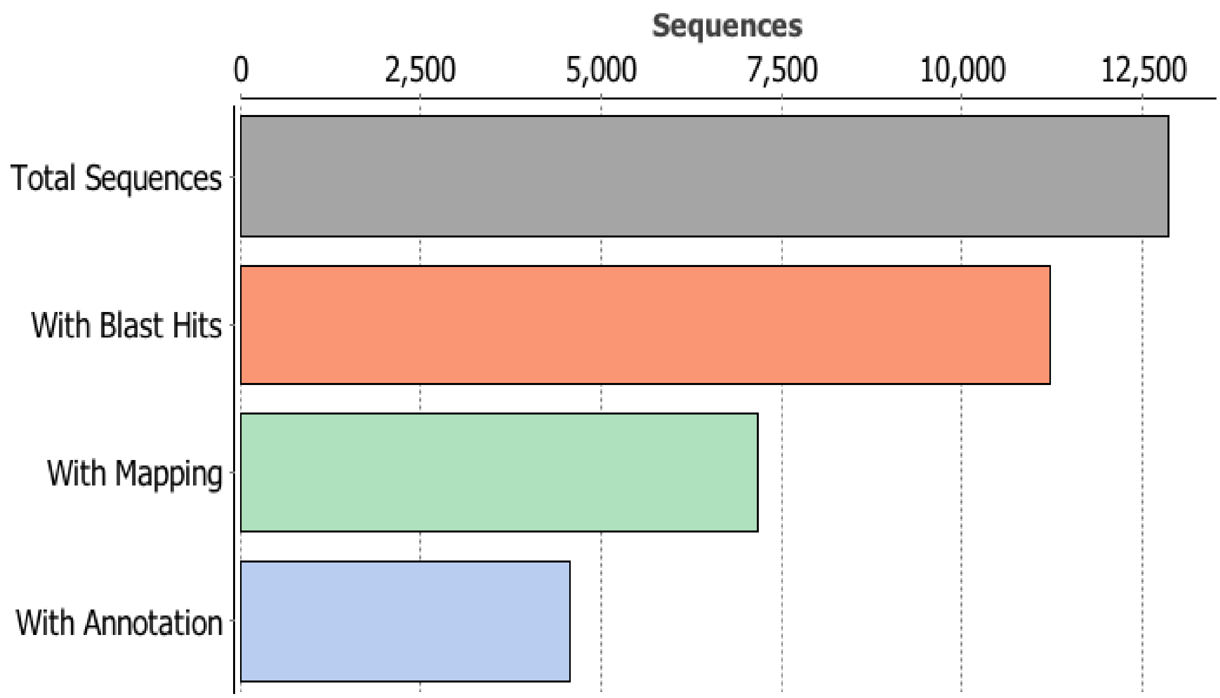

Figure 1: Blast2GO annotation of the *M. cribraria* transcriptome. Among the 12,857 contigs used for the BLASTx search against the NCBI nr protein database, BLASTx analysis revealed over 11,224 contigs shared significant identity with known arthropod proteins.

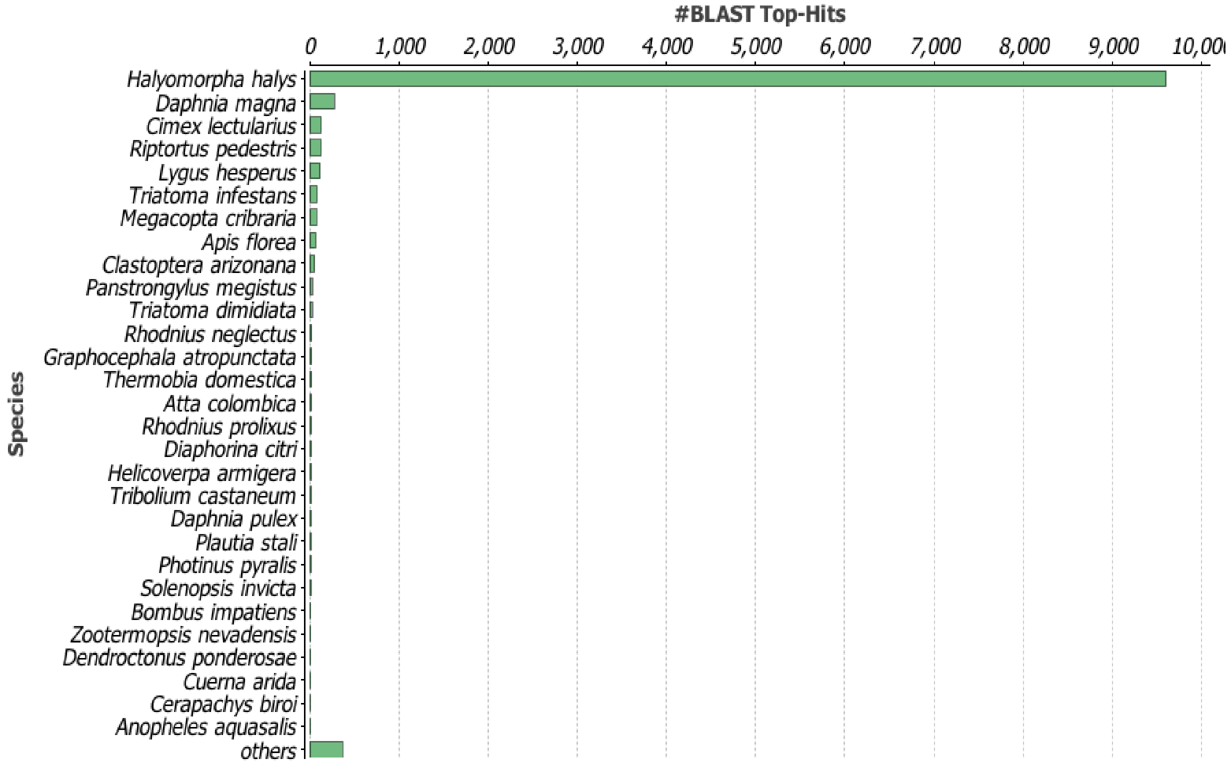

Figure 2: Top-Hits species distribution of *M. cribraria* transcriptome. The most represented species in the top scoring BLASTx-matches when compared to an arthropod-specific database.

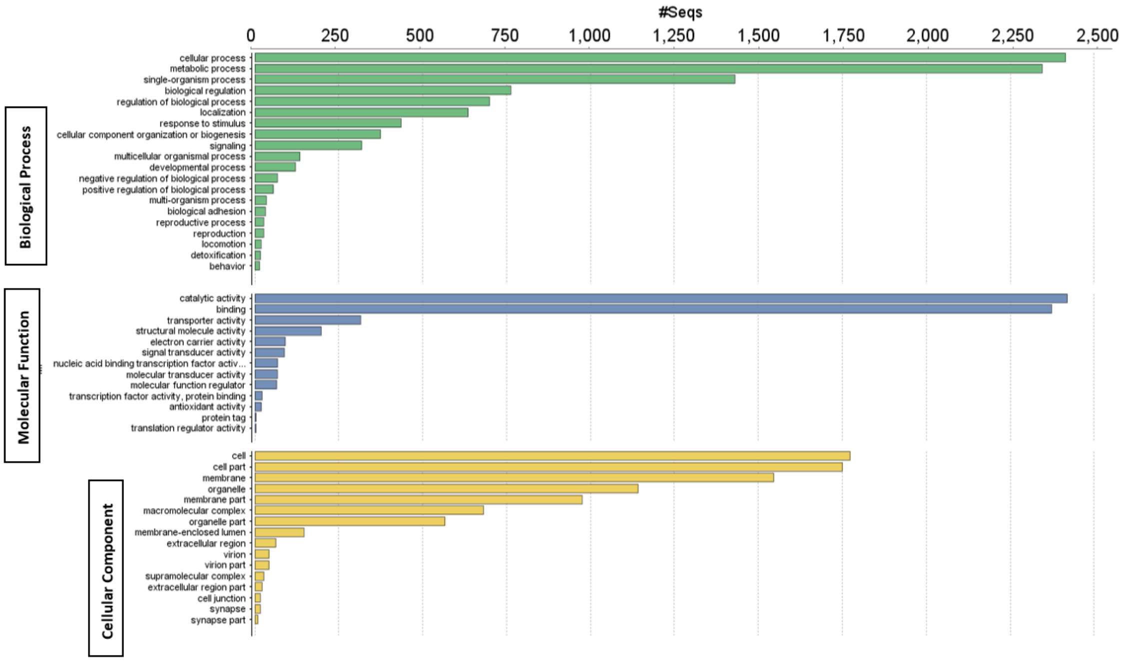

Figure 3: Gene ontology classification of the *Megacopta cribraria* transcriptome.

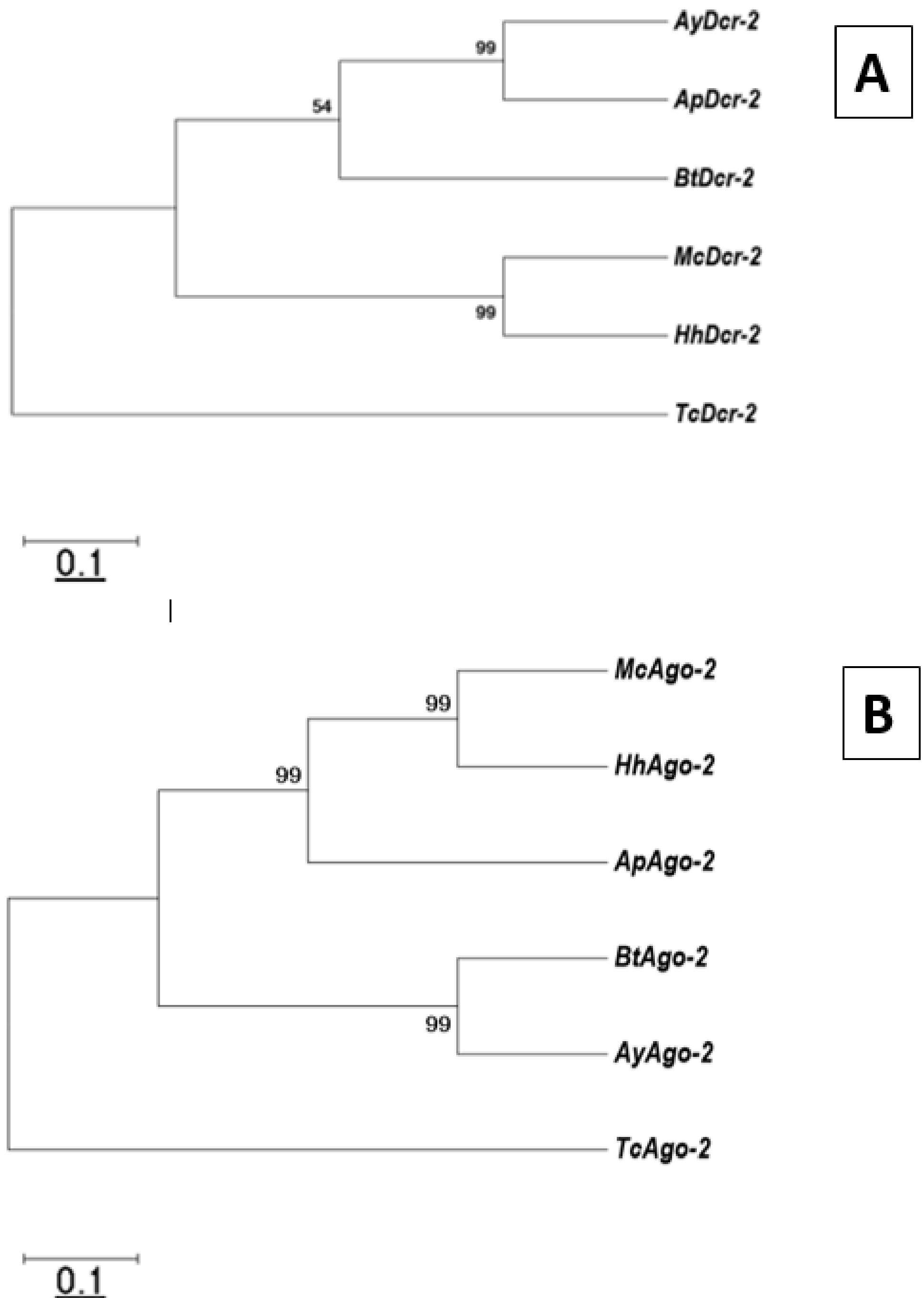

Figure 4: Phylogenetic trees of RNAi core genes constructed using maximum likelihood and 1000 bootstrap replicates. Protein sequences of Dcr2 (A) and Ago2 (B) from several species were compared. *Halyomorpha halys* (*Hh*), *Acyrthosiphon pisum* (*Ap*), *Aphis glycines* (*Ay*), *Tribolium castaneum* (*Tc*), *Megacopta cribraria* (*Mc*) *and Bemisia tabaci* (*Bt*). The scale bar indicates an evolutionary distance of 0.1 amino acid substitutions per site. Bootstrap values are given in percentages at the internodes.

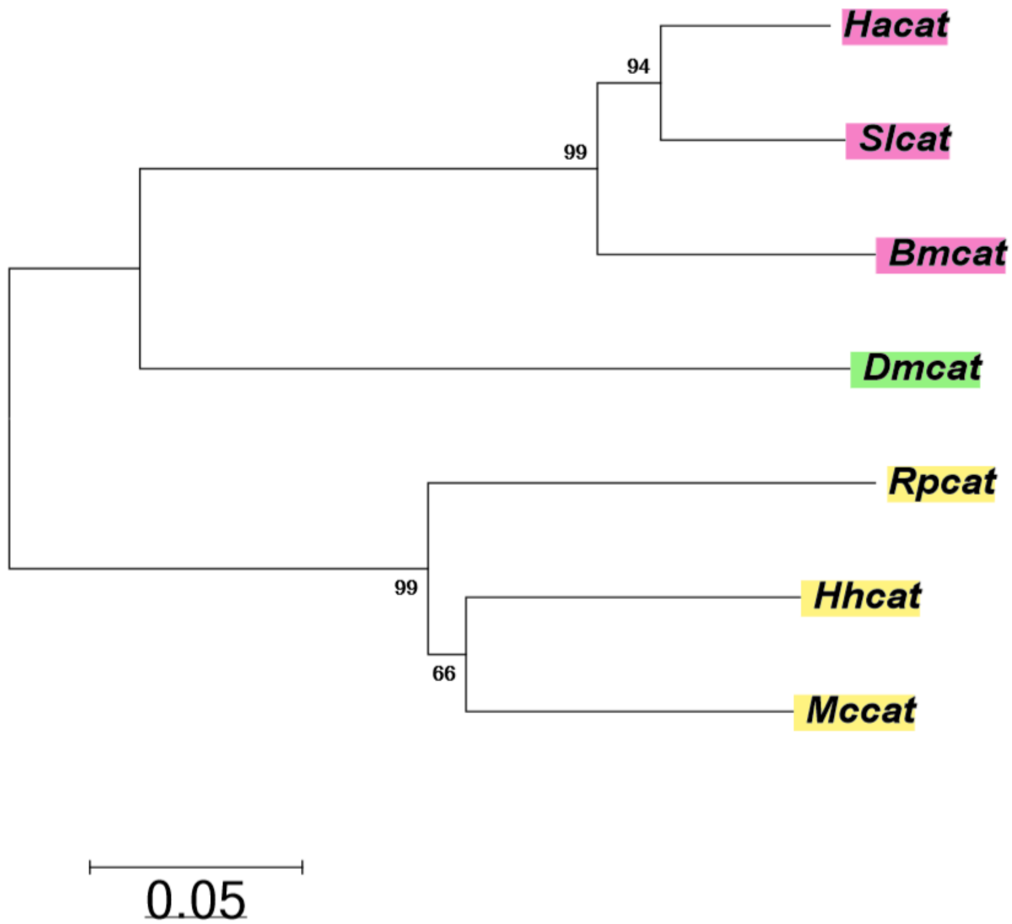

Figure 5: Phylogenetic relationships among insect species catalases found by maximum likelihood search with 1000 bootstrap replicates. *Halyomorpha halys* (Hh), *Drosophila melanogaster* (Dm), *Bombyx mori* (Bm), *Helicoverpa armigera* (Ha), *and Spodoptera litura* (Sl), *Riptortus pedestris* (Rp), and *Megacopta cribraria* (Mc). The scale bar indicates an evolutionary distance of 0.05 amino acid substitutions per site. Bootstrap values are given in percentages at the internodes.

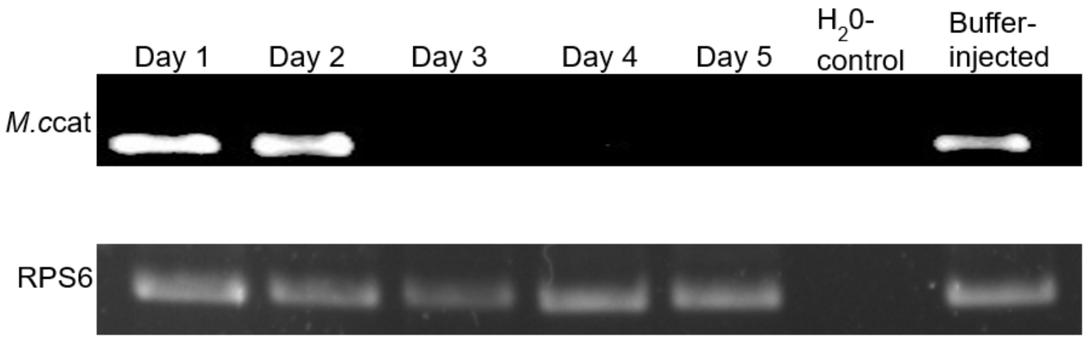

Figure 6: Effect of RNAi on the expression levels of the *cat* gene in *M. cribraria*. (Top) Knockdown for *Mccat* transcript determined by RT-PCR, showing day 1 through day 5 post injection, water control, and buffer-injected control on day 5 post injection. (Bottom) Internal loading control, *RPS6*.

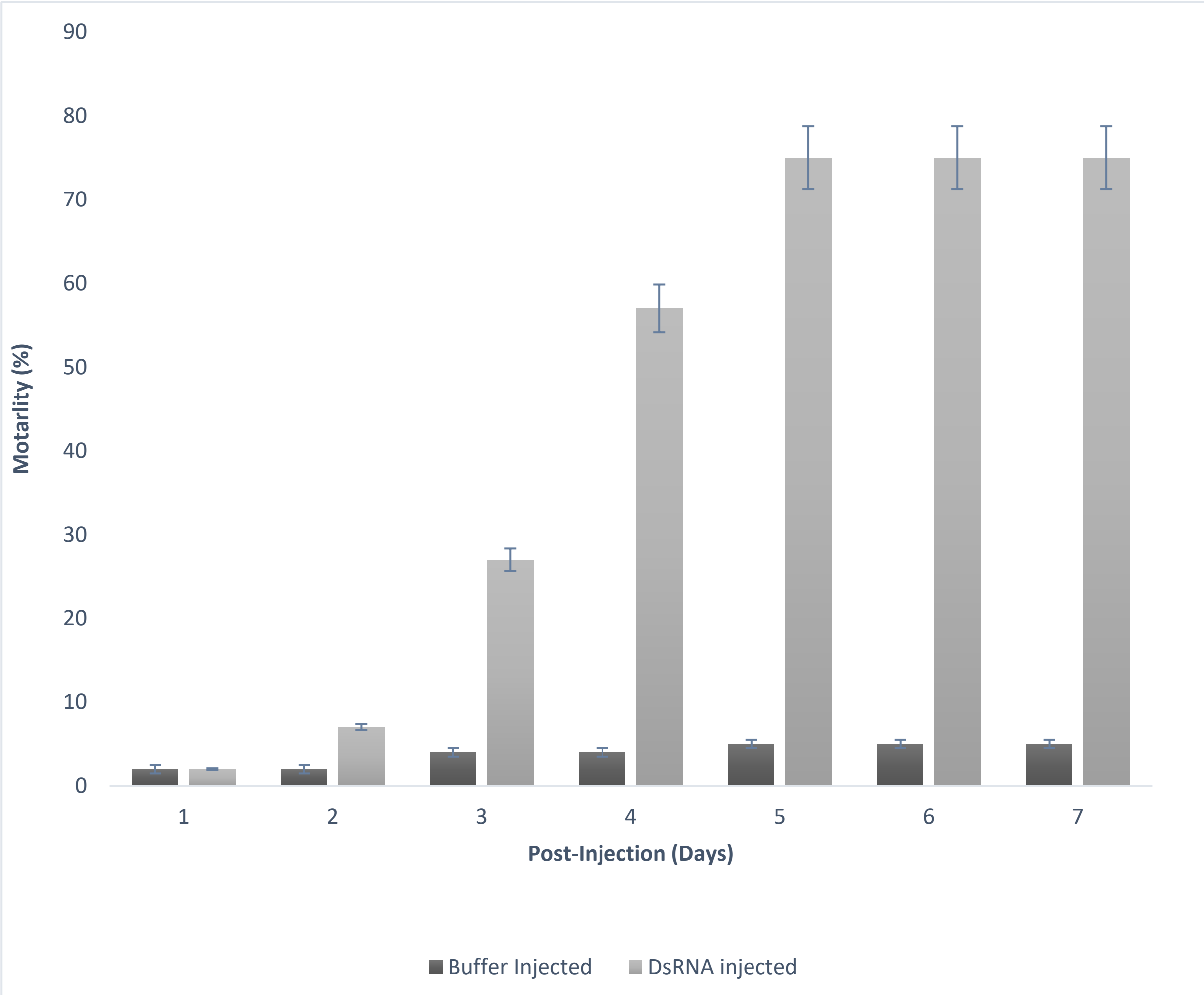

Figure 7: Effects of *Mccat* RNAi on the development of *M. cribraria*. dsRNAs were injected into fourth-instar nymph, and the mortality rates were recorded daily starting from 24 hours post injection until 7 days post injecton. Buffer was injected as a control.

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MpLac-2         ACAGCAGCATTACGTGAGTGGTCAAGTCGTAATCGTAGAGATGGGAGTTGGGGTCCAGTG
McLac-2         ACAGCAGCATTACGTGAGTGGTCAAGTCGTAATCGTAGAGATGGGAGTTGGGGTCCAGTG
                ************************************************************

MpLac-2         AGGGTGCCTGACGGATTGCGATACTGCCGTAGATACCATCCATCTTCTGGAGCCCAGTGT
McLac-2         AGGGTGCCTGACGGATTGCGATACTGCCGTAGATACCATCCATCTTCTGGAGCCCAGTGT
                ************************************************************

MpLac-2         GAGCATGCCAGAAATGTGTGCCTGCGTTTCCTGCAATCCACTGATACCTGAACGTGTTAC
McLac-2         GAGCATGCCAGAAATGTGTGCCTGCGTTTCCTGCAATCCACTGATACCTGAATGTGTTAC
                ****************************************************.*******

MpLac-2         CTTCGGAGATGGGGCACTGAGTGACGAAAGGTACACCGTCAGATATCTGAGTACCCCTCT
McLac-2         CTTCGGAGATGGGGCACTGAGTGACGAAAGGTACACCGTCAGATATCTGAGTACCCCTCT
                ************************************************************

MpLac-2         GGTGGATTCCGTGCCAATGTATGGTCAGTTCCAATCCTTGCATTGCATTGTGTACGTCGA
McLac-2         GGTGGATTCCGTGCCAATGTATGGTCAGTTCCAATCCTTGCATTGCATTGTGTACGTCGA
                ************************************************************

MpLac-2         TGACGACTTTGTCTCCTTCACAGACCTGTATGCTTGGACCTGGAAGCATTCTGTTGATAG
McLac-2         TGACGACTTTGTCTCCTTCACA-ACCTGTATGCTTGGACCTGGAAGCATTCTGTTGATAG
                ********************** *************************************

MpLac-2         TAAGCAATCCCCTTTCAACACCATCTGCGAGAACACACTGACAGTGACTCCATACCGTGT
McLac-2         TAAGCAATCCCCTTTCAACACCATCTGCGAGAACACACTGACAGTGACTCCATACCGTGT
                ************************************************************

MpLac-2         TGGTGGCGTTAGGTGTGCACACCTGGCAAGCCGCTCCTAGGACGGTGTAAAGCTCGGCTG
McLac-2         TGGTGGCGTTAGGTGTGCACACCTGGCAAGCCGCTCCTAGGACGGTGTAAAGCTCGGCTG
                ************************************************************

MpLac-2         TGAAGTGGTAGTAGCACACTTTTGGTGGCTCCCCTTCTCTGCAAGCCCTGGCGCATTCCT
McLac-2         TGAAGTGGTAGTAGCACACTTTTGGTGGCTCCCCTTCTCTGCAAGCCCTGGCGCATTCCT
                ************************************************************

MpLac-2         CGGGTGACGAAAGGATAGGGTTCCTCTGAAGTTCTTCCAGTCCTCTCCTATCGAAGTCGA
McLac-2         CGGGTGACGAAAGGATAGGGTTCCTCTGAAGTTCTTCCAGTCCTCTCCTATCGAAGTCGA
                ************************************************************

MpLac-2         GCGAGGATGCCGGAGCGTACTTGCTGGGATTGGTGTCAACGCTTTCCGGTCCGAACCCAG
McLac-2         GCGAGGATGCCGGAGCGTACTTGCTGGGATTGGTGTCAACGCTTTCCGGTCCGAACCCAG
                ************************************************************

MpLac-2         GACCGAGGGGGTGAGTTTGGAGGAGGCCATGGCTTGAAGCGAAGAAATCTGCCGATGTGT
McLac-2         GACCGAGGGGGTGAGTTTGGAGGAGGCCATGGCTTGAAGCGAAGAAGTCTGCCGATGTGT
                **********************************************.*************

MpLac-2         CGTCAGAGAAAGAAGACTGTCCGGGGGCCAGTTCCTGTCGCCACCATGCGGCCGGCGTCG
McLac-2         CGTCAGAGAAAGAAGACTGTCCGGGGGCCAGTTCCTGTCGCCACCATGCGGCCGGCGTCG
                ************************************************************

MpLac-2         AAGGGTCACCTGGTCGTAATGGTCCTGTTCGTTTCTTGACGCGGGTTGAAGTTGGCACTT
McLac-2         AAGGGTCACCTGGTCGTAATGGTCCTGTTCGTTTCTTGACGCGGGTTGAAGTTGGCACTT
                ************************************************************

MpLac-2         TGGTTGCGCTGGCCTCGAGGGCGATGGCAAAGAGGAGAAGAGCCGGTAGGAGCCGCATGT
McLac-2         TGGTTGCGCTGGCCTCGAGGGCGATGGCAAAGAGGAGAAGAGCCGGTAGGAGCCGCATGT
                ************************************************************

MpLac-2         CTTGCACTGACCGGGTGTAAGGGGAGACTGC
McLac-2         CTTGCACTGACCGGGTGTAAGG---------
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Figure 8: Alignment of the nucleotide sequence of the *Laccase-2* gene from *M. punctatissima* and *M. cribraria*. These alignments show that *Mplac-2* (top row) shares 99% sequence identity with *Mclac-2* (bottom row) orthologs and (*) indicate the conserved region. Four nucleotides in *Mplac-2* differed from *Mclac-2*.

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CHAPTER 5

Conclusion and Applications

CONCLUSIONS

Both *D. virgifera virgifera* and *M. cribraria* are agricultural pests in the United States, and while *D. virgifera virgifera* currently posses a greater threat to food security than *M. cribraria*, the latter has the potential to become a significant pest. Currently both species are fairly well controlled through the use of genetically engineered (GE) crops or foliar insecticides. While these control measures are effective today, increased use could lead to resistance, and as mentioned earlier, there are already populations of *D. virgifera virgifera* that are resistant to crop rotation, some insecticides and one or more *Bt* toxins. Since issues surrounding food security will only increase as the earth's population increases, finding new ways to control agricultural pests is of paramount importance.

My goal has been to learn, master, develop and test new control methods, ones expected to be more eco-friendly than traditional insecticides, and hopefully less harmful to non-target species, such as pollinators. Many studies, including those I performed during my dissertation work, suggest that RNA interference (RNAi) may be a viable control method for insect species such as *D. virgifera virgifera*. For example, I was able to interrupt the *D. virgifera virgifera* life cycle by introducing double-stranded RNA (dsRNA) designed to target critical ABC transporter genes. However, while ingestion of dsRNAs by *D. virgifera virgifera* can trigger "oral RNAi," this has not been shown to work in *M. cribraria*. Rather, in *M. cribraria* I was only able to trigger RNAi through injection of dsRNA.

In both cases I had to perform RNA-Seq to acquire target sequences, because neither *D. virgifera virgifera* nor *M. cribraria* had publically available genome assemblies, or high-throughput transcriptome data. To ensure the widest selection of transcripts, I sequenced a variety of developmental stages, and after selecting my targets, double-checked each target gene's expression profile. This allowed me to microinject each of the dsRNAs into *D. virgifera virgifera* or *M. cribraria* shortly before each gene product was required, thus generating a stronger phenotype.

Interestingly, my RNAi results from both *D. virgifera virgifera* and *M. cribraria* produced obvious knockdown phenotypes that were not only gene specific but also produced similar knockdown phenotypes as seen for the corresponding genes in other species. Of these, the most interesting phenotypes were those that impacted reproduction. Specifically, I tested dsRNAs targeting ABC transporter genes that resulted in egg-laying and -hatching defects in *D. virgifera virgifera*. This suggests their potential as insect birth control targets. In *M. cribraria*, injection of dsRNAs targeting an essential gene, *Mccat*, resulted in significant mortality and inhibition of nymphal growth.

However, while my results demonstrate the feasibility of RNAi as an alternative method for controlling these agricultural pests, to date oral RNAi has not been demonstrated in *M. cribraria*. Since RNAi needs to be triggered through ingestion of dsRNA to be practical in a field setting, I did attempt to feed dsRNAs to *M. cribraria*. My results were inconclusive, so were not included in Chapter 4, but it is unclear why my tests failed. One possibility is that the dsRNAs were broken down in the gut, but another possibility is that the concentration of dsRNA was too low. There have been reports of oral RNAi in insect species that had been thought to be immune to this technique. The difference was the use of very high concentrations of dsRNA. Again, it is possible that the dsRNAs are being broken down in the gut, but that having very high concentrations of dsRNA allows enough dsRNA to survive and trigger an RNAi effect.

As mentioned above, the fact that oral RNAi works exceptionally well in *D. virgifera virgifera* has been known for at least a decade, so it is thought that RNAi could offer an additional means of crop protection in the very near future. For example, the EPA recently registered Monsanto's new and innovative plant-protectant, SmartStax PRO, (EPA, 2017). In addition to expressing Cry3Bb1 and Cry34Ab1/Cry35Ab1, SmartStax PRO also expresses dsRNA that targets *Snf7* (Head et al 2017). Since SmartStax PRO pyramids *Bt* traits with an RNAi-based trait, it is expected to increase control of corn rootworms, even those that have developed resistance to *Bt* and traditional insecticides.

While RNAi has the potential of becoming a successful approach for insect control, practical use of RNAi in the field requires that dsRNAs function when ingested. In the case of Monsanto's SmartStax PRO, transgenic plants have been engineered to express dsRNAs targeting *Snf7* in the corn roots (EPA, 2017; Baum et al., 2007), and corn rootworms are highly susceptible to oral RNAi, thus making this product highly practical for field use. Another potential method for use in the field is application of engineered microorganisms (bacteria or yeast) designed to express pest-specific dsRNAs. Studies have shown that ingestion of bacteria or yeast designed to express dsRNAs can trigger RNAi in some pest species, even ones such as *D. suzukii*, which is known to lack systemic RNAi (Murphy et al., 2016; Zhu et al., 2011).

To further our understanding of dsRNA uptake and processing mechanisms in insects, RNAi pathways in different insect species and orders should be studied. Differences, such as what makes *T. castaneum* have strong systemic RNAi when *D. melanogaster* appears deficient needs to be understood. Likewise, we need to understand why *D. melanogaster,* which is not responsive to environmental dsRNA when unpackaged, has significant gene knockdown and high mortality when fed dsRNAs in transfection solution, or in the case of *D. suzukii*, is responsive to dsRNA when expressed in yeast. Taken together, this suggests that the presence of a robust systemic RNAi response may not be a precondition for RNAi-mediated insect control. Therefore, a better understanding of how dsRNA gets into midgut cells might increase our ability to improve oral RNAi in other insect species. Despite various setbacks associated with this technology, perhaps in the future, RNAi will be a widely-accepted tool for use in pest management.

However, several issues should be addressed before this technology gets used in the field. Although RNAi is known for its specificity, some studies have shown that off-target gene silencing can occur (Carthew and Sontheimer 2009). However, some instances of a single “species-specific” dsRNA triggering RNAi in more than one species may be less problematic than others. For example, Baum and co-workers (2007) administered a single dsRNA targeting the *DvvVATPase* gene to both *D. virgifera virgifera* and *Leptinotarsa decemlineata.* While this single dsRNA was effective in both pests, this has not been seen as a problem because both species are pests. However, if a pest-specific target triggers RNAi in a non-target species, and that non-target species is beneficial, such as the honey bee, this would have a very negative impact on the use of RNAi as a control method in the field.

Therefore, targeting highly conserved genes such as *polyubiquitin* (100% conservation between insects and humans at the amino-acid level) would be catastrophic to beneficial insects. Perhaps genes that are truly species-specific are better targets, or genes involved in species-specific biology, such as those involved in mate recognition, since this would reduce the possibility of silencing genes in non-target species. Clearly extensive studies would be needed to completely understand the factors behind off-target silencing and to prevent potential hazards to the environment.

Similar to insecticides and GE plants, there is also the possibility that insects will evolve resistance to a particular dsRNA sequence, due to mutations in the target gene, or due to mutations in one or more genes in the RNAi pathway. While creating transgenic plants expressing a different dsRNA, or targeting a different portion of the same gene or a new target gene, would overcome one of these resistance barriers, loss of the RNAi pathway would be devastating for RNAi as a pest-management tool. Therefore, research into mechanisms of RNAi resistance should be investigated before this technology is accepted on a large scale.

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APPENDICES

Appendix A: DvvABC naming chart

Subfamily	*Dvv* name	Contig numbers
A	DvvABCA_49125	DvvABC-A T49125_c1_seq2
A	DvvABCA_50718	DvvABC-A T50718_c0_seq1
A	DvvABCA_18330	DvvABC-A D18330
A	DvvABCA_266167	DvvABC-A C266167_7.0
B	DvvABCB_21313	DvvABCB_D21313+T40801_c0_seq1
B	DvvABCB_17742	DvvABC-B D17742
B	DvvABCB_19147	DvvABC-B D19147
B	DvvABCB_39715	D vvABC-B T39715_c0_seq2
B	DvvABCB_9796	DvvABC-B D9796
B	DvvABCB_13664*	DvvABC-B D13664+T8676_c0_seq1*
B	DvvABCB_17837	DvvABC-B T17837_c0_seq2
C	DvvABCC_41801	DvvABC-C T41801_c0_seq1
C	DvvABCC_44708	DvvABC-C T44708_c0_seq1
C	DvvABCC_48952*	DvvABC-C T48952_c0_seq2+T48952_c0_seq1*
C	DvvABCC_17573	DvvABC-C T17573_c0_seq1
C	DvvABCC_51687	DvvABC-C T51687_c0_seq1
C	DvvABCC_21020*	DvvABC-C S21020Locus_43217_0+T47823_c0_seq1*
C	DvvABCC_222633*	DvvABC-C C222633_3.0+T22098_c0_seq1*
C	DvvABCC_18126	DvvABC-C D18126+D19164
C	DvvABCC_49513	DvvABC-C T49513_c0_seq6
C	DvvABCC_14070	DvvABC-C D14070
C	DvvABCC_22628	DvvABC-C D22628
C	DvvABCC_20002	DvvABC-C D20002
C	DvvABCC_7536	DvvABC-C D7536
C	DvvABCC_47333	DvvABC-C T47333_c0_seq11
C	DvvABCC_49618*	DvvABC-C T49618_c0_seq2*
C	DvvABCC_45163	DvvABC-C T45163_c0_seq1
C	DvvABCC_43960*	DvvABC-C T43960_c1_seq1+D21270+T49513_c0_seq3*
C	DvvABCC_48940	DvvABC-C T48940_c0_seq1+D21306

(*) Represent short sequences

Appendix A: DvvABC naming chart continued

Subfamily	*Dvv* name	Contig numbers
C	DvvABCC_217405*	DvvABC-C C217405_3.0+D12550+S19317Locus_19671_1*
C	DvvABCC_10132*	DvvABC-C T10132_c0_seq1+D20603+T57212_c0_seq1*
C	DvvABCC_48300*	DvvABC-C T48300_c0_seq1+D21892*
C	DvvABCC_47673	DvvABC-C T47673_c0_seq1
C	DvvABCC_5345	Dvv ABC-C D5345
C	DvvABCC_22413	DvvABC-C D22413+T49258_c0_seq1
C	DvvABCC_18709*	DvvABC-C D18709*
C	DvvABCC_21941	DvvABC-C D21941
C	DvvABCC_15305	DvvABC-C D15305
C	DvvABCC_12562	Dvv ABC-C D12562+D20321
C	DvvABCC_10642	DvvABC-C D10642
C	DvvABCC_41602	DvvABC-C T41602_c0_seq1
C	DvvABCC_12703	DvvABC-C D12703
C	DvvABCC_14968	DvvABC-C D14968
D	DvvBCD_11014	DvvABC-D D11014
D	DvvABCD_11628	DvvABC-D D11628
E	DvvABCE_2830	DvvABC-E D2830
F	DvvABCF_2701	DvvABC-F D2701
F	Dvv BCF_802	DvvABC-F D802
F	DvvABCF_9935	DvvABC-F D9935
G	DvvABCG_9811	DvvABC-G D9811
G	DvvABCG_3712	DvvABC-G D3712
G	DvvABCG_14042	DvvABC-G D14042
G	DvvABCG_10897	DvvABC-G D10897
G	DvvABCG_22358	DvvABC-G D22358
G	DvvABCG_23081	DvvABC-G D23081
G	DvvABCG_13051	DvvABC-G D13051
G	DvvABCG_38769	DvvABC-G T38769_c0_seq1

(*) Represent short sequences

Appendix A: DvvABC naming chart continued

Subfamily	*Dvv* name	Contig numbers
G	DvvABCG_13829	DvvABC-G D13829
G	DvvABCG_49457	DvvABC-G T49457_c0_seq1
G	DvvABCG_36869	DvvABC-G T36869_c0_seq1
G	DvvABCG_79525	DvvABC-G T79525_c0_seq1
H	DvvABCH_20789	DvvABC-H D20789
H	DvvABCH_5118	DvvABC-H D5118
H	DvvABCH_18290	DvvABC-H D18290
H	DvvABCH_11818	DvvABC-H D11818

(*) Represent short sequences.

Appendix B.
Sequences of ATP binding cassette (ABC) transporters genes in *D. v. virgifera*

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>DvvABC-A T49125_c1_seq2
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PSDHIQRFGSENELLGYYYKNPNYTTVAIIFDDKNPKHFNYKIRYHKNYYQPEFLVTDRMYQRVYGYSPGSEYVYRDEDFLKIQLALDMSFLEENLR
SSNIEDTYSIQIQEFPYPPHKVDSAITTLFLEFLPLITLFSFIFLCPAVLKRVVEEKHSGTKELMKMVGMKSWMLWFGWFIYAMIPMFFAVSVISIF
MKVPMFGSDSPLVEFANGGILFVFLILYCMAAVAFCFAISSFFSRPTIALVAGILVWILSFFIPKYACGLDEANKLSWLSNVLLNLLPNMSLHYGYS
IISVFEEREVGINWSNFFKPGSGSSDDITMLNVYVMLIVDIVIYTIFTFYMDGVNPGKYGVRKSILFPLQNFMKLCRKPSITTVPVDSETVPLEKVE
AGHNLAKGIQINHLHKRYKQKQAVNNLNLDIYKNQITVLLGHNGAGKSTTMSIITGLIPATSGSVTINGLDINTDMDEIRKSLGLCPQHNLLFTDLT
VKEHLLFFAKLKGKSTKEANIEAKSLLAKLNMPDKEHSMAQTLSGGMQRKLCLAMALIGDSKVLILDEPSSGMDPQSRRELWDLLLQWRGEKTILIT
THFMEEADALGDWIAIMSDGSLNCYGTPMFLKKKYDTGYHLNLMIEEDADIDAISRRVKHFMPDAHLTSNNGNNLVFVLPYQNTNMTGLLGDLEKNR
SELHLSNISITITTLEDVFLKTRQEIEHSSDDTSSVATQDDIQPHASLTLITLLKKKVNFSLKKWSTYIVPVGVAVVLFSLTVFLSSGNDYYSERGP
ELPLKLSSYKQTSVYYSGDTSNEKINTLMKYYMSAVESQRSLPFKVDNVEKSILQRSLENIAYYKEHMIAGANFVYDRDFTLVALYNGIATHSTPIS
LNLITDSLAKTLLGPEYGISVSNWPLPQVQERLSSQEYSEAKVAVLWLILLPVGCLFIHGIFIIFPHTEISTRFLQIQYMAGVKPFFYWLVNWIADM
TFYIFLMFILSFLLWICSPVFQHNGTELGYLFSIFLCYGIAGIPFAYIFSRKKTASGAFALFVIMGMFLGIILTLTIAVLLESQDEYYVNIGNKIKY
VCFFLLPQVSLSDALVSFIRRTVNIYNFKISPQRLRVMCNQMESHACCVESSIECQNYKSYNNLFSEHYMFMIGCGVFYLTINIILDTYFMKKLKAM
VMRQCNLILKSFKDKDTALIPKNDKYVNEDVGDGYNTLRAKKIMKLYAGKQIVKNINFTLKHGHCLGILGVNGAGKTTTFKMLTREEVVDDGEIKIE
LDNNKQPLDITGSEYLETIGYCPQSDSLNFVLTGRQLLSTVAKLRGVTDETMIDRFLEAFDLKQYADIPCGHYSGGNKRKLSLAISLIGNRKFVLLD
EPTNGVDPATRRKCWDLIKLMKGNSGNKIGFILTSHSMTECEALCDELKIMKKGSFVEEGRLVDLKNRYGGFTLKLKLVSNQGQPINLVDDDVDEVD
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FSLTILYTAPEDKYYDDVIGFFKLIPKVNTQRVISSGELERISLAGNSSYYGIEFGGDRDNVEVNIRFPGETVYQLDSIGRQNWRTNLVYPVFQSSG
PRSPDNATGSAPNYFAEGFLAVQHFVTTALLLADKGITHEDPQEIFNFLMDKSNPFPLIKMQRFPFASWFSDQLLTALTSMLGMIVMLSFVYTCINT
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AATMAGLAWFISYAPYLFMQNNYTDLALSTKLLTSLLPNTAMAFGFQVVLMYEGTGDGVTWSTLFKPNTPDDTLSLGLIWIMIIINTIIYLLIALYI
EAVFPGEYGVAEKWYFPFTKKYWCGKGAVSDYNNYNDHSANEFFETEPNLRPGIQIFNLKKAFGKKTAVRNLSLNMFENQITVLLGHNGAGKTTTMS
MLTGMISPTNGTAKINGHDIRLDIAGVRNSLGLCPQHNIIFDELTVEEHLYFFSKLKGLSKSKITAEIDKYVKLLDLEPKRKEKSSTLSGGMKRKLC
VGMALCGNSKVVMLDEPTAGMDPSARRVLWELLQKQKEGRTILLSTHFMDEADLLGDRIAIMAGGELQCCGSSFFLKKKYGAGYSLIMDKAKTCNPH
KVTELLKKFIPEIEIHSNVGSELTYLLSENNAPVFEAMLKQIEQESNELGIRSYGISLTTMEEVFMKVGADHGQEEIYNEKQKKDKKEKNPILTSAD
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VLNGYGMSPTNIDNITRIMLDLTATNPNVVRRSYIIGSTFTEQEFEFGIIKTIHPVITAWFNNDPYHSPGIALGMALSSVYNHYTNGHIEFVNKPLP
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MGRLFFLLLLFGWSFMPIYYVASLIFTVPSTGYTRMTLVGIFIGNAAFLLVEVLKTQSTNLKRIGETLDNVFLVFPHYSLATGINKCYAIYSYNTLC
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KEKERIHMATDHDIRQTNILVVKDLTKYYNNFLAVNGLSIGIEKSECFGLLGINGAGKTTTFKMMSGDETVSYGDAWIEGKSVKTQLKQVQRNIGYC
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WYTNTNFTVFTKADPFVLLLFLMFYNCATITFCFALSVLFNKANTAATIAGMVWFLSYSPYLFMANVYDTLTLTSKLVASIGSNTAMAFGFQVILMY
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APGIARNMVYSFLTGIILFALLLAIEYKIFSRVHYYLTQKHFTKKPIPVEDEDSDVSKERERIHVATEIDIKQNYTLAVKDLTKYYKNFLAVNGLCV
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LLFTKHENST
>DvvABC-A C266167_7.0
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TETWKKMSNSKSSLEWVPYSAEDKVQEAYDQDHKFAPMAVIFKSDVPYVHTSLSYQIRTNPYYISTPSSNDIGWDKQSCRGGTNPNSNMEDGSTCPA
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QQEIENAAKKADIHTFIQTLPRGYQTVLGERGTQLSGGQKQKIAIARALVRTPEFLLLDEATSALDTTSEAEIQEALDSIRGTCTIIIVAHRLSTIR
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KSFAQEPREITSYNISIENVLKYCYKEAKARALFYGMTGFSGHIIIISVLYYGGVMVSSNTITVGNLSSFLLYAAYIGISVGGLSSFYSELNKSLGA
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Appendix C
Sequences of RNAi-related genes in *Megacopta cribraria*

siRNAi pathway

Dcr-2

cDNA

>Contig 7670, length 5375
GTTAGAATGCTTTGTGTCTCAGTCGTAGGTTATGACTGTTACCGGTGTTTATTTTTGGTTGGCATGTTCAAAGGAATTTTTTCTTTTTAATAAACAG
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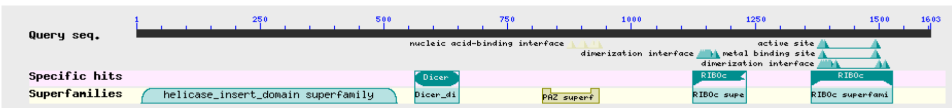
Graphical representation



Comparison with *Cylas puncticollis Dcr-2*

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Sbjct  6      NDFQPREYQVELFEKALKENTIIFLPTGSGKTFIAVMLIKHKSNDLKLPYSEGGKRTFFI  65

Query  80     VNTVALVDQHTKCIEQRTSFKVGSYSGDMNLDGWSKEKWLNEFDKYQVIVMTVQILANLV  139
              V+TVALV Q  + I Q+T   VG YSGD+ +D W  +KWL E + +QV+VMT  I  +++
Sbjct  66     VDTVALVSQQAQSIRQQTPLTVGEYSGDLGVDYWDIDKWLEELENHQVLVMTSAIFLDMI  125

Query  140    NQGFIDLNKVNLLIFDECHRGVNDHSMRQLCKSLENV-NEPPRIIGLTATLLNGNCKPGR  198
                 FI L +VNLL+ DECH  VN H MRQ+ +  E V N+ P I+GLTA LLN N KP R
Sbjct  126    LHKFISLTRVNLLVIDECHHAVNKHPMRQIMEQFEGVQNDRPHILGLTAALLNSNVKPNR  185

Query  199    VMDMVKDLEITYHGKVATVNGLDQVIGYSTNPWENIVEFKTHTLLPIENKVIGVLN---E  255
              +   + DLEIT H K+A       +  YST+P E I+ F     LP E++   V+N   E
Sbjct  186    IEKEIHDLEITLHAKIARAKNEAMIQVYSTSPKEEIIYFD----LPHEDECWTVINSSFE  241

Query  256    LIVTIGCVKIVSSYNDPPQIDLKPV------NKNKGLKQLQNLIRDIIFQIESLGSYGGD  309
               + +I  + ++   +  P I   P+      NK   + +++N++++I      LG Y
Sbjct  242    QLYSILDLIVLQDKSVKPMI--APLGAEQIFNKTDPINEIRNILKEISIITLELGGYASS  299

Query  310    KSLLAHLIQIERLRKHCDDVTLYKVLNYVGVTFMYVRGLFSQAMKDYDEFNKILLFSSEK  369
               +LL+ ++  ER+R   +D  L  VL  V   F+ +R      M   +E  KI  F+S K
Sbjct  300    YALLSRIVHFERMRISTNDPVLITVLGQVITQFLLIRKKLDLMMNVGNE--KIFKFASPK  357

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Query  430    SNPYNDTRECSYIRKKTRKILNSFGNKEINVLVASNVLEEGVDITMCSLVVKFEHPEDYR  489
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Query  609    SGLELIKVVIRLPTICPI-DIVEGIPMPSIKLAKRAAALQACKLLHQCGELDDNMLPKKA  667
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Query  668    GISEE-DVSFLFKHYPAEKEPDA----GTNKRKRLHKKVIPQYIRGPI-TSTKPVYLHII  721
               ++ E + S  F  +   KE  +    GT K +R++ K IP +I   +    KPVY+H++
Sbjct  653    DMNREVENSLHFPLWELFKEEKSSLKTGTKKCRRIYDKNIPNWICESLPVENKPVYMHVL  712

Query  722    EVTPAFKREENINRATMYDMYNSSLCYGIITPERVPEICDFPVFVSLGTLNISLKENYST  781
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Sbjct  713    NIRPNYSKPDSHRLLAFYNLLLSNKTFSVITSKKWPKICNFPLFMNVGEVSIVIQQNARK  772

Query  782    VNLTAENIDDIKAFNVLVYSDILTCLREFLIFDNSKDAESILIVP--VDKEHGCIDFSIL  839
              V L+ E I  I  F+ ++++   T  + FL+ D      S LIVP  VD +   ID+  +
Sbjct  773    VTLSKEQIKSIFDFHCVLFTQAWTYKKNFLVRDYENKENSYLIVPTIVDGDDVQIDWETI  832

Query  840    KEHKTVKSVMEPSQEEKLNVEVNLDTYLNKIVAPWYRNTG---FYIVTEVTFTKTARSVF  896
                HK + +V     E + N+ V+ + Y NKIV PWYR  G    Y+VT V   +T  S F
Sbjct  833    NNHKFIPAVKPVPIESRENIVVDKEKYFNKIVIPWYRPKGDTLKYVVTRVCEEETPLSEF  892

Query  897    PNESFGTYEQYFNDKHNLQLVNPNQPLLFVKSLSKKLNCFKPKG---AASRRKRDEMFEE  953
              P+  + +Y  YF +++N  ++N NQ L+ V+++S   N   P+G      +R+RDE  E+
Sbjct  893    PSRKYNSYSDYFLERYNQSILNKNQKLIEVRAISGMSNHILPRGRYKIGKKRRRDE--ED  950

Query  954    LDIHLIPELVIKQEFPASLWIQASLLPTILSRLSFLFRLEYLRVQIATEAGLGQKDVPNK  1013
              L+  L+PEL    EFPA   ++ +LLP++L R++ L   E LR +IA E GLG   +P
Sbjct  951    LEETLVPELCFLLEFPAVYMLKVTLLPSLLHRITMLLNAEELRQKIAAETGLGAVKLPKG  1010

Query  1014   A---SLELDLHLL  1023
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Sbjct  1011   VYWNAIEVDNNVL  1023
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Ago-2

cDNA

Contig7506, Length-4208

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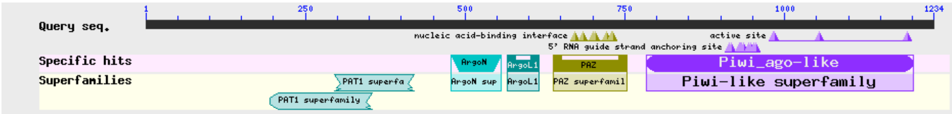
Graphical representation



Comparison with *Cylas puncticollis Ago-2*

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             GS P  Q + S  Q  P +     +T+  P  +  ++  S  Q     S+P + +  +G
Sbjct  352   GSAPSGQDARSVAQRPPPSSAQDKETRQPPPAKTPSQGPSRPQSHQGKSEPPSSSTGTGQ  411

Query  78    VSKVQIKPGTQ--GRRIKVESNHLKLSLGTLKEV-YHYDVNIVPDRPKKFLRAVVEKFRQ  134
             V +   +P     GR+I VE+NHL+L L   K V +HYDV + P++P +F R  ++  R+
Sbjct  412   VPRRLDRPKKTKAGRKIIVETNHLELKLKNPKMVVHHYDVTVNPEKPFRFYRRALDAVRE  471

Query  135   TRFPNKYPAYDGNKNMFTSFLLSGNLYDVLEEEVTIVDEE-GREKRFKIEVKWANTIDLT  193
               +P+++PA+DG KN+++   L     +++E  V I DEE  + K   + +K+AN +D++
Sbjct  472   ICYPSRFPAFDGKKNLYSYPELPLRSKELVET-VNIYDEEKDQTKEITVTIKYANAVDVS  530

Query  194   PLRN---LHSSPATPQLALQAVDIILRSAPVTTCLPVGRSFFVKPEGRIIDLGQGMEMYH  250
              +       ++  TPQ A+QA+D++LR       + VGRSFF  P GRII LG G+++++
Sbjct  531   IIGEYLRCGTTLNTPQEAIQALDVVLRQPSARRLVTVGRSFFSPPPGRIISLGDGLDLWY  590

Query  251   GFYQSAIRGWTPLLNVDVAHKAFPKSQNVIDTLVDLLSRPRQEFRRNDLQYLNPQQQEIL  310
             GF+QSAI GW P LN+DVAHK FP  +N +  L +++     E    + Q    Q++  L
Sbjct  591   GFFQSAIIGWKPFLNIDVAHKGFPTPENCVAALKNIIRSRDGELEHPNFQLQGYQRESFL  650

Query  311   SHFIKTLRVNYEIPGHPGTRRGYRVNGLGQPASQARFQHENRN------MTVAEYFRSVK  364
             S +IK L+V Y +P H   +R Y+V  L +     +F+  ++       MTV +YF S
Sbjct  651   S-YIKNLKVVYAVP-HGRGKRTYKVIDLSKCPRDNKFKSTDKTTQQTSEMTVEKYFLSQY  708

Query  365   NYALRYPDLPTLWVGSVQRTDKILLPLELCTIVEGQALNRKMTDIQTSNMIRQAATSTDV  424
              Y L YP LP L VGS  R   I LPLELCTI EGQ   +KM +IQT NM++QAA  TD
Sbjct  709   RYKLNYPHLPCLAVGSKDRP--ISLPLELCTIAEGQVTMKKMNEIQTRNMVQQAAVDTDR  766

Query  425   RKQKIMTGVQQASYNQSPCVREFGFSVGNEFQKLDARVLQPPQIQYN-RSNVRVSKGVWR  483
             RK+KIM  +++ S+N  PCV+EFG SV   F ++DARVL PP++ Y+ +  V V +GVWR
Sbjct  767   RKEKIMDSIKRISFNNDPCVKEFGLSVSESFTRVDARVLMPPKLDYSEKMQVDVKQGVWR  826

Query  484   NDVFLKGAVIKKWTIASVVSRYGPRPDDLKRMADMFHRAARDVGMIFETPAQEPFTTIGP  543
             N+ FL+GA +  W I +  +RY  R +D++ +A+   +  +  GM
Sbjct  827   NEKFLQGAELLTWRILNT-NRYI-RDNDIRGLAEGLIKHGKTCGMNISNNYGTAL-----  879

Query  544   RQDFQTISQYFNVQKEKQLDVIFVVVPDSGP-QYSYVKRAAEINVGCLTQCVKSTTVARK  602
             +     I  YF   ++  + ++ +++PD G   Y  VK+ AE+ VG LTQC+KS TV +K
Sbjct  880   KDKLSDIKDYFTQCQKDGVSLVIIILPDRGAVTYGGVKKCAELQVGILTQCLKSFTVQKK  939

Query  603   MNAQTALNILLKVNSKLNGINHTIADR--PPIMKRPVMIMGADVTHPGPDAQNIPSVAAV  660
             +++ T +NIL KVN+KLNG+NH+I     P    +PV+++GADVTHP PD  NIPS+AAV
Sbjct  940   LSSATFVNILQKVNAKLNGVNHSITQNIWPSYFHKPVIVVGADVTHPSPDQVNIPSIAAV  999

Query  661   TASHDPKAFQYNICWRLQSPRLEIIEDLQAIVVEQLKFFYAQTKCKPEAIVFFRDGVSEG  720
              ASHD KAF+YN+ WRLQ PR E+I+DLQAI+ + L  FY  TK KP AI+F+RDGVSEG
Sbjct  1000  AASHDVKAFKYNMIWRLQPPREEVIKDLQAIMKDHLLKFYLSTKQKPLAILFYRDGVSEG  1059

Query  721   QFQQVRDSEIRAIRAACKTLQQDGYEPKITFVVVQKRHHTRLFPTNPRDSEDKNCNVPAG  780
             QF+ VRD E+ AIR AC +L  D Y+P ITF VVQKRHHTR FPT+P+D+E +N NVPAG
Sbjct  1060  QFKIVRDIELNAIRRACSSLDAD-YKPPITFFVVQKRHHTRFFPTSPKDAEGRNKNVPAG  1118

Query  781   TCVDTDITHPFMQDFYLVSHASIQGVAKPTKYCTLWDDNLLDNDAVEQLAYYLCHMFSRC  840
             T VDT+ITHP   DFYLVSHASIQG A+PTKY  LWDD  L    +E++ +YLCH+F+RC
Sbjct  1119  TVVDTEITHPTELDFYLVSHASIQGTARPTKYHLLWDDAELSEQELEEITFYLCHLFTRC  1178

Query  841   NRSVSYPAPTYYAHLAAARAKVYIENDNLDMRALQREFQRFQIRDEIRKDLPMFFV  896
              RSVSYPAPTYYAHLAA RA+ Y+E +++ +  L+ E +R  I+D   K  PMFFV
Sbjct  1179  TRSVSYPAPTYYAHLAAFRARSYMETEHIHLERLEEEQKRRIIKDTFIKKNPMFFV  1234
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miRNAi pathway *Megacopta cribraria*

Dcr-1

cDNA

Contig11725, Length-4144

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Protein 1090(AA)

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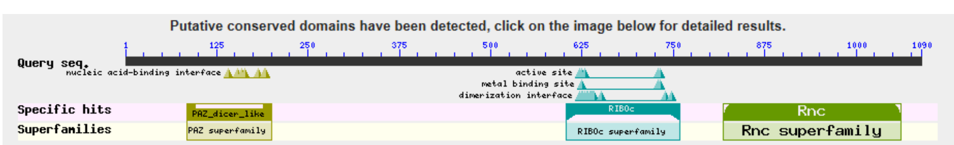
Graphical representation



Comparison with *Cylas puncticollis DCR-1*

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Sbjct  2     KEIPKVCPFPIFTRSGEVQVSLKLCSSSIRLSERNVETIATFLNFIFTSVLRLQKYLMSF  61

Query  455   KPELSDKNYLIVPTIQSEHGID-VDWEFIDIIYKNLHFVPRVIPDEDRKDYVFNTDDYKD  513
              P+  + ++ IVPT + ++G+  VDW+F+++IYK     P ++ DE+RK++VF+ + Y D
Sbjct  62    DPKAKENSFFIVPTKKDDNGLSQVDWDFLEVIYKRKDDNPHLVSDEERKNFVFDPEKYND  121

Query  514   AVVMPWYRNQDQPQYFYVAEICSFLNPTSAFPGSEYKSFEQYYLIKYAIQIQNLEQYLLD  573
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Sbjct  122   AVVMPWYRNQDQPQYFYVAEICYHLNPKSGFPGSFYNTFEDYYLKKYDIQIQNTTQPLLD  181

Query  574   VDHTSARLNFLTPRYVNRKGVALPTSSEETKRAKRENLEQKQILVPELCAIHPFSASLWR  633
             VDHTSARLNFLTPRYVNRKGVALPTSSEETKRAKRENLEQKQILV ELC +H   ASLWR
Sbjct  182   VDHTSARLNFLTPRYVNRKGVALPTSSEETKRAKRENLEQKQILVGELCEVHVVPASLWR  241

Query  634   KAVALPCVLYRINALLLADQIRTTVASDLNLGKTKLDDDFKWTPLNFGWSLSDVLKKSRD  693
             +AV LPC+LYR+NALLLAD+IRT VA ++ LG    L  DF+W PL+FGWSL+DVLK+++ 
Sbjct  242   QAVCLPCILYRLNALLLADEIRTKVADEIGLGLVNLPKDFEWPPLDFGWSLADVLKRTK-  300

Query  694   EEMKKQEEKLKSLREKTTELKITN-LVSDASEED---------PVNSDADISEAEEEEGN  743
             ++++ +E     + +   ++   N L+++ S  D            S+ +  E  E + +
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Query  744   DEGKGGDNWVVGTWSNEMAQ---SSQGDSTA---LVRYASPTSWLHGNSYDEDF------  791
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Query  792   ---------SDDMSDNSDFDSEESTHEWGRLRIEFTGDHQAEALDDDD---SKEDELYFV  839
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Query  840   EDVNAWTVDDN------SQETERLRHEFNNACLRNKEHILSSGILIKENEEFEKKSQNTP  893
             +D + W  D +        + E   H+F  A + N E +    ILIK  E F +  +   
Sbjct  474   KDFDVWKWDADDFISQVKNKVEEETHDFQKATIENVEMV--KKILIKSEEPFIRNKEELK  531

Query  894   ADDIPPVCPDNFDFD-------SLMIGDINIEQSSSAPQEPFVNVYDIS-EHIQNFSFDE  945
             AD+          F          +I     ++  S P  P   + DI  E    FSFD 
Sbjct  532   ADENLQSETKELGFKLRGYGMPESLIPKYQKKKFESYPY-PTERISDIVVEENSKFSFDH  590

Query  946   QPNLDTHPGPSPNVLLQALTMSNANDGINLERQETVGDSFLKYAITTYLYKTYENIHEGK  1005
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Sbjct  591   QPKLEGHPGPSPSILLQALTMSNANDGINLERLETIGDSFLKYAITTYLYCTHESIHEGK  650

Query  1006  LSHLRSKHVSNLNLYKLGKLKNLAEYMVATKFDPHDNWLPPCFYVPKQLEDALIDAQFPA  1065
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Sbjct  651   LSHLRSKQVSNLKLYRLGQKKMFGESMIASKFEPHDNWLPPCYLVPRDAEQRLLDSE-PQ  709

Query  1066  NCWTVADMAATRNMTIDEVCTLVRERGIYSLPNIIPYNLVTQHSIPDKSIADCVEALIGA  1125
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Sbjct  710   TT--------------------------------LPYNLVTQHSIPDKSIADCVEALIGA  737

Query  1126  YLIECGPRGALLFMAWLGIKVLPKNE-DGS----------------------YGELDLPK  1162
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Sbjct  738   YLIECGPRGALLFMSWLGIKVLPREEIDVSKRTSSSMKTVGRIKTNENTVVKFTTLSDPL  797

Query  1163  SPLLRNIPNPEEELEKLLDGYDTFEKHIGYKFRDRSYLLQAFTHASYSPNRLTDCYQRLE  1222
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Query  1223  FLGDALLDFIITKALFEDSRMHSPGALTDLRSALVNNTIFASLAVKHGFHKYFKHLSPGL  1282
             FLGDA+LD++IT+ LFED R HSPGALTDLRSALVNNTIFASLAVK+G HKYF+HLSPGL
Sbjct  858   FLGDAVLDYLITRHLFEDKRAHSPGALTDLRSALVNNTIFASLAVKYGLHKYFRHLSPGL  917

Query  1283  NEVIERFVRLQEESGHTIVDEHYLVVDTECEEVEDVEVPKALGDVFESVAGAIYLDSGMS  1342
              EV++RFV +QEE+ H I +E+YLV     EE EDVEVPKALGDVFESVAGAI+LDSGMS
Sbjct  918   AEVVQRFVTIQEENSHLISEEYYLV----GEEAEDVEVPKALGDVFESVAGAIFLDSGMS  973

Query  1343  LDAVWKVYHRMMKTEIEQFSNKVPKSPIRELLELEPETAKFGRPEKLADGRRVRVTVQVF  1402
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Query  1403  GKGTFKGIGRNYRIAKCTAAKCALKHLKRRGLLRNKND  1440
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Ago-1

cDNA

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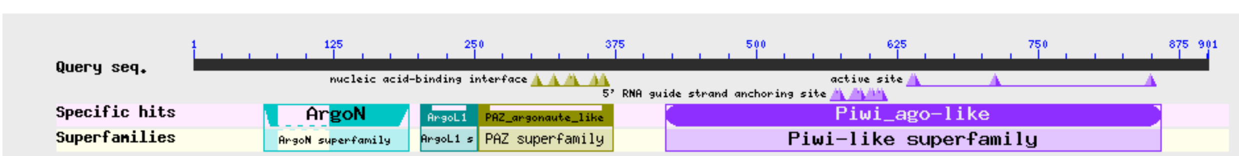
Graphical representation



Comparison with *Cylas puncticollis Ago-1*

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            +L    PP +PP   MF CPRRPNLGREGRPI L+ANHFQI+MPRGFVHHY+I+IQPDKC
Sbjct  34   ALAIQQPPHQPPDLPMFTCPRRPNLGREGRPIVLRANHFQITMPRGFVHHYEISIQPDKC  93

Query  90   PRKVNREIIETMVKSYGKIFGNLKPVFDGRNNLYTRDPLPIGNSREELEVTLPGEGKDRL  149
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Query  150  FRVSIKWVAQVSLYGLEEALEGRTRQIPYEAILALDVVMRHLPSMSYTPVGRSFFSSPEG  209
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Sbjct  154  FRVAIKWMAQVSLFALEEALEGRTRQIPYDAIMALDVVMRHLPSMTYTPVGRSFFSSPDG  213

Query  210  YYHPLGGGREVWFGFHQSVRPSQWKMMLNIDVSATAFYKAQPVIEFMCEVLDIRDINEQR  269
            YYHPLGGGREVWFGFHQSVRPSQWKMMLNIDVSATAFYKAQPVIEFMCEVLDIRDINEQR
Sbjct  214  YYHPLGGGREVWFGFHQSVRPSQWKMMLNIDVSATAFYKAQPVIEFMCEVLDIRDINEQR  273

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Sbjct  274  KPLTDSQRVKFTKEIKGLKIEITHCGSMRRKYRVCNVTRRPAQMQSFPLQLENGQTVECT  333

Query  330  VAKYFLDKYKMKLRYPHLPCLQVGQEHKHTYLPLEVCNIVAGQRCIKKLTDMQTSTMIKA  389
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Sbjct  334  VAKYFLDKYKMKLRYPHLPCLQVGQEHKHTYLPLEVCNIVAGQRCIKKLTDMQTSTMIKA  393

Query  390  TARSAPDREREINNLVRRADFNNDEYVQEFGLTISNNMMEVRGRVLPPPKLQYGGRVASL  449
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Sbjct  394  TARSAPDREREINNLVRRADFNNDAYVQEFGLAISNNMMEVRGRVLPPPKLQYGGRAPSL  453

Query  450  SGQ--------SKQQACPNQGVWDMRGKQFFTGVEIRVWAIACFAPQRTVREDALRNFTQ  501
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Sbjct  454  PSQLEYQGMLSAKQQALPNQGVWDMRGKQFFTGVEIRVWAIACFAPQRTVREDALRNFTQ  513

Query  502  QLQKISNDAGMPIIGQPCFCKYATGPDQVEPMFRYLKTTFQSLQLVVVVLPGKTPVYAEV  561
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Sbjct  514  QLQKISNDAGMPIIGQPCFCKYATGPDQVEPMFRYLKSSFQALQLVVVVLPGKTPVYAEV  573

Query  562  KRVGDTVLGMATQCVQAKNVNKTSPQTLSNLCLKINVKLGGINSILVPSIRPKIFNEPVI  621
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Sbjct  574  KRVGDTVLGMATQCVQAKNVNKTSPQTLSNLCLKINVKLGGINSILVPSIRPKVFNEPVI  633

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Sbjct  634  FLGADVTHPPAGDNKKPSIAAVVGSMDAHPSRYAATVRVQQHRQEIIQELSSMVRELLIM  693

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Sbjct  694  FYKSTGGYKPHRIILYRDGVSEGQFLHVLQHELTAIREACIKLEGDYKPGITFIVVQKRH  753

Query  742  HTRLFCADKKEQSGKSGNIPAGTTVDVGITHPTEFDFYLCSHQGIQGTSRPSHYHVLWDD  801
            HTRLFCADKKEQSGKSGNIPAGTTVDVGITHPTEFDFYLCSHQGIQGTSRPSHYHVLWDD
Sbjct  754  HTRLFCADKKEQSGKSGNIPAGTTVDVGITHPTEFDFYLCSHQGIQGTSRPSHYHVLWDD  813

Query  802  SHLDSDELQCLTYQLCHTYVRCTRSVSIPAPAYYAHLVAFRARYHLVEKEHDSGEGSHQS  861
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Sbjct  814  NHFDSDELQCLTYQLCHTYVRCTRSVSIPAPAYYAHLVAFRARYHLVEKEHDSGEGSHQS  873

Query  862  GSSEDRTPGAMARAITVHADTKKVMYFA  889
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Loquacious
cDNA
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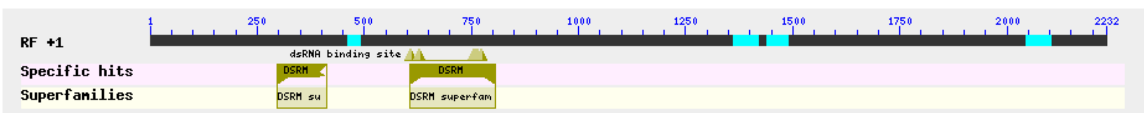
Graphical representation



Comparison with *Cylas puncticollis* Loquacious

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Sbjct  27   GGRSRMRNIPSCKFSPPEPVPLEEAAK----RELQTMPTKTPVSMLQELLSRRGTTPKYE  82

Query  79   LVQIEGAIHEPVFRYRVFL-----SNDLVATGTGRSKKDAKHAAAKNLLDLIVGKQTPEQ  133
            LVQ+EGA+HEP FRY V +      SN   A GTGRSKK+AKHAAAK +LD I G    E
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Query  134  ANQTNGTPGSTDITAQVVSPFDDKVMGNPIGWLQEMCMSRRWPPPLYEMEQEEGLPHERQ  193
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Query  311  IASEQNFEVTYVDVEEKSLSGRCQCLVQLSTLPVAVCFGTGKTPKDARANAALNALEYLK  370
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Sbjct  320  IATEQQFEVTFVDVEERSVSGKCQSLVQLSTLPVAVCYGTGMSSSEAQMCAAYNALQYLK  379

Query  371  IMTKK  375
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Sbjct  380  LMTKK  384
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Exportin-5
cDNA

Contig 4070, Length-8269

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Protein 1889 (AA)
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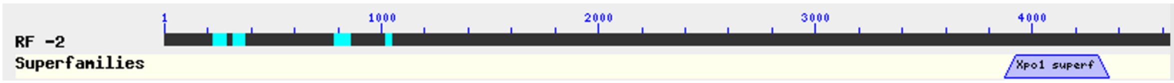
Graphical representation



Comparison with *Cylas puncticollis* Exportin-5

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             KKL +V  GL  Q+ +LW KD   +P NF M+LEAI+ ++ H SL L   AN LW +++K
Sbjct  315   KKLTRVLTGLGTQLSSLWTKDSQSRPPNFQMYLEAIVTFTRHPSLSLVCYANSLWLALMK  374

Query  69    QEHVARDLTFLSFLPKWVQCTAPKIIKFNYPAGKSPTLGEDISETVAYAKIDFDSEEEFS  128
              + +++D  FLSF+PKW++   PKI+K  +P+ KS  L  +  E  AYA  DFD+E+E++
Sbjct  375   HDQISKDEVFLSFVPKWIEAAGPKIMKVPFPSSKS-NLEPNTPE--AYAVQDFDAEDEYN  431

Query  129   AYFYRCRSDFLDSFRQATLVAPLITFNYVEQWLLKCLQ---VPNTTFGLSVSDPVYQEWE  185
             A+F++ R + LD+F+QATLV+PL+ ++YVE+WL   +Q     N     +++   Y EWE
Sbjct  432   AFFHKHRVELLDTFKQATLVSPLVAYSYVERWLEVQMQKTVSQNNMEPCTLTSVAYLEWE  491

Query  186   ALANFLESVLSRVLQAHERPSIPSGLRLLEMCLRYQPADPLIMSTLLTCISALFVFLSMS  245
             AL+  L++VL +++ A ERP + +GL+LL +CL  +P DPLI+S +L+CISALFVFLSM
Sbjct  492   ALSLALDAVLGKLVMAKERPGVNNGLKLLVLCLALEPTDPLILSAMLSCISALFVFLSM-  550

Query  246   TGQMAPAANSIAVSGAALLPQVLEKIFSTLVYNPNNQSKEVRSRPLKNVRRHAASLMVKI  305
                 AP   +     A  LP+VL+KIF+TLV+    + K  RSR +KN+RRHAASLMVKI
Sbjct  551   ----APPETT-----AIYLPKVLDKIFATLVFTLPGEPKNQRSRSVKNLRRHAASLMVKI  601

Query  306   GNKYPLLLLPVFDQIRTTVENLSKPDGPAQLSTLEKVTLREALLLISNHFADYERQSAFV  365
               KYPLLLLPVF +I   V +L     P  LST+E + L+EALLLISNH  DYER+  F+
Sbjct  602   AQKYPLLLLPVFSRIHGIVVSLQAK--PHTLSTMEALCLQEALLLISNHLCDYERECRFI  659

Query  366   GEVLREASAQFISIVNSGALKGAASFISFVGLDKPSVPANTKDICGHNRSNLVFCVNLVL  425
             GEV+      + ++ ++  L   A F+S+VGLDKP V  ++ DI G NRS +++C+ ++L
Sbjct  660   GEVMNPVIGPWTNMASTAFLSTPA-FMSYVGLDKPPVEPSSDDINGQNRSQIMWCLGVIL  718

Query  426   GAIKRCSWPDDPERATRGGFVVSLTESGNPVCRNPAAPHVIPLLPHMLSLICIFNELFTN  485
               +KR  WP DPE A RGGF+V  TE+GNP+ RNPA PHV+PLLP + SL C+ N L +
Sbjct  719   AVMKRVMWPSDPELAARGGFLVCTTEAGNPIYRNPATPHVLPLLPGLFSLSCVLNGLSSP  778

Query  486   EAQNLIHQSYKGCLAMPETEKSNLLGLIGHSSD--NGDNLIIQSPLERMQRFLTSLHESF  543
              A   + + Y+G   M E E+ NLLG IG +S+  N ++    +PL+RMQ F+++++E
Sbjct  779   AALTNLSEGYRGAYTMLELERQNLLG-IGSTSEVMNNESKGETTPLQRMQNFISNVNEDC  837

Query  544   YHLIGSMGPSLGRDLYNIPDLALAVINSVLAYLQYVPDYRIRPIIRVFLKSFIFACPVPY  603
              H +     +L  D+Y++P+LA ++I +V + L+ VPD+R+RP +RVFLKSF+ +CP P
Sbjct  838   CHTLAHAFHALSHDIYHVPNLAHSLIATVFSNLELVPDHRMRPFVRVFLKSFVTSCPPPC  897

Query  604   YEIVILPVLGHITPIIFNRLHSNWQRVIEFR----NREVQEDNADTQEVLEDILTRALTR  659
             Y+ V++PVL H TP +F RL + WQ + E      N +  E+N DTQE+LED+L R LTR
Sbjct  898   YDSVLIPVLAHFTPYMFTRLSARWQHLSEISGENGNVDEHEENTDTQEMLEDMLNRTLTR  957

Query  660   EYLDLLKVALVGGSLTPESTSETMETEELSNSPTPPPVRSNLTSEVISDLGLILLRNTKT  719
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Sbjct  958   EYLDVLKVVLYGGTDTGTASGGNMEEEGQDVKPQ---------SDVISELGMRVLAFDPT  1008

Query  720   CQPIVLAVLGALSWIDSNASLKATLLTGPIVRQLSQDNSLNGEMATHIMAAILNALMLHG  779
              QPI+L +L AL W DS ASLK T L G ++  L+    +  ++A H + ++L  L  HG
Sbjct  1009  SQPILLCLLRALYWGDSTASLKGTSLLGGVMFHLASTGKMTSDLACHALTSVLFGLQCHG  1068

Query  780   QHEANQGSLLTLGAQIYELLRPSFVEVLGVMQQIPGVNPVDLQKLDERISGSTSKGNKVE  839
             QH+ANQGSLL LG  +Y +LRP    +L VM+QIP VN +DLQKLD+R+     KG+KV+
Sbjct  1069  QHDANQGSLLVLGTLMYGILRPMAPPILQVMKQIPDVNMIDLQKLDDRMMKEIQKGSKVD  1128

Query  840   KVKKDLFKKITANLIGRSVGQLFKKEVKIQDLPQLVIPKKAEKSEVIGDL  889
             K KK++FKK+T+ LIGR+VGQLF+K+V I+DLP++    +  KS++  DL
Sbjct  1129  KAKKEMFKKVTSPLIGRNVGQLFRKKVAIRDLPKI----ENSKSKLHTDL  1174
```

piRNAi pathway *Megacopta cribraria*

AGO-3

cDNA

Contig 1655, Length-3033
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Protein 483(AA)
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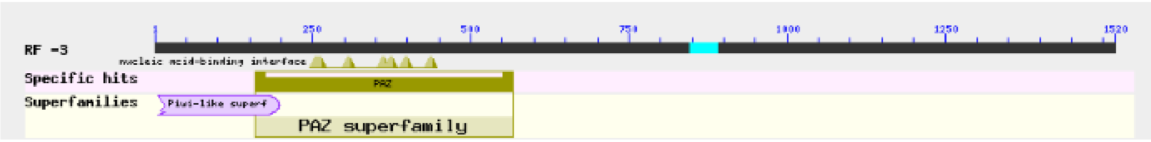
Graphical representation



Comparison with *Cylas puncticollis* AGO-3

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Sbjct  76   SEKPKADPDLE-VSKQLQQVSIS---EEEKVPALYKGESGSPLKLSANYIRLDVEKGRGV  131

Query  148  FQYDVQYDPPLESRSLKFGVLNSLKHVIGETRLFDG-MVLYLPIQLPKKITLLKTTLAHD  206
            F+Y+V+++P L++++ +  ++N +   +   ++FDG   LYLP ++ ++  + K TL
Sbjct  132  FEYEVRFNPELDAKNERIKMVNQMMRDMESVKVFDGGHCLYLPQKIKEEQKVYKGTLPGG  191

Query  207  NSVVNVKITYTKERKFGDPEAVHLYNVLFRRIMVILGLALHGKNFFDPKSAMPIPMHKLE  266
            +  V+V I Y ++++FGD E +HLYN+LF+RIM IL     G+N+F+P     IP HKLE
Sbjct  192  DQEVSVTIIYKRQKRFGDRECLHLYNILFKRIMHILLYTQMGRNYFNPAHKHLIPQHKLE  251

Query  267  VWPGYITAIDEFEGGLMLCCDASHRVLRNQTVLQLMDDIQ-NSNHSHWKEAFVQLILGQS  325
            V+PG+   +DE EGGLMLC D  HRVLR Q   +L+ +I+  S+   +KE  ++ I+G
Sbjct  252  VYPGFAVTVDELEGGLMLCLDTQHRVLRTQNAYELLTEIRCASDPRTFKENAMKNIIGSC  311

Query  326  VLTKYNNKVYRIDDVSFDESPNDSFEKSNGEKVRYVDYYRLQYNIKISDENQPLLKSRVK  385
            V T+YNNK Y IDD+ +D +P+D+F   +G  + +V+YY+ QYNI I+D NQPLL  R
Sbjct  312  VFTRYNNKTYIIDDILWDMTPSDTFPTRDGNTITFVEYYKQQYNININDVNQPLLLHRRS  371

Query  386  TRIKGKETRQ--LVSLVPELCFLTGITDTMRADARVMKDITQCISISPNQRHRAIKQFIN  443
             ++ GK  ++  ++ LVPEL FLTG+TDTMR D RVMKD+ Q   ++P+QR +A++ +++
Sbjct  372  VKVSGKAEKEDRMICLVPELSFLTGLTDTMRNDFRVMKDVAQYTRVTPHQRMQALRVYLD  431

Query  444  NIRVSPEATKVLSDWGMSLDDAYLVLEGRNIPPIDILFG  482
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Sbjct  432  NVRSSEKAQQVLSQWGLSVAEGNIDLQGRQLEHEKIRFG  470
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Aubergine/PIWI

cDNA

Contig 1655, Length-3033
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Protein 796(AA)
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PIEGHDGDWTRQMRGRIMFNNMPLQNWFVVIHKFHAKDKTGKNVFDIFLQEISRIAKSLKYEVHRPEVIFINDERPLGYVEAIEKQLSVMSKIDLVM
CIINGSKSDIYGAIKKKCCCDRGVASQVVATKTLSHKNLPSVVTKIIIQINCKLGGSPWFTPIPFKIVPDHCNVSMVVGFDVCHDSKVKDKSVGAMV
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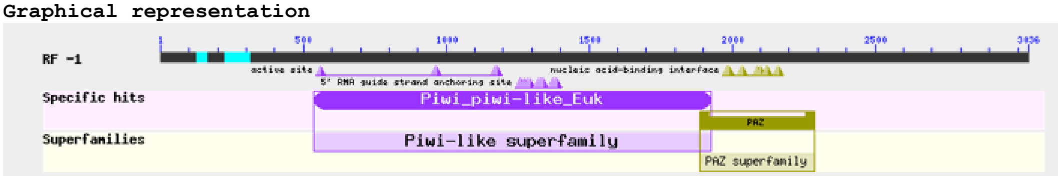
Graphical representation



Comparison with *Cylas puncticollis* Aubergine

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Query  130  VRGRTNRNEIISTRPSHIQSKKGFDGTAIRLRANYFRFIPKGHWGLNQYRVDFSPDLDST  189
            +RGR      I TRP +++ K+G DG  I + +N+FR I K  W L QYRVDFSP+ + T
Sbjct  1    MRGRFELVPPIKTRPDNLEVKQGTDGKGIEVVSNHFRLIKKTDWALYQYRVDFSPEEERT  60

Query  190  STRKYLVRTGMKNKNVSGYLFDGTVLYTPNRIQPEPLQ-FVVDTDDGTHTTVTIRLVGEV  248
              RK ++R   K++    Y+FDGT+L+T  R++P+  + F +   D     +TI+L  E+
Sbjct  61   KIRKAMLRDH-KDRLGEAYMFDGTMLFTIQRMRPDEFEVFSIRESDQAKIRITIKLTNEL  119

Query  249  KWGDYHYLQLFNIIMRKCLESMQLQLMNRNYYDPKLKISVPEHNLELWPGFFTSIRQYEK  308
              GD+ Y+QL+NII+R C+++M+ QL+ R Y+DP    ++    LE+WPG+  SI QYE
Sbjct  120  AVGDFQYIQLYNIILRHCMDAMKFQLVGREYFDPTRTTTLESFALEIWPGYNNSINQYEY  179

Query  309  DIMMNTDLAFKTVRTDNVYDLF--LECLQGRNPQNEFRSRIIGSVVLTYYNNKTYRIDDV  366
            ++MM  D++ K +RTD V D    L+ +   +    F   ++G VV T+YNNK YR+DD+
Sbjct  180  NVMMLIDVSHKVLRTDTVLDFLNDLKRVHRHDWMTHFNRHVLGCVVFTFYNNKPYRVDDI  239

Query  367  DFKQTPASTFQMKDGSQISYAQFLQNRWRVSVNTMDQPMLISRASMREVRLGMPETIILV  426
             F   +P  TF+ K  + ISY ++   ++  ++    QP+LISR   R++R G  + I+LV
Sbjct  240  AFDMSPLDTFK-KGNTNISYIEYYGQKYNANIKDPKQPLLISRPRARDIRGGRNQNIVLV  298

Query  427  PSTCIMTGLTDKQRENFHLMKALGEYTRVNPQNRMQKLREFSQRLQNCPEAMNEIRRWDL  486
            P  C MTGL+D+ R NF+LMKA+ E TR+ P  R+     F  RL+   E  +++  W+
Sbjct  299  PELCQMTGLSDEMRTNFNLMKAVAEKTRIGPTARIASYYRFMDRLKESKEVQSKLSIWNF  358

Query  487  DVARDIIELEGRVLPEESLLLRNGAMITGGP----EADFTKQLRSAPMYT-IAQADKLAV  541
              A D+  ++ R L  E L +         P    + D+T+Q+R   M+  +   +   V
Sbjct  359  KFASDLERIKARRLDPEPLYMNQFVAKDKSPIEGHDGDWTRQMRGRIMFNNMPLQNWFVV  418

Query  542  ICPGRFRQGTNE-----FINCLVKAGRGMHFNLGNPKILEMQDDRPQSYLDILEHVITSL  596
            I     +  T +     F+  + +  + + + +  P+++ + D+RP  Y++ +E  ++ +
Sbjct  419  IHKFHAKDKTGKNVFDIFLQEISRIAKSLKYEVHRPEVIFINDERPLGYVEAIEKQLSVM  478

Query  597  -QPRMVLVVLPNNSADRYNAVKKKCYVDRAMPCQVVVGRTLQNKGVMSIATKVAIQMNCK  655
             +  +V+ ++  + +D Y A+KKKC  DR +  QVV  +TL +K + S+ TK+ IQ+NCK
Sbjct  479  SKIDLVMCIINGSKSDIYGAIKKKCCCDRGVASQVVATKTLSHKNLPSVVTKIIIQINCK  538

Query  656  MGGAPWGTALP--------KATMVVGYDVCRDTANRGKSFAGMVASMDTACSQYFSLTIE  707
            +GG+PW T +P          +MVVG+DVC D+  + KS   MVAS+D   ++++S   +
Sbjct  539  LGGSPWFTPIPFKIVPDHCNVSMVVGFDVCHDSKVKDKSVGAMVASLDYHFTKWYSAVSK  598

Query  708  HEQEQELSSNIATFMLLACKNYQERNK-VIPERIVIFRDGVGDGQIQYVKEHEVEQLKKK  766
            H   +ELS++IA  +++A   ++E NK  +P RI+++RDGVG+  + YV EHEV  +K +
Sbjct  599  HNFGEELSNDIAAHIVIAVYKFKEVNKGALPPRIILYRDGVGESNVGYVLEHEVSAIKSR  658

Query  767  LNAEIYQTQQLKMAFIIVSKRINTKIFRAQGVGPRNDYNPPPGTVVDDVITWPERYDFYI  826
            LN+  Y   ++K+  ++VSKRI T+IF  +G   RN YNP PGTVVDD+IT PE+YDF++
Sbjct  659  LNSS-YPGNKIKLMIVLVSKRIQTRIFLLEG---RNAYNPQPGTVVDDIITSPEKYDFFL  714

Query  827  VSQCVRQGTVAPTSYNVIEDSLGIDANKLQRFTFKLCHMYYNWSGTVRVPAPCQYAHKLA  886
            VSQ VRQGTV PT+Y+VI D++    AN +QR T+K+CH+YYN S TVRVPA  QYAHKLA
Sbjct  715  VSQSVRQGTVTPTNYHVIYDTMATPANIIQRITYKMCHLYYNCSTTVRVPAQVQYAHKLA  774

Query  887  FLTAQSLHRSANPALKNTLYYL  908
            FL  Q    +    L   L++L
Sbjct  775  FLVGQVTILAPLEVLTRCLFFL  796
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Antiviral RNAi in *Megacopta cribraria*

Ars2

cDNA
Contig 4509, Length-2647
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Protein 757(AA)

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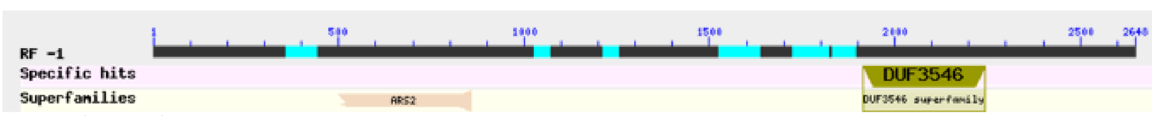
Graphical representation



Comparison with *Cylas puncticollis* Ars2

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Sbjct  1    MGDSEDEYDKKRRDKFQGERSD-SYRTDKR---------KDDDWGRPRMRNDYR--DRYQ  48

Query  60   SPSMEPTAKRMRHD--------YYGEGY--YNHYTPYHQPPHREQTMSQMEGQQPPMMSF  109
                 P AKRMR+D        Y    GY  YN + P  +PP+    +       QPP+M+F
Sbjct  49   YQGDIPPAKRMRYDSDDIRRMRYNDPGYGPYNSWGP--EPPYPGNSRLGEMDTQPPIMTF  106

Query  110  KAFLATQDDNISDSEAIEKYNDYKLEFQRQQLNEFFVAHKDDEWFRLKYHPEDSVRRKQE  169
            KAFL +QDDNI+D EAI KY +YKLEF+RQQLNEFFVAHK++EWF+LKYHPE+SV+RK+E
Sbjct  107  KAFLQSQDDNITDEEAISKYAEYKLEFRRQQLNEFFVAHKEEEWFKLKYHPEESVKRKEE  166

Query  170  QAAALKKRLEVFIDLLNSGKIESTTVDCARTTDLLKLLDTVVIKLEGGTDEDLAALEQEY  229
               ALKKR +VF++++NS ++E+   VD  +   D++KLLD VVI+LEGGTD DL   L+Q
Sbjct  167  LNTALKKRCDVFLEMMNSDRMENIRVDTEQGDDVVKLLDAVVIRLEGGTDLDLTILDQP-  225

Query  230  EEMEQKYREQKEKEAAAERAREARMAETASQKEEGE  265
               E +  EQKEK+   E+ +E   +E   + +E E
Sbjct  226  ---EGQKEEQKEKDKIDEKPKENNKSEDEEKVKEHE  258
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Egghead

cDNA

Contig 3764, Length-3819
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TGAAAATTTAGGTAAACAAAAATGTTCATGAACATATTGCAAAATCTTAAGCTCGTATTTGAAACATTATAATAAAAAATTTCGCGGTAGGGAGTAA
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Protein 457(AA)
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RIVTRGDYPQLVKNNVSRNLSKCLNAGLEHFIIEVVTDKPIHLIKDRRIIETVIPANYKTKSGALFKARALQYCLEEGVNTLSDSDWIVHLDEETLL
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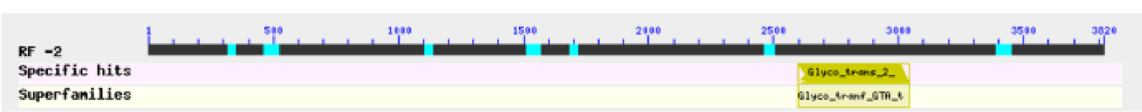
Graphical representation



Comparison with *Cylas puncticollis* Egghead

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Sbjct  1    MLRSKTKHVLHCVLLFTVIIVFELVTGGVKFSSDDVI-----IDPWEEYGFVLTTLLYVL  55

Query  61   RLVTFLPLPQVIFNFVGLIFYNAFPEKVSLKGSPLLAPFICIRVVTRGDFPQLVKNNVNR  120
            RL+ FLPLPQ++ NF GL FYNAFP+KV LKGSPLLAPFICIR+VTRGD+PQLVKNNV+R
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Query  121  NMNKCLDTGLENFLIEVVSDKPIGLEQHRRVRELVVPSDYRTPTGALFKARALQYCLEEK  180
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Query  181  INILSDNDWVVHLDEETVLTENSIRGILNFVMDGKHHFGQGLITYANEEVVNWITTLADS  240
            +N LSD+DW+VHLDEET+LTENSIRGILNFV+DGK+ FGQGLITYANEEVVNWITTLAD+
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Query  241  FRVTDDMGKLKLQFLWFHKPLFSWKGSFVVTQVAAEKDVSFDNGLDGSIAEDCFFAMKAY  300
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Query  301  SMGYSFNFIEGDMWEKSPFTLWDFIQQRKRWIQGILLVVHSRSIPIRNKLLLACSCYSWV  360
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Sbjct  296  TMGYSFNFIEGEMWEKSPFTLCDFLQQRKRWLQGILLVVRSKKIPFRNKIFLSISCYSWV  355

Query  361  TLPLSTSNIFLATKFPIPCPALVDFLVAFIGAVNIYMFIFGVIKSFNVYRFGLARF  416
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Sbjct  356  TMPLSTSNIILAAICPIPCPPIIDFLCAFIGAVSIYMYIFGVIKSFSLYRFGIVKF  411
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Nucleases* RNAi in *Megacopta cribraria

dsRNAse

cDNA

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PROTEIN 409 (AA)
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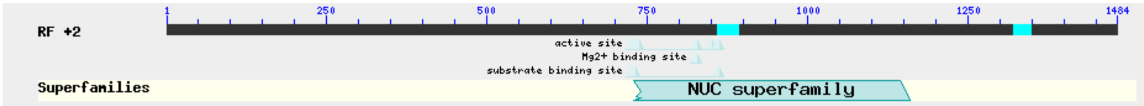
Graphical representation



Comparison with *Cylas puncticollis* dsRNAse

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Query  45   SGTSDFIYPK--PFEKTLKFSSGQSLDFVCPERTLILGATKTNDSVLQGTCVKDDTFKIN  102
            SG+ +F YP+        +    G+ L    CP R    L   KT + + + +C + +    ++
Sbjct  53   SGSLEFAYPELEGRRGVIALREGEELVISCPGRRNYL--QKTKNDIAKTSCAEGNRLTLD  110

Query  103  GGEVLWNQISCSNYPYRVAKRTGLSCENG-GTDIEIGFEVGDGRFLRSLSVCFNESSQIA  161
              +    ++  C++      +K T    C  G G  +++GF VG+  +L   +  C N    +
Sbjct  111  DKKYNSDEFECNSRVAASSKPTEQKCAGGKGIIVQLGFNVGE--WLPLIDSCHNVDESVT  168

Query  162  LYSFHNMTTAI--NQRVLATPRPSWLQGSGLY--TISTITNYYVRNKQRSTINTLLGLDI  217
             YS H +   AI    +      T RP + +G   +      +     Y   RN+QR   ++   LG +
Sbjct  169  YYSNHTIHGAILGGKVRRTTGRPKFDRGDAILFKGFNPEIAYTQRNQQR-ILSRDLGKE-  226

Query  218  NSTKYIEDNSNYYLARGHLSARSDHYYAAQQNATFFLINVAPQWQTFNSLNWNQVEIDVR  277
             +     ++    + ++ARGHL+    +D    +++ Q   T+F +NVAPQWQ+ N+ NW +VE + R
Sbjct  227  TAEGLLDTKKSLFMARGHLAPDADFLFSSHQFLTYFYVNVAPQWQSINAGNWLKVEENTR  286

Query  278  DYAEERGINLQVWTGIYGVTILPHEQTGRPVELYLYVDDNNNKALPVPEIYWKVAYDPIT  337
             +A      +L  V TG YGV   L          + + L                LP PE++WKV    +
Sbjct  287  RFARRLAADLDVVTGTYGVLKLKGTDGEKEIRL-------QESRLPAPELFWKVVRNTQD  339

Query  338  EKGLAMIGVNNPYLANYTE-ICNDVSDRITWLHWKKDDQARGYSYACAVDVFRRVVTSLP  396
            +   +A +   NNP+L +    + IC D+        W   + +DD ++GY Y C        ++VV   +P
Sbjct  340  DSCIAFVSTNNPFLESKPKPICTDICKMANWPTF-QDDLSKGYVYCCTYQELKKVVAEMP  398

Query  397  DIPVRGLL  404
            D+    +L
Sbjct  399  DVTCNSVL  406
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Exosome

cDNA

Contig 2692, Length-3677

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PROTEIN 809 (AA)
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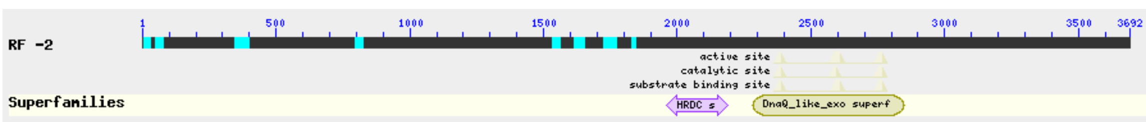
Graphical representation



Comparison with *Cylas puncticollis* Exosome

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            M  ++++N ++       LE+  E +I++ D  L+RV NN+ E++G +KN + P     V
Sbjct  76   MECLMKRNGIRK------LEQGFESVIDSNDRCLDRVNNNLLELDGRKKNPLPPKPATNV  129

Query  61   SVQLPVNGSWNRVSKPVMSATSAITSSQTTASGSSTQTIRLITAENIVRPQKFFKDKIDN  120
            + Q   +G W                 + T S  S + I L  +   VRPQ  FKDKIDN
Sbjct  130  APQAVPSGGW---------------FEKQTNSYPSKEEITLCASSGTVRPQTLFKDKIDN  174

Query  121  SRQRPWEPRIKEKPNSIKPLAIFLEETENGQE-YSHPYECELDKFSPPEDQLRKSDVVKP  179
            S   PW PRIKEKPNS+KPL+I LE  + GQ+ +SHPY+ EL   + P E  L   +V  P
Sbjct  175  SNS-PWIPRIKEKPNSLKPLSIMLELNDLGQDCFSHPYDYELTLWKPDESLLTNVEVKTP  233

Query  180  KLLKDTPLVEITQEEQLNDLVEDLRSAKEIGIDLEHHSYRSFMGITCLLQISTLEKDYLI  239
              L DTP + I  EEQLN L++DL   +E  +DLEHHSYR+FMG TC++QIST EKDY+I
Sbjct  234  LPLADTPFIYIETEEQLNGLLQDLSEVQEFAVDLEHHSYRTFMGFTCVMQISTWEKDYVI  293

Query  240  DTLVLRDKLYILNEIFTDPKIIKIFHGAKHDIQWLQRDLSLYVVNMFDTHFAAKQLEYPG  299
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Sbjct  294  DALKLRDKLHILNEVFTKPSILKVFHGADSDIEWLQRDLSIYVVNMFDTYQASKLLGFAR  353

Query  300  LSLAYLMQKFCNFAPNKQFQLADWRIRPLPHELKTYAREDTHYLIYIYQNMKNELIDKYN  359
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Sbjct  354  LSLAHLLYKYCKVEANKEYQLFDWRKRPLPESALKYAREDTHYLLHIYQHMRNDLIQHAN  413

Query  360  GQPNLLKSVIQMSTDLCKTRYVKPVFTSDSYLNLYRRCSRMFHNRQLFALQELYRWRDEI  419
            G+ NLL++V   S + CK  Y KP    DS++ +YRR    F NRQL+AL+E+YRWRD I
Sbjct  414  GKTNLLEAVFDRSKETCKKVYCKPSLEEDSHMAIYRRLKLCFDNRQLYALKEIYRWRDRI  473

Query  420  SREEDESTGYVLPNNMLLEISERLPREMQGILACCNPTPPLVKANLLDLHKIMLKALEQP  479
            +R+EDES GYVLPN+M+++I   LPRE+QGILACCNP PPLV+  LL+LH+I+LKA EQP
Sbjct  474  ARQEDESCGYVLPNHMMVQICRTLPREVQGILACCNPIPPLVRTCLLELHQIVLKAKEQP  533

Query  480  FESPILKEDTRSRGITTKISKIDVNNPLHCPHDLTKREEVCDNLPTILSGDSINLDSIFT  539
                +++E ++S       + ++ +  L  P D     E  D+LPT+L G    + S
Sbjct  534  LVKSLVEETSKS------ATGVERDLRLILPQD-NSGFEFRDDLPTLLGGGLPEIPS---  583

Query  540  HYIEEDSSVSSIFDFPVNAANETRLPNKLEGV--LKFLSPYARYKLIKPF  587
              + E +    IF F  N  +++   ++      L+F+SPY RY  + P+
Sbjct  584  --VPEQNCAPIIFAFESNHKDKSSHHSEESSTVKLRFVSPYERYLNVLPY  631
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Polymerase

cDNA

Contig 7462, Length-2376

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PROTEIN 610 (AA)
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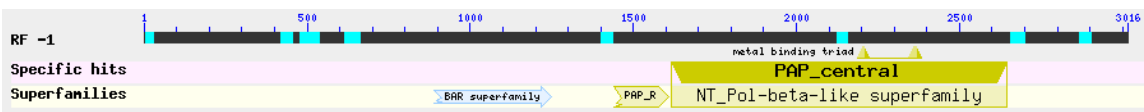
Graphical representation



Comparison with *Cylas puncticollis* Polymerase

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Sbjct  20   TLGLTSAITLAGPKPIDYQKTNELTEALKPYNVMETEEELNHRMEILSKLNSLVKEWIKE  79

Query  85   LSIKCNMPESVAENVGGKVYTFGSYRLGVHNKGADIDALCVAPKHICRSDFFTSFYELLK  144
            +SI  NMPESVA +VGGK+YTFGSYRLGVH+KGADIDALCVAP+HI RSD+FTSF+E LK
Sbjct  80   VSISRNMPESVASSVGGKIYTFGSYRLGVHHKGADIDALCVAPRHIDRSDYFTSFFEKLK  139

Query  145  KQPEVTELRAVEEAFVPVIKMSFDGIEIDLLFARLLQKEIPDSMDLRDDNLLKNLDQKCV  204
               EVT+LRAVEEAFVPVIKM+FDGIEID+LFARL  KEIPDSMDL+DD LLKNLDQKCV
Sbjct  140  LNSEVTDLRAVEEAFVPVIKMNFDGIEIDMLFARLALKEIPDSMDLKDDLLLKNLDQKCV  199

Query  205  RSLNGCRVTDEILRLVPNIETFRLALRAIKLWAKRHGIYSNVLGYLGGVSWAMLVARTCQ  264
            RSLNGCRVTDEILRLVP+IE FRL LR IKLWAK+HG+YSNV+GYLGGVSWAMLVARTCQ
Sbjct  200  RSLNGCRVTDEILRLVPDIENFRLTLRTIKLWAKKHGVYSNVMGYLGGVSWAMLVARTCQ  259

Query  265  LYPNAAPATLVHKFFLIFSKWQWPQPVLLKQPTNASLGFTVWDPRVNIQDRYHLMPIITP  324
            LYPNA  ATLVHKFFL+FS+W+WPQPVLLKQP    LGF VWDPRV + DRYHLMPIITP
Sbjct  260  LYPNAVAATLVHKFFLVFSQWKWPQPVLLKQPDQVNLGFPVWDPRVTVSDRYHLMPIITP  319

Query  325  AYPQQNSTFNVSNSTRNIIMEEFERGLKITDQIMLNKSTWERLFVQPPFFMKYRHFIVLI  384
             YPQQNSTFNVS STR I+ E F  GL ITD+I   K+TW++LF  P FF+KY+HFIVL+
Sbjct  320  VYPQQNSTFNVSASTRTILQEAFNNGLSITDEIFNGKATWDKLFEAPNFFLKYKHFIVLL  379

Query  385  ISAETSKDLLEWSGLVESKIRLLISTLERNGAITLAHINPENFML-PEPLRKPKFQYSMW  443
              + + ++ LEW GL+ESK+R L+  LERN  I+LAH+NPE F   P P  +P+   SMW
Sbjct  380  AKSGSQEEQLEWCGLIESKVRHLVGNLERNQYISLAHVNPECFAGPPTPPGEPQGPTSMW  439

Query  444  FIGLEFRKMEGLNVDLTQDIQQFTETVNKHAMHIQMFKDTMKLEARHVKRKMLPNYLPSG  503
            FIG+ FRK+E LNVDLT DIQ FT +V++ A   +M KD+MK+EARHVKRK L  YLP+
Sbjct  440  FIGIVFRKLENLNVDLTYDIQSFTTSVHRQASATKMIKDSMKIEARHVKRKQLSAYLPAQ  499

Query  504  VLKREKKYLATFTE--------CKEQKEG---RKRQSESSDSETTVKKTRLS---NEMNG  549
            +LKREKK  A             +Q+ G   +KR S+SS  +   KK +L     EM+G
Sbjct  500  ILKREKKVAAARNSSSPIHKNGVSQQQSGDVNKKRHSDSS-LDLIQKKQKLHPHLPEMDG  558

Query  550  --------TNFDDSSNNSLNNDD  564
                     +  + SN+SL+ D+
Sbjct  559  DPPMNRIVVSCGEDSNSSLSADE  581
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dsRNA uptake in *Megacopta cribraria*

Hermansky(CG4966)

cDNA

Contig 5140, Length-2217
ATTTAGTTTATCTCTTGTCTACATTTCAATTAAAATACCCTGAATACCATTGACTAGTTAAAAACTGGCATCAATTTATTCATTCAATAGCAACATT
AACATCCGATGTTAACATCGGAAAGTAAATCATAACAAAATCTCAAATTTGCATAAACTTTATAAACTTAATACAACAGGCTATAAACAATTTATAG
AAATGTCTTTTAAACCTACTTTAACATTAGTAACTTTTAAAAATTTTACAAAGGTCACAAATTGTATTATAATAAGGTCTTGGTTTTTTCCTATGTG
AAGTTTCACACCATTCAGGATTAAGAGAAGGCAGACCTATACTGTAATACCTTATAGGAATTTTTTTTGTGGTAAGATCATCAGGGGTCATAGCTGA
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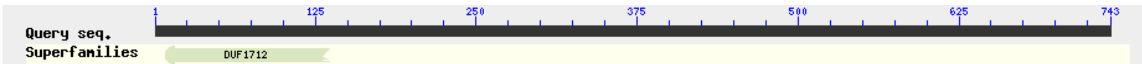
CCCTATTTTGATAAAGCAGTACACCTCCAAGGATTCCCTTTATTTCTTGAAATCCTTGTAAAACTTGCCTGGCTTCTAAATACAGAGTACTTGCACT
CTTAGGAATTTTGAATAATGGAATATTTCCAAATTTATTAGTGGCATATTGCAATATCGGTAAATAAATCTGGAGCAGTTCAGACAATTTTTCAGAA
ATATCATCATCTAATAATGATTCTTGTAATGTTTCAATACTGTTATGAAACAACCTTATTAACTTATATAAAATCTTAACTCTTGTTTCCAATACTA
TATCAGGAATATTTCTGTCAGTTCCTACACACAAAGCATATTTACCTAATTTTTTCAAAGCAAATTTGCCACTTTGTAGAGAAATAATATTTGGAGG
AGAAAATGATGTAGAACAAAATTGGGTAACACCCATTAATTGACTACACAAGGCATGTCTCTGTTCATCGGTGACCCAAGAGGGGTAGAAGTAAAGA

ATAGAATTTTGTGGATCATCTTCTTCTCCTTTACATAATTCACAATCATAAATAAAAACTATCAACAATTCCTTTGCCATTGAGCTGATGTAAAATT
TCTATCAGTATTACATAACAGACATATCCAACAGTTGTTTGACTGTTTATTTTGAG

PROTEIN 405 (AA)
MAKELLIVFIYDCELCKGEEDDPQNSILYFYPSWVTDEQRHALCSQLMGVTQFCSTSFSPPNIISLQSGKFALKKLGKYALCVGTDRNIPDIVLETR
VKILYKLIRLFHNSIETLQESLLDDDISEKLSELLQIYLPILQYATNKFGNIPLFKIPKSASTLYLEARQVLQGFQEIKGILGGVLLYQNRVVATQL
AKSLTKLFVVTDPYRIKLPAEIVSTPFHLPFGVQLMKVYISSAEIKRLKDEYNELHNTLKDVAIWRNQLEDSMIQNQNKNTCLKTSDSYISMCGLKR
DVSRIFTVLEEEGNENLEGKDQGDIPDVVRDAVKARHLSRIEAVVPNNFIIPEASSNVRSAMTPDDLTTKKIPIRYYSIGLPSLNPEWCETSHRKKP
RPYYNTICDLCKIFKSY

Graphical representation



Comparison with *Cylas puncticollis* Hermansky(CG4966)

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Query  1    MAKETTIIFVYDTDKLQNEEDDPASAILYFHPTWVSDQQKTALCGQIVGTISCLKSIFSM  60
            MAKE  I+F+YD +   + EEDDP ++ILYF+P+WV+D+Q+ ALC Q++G      + FS
Sbjct  1    MAKELLIVFIYDCELCKGEEDDPQNSILYFYPSWVTDEQRHALCSQLMGVTQFCSTSFSP  60

Query  61   PKVVCLQTGKFYIIENGQYILAVGTDRNIADWLLEHRGTLLYSLVTLFNKDFDMLGRIYK  120
            P ++ LQ+GKF + + G+Y L VGTDRNI D +LE R  +LY L+ LF+   + L
Sbjct  61   PNIISLQSGKFALKKLGKYALCVGTDRNIPDIVLETRVKILYKLIRLFHNSIETLQESLL  120

Query  121  DEALKAKLYHLFETYLRMLFYGGSIFSHVPVLCLPKSASAVFTEAVTFLEACREYSHVLG  180
            D+ +  KL  L + YL +L Y  + F ++P+  +PKSAS ++ EA   L+  +E   +LG
Sbjct  121  DDDISEKLSELLQIYLPILQYATNKFGNIPLFKIPKSASTLYLEARQVLQGFQEIKGILG  180

Query  181  GTLLYHNKVVATQLPTDITKRIVIADPYRIKSPAEPAETAFKLPLGVQLLQVYITN----  236
            G LLY N+VVATQL   +TK  V+ DPYRIK PAE   T F LP GVQL++VYI++
Sbjct  181  GVLLYQNRVVATQLAKSLTKLFVVTDPYRIKLPAEIVSTPFHLPFGVQLMKVYISSAEIK  240

Query  237  --KDFCDLLETSMRNKCIFQYLNNKSIKRAHSKS----SSEAPI-VSAMKRDQSLLFTA  288
              KD  + L  ++++  I++     S+ +  +K+    +S++ I +  +KRD S +FT
Sbjct  241  RLKDEYNELHNTLKDVAIWRNQLEDSMIQNQNKNTCLKTSDSYISMCGLKRDVSRIFTV  299
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FBX011

cDNA

Contig 3711, Length-6097
AAATGGGTATTTTGCCAGACGTAAAGGCTCAGTACATACATTATTGACAGAATACAACATCCTATAATAGGTAAAACACAAACACCTCTCACAGTAG
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TTGTTTGGAAATTGGAGAAAACTGCAGCCCCACAATTGACCATTGTATTATTAGAAGCACTTCAGTTGTTGGAGCTGCTGTTTGTGTTAGTGGTGCT
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GGATTACTACAGGTTCTACTCCAGTTCTCCGCCGTAATAGGATTCATTCTGGAAAACAAGTTGGCGTTTATTTTTATGATAACGGCCATGGGAAGTT

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CTAACCCAACTCTTAAGCGGAATAAAATTTTTGATGGAAGGGATGGAGGCATTTGTATATTTAATGGCGGCAAAGGTATTTTAGAAGAAAATGACAT
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TGTTTAAATTGTTATTTCAATGTTGGAAACATCATTGTTGCTTGATATTCCATTTCTAAGTATATAAAATTATTTGAATATTAGGGGAATGATCAGT
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AAGAATTTTTATAATGAAAATTTTCTAACCTTATGGCTTGAACTTCGATTTTTTCATATAGTAATCATTTACATTCTTCTTTTTTATCTGTGTTTCT
ATATTTCTGATAGTTTTTTGCATAATTGCAAG

PROTEIN 871 (AA)
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FTPDVASSVPHHKHYCLEIGENCSPTIDHCIIRSTSVVGAAVCVSGAGAAPTIKHCDISDCENVGLYVTDYAHGTYEDNEICRNALAGIWVKNYANP
IMRRNHIHHGRDVGIFTFDNGLGFFEANDIHNNRIAGFEVKAGANPTVVQCEIHHGQTGGIYVHENGLGQFIDNRIHSNNFAGVWITSNSNPTIRRN
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KQVGVYFYDNGHGKLEDNDIFNHLYSGVQIRTGSNPIIRGNKIWGGQNGGVLVYNGGLGLLEQNEIFDNAMAGVWIKTDSNPTLKRNKIFDGRDGGI
CIFNGGKGILEENDIFRNAQAGVLISTQSHPVLRHNRIFDGLAAGIEITLNATATLESNQIFNNRFGGLCLATGVNPIVRCNKIFSNQDAVEKAVRN
GQCLYKISSYTSFPMHDFYRCQTCNTTGRNAICVNCIKTCHAGHEVEFVRHDRFFCDCGAGTLCNQCQLQGEPAQDTDTLYDSAEPMESHTLMVN

Graphical representation

Comparison with *Cylas puncticollis* FBX011

```
Query  86   HQSPYDLRRKSPSHNHGGGAPVADGGPGPSTSAATASGSPASPTTPCNLPAAQGAYSSAM  145
            H  PYDLRRKSP +      P+ D G                       P
Sbjct  56   HNPPYDLRRKSPPY------PILDAG----------------------FPNL--------  79

Query  146  LPARKRPRRTCSASYENCTNTAAHYLQYELPDEVLLTIFNYLLEQDLCRVSQVCKRFQVI  205
               RKRPRR+CS S + CT  AAHYLQYELPDEVLLTIF YLLE+DLCR+SQVCKRFQ I
Sbjct  80   ---RKRPRRSCSVSTDVCTPPAAHYLQYELPDEVLLTIFGYLLEKDLCRLSQVCKRFQTI  136

Query  206  ANDTELWKRLYQNVYEYDLPLFNPSPCRFEFVSSEESELANPWKESFRQLYRGIHVRPGY  265
            +ND  LWKRLY N++EYD+PLFNP PC+FEF+    + E ANPWKESFRQLYRGIHVRPG
Sbjct  137  SNDNGLWKRLYHNIFEYDVPLFNPEPCKFEFIPPNDCEYANPWKESFRQLYRGIHVRPGQ  196

Query  266  -QELSFKGRNLVYFNTVQGALDYADERSGSGSGTGLAVSGGGSHSSENAGQGALIFLHAG  324
                  +GR+L +F+TVQ ALD+ADE                   ++  G  A++FLHAG
Sbjct  197  GSRYKARGRSLAHFDTVQTALDHADE-------------------NQTPGVPAIVFLHAG  237

Query  325  TYRGEFLVIDSDIALIGAAPGNVAESVILERESESTVMFVEGAKNAYAGHLTLKFSPEPA  384
            TYRGEFLVIDSD+ALIGAA GNVAESV+LER+SEST+MFVEGAK+AYAGHLTLKF+P+ A
Sbjct  238  TYRGEFLVIDSDVALIGAAAGNVAESVVLERQSESTMMFVEGAKSAYAGHLTLKFTPDVA  297

Query  385  SATPHHKHYCLEVGENCSPTIDHCIIRSTSVVGAAVCVSGVGANPVIRHCDISDCENVGL  444
            S+ PHHKHYCLE+GENCSPTIDHCIIRSTSVVGAAVCVSG GA P I+HCDISDCENVGL
Sbjct  298  SSVPHHKHYCLEIGENCSPTIDHCIIRSTSVVGAAVCVSGAGAAPTIKHCDISDCENVGL  357

Query  445  YVTDYAQGTYEDNEISRNALAGIWVKNYANPIMRRNHIHHGRDVGIFTFDNGLGYFEAND  504
            YVTDYA GTYEDNEI RNALAGIWVKNYANPIMRRNHIHHGRDVGIFTFDNGLG+FEAND
Sbjct  358  YVTDYAHGTYEDNEICRNALAGIWVKNYANPIMRRNHIHHGRDVGIFTFDNGLGFFEAND  417

Query  505  IHNNRIAGFEVKAGANPTVVHCEIHHGQTGGIYVHENGLGQFIDNKIHSNNFAGVWITSN  564
            IHNNRIAGFEVKAGANPTVV CEIHHGQTGGIYVHENGLGQFIDN+IHSNNFAGVWITSN
Sbjct  418  IHNNRIAGFEVKAGANPTVVQCEIHHGQTGGIYVHENGLGQFIDNRIHSNNFAGVWITSN  477

Query  565  SNPTIRRNEIYNGHQGGVYIFGEGRGLIEHNNIYGNALAGIQIRTNSDPIVRHNKIHHGQ  624
            SNPTIRRNEIYNG QGGVYIFGEGRGLIEHNNIYGNALAGIQIRTNSDPIVRHNKIHHGQ
Sbjct  478  SNPTIRRNEIYNGQQGGVYIFGEGRGLIEHNNIYGNALAGIQIRTNSDPIVRHNKIHHGQ  537

Query  625  HGGIYVHEKGQGLIEENEVYANTLAGVWITTGSTPVLRRNRIHSGKQVGVYFYDNGHGKL  684
            HGGIYVHEKG+GLIEENEVYANTLAGVWITTGSTPVLRRNRIHSGKQVGVYFYDNGHGKL
Sbjct  538  HGGIYVHEKGEGLIEENEVYANTLAGVWITTGSTPVLRRNRIHSGKQVGVYFYDNGHGKL  597

Query  685  EDNDIFNHLYSGVQIRTGSNPVIRGNKIWGGQNGGVLVYNGGLGLLEQNEIFDNAMAGVW  744
            EDNDIFNHLYSGVQIRTGSNP+IRGNKIWGGQNGGVLVYNGGLGLLEQNEIFDNAMAGVW
Sbjct  598  EDNDIFNHLYSGVQIRTGSNPIIRGNKIWGGQNGGVLVYNGGLGLLEQNEIFDNAMAGVW  657

Query  745  IKTDSNPTLKRNKIFDGRDGGICIFNGGKGILEENDIFRNAQAGVLISTQSHPILRRNRI  804
            IKTDSNPTLKRNKIFDGRDGGICIFNGGKGILEENDIFRNAQAGVLISTQSHP+LR NRI
Sbjct  658  IKTDSNPTLKRNKIFDGRDGGICIFNGGKGILEENDIFRNAQAGVLISTQSHPVLRHNRI  717

Query  805  FDGLAAGVEITNNATATLEFNQIFNNRFGGLCLASGVQPIVRGNKIFSNQDAVEKAVANG  864
            FDGLAAG+EIT NATATLE NQIFNNRFGGLCLA+GV PIVR NKIFSNQDAVEKAV NG
Sbjct  718  FDGLAAGIEITLNATATLESNQIFNNRFGGLCLATGVNPIVRCNKIFSNQDAVEKAVRNG  777

Query  865  QCLYKISSYTSFPMHDFYRCQTCNTTDRNAICVNCIKTCHAGHDVEFIRHDRFFCDCGAG  924
            QCLYKISSYTSFPMHDFYRCQTCNTT RNAICVNCIKTCHAGH+VEF+RHDRFFCDCGAG
Sbjct  778  QCLYKISSYTSFPMHDFYRCQTCNTTGRNAICVNCIKTCHAGHEVEFVRHDRFFCDCGAG  837

Query  925  TLTNQCQLQGEPTQDTDTLYDSAAPMESHTLMVN  958
            TL NQCQLQGEP QDTDTLYDSA PMESHTLMVN
Sbjct  838  TLCNQCQLQGEPAQDTDTLYDSAEPMESHTLMVN  871
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Auxiliary factors RISC in *Megacopta cribraria*

Tudor-SN

cDNA

Contig 2299, Length-3663
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AATTATATTACGGAGTGTGGTTGTGTTGATAGAATAAATATTGTTGGAAATGATAAAATTTATTATTA

PROTEIN 907 (AA)
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KAANQTRDYGTLFIDLPNGVRENINELLVKEGLVSVRTVPGSKDPVLQHLTELQEQAKAAKKGKWADDASSHVRQIRWSVEADKMMNFVDKAEGKPI
KAVIEHVRDGSTIRAFLLPDFTYITLMMSGIRCPGFKLDSEGKPDLTVKVEFADEAKYFTEARLLHQEVEIVLESVNNNNFVGTILHPKGNIAEELL
KVGHAHCVDWSIAKMKKADADRLRQAEKMAKEKRLRIWKDWTPPPQISDREFTGTVVEVVNGDALMVKLPNGTVKKIFLASIRPPRDTSAAAEERAA
SERPRTGRVRPLYDIPWMFEAREFLRKKLIGKKVNVTVDYIQPARETLPEKICCTVTISNVNVAEAMVSKGLATVVRYRQNDDQRASAYDALLAAEN
KAAKSLKGVHAKKDIPIHRVNDITADPSKAKNLLPHIMRYSRIEALVEFVVNGSRMRLYVPKDSHLITFLLSGIEVRCDKNSAVNTEEAALQFTRER
CMQREVEIQVEGIDRNGNFIGWLWVDNVNLSVALVEAGLARIHSSGENSRYSKDLYNAKNTAKANGVWKYEEKEEKPDTIEEDKTIDRKTDYKEILV
VEVSEVGFYCQYDSSKSKLNSLQAKMAQEMGANPPLPGAYTPKKGDVCAAKYPLDNMWYRAKVEKLAGSGKVSVFYIDYGNRAEVQNVQCAPLPPGL
DINTDKPYAHYFALAFVSVPNEPEDKKAAENEFRDCVVDRKFLMNYEYELNGVRHATLLDPEMDKEKDKQDVGRSLVADGFLLVAKRREKRFEKIMS
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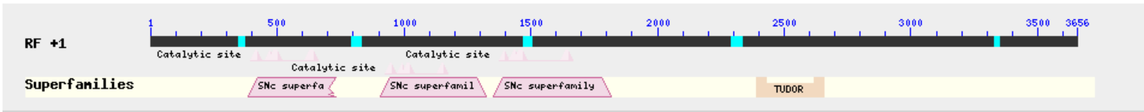
Graphical representation



Comparison with *Cylas puncticollis Tudor-SN*

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Query  27   PQIFKRQFSVVFVFRQRNVRHDVFGGERLIGRIGGG  62
            PQI  R+F+   V        +V  G+ L+ ++  G
Sbjct  336  PQISDREFTGTVV--------EVVNGDALMVKLPNG  363
```

Vasa Intronic (VIG)

cDNA

Contig 2606, Length-2579
CAATTATCATACTAAAACAAACAAAACAAGAATATAATAGTTTATGATCATAATAATGTTAATCAATAACTGTGAATACAACCATCTCAGAGATTAT
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TGAGTCTTGGGTTTTCCTGAGACAAACATTGATCCAATCATTGTGAAAATCACTGGCATTAAAGAAGAGAAAAGCGCAGAAGATAAGCATAAGGTCG
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PROTEIN 395 (AA)
MSATEYGIGIVKNRFALSGIEEEIDPLELLKRHELEKEARKKSKLLDKVTKTKDSAKLKSSKAGKDSVAKHNEVISHKDDVIIKNKPRDADFTKKHV
TIVENFNKHYPADVPESQQFGDYFEEGDKSDLINTGAAFEGDSADRGRNNRRGLPRGVFVRGGGRGGHRGGFPRSTFDTRGKREYDRQSGSDKTGIK
SIDKREGSGAHNWGNPRDDIDNLQTSFAAEEPWSSEKVEDEPPVECPEILNEEEDDNVETNVEEDEERRELTLDEWKALKTPRKTPTYNIRKAGEGE
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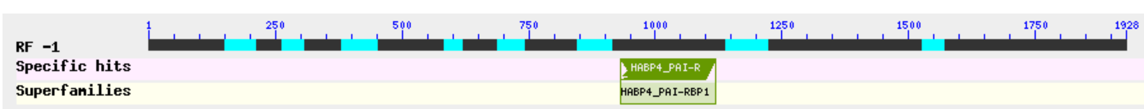
Graphical representation



Comparison with *Cylas puncticollis Vasa Intronic (VIG)*

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Query  5    YGIGVA-NRYALF-LDDESDPLETLSIKEQEKELKKKAKVAEKENKGKNEQPKAKPAANV  62
            YGIG+  NR+AL  +++E DPLE L   E EKE +KK+K+ +K  K K+   K K +
Sbjct  6    YGIGIVKNRFALSGIEEEIDPLELLKRHELEKEARKKSKLLDKVTKTKD-SAKLKSSKAG  64

Query  63   QKKPIKETTINKAQENKREDNKPNQRAAVDGKPERTFTKFNNENREERNNRRNREDRPYN  122
            +    K   +   +++    NKP             +  FTK +    E  N        P +
Sbjct  65   KDSVAKHNEVISHKDDVIIKNKPR---------DADFTKKHVTIVENFNKHY-----PAD  110

Query  123  GPAENRDRDRE---NRPRRENNSENFENRNRDRGERGERR------EGRAIGNRPGGPRG  173
             P   +  D     ++    N    FE  + DRG R  RR         R  G
Sbjct  111  VPESQQFGDYFEEGDKSDLINTGAAFEGDSADRG-RNNRRGLPRGVFVRGGGRGGHRGGF  169

Query  174  PRKTFDDRRGKREFDRQSGSDKTGVKPIEKRDGAGAHNWGSHKDIIEAETERPSEADQSW  233
            PR TFD  RGKRE+DRQSGSDKTG+K I+KR+G+GAHNWG+ +D I+   +    A++ W
Sbjct  170  PRSTFD-TRGKREYDRQSGSDKTGIKSIDKREGSGAHNWGNPRDDID-NLQTSFAAEEPW  227

Query  234  GETEKIE---PIE---VEKKEEQPEVEA-VPAEEEPKELTLDEWKAQRAGRAKPQYNIRK  286
              +EK+E   P+E   +  +EE   VE  V  +EE +ELTLDEWKA +  R  P YNIRK
Sbjct  228  S-SEKVEDEPPVECPEILNEEEDDNVETNVEEDEERRELTLDEWKALKTPRKTPTYNIRK  286

Query  287  AGEGEDPSQWKKMFELKKKEKEEESEEEEFDASEYPQRAGRQKLCHSIDIQFNDNRRPGG  346
            AGEGED SQWKKM+ L+KK++ ++ + EE++  EYPQR G+QK+   IDI + D+
Sbjct  287  AGEGEDLSQWKKMYALEKKKETDDDDYEEYELGEYPQRVGKQKMLE-IDIHYKDS-----  340

Query  347  GRGRGQRSGVRGGRGGSQRGGGPPRDGGERPRFREEQ---GDEKGTPRAPKVDDERDFPS  403
                  RS   G   G  RG GPP   G R +F   Q    + +    APKVDDERDFPS
Sbjct  341  ------RSLGGGRGRGFGRGWGPPNQSG-RGQFSPRQSASANNRTLIPAPKVDDERDFPS  393

Query  404  LV  405
            L
Sbjct  394  LA  395
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FXMR1

cDNA

Contig 1649, Length-4242
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GGCAGCACTGTAGCAGTAACCGATCTAGCAGGCTGTGTTAATTACTTCTTTCTTCGTAATATTTTATCTTTTTTAATTATTATGCCTTAAAATACTT
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PROTEIN 563 (AA)
MDDLEVEVCGENGAYYKAYVTDVFEKEVSVAFENEWQAESRFTFNLVRLPPPKDAPKTEFKENEEVEVLSRSNDHESCGWWRAVIKMMKGDFLVLEY
LGWETTYTEIVPSDRLRHKNSNPPITAQTFTKFEIEVPEELREYLYDCSAKKENVHKDFQKAITASICRYIPESGVLSFISRCEGSKKRAAMLQEMH
FRNLHQKLLLLKRTEEAQKQLESTKLQNTGGFSDEFSVKEDLMGLAIGAHGVNIQQARKLDGITNIELEEGCTFKIYGESSEAVKKARTMLEYSEES
MQVERSLVGKVIGKNGRIIQEIVDKSGVVRVKIEGDNEPSPSVPREEGLVPFMFVGTIESITNAKILLEYHLAHLKEVDKLRQNKEAIESQVRNMQG
TNMGSMMGFPIQRRNERGYNSDMEVGGGRGRGGPPRGRGGRGRGGPGRHDSRYQGSRHQTPDTDERVKEGGRGYSGGGRGGGGNYMQRRDRGDRGGP
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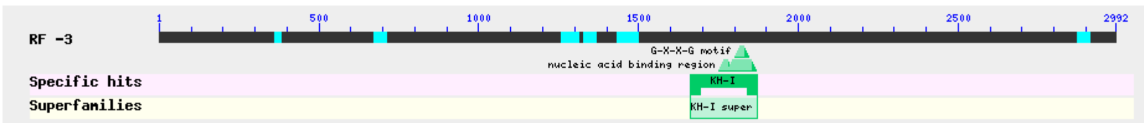
Graphical representation



Comparison with *Cylas puncticollis FXMR1*

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Sbjct  1     MDDLEVEVCGENGAYYKAYVTDVFEKEVSVAFENEWQAESRFTFNLVRLPPPKDAPKTEF  60

Query  86    TENMEVEVFSRSNNQEGYGWWKARIKMMKGDFYVLEYLGWDSTYTEIVSIDRLRMKNSNP  145
              EN EVEV SRSN+ E  GWW+A IKMMKGDF VLEYLGW++TYTEIV  DRLR KNSNP
Sbjct  61    KENEEVEVLSRSNDHESCGWWRAVIKMMKGDFLVLEYLGWETTYTEIVPSDRLRHKNSNP  120

Query  146   PIERGMFHKFEIEVPEDVRDY---C---KKDTYKEFQKAIGAGRIFYNPDKGVLVVISRC  199
             PI    F KFEIEVPE++R+Y   C   K++ +K+FQKAI A    Y P+ GVL  ISRC
Sbjct  121   PITAQTFTKFEIEVPEELREYLYDCSAKKENVHKDFQKAITASICRYIPESGVLSFISRC  180

Query  200   ESSRKRASLLQDMHFRSLQQKVLLMKRTEEAARQLESTKLATIGGFSDEFHVKEDLMGLA  259
             E S+KRA++LQ+MHFR+L QK+LL+KRTEEA +QLESTKL   GGFSDEF VKEDLMGLA
Sbjct  181   EGSKKRAAMLQEMHFRNLHQKLLLLKRTEEAQKQLESTKLQNTGGFSDEFSVKEDLMGLA  240

Query  260   IGAHGVNIQQARKVEGITNIELEENSCTFKIYGETDEAVKKARSMLEYSEESLQVPRALV  319
             IGAHGVNIQQARK++GITNIELEE  CTFKIYGE+ EAVKKAR+MLEYSEES+QV R+LV
Sbjct  241   IGAHGVNIQQARKLDGITNIELEE-GCTFKIYGESSEAVKKARTMLEYSEESMQVERSLV  299

Query  320   GKVIGKNGRIIQEIVDKSGVVRVKIEGDNEPQPTFPREEGQVPFVFVGTVESISNAKVLL  379
             GKVIGKNGRIIQEIVDKSGVVRVKIEGDNEP P+ PREEG VPF+FVGT+ESI+NAK+LL
Sbjct  300   GKVIGKNGRIIQEIVDKSGVVRVKIEGDNEPSPSVPREEGLVPFMFVGTIESITNAKILL  359

Query  380   QYHLAHLKEVEQLRQEKLEIDQQLRSIHHGSNLGSMQSLSMSGRRNDRGYNSDMDGRSSG  439
             +YHLAHLKEV++LRQ K  I+ Q+R++  G+N+GSM    +  RRN+RGYNSDM+
Sbjct  360   EYHLAHLKEVDKLRQNKEAIESQVRNM-QGTNMGSMMGFPIQ-RRNERGYNSDMEVGGGR  417

Query  440   RGGSMRGRGGGRGRGGPRQNDRYNSGSRHQTPDTADERVQDGGGPRRYGGYRGGRGGGGG  499
               G      GGRGRGGP ++D    GSRHQTPDT DERV++GG     GG  GG
Sbjct  418   GRGGPPRGRGGRGRGGPGRHDSRYQGSRHQTPDT-DERVKEGGRGYSGGGRGGGGNYMQR  476

Query  500   RGRGDARRGGEDRRRN----NDDEETVLDSQEVSSADRVNNHSDQA---PATDNGVDNQP  552
             R RGD  RGG  R  N    +D+++    +Q+  + D  ++HS  A      +N  +
Sbjct  477   RDRGD--RGGPPRANNPRVRHDEDQP--PTQDFETGDSGSHHSLAAINIAPVENSKEAVN  532

Query  553   RGGGPKNRYNRGPPPRRGGGVDKHQQHQQQQQQKEALVNGTSA  595
                GPK            G    ++Q +  ++ KE L NGTS
Sbjct  533   SNDGPK------------GQRKNNRQKRTTEKVKEPLYNGTST  563
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p68 RNA helicase

cDNA

Contig 211, Length-1773
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AGAAATAACGAATTAAGTTCACAATAAAAAAAGTTTAATAACTAACATTAATTATAAAATAGATAAATTATGTTCTTCTTATTTACATTTTATTAGC
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CATAGGCTCAACAATTTTTTTTTTGTATACAATCATAATTAAGGAATAAAAGTTCTTAACTTTATAGGAATTAATCAAAATCAAATCTTTTATAATT
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PROTEIN 533 (AA)
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QCGQKSVAIFGGAPKGPQARELERGVEIVIATPGRLIDFLARGTTNLRRCTYLVLDEADRMLDMGFEPQIRKIMQQIRPDRQVLMWSATWPKEVKAL
AEDFLQDYVQVNIGSLELAANHNIQQIVEVCQEGDKQSKLNNLLEEIGNQKLERTIIFVETKKKVEAIANALKKVGWPAVCIHGDKSQNERDYVLRD
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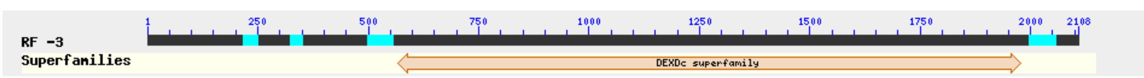
Graphical representation



Comparison with *Cylas puncticollis p68 RNA helicase*

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Query  28   KSGYEGGSYRNSRAGFNNRLRTVEWSSKQLRPFKKDFYVPHPSICSRSTFEVDQFRSAKE  87
            K G+ G    + R  F   L+ V W + +L  FKKDFY PHP++ +R   EV ++R +K+
Sbjct  22   KPGFRGRVNNDDRGNFGGGLQAVAWENHELSDFKKDFYCPHPNVLNRPYTEVKRYRESKD  81

Query  88   ITVEGEAP---KPIQSFHEANFPDYVMDEIVSQGYEFPTAIQAQGWPIAMSGNDMVGVAH  144
            ITV+G +     PIQ F E NFPDYV   I   G++FPT+IQAQGWPIA+SG +MVG+A
Sbjct  82   ITVKGASDAIFNPIQFFEEGNFPDYVASNIKKMGFDFPTSIQAQGWPIALSGKNMVGIAQ  141

Query  145  TGSGKTLAYILPAIVHINNQPEVQRGDGPIVLVLAPTRELAQQIQQVANDFGRRSKIRNS  204
            TGSGKTLAY+LPA++HI NQP VQRGDGPI LVLAPTRELAQQIQ VA+ FG +   ++
Sbjct  142  TGSGKTLAYMLPAVIHIRNQPRVQRGDGPITLVLAPTRELAQQIQTVASHFGGQCGQKSV  201

Query  205  CVFGGAPKGPQARDLERGVEICIATPGRLIDFLEKGTTNLERCTYLVLDEADRMLDMGFE  264
             +FGGAPKGPQAR+LERGVEI IATPGRLIDFL +GTTNL RCTYLVLDEADRMLDMGFE
Sbjct  202  AIFGGAPKGPQARELERGVEIVIATPGRLIDFLARGTTNLRRCTYLVLDEADRMLDMGFE  261

Query  265  PQIRKIIGQIRPDKQTLMWSATWPKEVKKLAQDFMNNPIQLNVGSLQLSANHNILQIVDV  324
            PQIRKI+ QIRPD+Q LMWSATWPKEVK LA+DF+ + +Q+N+GSL+L+ANHNI QIV+V
Sbjct  262  PQIRKIMQQIRPDRQVLMWSATWPKEVKALAEDFLQDYVQVNIGSLELAANHNIQQIVEV  321

Query  325  CQEHEKESKLNNLLQEIGTNGEPDAKIIIFVETKKKVEGITKTIRRLGWPAVCMHGDKSQ  384
            CQE +K+SKLNNLL+EIG   +   + IIFVETKKKVE I    ++++GWPAVC+HGDKSQ
Sbjct  322  CQEGDKQSKLNNLLEEIGN--QKLERTIIFVETKKKVEAIANALKKVGWPAVCIHGDKSQ  379

Query  385  QERDYVLREFRSGKSTILVATDVAARGLDVDGIKYVINYDYPNSSEDYIHRIGRTGRSDT  444
             ERDYVLR+FR GKS ILVATDVAARGLDV+ + YVINYD+PNSSEDYIHRIGRTGRS
Sbjct  380  NERDYVLRDFRRGKSLILVATDVAARGLDVEDVMYVINYDFPNSSEDYIHRIGRTGRSTA  439

Query  445  TGTSYAFFTPSNIRQAKDLVSVLKEANQVVNPKLSDMASKSSGFGGFQKGGRWG  498
            +GT+Y FFT +N +QA+DLV+VL EA Q ++P+L  M   S G  G+ +  R G
Sbjct  440  SGTAYTFFTSANQKQARDLVAVLAEAKQSISPELQAMTRFSGGGNGYSRNFRNG  493
```

Translin associated factor X

cDNA

Contig 5300, Length-1018
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PROTEIN 282 (AA)
MKRKLSASYDENNRKYDKPSQTKKNNNPKTPIIEAFEKYSKELEFKQDKYERIIKLSRDVAIASKRIIFSLHALLRSSNYEQDLAKITENLKTVRNT
HLKNIAFELKDDDPYQYCRAYTAGLQEYIEAVTFFHFITKGDLFDLKLLEKELTFHENFMNQVDQSKESISLFIPLFDYILGIQDLTGELMRHCINS
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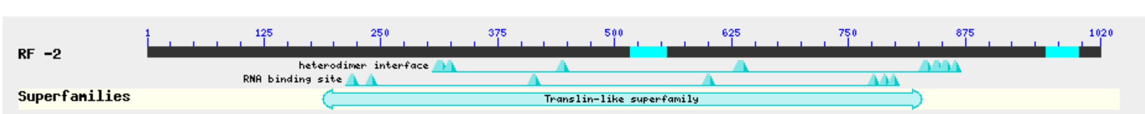
Graphical representation



Comparison with *Cylas puncticollis Translin associated factor X*

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            P+I+ F++++ EL+ K D+YER++K+SRD+ I +KRIIF LH+      ++D  L +
Sbjct  33   PVIQMFQEFTLELDDKHDRYERVVKISRDITIEAKRIIFLLHSTNTDIESKRDSVLEEAF  92

Query  89   ENLKTVRNTHLKNIAFELKDDDPYQYCRAYTAGLQEYIEAVTFFHFITKGDLFDLKLLEK  148
            E L T+   + KNIA EL+D D Y Y +A+T G+QE+IEA+ F+H+   G++     L K
Sbjct  93   ERLSTLYKNNFKNIAMELRDKDHYLYHKAFTCGMQEFIEALCFYHYTKNGNITSWLELNK  152

Query  149  ELTFHENFMNQVDQSKESISLFIPLFDYILGIQDLTGELMRHCINSFSARNLNAGNADCN  208
                   F    DQ +E ++L    +D+ILGI D TGELMR CIN  S  N+N     C
Sbjct  153  -------FFQYKDQDEEDLNLLFTQYDFILGIADFTGELMRKCINVLSVGNVNECFKLCK  205

Query  209  FVKNLYTGMLLLNLSGTSLSQNMQGRDFSRKLVVALQSLNKMELVRYASHIRGSE  263
            FV+N++TG + L+ +G         ++ S+K  V  QSL KMELV Y   IRGSE
Sbjct  206  FVRNIHTGFVGLSFAG--------NKELSKKAYVLRQSLAKMELVCYNIKIRGSE  252
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Armitage

cDNA

Contig 5309, Length-2219
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PROTEIN 797 (AA)
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DNDLIPNVSEDSSEEAALLRALASLLPCRTFGGYAPPLLFHGVRGTNCQETESHSWYNPQEVFQAFVYLNLLYKAGLRPDQVGIITPYQLQSNKIRF
MLERINVEPPKVGSVEEFQGQEKMAIIVSVVRSSPDLISYDMQRALGFVANARRLNVALSRARGILIIILGNPHLLYLDMHWRSVLRHCVKKKFYTGC
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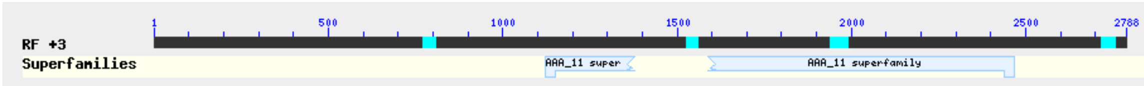
Graphical representation



Comparison with *Cylas puncticollis* Armitage

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Query  414   GQRN-STVRFKSVKIPDYPVPKKLLDLIVKYHNQIDKINLIEELKVTKRSLFNNLTSTNY  472
             G+R+ S   F  VK+  +P+ +K+L +      +++  +L+  ++     L  +L+   Y
Sbjct  3     GRRSFSPAAFVPVKLGQFPLSEKIL-IAALPDVKMNLDDLMIRVEKVLPCLKEDLSPRTY  61

Query  473   EDKFHTLLHLDEIANLICIRNYDQDLACFIRNGEFLMLEIENLSERRPSIVLGDRIIASD  532
               + H LL+L+E+A L  +     D A F +  + L+L++  LS     +V GD +IAS
Sbjct  62    LARMHGLLYLEEVAMLKQVGELQMDRASFRKEKDCLILDVPPLSPYTSKLVAGDMLIASL  121

Query  533   PLRIAKEDYEGNVFKVGAHHVYLKFSALFHDKYN-GEDYSIRVIPGRSTYRRQHHAIYMV  591
             P    +  YEG + +V    ++L+F+  FHD Y  G  YS+  +  R++ RR H AI +
Sbjct  122   PWAADERKYEGVIHRVTQTELWLQFAKDFHDSYGEGIQYSVSFVTSRASLRRMHQAINLA  181

Query  592   ARNLGQDWLFP----SKIVERDVQVRFTYDHYSRVMR--NIKKRLR--------------  631
             A++LG  WLFP    S++ +  V+         R+ R  N  K+L
Sbjct  182   AKHLGFGWLFPTGVTSRLPQVIVEEEIEESESVRIARKENYSKKLHCVPTPESKDLLYSP  241

Query  632   -PREL------------------YQIAVEENRRKSEANATEVEETGS-------------  659
              PR++                  Y+       RK      +    GS
Sbjct  242   DPRKISVAGQANLSIEHKFQAASYKSGYHGRGRKYNNRDIQWNRLGSGYGMHCTVDNEVR  301

Query  660   --IDDSSLLKLQWFNQQLNCKQKDAVVNILKGVARPLPYIIFGPPGTGKTVTVIEAILQI  717
               I    + K++WFN+ LN +QK+AV N+L G ARPLPY+IFGPPGTGKTVTV+E ILQI
Sbjct  302   VNIGLERIKKIRWFNKGLNRQQKEAVNNVLLGEARPLPYVIFGPPGTGKTVTVVETILQI  361

Query  718   IRLIPESRLLVTAPSNSAADLIALRLIDSGVLKPGNLVRLVSVNYAVGDNIPARLVPYCA  777
               LIPESRLLV  PSNSAADLI  RL+D+G L+ G+L+R+V  +Y     I A +VPY A
Sbjct  362   HALIPESRLLVATPSNSAADLITERLLDAGDLEQGDLLRMVGYHYLEQGRIAASIVPYAA  421

Query  778   TAGFAKEGTAEANNVLENGMICDCSRSVLGRHKITVSTCSSAGSLYQMGFPRGHFTHIIV  837
                      A  +     G +  C R +LG+H++TV T    G LY MGFPRGHFTH+IV
Sbjct  422   VPDVKAINVAGLSGASHEG-VQMCGRELLGQHRVTVGTLGCLGLLYNMGFPRGHFTHVIV  480

Query  838   DEAGQAAEPEVMIPISFLDKWNGQIILAGDPMQLGPVVISRIAEECGLNESFLERLTNRF  897
             DEAGQA EPE++IP+ FL    GQ++LAGDP+QLGPVV SR+A  CGL +S L R  NRF
Sbjct  481   DEAGQATEPELLIPMVFLHMEYGQVVLAGDPLQLGPVVTSRLASRCGLQDSLLARFLNRF  540

Query  898   PYIRDAEGFPDTEGFDPRLVTKLLYNYRSLDVILELFSSMFYHGDLIPTISDRDSKEAMF  957
             PY RD  GFPD+ G+DPRLVTKL+ NYRSL  ILEL S +FY  DLIP +S+  S+EA
Sbjct  541   PYSRDPHGFPDSSGYDPRLVTKLVNNYRSLPTILELPSMLFYDNDLIPNVSEDSSEEAAL  600

Query  958   LTSLSEILPKRD-DGSVPSIVFHGVKGENYQTNDSPSWYNPHEVAQVFYYVNELYRLGCE  1016
             L +L+ +LP R   G  P ++FHGV+G N Q  +S SWYNP EV Q F Y+N LY+ G
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Query  1017  PTNLGIITPYSKQVKEIKSILREAEFDLPKIGTVEDFQGQEFGVIILSTVRSSRDYIPSD  1076
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Sbjct  661   PDQVGIITPYQLQSNKIRFMLERINVEPPKVGSVEEFQGQEKMAIIVSVVRSSPDLISYD  720

Query  1077  LEHSLGFVSSPRRLNVAISRSKSLLIIIGNPNLLCYDTYWRTVITYCMEKGAYTGCDL  1134
             ++ +LGFV++ RRLNVA+SR++ +LII+GNP+LL  D +WR+V+ +C++K  YTGCDL
Sbjct  721   MQRALGFVANARRLNVALSRARGILIILGNPHLLYLDMHWRSVLRHCVKKKFYTGCDL  778
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Homeless (spindle-E)
cDNA

Contig 4827, Length-3647
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PROTEIN 1771 (AA)
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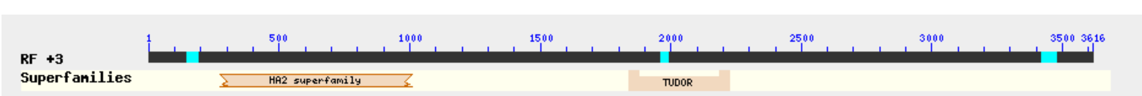
RRYLTGALCGLGFDPETGVAFYPENDIEITFDTKLTLLDLEMINKLRFWMDYMMGGGDGPNSEISRPGILKAQEKIKSYIIDLLSKRRPSVTSYITS
YPYEWDQLEPDELLDPQGSVVSLYPLIWGISLVGEGARDSAVLSRVETLNMIAEGKEPFKTAVQCELCNIYNETLQELKLHLTTTLHTVKLTDFKES
MKPRRRH

Graphical representation



Comparison with *Cylas puncticollis Homeless (spindle-E)*

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             +  N+F+ YF R   G  I  PII +     +++    +YLD ++N++    K P+ DI  P
Sbjct  1     MNVNQFSDYFSRSVNGVLIEPPIIELGHAPKFSVQFYYLDSLVNRLPGIKIPEIDISSPS  60

Query  331   ISEEVWAVFVFLISIFDRLEEGEATVNKN-GTVLVFLPGIYEIEEAHRRLMNEETNTNKW  389
             IS   + +   LI +F  ++E E     +  G+VL+FLPGI EIE  + +L+N   +  KW
Sbjct  61    ISSCTYELARALIEVFHVIDEHEHHDTRFIGSVLIFLPGIAEIENMYAKLINYCGSNEKW  120

Query  390   EIIPLHSSLPNDEQGRAFAPRKPGLRKIILSTNIAESSVTVPDSSFVIDFCQTKVMTVHP  449
              + PLHSS+  DEQ + F P   G RKIIL+TNIAESS+TVPD  +VIDFC +K    + P
Sbjct  121   WLCPLHSSVTYDEQMKVFQPAPRGHRKIILATNIAESSITVPDIKYVIDFCLSKQQILEP  180

Query  450   ETKYMSLKLEWASHVNCDQRAGRVGRTCNGRVYRLVNRQFYMSEMEKHSKPEILSAPLER  509
              T Y  L+L W S      QRAGRVGR   GRVYRL+ + +YM E+ +    PEI+  PL++
Sbjct  181   NTNYSCLQLTWISRSQGTQRAGRVGRVMPGRVYRLMPKNYYM-ELPEDITPEIMRCPLDQ  239

Query  510   IVLQAKMLELNETPAQILALAMTPPGLKNIEDTIWQLKEIGGMLRTCRGIQANADGDITF  569
             +VL+AK L++    PA +L  A+ PP L NI  TI  LKE G +L T  G     DGD+TF
Sbjct  240   LVLKAKQLKMG-PPATLLGFAIDPPDLSNIHKTILHLKEAGALLLTADGKYNANDGDLTF  298

Query  570   LGQVMANLPIDVHLSKLIVLGQLFSCLEETIIIAAGCSIQNIFSIPFQKRLDAYRKQLLW  629
             +GQ+MA+LP+D+HLSKLI+LG +FSCL + II+A+  S+++IFS PF+++L+AY  +L W
Sbjct  299   IGQIMASLPLDIHLSKLIILGHMFSCLSDAIIMASALSVKSIFSTPFRQQLEAYNSKLTW  358

Query  630   SDGSCSDLIALLNLYTVWLNLKRENAF--GSNRQELEWCRTNLVSLKGLKEWNLLITEIR  687
             +D SCSD IA LN Y++W    +   F         E++WCR    +    +KE   L  EI
Sbjct  359   ADSSCSDPIAYLNAYSLWRYKSKMGYFKRSGGESEVDWCRKYFIQGNLIKEVLRLENEIT  418

Query  688   QRLERMQIKETDGPGRVILSDIEKPTVLKIIMAGAFYPNFFIKSPHSSQMTEREAVKIVG  747
             QRL  + ++E       V  S  EKP VLK+I+AGAFYPN+FI  P+ S   E+++VK++G
Sbjct  419   QRLRVLGVEEIKLETGVSWSASEKPLVLKLILAGAFYPNYFI--PYGSD--EKDSVKLLG  474

Query  748   GRDPFSTVYFTGMDPRQPGQVYVRPIKKLIRENGEREMDVQVGFDGSSKIYVEFKNV--L  805
             GRDPF+TVY  GM   QPG +Y   I+       G    +++V FDGSSK+Y+ F +   L
Sbjct  475   GRDPFNTVYLMGMPNNQPGPLYTHGIRSHFLNCGS---NIEVSFDGSSKVYLSFGSSIPL  531

Query  806   QREPITVNVDGFQKLTNIPGRIPMSMYEILRKRQLQYPFQLKVLPYNEAWEFAEKHGLKR  865
               EP  + V         +PG+I M++Y  ++ RQLQ P ++ VL  +EA + A++   +R
Sbjct  532   NTEPENIGV---------VPGKISMAVYRSIKLRQLQIPIKIPVLLPHEARKRAQEIFGER  583

Query  866   NMPSGKLPYQERNCYSSVEYSPLPSMDTTYISLNISNHIDAGHFWAQNATEETNVFLQQI  925
               P+       +RN  + V+ S +PS+ T  +S+ I++  +   FW              + I
Sbjct  584   LRPT-LFNVNKRNAVTPVKKSNMPSLRTNILSVVITHVENPSKFWTSINEPVNANKVYWI  642

Query  926   EEALNK--QVLKQVTENIKTDKIYAARYAEDG----QFYRCKVTV------LGGQLN--Q  971
               +LN+  Q L                A Y  DG    Q++R ++          G++   Q
Sbjct  643   HSSLNRRLQPLPPYYGPYDDGSECIAPY-RDGNAPIQYFRARIISSIETDRFSGKVTRVQ  701

Query  972   ILFIDYGNLQEVRSDELY-YVPQRPQCVMAP-LAFECILHGVKPTYRLNPVGMWDGKVNE  1029
             I F DYGN + V + EL  Y P+        P LA E  L  V P+   NP G W  +  +
Sbjct  702   IFFYDYGNQESVYTKELKDYPPELSSIKEEPALAMETSLAEVGPSVSKNPRGDWSFETIK  761

Query  1030  DFKRLTDGILLYGEVYSVVGDVVELILYRSQ------NRDL----SLNQYLLNRQFAEPS  1079
             +F++L          ++YSVV +V+ + LY  +        + D     S+N YL+    FAE
Sbjct  762   EFRKLLIKDQAVVKIYSVVNEVMAVTLYTHEALENCTDTDFPFKRSINYYLIKHGFAEAI  821

Query  1080  TPSFLSKQNHEQRQTVQMAENPDQEASRLNYDKI---ISYSDFVTPQLNHSKCSTIYLKG  1136
                +LS+ NH  R+  +    P    + ++ D      +S  +F  P+      + S I LKG
Sbjct  822   DEPYLSRDNHLLREASEKI--PGLITTTMDNDLFNDNLSDINFTPPRPEECR-SKITLKG  878

Query  1137  PFSPLEVKLYSCTNMGSTKSVFVEGTSVNAVLLDNEPESPHSRLVVAVHVGQSVDGMKLK  1196
             P SPLE+ LYS        K    +E +SVN+VLLD  P  PHSRL+VA  V Q+ +  +L
Sbjct  879   PRSPLEMNLYSLPKKCQAKETLIEWSSVNSVLLDTCPMDPHSRLLVAASVTQNANSSRLT  938

Query  1197  LRQTTLMPSLPGFPMLMTAMFCPTMEPKLTSDNMLVAAILCGLGYNEITGKALYPAHDIC  1256
             LR TTLMP++ G   L+  +F P +E +   +   +    LCGLG++  TG A YP +DI
Sbjct  939   LRNTTLMPNIHGLGSLICLLFSPRVELRADPERRYLTGALCGLGFDPETGVAFYPENDIE  998

Query  1257  LGLDTELKIEELEMVNRLR----YLMNNGIKLLHDIEQNMSNQNELIHTQIKIKENLFDL  1312
             +   DT+L + +LEM+N+LR    Y+M  G      D    +  ++   ++   Q KIK  + DL
Sbjct  999   ITFDTKLTLLDLEMINKLRFWMDYMMGGG-----DGPNSEISRPGILKAQEKIKSYIIDL  1053

Query  1313  IRMERNPIERRNVVPQNTTWGKHAAGLGLLKPSMDNDEQ----DIWSLLWFVKLAGYNPR  1368
             +   +R P      +       W +        L+P    D Q      ++ L+W + L G    R
Sbjct  1054  LS-KRRPSVTSYITSYPYEWDQ-------LEPDELLDPQGSVVSLYPLIWGISLVGEGAR  1105
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Homeless Maelstrom

Cdna

Contig 9069, Length-1803
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GCATACCTGTCAGTGACCCATCTTGGAAAGAGGGAATAAAAGATCCATTAGAAATGTATCGAAGAGTTAAAGAATTCATCAAGAAATTTACAGTTGG
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AATTGTTTATAAATAAATATACAGGAC

PROTEIN 477 (AA)
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IMIATIKNTIANLDLNSTLKSHIFFVCHANYFYKSEKQVYFPAEVAVAAFSLELGVLATLHFFVDPGKIPLGFKYESSEWSSRTHRIPVSDPSWKEG
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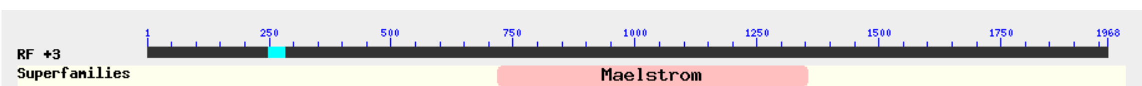
Graphical representation



Comparison with *Cylas puncticollis Maelstrom*

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Query  1    MAPKKPAKP--NGFFMFASEFKNRH---GRKYASMKEACDAAAPYWAKMNAQEKQKYQDM  55
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Sbjct  1    MPPKKKQKGGRNGFYYFMLDLQKQEALKGNRY-SLQEISGLANPLWSDMSLEERKPFTDL  59

Query  56   AREE--KGSG---KKYTSEGLDVEELTRKEKEQEQFQEKMRQDIRQIIELASMKGSEALA  110
            A +   K SG   KK+TS G+   EL  +E+E E  +  M   I+  I  A++  +  L
Sbjct  60   ALKNASKNSGDLTKKFTSLGISYAELDAEEREIEDARNIMIATIKNTI--ANLDLNSTLK  117

Query  111  SETFFLIHFNIFCFHPPSDQYYPAEVAAVCFNLKDGVKPENVFHEFVKPGPMPLGYSFDA  170
            S  FF+ H N F +      Y+PAEVA   F+L+ GV      H FV PG +PLG+ +++
Sbjct  118  SHIFFVCHANYF-YKSEKQVYFPAEVAVAAFSLELGVLA--TLHFFVDPGKIPLGFKYES  174

Query  171  KQHSEETHKISVP---YDDGENNMEEVFVKLTTFLKKKKPANVTRLPILF-----ANDKY  222
             + S  TH+I V    + +G  +  E++ ++  F+KK      T +P ++     +N  Y
Sbjct  175  SEWSSRTHRIPVSDPSWKEGIKDPLEMYRRVKEFIKKFTVG--TEVPPIYTLFETSNSHY  232

Query  223  Q----KMFQNILDRWSWEYGGEENLFRVYSLQVLLFWLRNKVSGGEVWHTVTFSDREIEK  278
            +    K   N++   ++E   + +LFRVY L  L F +RNK S  E+  +V     E+EK
Sbjct  233  RLSVVKSALNMMCEAAYE---DTSLFRVYCLAHLFFEIRNKCSA-EI-PSVAIMKNELEK  287

Query  279  DVYAYVPDIACHYHSKMSSSLYCSQSNVLRMAYVVCDNCCEDLDIELLPGQHVP  332
            DV++Y  D+ C+YH +   S++CS S V R  +++CD+CC+ L I+L+ G+HVP
Sbjct  288  DVFSYARDLGCYYHEEKDLSIHCSLSIVTRWVFIICDHCCKHLGIKLILGRHVP  341
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Homeless RNA helicase Belle

cDNA

Contig 3595, Length-2233
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CAATTCTATGGACATATTCTTCAATATCATTTGGTAAGTCAAAATTAATGACGTGTTTCACATGAGGAATATCCAAACCTCTAGCAGCAACAGCAGT
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GGTCTAATAGGAAACCCCTTTTGTCATTTTCTTCAACCCAAACAATATTCTGAGTAATGTTTTCTGAGGTAGACCCAACACGACCAATAGCCAAAAA
TATGTAGTCATTTAAAAAATCTAAGGCCAACATCTGAATTTCTTTTGGAAAAGTAGCTGAAAACATCAAAGTTTGCCTATCACCAGTAGGAGGCATT
GAGTGTTTTTCTACAATCCTCCTTATTTGTGGTTCAAAACCCATATCTAACATTCTATCAGCTTCATCAAGTACTAGATACTTGCAATTTTCTAATC
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CAGCAGTTTTACCACTACCAGTTTGTGCACATGCCATCAGATCTCTCTTGGCCATAATTATAGGGATAGCATGCTTCTGAACAGGGGTAGGCTTATC
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PROTEIN 678 (AA)
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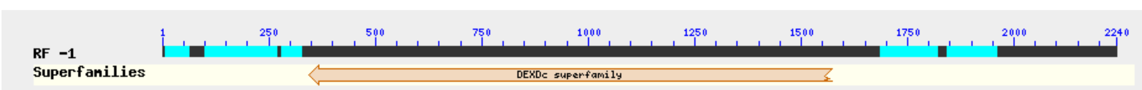
Graphical representation



Comparison with *Cylas puncticollis RNA helicase Belle*

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Query  1    MSNAPNQNGSGLEQQFAGLDLQ-SRGISDRYVPPHLRNKQQHSS----QPESGSSYDREK  55
            MSN PNQNGSGLEQ+FAGLDL+ SR  +  Y+PPHLRNKQ   S    QP S  S   +
Sbjct  1    MSNVPNQNGSGLEQRFAGLDLEGSRKETGPYIPPHLRNKQAGESRSGEQPPSSFSSYSDS  60

Query  56   GRGESRGGGRNFNRGGGSGGSRDAR---ENRGDFSSFN-TRNRRDNFQNGEVFENREKEE  111
                SRG G NF   GGSG S + R      GDF S N  R+  D   +          +
Sbjct  61   RDFSSRGSG-NFRSSGGSGRSDNYRGGSRRNGDFDSQNGDRSWGDRGGSSSFRSGGRDRD  119

Query  112  WGREARG-GGRFQERERDLPRNDRWQEPEKPKDRWNESSNSREGGNGRWNDNRERRNEND  170
              R+    G R          NDRWQE  KP+        S  G
Sbjct  120  RERDRDDWGSRRGGGGTPSGGNDRWQE--KPQ-------GSSAG----------------  154

Query  171  WTIPLARDERLEMELFGTGNTGINFSKYEDIPVEATGDKVPRHIASFEEVQLTEIIRSNI  230
            WT  L +D+RLE ELF   NTGINF+KYEDIPVEATGD+VP HI+SFE++Q+TEII +NI
Sbjct  155  WTTLLPKDDRLEFELFENANTGINFNKYEDIPVEATGDQVPPHISSFEDLQMTEIIGNNI  214

Query  231  AAARYDTPTPVQKYAIPIILSKRDVMACAQTGSGKTAAFLVPILNQMYEVGPPNIQHGRS  290
              ARYD PTPVQK+AIPII++KRD+MACAQTGSGKTAAFLVPILNQM E GP + ++
Sbjct  215  RLARYDKPTPVQKHAIPIIMAKRDLMACAQTGSGKTAAFLVPILNQMLERGPQSTRYPGK  274

Query  291  RRSKQYPLGLVLAPTRELATQIYDESKKFAYRSRVRPCVVYGGAHIGDQLRDLERGCHLL  350
            R  KQYP+GLVLAPTRELATQIYDE++KFAYRSR+RPCVVYGG H+ DQ+RDLERGCHLL
Sbjct  275  R--KQYPMGLVLAPTRELATQIYDEARKFAYRSRLRPCVVYGGLHVADQMRDLERGCHLL  332

Query  351  VATPGRLLDMIDRGRIGLDYCKYLVLDEADRMLDMGFELQIRRIVEKESMPRTGERQTLM  410
            VATPGRL+DM+ RGRIGL+ CKYLVLDEADRMLDMGFE QIRRIVEK SMP TG+RQTLM
Sbjct  333  VATPGRLVDMLARGRIGLENCKYLVLDEADRMLDMGFEPQIRRIVEKHSMPPTGDRQTLM  392

Query  411  FSATFPHPIQMLARDFLDNYIFLAVGRVGSTSENITQKVMWVEEHDKRSLLLDLLNVNDL  470
            FSATFP  IQMLA DFL++YIFLA+GRVGSTSENITQ ++WVEE+DKR  LLDLLN +
Sbjct  393  FSATFPKEIQMLALDFLNDYIFLAIGRVGSTSENITQNIVWVEENDKRGFLLDLLNASK-  451

Query  471  HQPSAESLTLVFVETKKGADSLEDFLHQEGYPVTSIHGDRTQREREDALKQFRSGNTPIL  530
               +A SLTLVFVETKKGADSLEDFL   GYPVTSIHGDR+Q+ERE+AL+ FR+G TP+L
Sbjct  452  ---NAVSLTLVFVETKKGADSLEDFLFGSGYPVTSIHGDRSQKEREEALRSFRTGQTPVL  508

Query  531  VATAVAARGLDIPHVKHVINFDLPSDIEEYVHRIGRTGRMGNLGLATSFFNDRNRNLASG  590
            VATAVAARGLDIPHVKHVINFDLP+DIEEYVHRIGRTGRMGNLGLATSFFND+NRNLA
Sbjct  509  VATAVAARGLDIPHVKHVINFDLPNDIEEYVHRIGRTGRMGNLGLATSFFNDKNRNLARD  568

Query  591  MLDLLIEAKQEYPSWLESVASDSRMP  616
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Sbjct  569  LYDLIQETNQDMPSWLQRMASESKQP  594
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PRP16, mut6 homolog

cDNA

Contig 3764, Length-3819
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TCCTATCCCTTTCAATCGAGCTCCTTGATGGAAGTAAGCTGAGCAAATACATTTTCTCACAATGTCCCAATCAGTTCCGCAGGAGATAACTTCCATC
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PROTEIN 1203 (AA)
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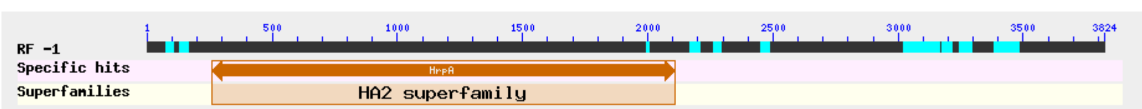
Graphical representation



Comparison with *Cylas puncticollis PRP16, mut6 homolog*

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Query  1     MDEEDGVHRLEGTTGNEKGGLVVKKKT----GSTFKVPQVSLLGLDRLAAIKRKEKEEAA  56
             ++++ GV+RLEG    +KGGL++KKK        FKVPQ SLLGLDRLAA++RKE+E
Sbjct  3     VEDDSGVYRLEGVE-EQKGGLIIKKKPEPKGNFEFKVPQTSLLGLDRLAALRRKERENED  61

Query  57    RKMSFSMDDEAAAENSDDHEGRKVPKDGRKFRSPAEETPTYTGGVSKEAKDRLREHMKNK  116
             +K +     E   E     +  K   + R +R   +ETPT+TGGV++EAK+R+ E  K +
Sbjct  62    KKETEKKLKEGKEEKCTFAKPEK--HNDRHYREKFDETPTHTGGVTREAKERMDERRKRE  119

Query  117   YKEKGVY--ASTKDRRDRERKRDRGDRSERRRNKDSSRR---------------------  153
              K++G++  A +K+  + E  + + +R  + R++D  +
Sbjct  120   EKKRGIHVTADSKNNDENEEDKRKDERQGKSRDRDRYKERSRDRERNRDRDRSRGDRDRE  179

Query  154   -----------------------EETPKFRDEPRTPNIKIKDNTARTSWEDEDESVPVKR  190
                                     E+P+F DEPRTP   +KD  +R  W+++D +   K+
Sbjct  180   RDRRDDRSDRRSERSYGRSQRSWSESPRFHDEPRTPMFSVKDTPSRCGWDEDDITPDAKK  239

Query  191   SSWDFPTPTSYKREDPSWSERSFRTKYESSRSFKHERSSRDSKSFRRYSDDTPRATPAHK  250
             SSW+ PTP +  RED  WS R                                R TPAH+
Sbjct  240   SSWEQPTPKAEPRED-DWSMR--------------------------------RPTPAHR  266

Query  251   FNNWMKDRKRTGATPGTGRDKDEPLKWDATVDRENWEEEQKRLDREWYNMDEGYDDENNP  310
             FN+W  +R RTGATP  G++++ P  W +  DR  WEEEQKRLDREWY +D+G+++  +P
Sbjct  267   FNSWAPERARTGATPLVGKEEEVP--WGSEKDRILWEEEQKRLDREWYGLDQGFEEGRDP  324

Query  311   FSSVSDEYTKKKEEQLEQRKKKRMSAQQRQINKDNELWERNRMLTSGVVQSVDLNEDFDE  370
             F SVS EY  K+E+QLE+ KKKRMSAQQRQINKDNELWERNRMLTSGVVQ++DL+EDFDE
Sbjct  325   FGSVSQEYINKREKQLERSKKKRMSAQQRQINKDNELWERNRMLTSGVVQNLDLDEDFDE  384

Query  371   ESIDRVHLLVHNIVPPFLDGRIVFTKQPEPVIPVKDPTSDMALVARKGSHLVRVYREQKE  430
             E+  RVHLLVHNIVPPFLDGRIVFTKQPEPVIPVKDPTSDMALV+RKGS LVR YREQKE
Sbjct  385   EAEARVHLLVHNIVPPFLDGRIVFTKQPEPVIPVKDPTSDMALVSRKGSLLVRAYREQKE  444

Query  431   RRKAQKKHWELGGTKIGNIMGIKKKEDEEDKKYNKEDDTTDYKADHKFAEHMKGSSEAAS  490
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Sbjct  445   RKRAQKKHWELSGTTIGNIMGVPKKDEKEDDKIDGEVEA-DYKTSQKFAEHMKDMTPAAS  503

Query  491   DFARKKSISEQRRYLPVFAVRQELLNVIRENSVVIIVGETGSGKTTQLTQYLHEDGYSKY  550
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Sbjct  504   EFAKKKTIQQQRQYLPVFAVREELLNIIRENSVVVVVGETGSGKTTQLTQYLHEDGYSRS  563

Query  551   GMIGCTQPRRVAAMSVAKRVSDEMGTQLGDEVGYAIRFEDCTSENTVIKYMTDGILLRES  610
             GMIGCTQPRRVAAMSVAKRVSDEM + LG  VGYAIRFEDCTSE+TVIKYMTDGILLRES
Sbjct  564   GMIGCTQPRRVAAMSVAKRVSDEMASPLGKTVGYAIRFEDCTSEDTVIKYMTDGILLRES  623

Query  611   LREPDLDHYSAIIMDEAHERSLSTDVLFGLLREIVARRHDLKLIVTSATMDSSKFSMFFG  670
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Sbjct  624   LREPDLDNYSAIIMDEAHERSLNTDVLFGLLRQVVARRQDLKLIVTSATMDSSKFSMFFG  683

Query  671   NVPTFTIPGRTFPVEVLFSKNPVEDYVDAAVKQALQIHLQPPSGDILIFMPGQEDIEVTC  730
             +VP +TIPGRTFPVEVLFS+NPVEDYV+AAVKQALQIHLQP  GDILIFMPGQEDIEVTC
Sbjct  684   HVPVYTIPGRTFPVEVLFSRNPVEDYVEAAVKQALQIHLQPTKGDILIFMPGQEDIEVTC  743

Query  731   EVLAERLGEIDNAPELSILPIYSQLPSDLQAKIFQRSPEGIRKCVVATNIAETSLTVDGI  790
             EVL ERLGEID AP LSILPIYSQLPSDLQAKIFQ SP+G+RKCVVATNIAETSLTVDGI
Sbjct  744   EVLGERLGEIDAAPPLSILPIYSQLPSDLQAKIFQASPDGVRKCVVATNIAETSLTVDGI  803

Query  791   IFVIDSGYCKLKVYNPRIGMDALQIYPISQANSNQRSGRAGRTGPGQAFRLYTERQYKDE  850
             ++V+DSGYCKLKVYNPRIGMDALQIYPISQAN+NQRSGRAGRTGPG A+RLYTERQYK+E
Sbjct  804   MYVVDSGYCKLKVYNPRIGMDALQIYPISQANANQRSGRAGRTGPGHAYRLYTERQYKEE  863

Query  851   LLVTTVPEIQRTNLANTVLLLKSLGVQDLLQFHFMDPPPQDNILNSLYQLWILGALDHTG  910
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Query  911   VLTKLGRQMAEFPLDPPQCQMLIVSTQMGCTAEILIIVSMLSVPSIFYRPKGREEEADGV  970
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Sbjct  924   SLTALGRQMAEFPLDPPQCQMLIVSNQMGCTAEILIIVSMLSVPTIFYRPKGREDEADSV  983

Query  971   REKFQVPESDHLTFLNVYNQWKQNNYSSHWCNEHFIHVKAMRKVREVRQQLKDILVQQKF  1030
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Query  1031  EVKSCGTDWDIVRKCICSAYFHQAARLKGIGEYVNCRTGMPCYLHPTSALFGLGNTPDYV  1090
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Sbjct  1044  EVISCGTDWDIVRKCICSAYFHQGARLKGIGEYVHLRTGMPCHLHPTSALFGMGFTPDYV  1103

Query  1091  VYHELVMTAREYMQCVTSVDGHWLAELGPMFFSLKETGKSGRAKKKQAAEHLLEMENQMQ  1150
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Sbjct  1104  VYHELVMTSKEYMQCVTAVDGVWLAELGPMFFSIKETGRSGSSKRREAMEG---MEAEME  1160

Query  1151  VAQEEMKARKEAADKKEAAMYKGQEIV----SAGTTPRRTPAR  1189
              AQ++MK R+   +++     K    V    + G+TP RTP R
Sbjct  1161  AAQKQMKDRERQEEEERGRWSKRSNQVAEPGAPGSTPLRTPFR  1203
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Gawky

cDNA

Contig 602, Length-3560
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PROTEIN 1452 (AA)
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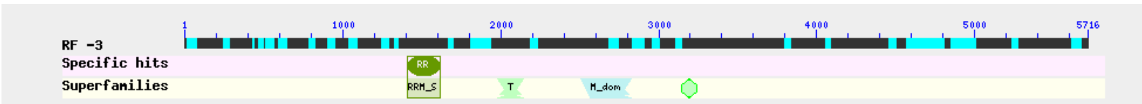
Graphical representation



Comparison with *Cylas puncticollis* Gawky

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Query  361   NNGTELWEANLRNGGQPPP--QPQQKTPWGHTPSTNIGGTWGEDDDAADSSNVWTGVPSN  418
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Sbjct  414   NNGTDLWEANLRNGGVPPPVSQQNQKTPWVHTPSTNIGGTWGEDDE-GDASNVWTGVPQT  472

Query  419   QQQWGNNGSNAMWGGAAAASAGTGGAAPTSG-WGDPRSADPRAAVAAVSAMDMRP-DMRV  476
             Q      G    W   A       A    G WG P   D R       + D+R  DMR
Sbjct  473   QA-----GCGPQW---PAQPPPIWPATKKEGDWGGPNWNDQR------DSRDLRHNDMR-  517

Query  477   AAAAGNLDPRQLDPREQMR-----HMTGGGD---MRGDPRGITGRLNGAGAEF-------  521
                      + +D R+ MR     H + GG+   MRGDPRGI+GRLNG  +E
Sbjct  518   ---------QMMDARDHMRPTSIDHRSMGGNDVIMRGDPRGISGRLNGVTSEAMWPGPGP  568

Query  522   ---------------------WGQTGPLGGPAGMHHQNKMPGVGPGNGTAWDEPSPPSQR  560
                                  W   +GP             M G+G G  T  W+EPSPP+QR
Sbjct  569   HHHIPHHQGKLPAQPNQPVNQWTSSGP--------QMKDMTGLG-GKSTGWEEPSPPAQR  619

Query  561   RTMPNYDDGTSLWG--NPQQGAGG---------MGGRGGGPGG---PPGMA-PSRVGGGG  605
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Sbjct  620   RNMPNYDDGTSLWGPQHPRPSIQGQNKVSHWKEMPAPGIGRGGLQCPPGRANPS------  673

Query  606   LKPDGSVWGGGP---AGGAGVGRGNGWDDVAAGPTAASGWDDPT--VGPWPKQKIPGAAG  660
             +KPD  +W   P    G  G   G  W D           D PT    PW +Q +  ++
Sbjct  674   IKPDQPLWPHHPRNERGWEGGMEGGPWVD-----------DKPTQSAAPWMEQGLTPSSW  722

Query  661   GGG---GGLWDTGDLD---WGH-KQSIKPPQLTKEMVWNSKQFRTLVDMGHKKEDVENAL  713
              GG      WD  DLD   W H KQ  KP  ++KE +W SKQFR L DMG+KKED+E+AL
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Query  714   RMREMNFDEALDMLS-----ISRNRGDPGWITRHDDHYDHPQFPGMGAQRGFPNVGPTNP  768
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Sbjct  781   RNSGMSLEDALEQLNSNSRGLSSGGGASDRWPRGDLDADHAA------------------  822

Query  769   LSNAFPPNNAPNLL------NNMPGTGGGQSNSSLINNISPAIMQKMLTQQGGGGGAAQS  822
             + NAFP    P  L            G+G G       +  I+PA+MQK+L QQ
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Sbjct  883   QPSR---------TQQTQQPSAQQLRMLVQQIQMAVQTGYLSPQILNQPLAPQTLILLNQ  933

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Query  943   KQQQNNGNIGYDTFKTNTMHDTIHALQGNFGELAITKDSQVN--QQQSRLNQW----INK  996
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Query  997   DKEE-NGEFSRAPGSSSKP--VATSPNMAPLGLTQPDGPWSTGRTADTGWPDSSGGDSSN  1053
             D +    GEFSRAPG+++K    ++SPN   L L Q DG WS+     ++GWPDSSG DSS
Sbjct  1051  DPDIGTGEFSRAPGTTAKSGQGSSSPNTN-LLLGQADGTWSS-VNRESGWPDSSGDDSSG  1108

Query  1054  DKDAQWATTAQP---SLTDLVPEFEPGKPWKGNQIK-IEDDPSITPGSVVRSPLSIATIK  1109
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Query  1110  DNELFSMNT---SKSPPVS---DAMQSLSLSSSTWSFNPTSTSSAFTSSPQIKLPTSKGG  1163
             D  + S NT     SP  S   D + SL LSSSTWSFNP  +SS+ +    +KL +S GG
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             +    +                  +SELW APK RGPPPGL  K G  G   ANGWSS
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Query  1209  AGSVP-----WAGASGSAAQRNSGNWGVSQSQWLLLRNLTAQIDGSTLRTLCMQHGPLQS  1263
             +         W G +  A+ +        S WLLLRNLT QIDGSTL+TLCMQHGPLQ+
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Query  1264  FHLHLHQGFALAKYSSREEATKAQTALNNCVLGNTTILAENPTDWDASTLLQSIANQQGA  1323
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Query  1377  SFLPNDLLGGESM  1389
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Staufen

cDNA

Contig 522, Length-1684
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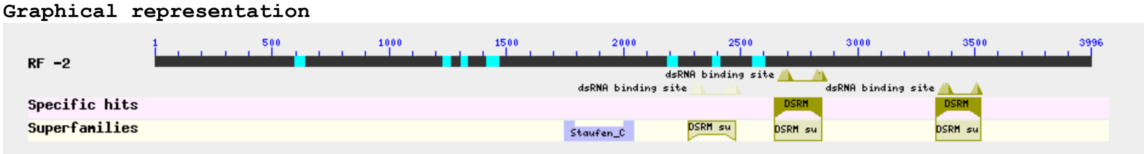
Graphical representation



Comparison with *Cylas puncticollis* Staufen

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Sbjct  98   KEKTPMCLVNELARYNKIEHQYRLTSEDGPPHKKKFTVTLKLGNEEYTAEGASIKKAQHA  157

Query  192  AAAKALTKTEFKHPPQKTIINRPGNRPSNPGVVTPTVELNALAMKRGERTVY-VVESGGA  250
            AA  AL  T +KHPP K+     G++ +    +TPTVELNALAMKRGE TVY +VES
Sbjct  158  AAGIALKSTTYKHPPPKSSRQSRGSKSN----ITPTVELNALAMKRGEPTVYTLVES---  210

Query  251  PPHQGYMNQPSYYPRHNINYPQ---AQPRYGYD-ARRNIRG-HYTYDNRYYGQFRPGAPH  305
             P Q  ++  +Y+  H   Y Q    Q  + Y   + N RG +   D R+YG
Sbjct  211  -PQQ--IHHYTYHHSHRGMYTQPYNDQFSFPYGRGKANFRGFNRGVDPRFYGS-------  260

Query  306  HNPGDPYTVRLRVGEREYPGHGYTVQAARHDAAAKAIEHIKQLGGVEGADSVPANEN--G  363
             N    Y V ++VGERE+ G G + QAARHDAA+KA++H+  L      D+ PAN    G
Sbjct  261  GNKAPLYKVVVKVGEREFTGEGNSAQAARHDAASKALQHLHSL---PLEDTCPANSTICG  317

Query  364  QMSDQQQAQSSLTNDVNSELKSPISLVYEIALKRNLNVTFEVLSEKGPPHMKVFVTQCRV  423
             +++Q+           SELKSPISLV+EIALKRNL V FEV+SEKG PHMK FVT+C V
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Query  424  GS-FVAEGEGNGKKISKKRAAEKMLEELSKLPPLPNV------ANISQMKRKRVTNKKKT  476
            G  F   GEGNGKKISKKRAAEKMLE+L  LPP   V      + +++ KRK  T KKK+
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Query  477  RNLIK-------VNVDKNSETQEEINPISRLIQIQQANKEREPVYTVLEERGAPRRREFV  529
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Query  530  IEASVSGHSCTGVGPNKKVAKRNAADALLTELGYS--TTVPKPQTQTKSEKEPEPSTSSD  587
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Query  693  LGTNPPQVCHGEGPTTEASHEKAALEALKVLSELGLD  729
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Sbjct  660  LDTDPPQVCHGGGATIELSHEQAAMNALRSLAKVGLD  696
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Clp1 homolog (kinase)

cDNA

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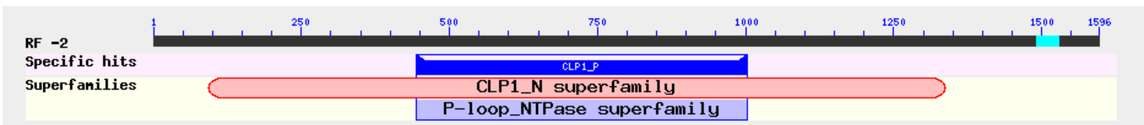
Graphical representation



Comparison with *Cylas puncticollis* Clp1 homolog (kinase)

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Query  69   TPMVIYSNCHAALELMRIEAEKDN--KRGPIAMIVGPCDVGKSTVCRILLNYAVRMGRRP  126
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Sbjct  86   TPMMFYLNCHACLEQLRMKAENESEVKRGPITMVVGPTDVGKSTVCRILLNYAVRMGRAP  145

Query  127  IYVDLDVGQGSVSIPGTVGALVIERPAGIDEGFSQEAPLVYNFGHKSPGHNTKLYRMIVD  186
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Sbjct  146  VYVDLDVGQGQISIPGAIGAILVERPADVEEGFPHNAPLVYHYGHTSMEKNTQTFNLLVN  205

Query  187  QLATIVKERLEVNKKTRQSGVIINTCGWIKGEGYKQILQSGKSFEVDVIMVLDQERLYNE  246
            ++A +V ERL+ N+K+  SG+IINTCGW+KG+GY+ +   + ++FEVD+I+VLDQE+LYNE
Sbjct  206  KMAEVVHERLQTNRKSNVSGIIINTCGWVKGDGYRHLTHAAQAFEVDIILVLDQEKLYNE  265

Query  247  LVRDMPNYVKIVFLQKSGGVVERSKQARSEARDQRIREYFYGTPKNSLYPHSFDVKFSEI  306
            LVRDMPN+VK+V L KSGGVVER+K+ R   +RD R+REYFYG  K   L+PHSFDVK+S++
Sbjct  266  LVRDMPNFVKVVLLPKSGGVVERTKKFRMNSRDSRVREYFYGG-KTPLHPHSFDVKWSDL  324

Query  307  KIFKIGAPALPDSCLPLGMKAEDHLTKVVPITPNPGILHHLLGVSFAEKEEDDIILSHVA  366
            +++KIGAP LPDSC+PLGMKAED++TK+V + P P +LHH+L VSFA   ++D+I ++VA
Sbjct  325  RVYKIGAPPLPDSCMPLGMKAEDNMTKLVAVQPGPNLLHHILAVSFATSTDEDVITTNVA  384

Query  367  GFVCVSNVDLERQTITLLSPQPKPLPNNMLVLSEIQFMDSH  407
            G++CV+NVD+E QT+T+LSPQP+PLP+ +L+LS++QFMDSH
Sbjct  385  GYICVTNVDVENQTLTVLSPQPRPLPDTLLILSDVQFMDSH  425
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Elp-1

cDNA

Contig 10864, Length-3825
CACAACAAAATACTACTTACCTCTGAATTTATAATTTGTAATATAACTAGTTTGTGTGATGATGTTGTCACAAGTAGATAAGGATCTCTTAAAATAA
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CTACTGCTTCTTTGAATGAGGTAAGCAAAATTGAATCATTGTCTATAACACCAACATAAGATTTTTCTTCACAATAGGAATAATAACTGTCATTAAC
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GAATTTATTAAAATTAGTAAGTTTGAGGTGGAAACAACAACAGCAAACTCCTCATCTGGGCTCCAGTGAATCTTTAAAACATCAATATTTAAATGAT
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AAAATATTATTAGACAAAACAAAAACATTCTTAGTTTTAGAACACAGATCATTGTCCTGCAAACTTTGACCGCTAATAATTATTGTAGAATCTACAA
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PROTEIN 639 (AA)
MRNLKLLLNFKIHREVFVDSTIIISGQSLQDNDLCSKTKNVFVLSNNILYCVELPDGKVLEYYDLRVLFSGNVPKIREMWYRDLYKTVYICFETGEI
YSFLLDDRGVQHSRSCHHLNIDVLKIHWSPDEEFAVVVSTSNLLILINSEFFILAEIDLSDTFLGENELISVGWGKKETQFHGSEGKNAALSKPVIH
SPHQDDDHTTNVTWRGDSNLFAVSYWCSHTNIRRVKIFNSEGILQSTSEDIQGLNEPICWKPSGSLITVPQQLPNKKVISFLEKNGLKHGDFTLPSN
IKVKEVMWNEASTILCTICENQDNSEEEVMLWTVGNYHWYLKQKFKFTSLSIKVYWDKECPNRMIALCKGGLLQILEWAFVVNDSYYSYCEEKSYVG
VIDNDSILLTSFKEAVVPPPMSSYKLKCSDAVNHILFAPVNREECSPYMLCVILYSGDILIFKDPISEPLIMPGLVKQHNFSIEMLSLSHWQWVSAD
ILVFCYSNEFNETLIHQLYISKDEIELSNVFFFNGRIITSNRICEEIIMQTSCGKLFKYNTKSMMVTESLALIEPCYDIKVHPTGLFCLSELSRLYL
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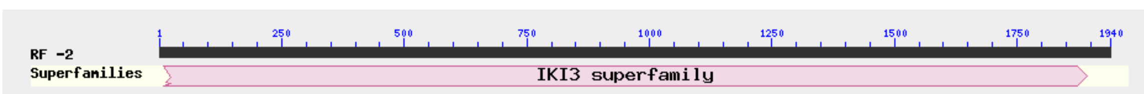
Graphical representation



Comparison with *Cylas puncticollis* Elp-1

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Query  57   NIREVRYLQYLSIHQVLFITND----FDLIIYNGNSKEFVVVYSSPIKIESVAWNPSETF  112
            N+ ++R + Y  +++ ++I  +    +  ++ +   +     +   I +  + W+P E F
Sbjct  72   NVPKIREMWYRDLYKTVYICFETGEIYSFLLDDRGVQHSRSCHHLNIDVLKIHWSPDEEF  131

Query  113  LILCDTEENLYGLTFECNIGFKEYRFIETCKSNLHDPVPNS---VYVGWGSHNTQFKGSK  169
             ++  T   L  +  E         F    + +L D         + VGWG   TQF GS+
Sbjct  132  AVVVSTSNLLILINSE---------FFILAEIDLSDTFLGENELISVGWGKKETQFHGSE  182

Query  170  ---KIIDEEIQEIPQQYSPPI--ISWRGNGEQFVINFWKEER--RYLKLFDSTLRPLYQS  222
                  + + +    P Q        ++WRG+    F +++W      R +K+F+S      S
Sbjct  183  GKNAALSKPVIHSPHQDDDHTTNVTWRGDSNLFAVSYWCSHTNIRRVKIFNSEGILQSTS  242

Query  223  ESYPNLLALTSFKQQGNFIACATIHNNQNKIVIFEKNCLVKSEFLVPE-VKGVIRNILYH  281
            E    L      +K  G+ I         N+  I   EKN L   +F +P   +K  ++ ++++
Sbjct  243  EDIQGLNEPICWKPSGSLITVPQQLPNKKVISFLEKNGLKHGDFTLPSNIK--VKEVMWN  300

Query  282  PFLHIL-AIYSLEEAGNGYINIFVNSNAKWYLKQQLLYVTEKQVKCLNWADSLEN---SI  337
                IL   I    ++       + ++     N   WYLKQ+   + T    +K + W      N   ++
Sbjct  301  EASTILCTICENQDNSEEEVMLWTVGNYHWYLKQKFKF-TSLSIK-VYWDKECPNRMIAL  358

Query  338  CKLNILTSSSIERIVFRMVINRSPNNGTVAVVDGSIVHFTFFDSEIVPPPMSSAFLKFDK  397
            CK  +L        +V     +        V V+D    +   T F    +VPPPMSS   LK
Sbjct  359  CKGGLLQILEWAFVVNDSYYSYCEEKSYVGVIDNDSILLTSFKEAVVPPPMSSYKLKCSD  418

Query  398  PINRIQFHP-NLPQC  411
             +N I F P N  +C
Sbjct  419  AVNHILFAPVNREEC  433
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GLD-1 homolog

cDNA

Contig 3261, Length-3219
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CATTTAAATGAAGATCTGCACGTTCTGATTACAGTAGAAGATACTGAAAATAGAGCTAAAGTCCGCCTTGCCAGGGCAGTTGAAGAAGTTAAAAATC
TCATCATCCCAGCTGATGGAGAAGATGAGCTGAAGAAGAGGCAGTTGATGGAGTTAGCGATCATTAATGGAACTTACAGAGATTCCAACACAAAAGC
TCTTGCTGCTGCAGCTGACGAGGAATGGCGAAGAATGGCCCTAACTGCAGCCGCTGCTGAGACTCAGCGTTTGATGTCGCCAGGAATCCCTGGGATG
GCCACGCCCCTAAGGACACCTGCTGCCAATCCTCTGGGAGCTCCTCTCATTCTGTCCCCTAGGATCCCAGTGCCTACTTCAGCAACTCCCCTCCTGT
CACCACCCGAAGCACACCCTCATCAGCTCTTGTACACTCCCTTTCCAGACTACACCAACTATGCAGCTCTCACGGGCACTCCTCTGATATCAGATTA
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PROTEIN 342(AA)
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RGMTAKQLELETGCKIMVRGKGSMRDKKKEEASRGKPNWEHLNEDLHVLITVEDTENRAKVRLARAVEEVKNLIIPADGEDELKKRQLMELAIINGT
YRDSNTKALAAAADEEWRRMALTAAAAETQRLMSPGIPGMATPLRTPAANPLGAPLILSPRIPVPTSATPLLSPPEAHPHQLLYTPFPDYTNYAALT
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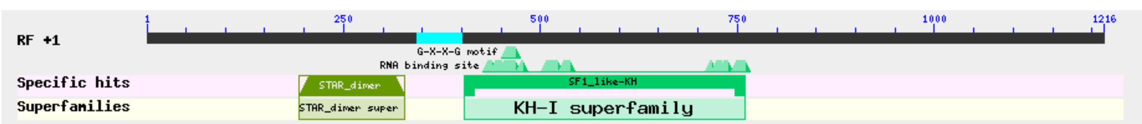
Graphical representation



Comparison with *Cylas puncticollis* GLD-1 homolog

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            M DQ    STQSIADYLAQLLKDRKQ+ AFPNVF+HVERL+DEEI +VR+SLFQ++GVKK
Sbjct  1    MSDQTGN-STQSIADYLAQLLKDRKQVTAFPNVFMHVERLIDEEIGRVRSSLFQVDGVKK  59

Query  61   EPLILPEPDGPVTTLTEKVYVPVKEHPDFNFVGRILGPRGMTAKQLEQETGCKIMVRGKG  120
            EPL+LPEP+G  TTLTEKVYVPVK+HPDFNFVGRILGPRGMTAKQLE ETGCKIMVRGKG
Sbjct  60   EPLVLPEPEGETTTLTEKVYVPVKDHPDFNFVGRILGPRGMTAKQLELETGCKIMVRGKG  119

Query  121  SMRDKKKEDQNRGKPNWEHLSDELHVLLTVEDTENRAQIKLQRAVDEVRKLLVPQAEGED  180
            SMRDKKKE+ +RGKPNWEHL+++LHVL+TVEDTENRA+++L RAV+EV+ L++P A+GED
Sbjct  120  SMRDKKKEEASRGKPNWEHLNEDLHVLITVEDTENRAKVRLARAVEEVKNLIIP-ADGED  178

Query  181  ELKKRQLMELAIINGTYRDSSAKAASASACDEEWRRVA--AAAVDAQRLLSPAIPGLAAP  238
            ELKKRQLMELAIINGTYRDS+ KA +A+A DEEWRR+A  AAA + QRL+SP IPG+A P
Sbjct  179  ELKKRQLMELAIINGTYRDSNTKALAAAA-DEEWRRMALTAAAAETQRLMSPGIPGMATP  237

Query  239  MRGPAA-PLGAPLILSPRMSVPTTAASILNGSAPPGSLLSPGDPHGLLYAPYADYTNYAA  297
            +R PAA PLGAPLILSPR+ VPT+A  +L   +PP +      PH LLY P+ DYTNYAA
Sbjct  238  LRTPAANPLGAPLILSPRIPVPTSATPLL---SPPEA-----HPHQLLYTPFPDYTNYAA  289

Query  298  LAATPLLTEYATADHS  313
            L  TPL+++Y  ADHS
Sbjct  290  LTGTPLISDYPGADHS  305
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ACO-1 homolog

Cdna

Contig 3707, Length-2990
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CCTTCAGCCATATATCTTTCGGCAGCATCAAAGACATCCATCTCATCTCCAGAGGGGATATGAACAGTTCTTGGAGCAGCTCGGTTGAGAAACTTAT
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PROTEIN 893 (AA)
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EQLLYPDSVVGTDSHTTMINGLGVVGWGVGGIEAEAVMLGQAISMLLPQVIGYKLVGKLNQYATSTDLVLTITKNLRQLGVVGKFVEFFGPGVAELS
IADRATISNMCPEYGATVGFFPVDENSLYYLSQTNRDPAKINAIRKYLQAVGMLRDFSNAAQDPVYSEVIELDLSTVVSCVSGPKRPQDRAPVTEVK
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DHISPAGSIARNSPAARYLASKGLTPREFNSYGSRRGNDEVMARGTFANIRLVNKFLNRAAPRTVHIPSGDEMDVFDAAERYMAEGTPLIAIVGKDY
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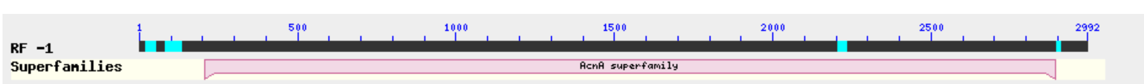
Graphical representation



Comparison with *Cylas puncticollis* ACO-1 homolog

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Sbjct  1    MSGSNPYNKILKTLDVDGVSYKFYSLGELGPQYAKLPFSIRVLLESAVRNCDNFEVKQTD  60

Query  61   VQNVLNWESNQNIEDGVEIPFKPARVILQDFTGVPAVVDFAAMRDAVRDLGGNPEKINPI  120
            V+N+LNWE     E  VE+ FKPARV+LQD TGVPAVVDFAAMRDAV+ LGG+P+KINPI
Sbjct  61   VENILNWEKTGKTESSVEVAFKPARVLLQDLTGVPAVVDFAAMRDAVKSLGGDPDKINPI  120

Query  121  CPADLVIDHSVQVDFARSPDALQKNQDLEFERNFERFVFLKWGAKAFNNMLIVPPGSGIV  180
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Sbjct  121  CPSDLVIDHSVQVDFARVDKALQKNEEIEFERNKERFTFLKWGAKAFRNMLIVPPGSGIV  180

Query  181  HQVNLEYLARVVFTGSNKPILYPDTVVGTDSHTTMINGLGVLGWGVGGIEAEAVMLGQAI  240
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Sbjct  181  HQVNLEYLARVVFT---EQLLYPDSVVGTDSHTTMINGLGVVGWGVGGIEAEAVMLGQAI  237

Query  241  TMLLPQVVGYKLYGSLGPYVTSTDLVLTITKHLRQIGVVGKFVEFYGPGVAALSIADRAT  300
            +MLLPQV+GYKL G L  Y TSTDLVLTITK+LRQ+GVVGKFVEF+GPGVA LSIADRAT
Sbjct  238  SMLLPQVIGYKLVGKLNQYATSTDLVLTITKNLRQLGVVGKFVEFFGPGVAELSIADRAT  297

Query  301  ISNMCPEYGATVGYFPADEISLSYLRQTNRSEEQVKLIEAYLLATRQMRNYE-SEENPVF  359
            ISNMCPEYGATVG+FP DE SL YL QTNR   ++  I  YL A   +R++  + ++PV+
Sbjct  298  ISNMCPEYGATVGFFPVDENSLYYLSQTNRDPAKINAIRKYLQAVGMLRDFSNAAQDPVY  357

Query  360  SQSVELDLSTVVSSVSGPKRPNDRVSVSNMKKDFLSCLTNKIGFKGFGIPENKIGTKTKF  419
            S+ +ELDLSTVVS VSGPKRP DR  V+ +K+ F   LTNK+GF+GFG+    +     F
Sbjct  358  SEVIELDLSTVVSCVSGPKRPQDRAPVTEVKELFTKALTNKVGFQGFGLKPAAVEASGTF  417

Query  420  MFDGKQYTIGHGSVIIAAITSCTNTSNPSVMLGAGLLAKKAVEAGLSVEPYIKTSLSPGS  479
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Sbjct  418  AFEGSEYTIRHGSVVIAAITSCTNTSNPSVMLGAGLLAKKAVEAGLKVAPYIKTSLSPGS  477

Query  480  GVVTYYLRESGVIPALEQLGFNIVGYGCMTCIGNSGGIDENIANAIEQNDLVCCGVLSGN  539
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Sbjct  478  GVVTHYLQESGVVPYLDKLGFTTVGYGCMTCIGNSGPLPEPMIDAIEKNELVCCGVLSGN  537

Query  540  RNFEGRIHPNTRANYLASPLLVIAYAIAGRVDIDFETEPLGVNANGTQIFLRDIWPTRRE  599
            RNFEGRIHPNTRANYLASPLLV+AYAIAGR+DIDFETEPLG   +GT I+LRD+WP R E
Sbjct  538  RNFEGRIHPNTRANYLASPLLVVAYAIAGRIDIDFETEPLGKKPDGTNIYLRDVWPLRSE  597

Query  600  IQSVEQQHVIPAMFKEVYAKIESGSSQWQTMKAPEGKLYPWSNESTYIKKPPFFDGMTRE  659
            IQ VE++ VIPAMF++VYA+IE+GS+ W+++ AP+ KLYPW  +STYI++PPFFDGMTR+
Sbjct  598  IQEVEKKTVIPAMFRDVYARIENGSNNWRSLNAPDDKLYPWDPKSTYIRRPPFFDGMTRD  657

Query  660  LPKSKPIQNARVLLYLGDSVTTDHISPAGSIGRNSPAARFLASKGLTPKDFNSYGSRRGN  719
            LPK K I+NA+VLL+LGDSVTTDHISPAGSI RNSPAAR+LASKGLTP++FNSYGSRRGN
Sbjct  658  LPKPKKIENAKVLLFLGDSVTTDHISPAGSIARNSPAARYLASKGLTPREFNSYGSRRGN  717

Query  720  DAIMARGTFANIRLVNKFMSKSGPKTLYLPNNEEMDIFDCAQRYATSGTPLIIIAGKDYG  779
            D +MARGTFANIRLVNKF++++ P+T+++P+ +EMD+FD A+RY   GTPLI I GKDYG
Sbjct  718  DEVMARGTFANIRLVNKFLNRAAPRTVHIPSGDEMDVFDAAERYMAEGTPLIAIVGKDYG  777

Query  780  SGSSRDWAAKGPFLLGVRAVIAESFERIHRSNLVGMGLVPLQFLPGENAESLGLTGKEIY  839
            SGSSRDWAAKGP LLG++AVIAES+ERIHRSNLVGMG+VPLQFL GE+AESLGLTGKE Y
Sbjct  778  SGSSRDWAAKGPLLLGIKAVIAESYERIHRSNLVGMGIVPLQFLEGESAESLGLTGKERY  837

Query  840  NIDLPENLKPHEHITVSTDTGKSFKVLLRFDTEVDLLFYKHGGILNYMVRKML  892
             I+LP + +PH+ ITV TD+GKSF+V++RFDTEVDLL++KHGGILN MVR+ML
Sbjct  838  TINLPADPRPHQRITVQTDSGKSFEVIVRFDTEVDLLYFKHGGILNCMVRRML  890
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