

Review Article

<https://doi.org/10.20546/ijcmas.2020.905.339>

Epigenetics Mechanisms in Insects: A Review

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ABSTRACT

Keywords

Epigenetics, Insects,
DNA methylation,
Histone
modification and
RNAi

Article Info

Accepted:
23 April 2020
Available Online:
10 May 2020

Epigenetics is the study of heritable changes in gene expression that do not involve changes in the underlying DNA sequence (or) a change in phenotype without a change in genotype. Phenotype is the observable or measurable characteristics of an organism i.e., height, behaviour, colour, shape, and size. Insects are being examined for their epigenetic phenomena and the underlying mechanism behind it. Epigenetics is well studied in fruit fly, *Drosophila melanogaster*. Gene is segments of the DNA sequence that store the information to synthesize proteins or RNAs that carry out specific functions. Epigenetics is important in cellular differentiation which is responsible for the phenotypic plasticity. Epigenetics is been investigated in plants and animals. On comparing other organisms insects possess a high degree of phenotypic variation. This variation is due to switch on and off mechanism of gene. Gene expression and repression in insects is regulated through epigenetic mechanisms i.e. DNA Methylation, Histone modification and Noncoding RNAs which influence the phenotypic modification. In recent days insects are used as models in studying epigenetics. RNA interference (RNAi), also known as RNA silencing, refers to a set of molecular processes in which noncoding RNA molecules target and silence the expression of specific nucleic acids. Silencing Dnmt3 expression in newly hatched honeybee larvae mimics the effect of royal jelly, namely, the larvae destined to become workers develop into queens with fully developed ovaries. The detailed mechanisms of epigenetics in insect were discussed in the paper.

Introduction

The growing population and degrading environment are two major problems at international level. Satisfying the growing population's requirement is somewhat difficult. Although there were legal and social constrains in utilizing the biotechnology researches in field level, these tools improve agriculture and human life to a great extent

(Ahmad *et al.*, 2012). Genetically modified mosquitoes created possibilities for controlling diseases like malaria (Catteruccia *et al.*, 2003).

In 1994, the "flavr savr" (first GM tomato) was commercialized (Yang *et al.*, 2005). Bt cotton was the first GM crop approved for use in India (Kapur *et al.*, 2010). Almost in the entire living organism's gene-modification

plays an important role in developing transgenic organisms. In an organism genes are controlled by some Non-gene mechanisms. The expression and repression of gene without change in respective DNA sequence occurs in all living organisms. Ultimately their study is called epigenetics. Similar to genetic engineering this study leads to a profitable/beneficial research outcome in the science of plant breeding, entomology, pathology, nematology, biotechnology, microbiology, agronomy, soil science etc in various branches of agriculture.

Epigenetics is one of the emerging branch of science yet to be reviewed and more research work has to be carried out for clear cut configuration about the phenotypic plasticity. “Epigenetics term was coined by Conrad H. Waddington in the year 1942”. In view of Conrad Waddington, epigenetics is study of epigenesis, i.e. contribution of genotypes to phenotypes during development (Waddington, 1942). According to Arthur Riggs and colleagues it was “the study of mitotically and/or meiotically heritable changes in gene function that cannot be explained by changes in DNA sequence”. The study of heritable changes in gene expression that occur without a change in DNA sequence is known as Epigenetics. *Without the bullock, the cart cannot be driven*. There is “gene” to study for geneticist but no “epigene” for epigeneticist. Epigenetic mechanisms are essential in regulating the genome. Gene expression and repression is regulated by three common mechanisms namely DNA methylation, histone modification, noncoding RNAs occurs in all eukaryotic cells. Additional research works in the recent years are proving the significance of epigenetics in plants, animals and as well as in insects. Many organisms are capable of developing distinct phenotypes from the same genotype (Glastad *et al.*, 2013). Comparing all living organisms in the world insects contribute a

high phenotypic plasticity as evident in most of the insects i.e. holometabolous insects having egg, larvae, pupa and adult stages all with same genome. The fruit fly, *Drosophila melanogaster* is used as a model by the geneticist for studying the biological processes and nothing to get excited, they are preferred for studying epigenetics (Burggren, 2017). Epigenetic inheritance deals with Intra generational and intergenerational epigenetic inheritance. The former is concerned with the development process i.e. how an egg with a single set of genetic instructions is able to develop into a multicellular organism made up of distinct tissues (Waddington, 1942). The later Heard and Martienssen (2014) is concerned with transmission of epigenetic information to offspring. This paper is aimed to describe and understand the basic knowledge on insect epigenetics to the readers.

DNA methylation

Addition of methyl group to the cytosine in the genes is termed as “DNA methylation”. It occurs in all three domains of life Archaea, Bacteria, and Eukarya (Klose and Bird, 2006; Suzuki and Bird, 2008). In insects DNA methylation mostly occur in genes (Glastad *et al.*, 2011) and primarily target the transcription initiation site of genes (Fig. 1). Nearly one half of DNA may be methylated (Glastad *et al.*, 2011; Bewick *et al.*, 2018). The regions where cytosine is followed by guanine are known as CpG sites or CpG islands. CpG methylation is common in eukaryotes (Delcuve *et al.*, 2009). In insects, methylation sites are predominantly restricted to the coding sequence of genes at CpG sites i.e. pea aphid (Walsh *et al.*, 2010). DNA methylation is highly enriched in exon sequences e.g. Holometabolous insects such as Coleoptera (Cunningham *et al.*, 2015), Hymenoptera (Glastad *et al.*, 2017) and Lepidoptera (Xiang *et al.*, 2010; Hunt *et al.*,

2013). DNA methylation occurs in larger proportion of the genome e.g. Hemimetabolous insects such as Orthoptera (Wang *et al.*, 2014), Hemiptera (Bewick *et al.*, 2019), Blattodea (Glastad *et al.*, 2016). De novo DNA methyltransferases (*Dnmt3* proteins) and maintenance DNA methyltransferases (*Dnmt1* proteins) are the enzymes that facilitate DNA methylation (Lyko, 2018). Gene expression is inhibited by DNA methylation due to interference with DNA-binding transcription factors in promoter regions (Watt and Molloy, 1988).

Low level DNA methylation

Very low methylation rates of approximately 0.11% were observed in the genome of the silkworm moth, *Bombyx mori*, but all of this methylation occurs in CpG islands (Xiang *et al.*, 2010). In dipteran insects dramatic loss of DNA methylation has been observed, where *Dnmt1* or *Dnmt3* proteins have not detected in the genome sequencing projects (Hung *et al.*, 1999; Tweedie *et al.*, 1999; Marhold *et al.*, 2004). CpG methylation is virtually undetectable in most developmental stages of *D. melanogaster* due to absence of *Dnmts* (Zemach *et al.*, 2010).

High level DNA methylation

Unusually high levels of DNA methylation occur in the desert locust *Schistocerca gregaria*, which also has an unusually high level of phenotypic plasticity, suggesting DNA methylation involvement in insect polyphenism (Falckenhayn *et al.*, 2013).

Gene specific DNA methylation played a role in mediating insecticide resistance in the hemipteran aphids *Myzus persicae* (Field *et al.*, 1996; Field *et al.*, 2004) and *Schizaphis graminum* (Ono *et al.*, 1999). In termites over 12% of genomic CpGs and 58% of exonic CpGs were methylated.

Application

Epigenetic mechanisms play key roles in adaptation to a changing environment and have been implicated in the regulation of phenotypic plasticity (Moczek and Snell-Rood, 2008). *Nemoria arizonaria* caterpillars mimic different plants depending on their food uptake (Nijhout *et al.*, 2009). Interest on the role for DNA methylation in insects surged after an experiment reduced expression of *dnmt3* in honey bee larvae and led to a dramatic shift from worker to queen developmental fate (Kucharski *et al.*, 2008).

Histone modification

The eukaryotic DNA is wrapped around histone octamers, which consist of four different histone proteins, H2A, H2B, H3 and H4. The N-terminal tail of histone protein is post-transcriptionally modified. Histones play important roles not only in regulation of gene expression but also in DNA repairing mechanisms, DNA replication and recombination. Histones are the small basic proteins that together with DNA form chromatin structures in the cell nucleus. Histones are modified at several different amino acid residues and with many different modifications (Lennartsson and Ekwall, 2009). Chromatin arrangement (the level of gene transcription) is relaxed or condensed according to the degree of acetylation, methylation, phosphorylation and/or ubiquitylation of associated histones (Burggren, 2017). Replacement of canonical histone proteins with sequence variants can considerably alter gene expression (Talbert and Henikoff, 2010). Therefore, histone modification and replacement are both important epigenetic modifications across eukaryotes (Fig. 2). Histone proteins may be more directly implicated in the mediation of phenotypic plasticity than DNA methylation (Simola *et al.*, 2013).

Histone acetylation

In eukaryotes, an epigenetic process of gene expression is regulated by histone acetylation/deacetylation which is mediated by two enzymes namely histone acetyl transferases (HATs) and histone deacetylases (HDACs). The acetylation of histones by HATs increases DNA accessibility and promotes gene expression, whereas the removal of acetyl groups by HDACs has the opposite effect (Mukherjee *et al.*, 2012). DNA bound to nucleosomes is less accessible to other proteins. For example, transcription factors (eg. RNA polymerase) typically bind only to sites lacking nucleosomes (Bell *et al.*, 2011).

Histone methylation

Histone methylation in general associated with transcriptional repression (Black *et al.*, 2012). Histone methylation occurs predominantly on histones H3 and H4. Histone methylation is commonly targeted at arginine (R) or lysine (K) residues. H3-K9 dimethylation and H3-K27 trimethylation are both associated with heterochromatin formation thus silencing gene expression, whereas H3-K4, H3-K36, or H3-K79 methylation is associated with euchromatin formation (Maison and Almouzni, 2004; Peterson and Laniel, 2004).

Histone phosphorylation

Histone phosphorylation is mediated via protein kinases (which adds phosphate groups) and protein phosphatases (which removes phosphate groups) (Ellenbroek and Youn, 2016). All core histones contain phosphoracceptor sites in their N-terminal domains: H2A is phosphorylated on Ser1, H2B on Ser14 and Ser32, H3 on Ser10 and Ser28, H4 gets phosphorylated on Ser1 (Loury and Sassone-Corsi, 2003).

Histone ubiquitination

Histone ubiquitination is a modification mediated by the attachment of ubiquitin (Ub), which is a 76-amino acid protein that is ubiquitously distributed and highly conserved throughout eukaryotic organisms (Kerscher *et al.*, 2006; Zhang *et al.*, 2018).

Histone variants

Replacement of canonical histone proteins with sequence variants can considerably alter gene expression. Key histone variants are conserved between insects and mammals and are also linked to gene regulation in *Drosophila*. Specifically, H2A variants increase the mobility of, or destabilize, the nucleosomes in which they are found, resulting in increased accessibility of DNA (Talbert and Henikoff, 2010). In invertebrates histone H2A.v (H2A.Z in vertebrates) is a variant of the canonical histone H2A (Baldi and Becker, 2013).

Applications

Studies have been made on histone acetylation/deacetylation in associated with regulation of pupal diapause in the flesh fly, *Sarcophaga bullata* (Reynolds *et al.*, 2016). Histone-modifying enzyme systems are differentially expressed in brain tissues of solitary and gregarious migratory locusts *Locusta migratoria*, although the varying gene expression leads to the gregarious and solitarius phase changes which results in their different phenotype (Guo *et al.*, 2015).

Suppression of histone deacetylases (HDAC) by injection of HDACi (inhibitor) or small interfering RNAs (siRNAs) against the HDAC encoding gene *Rpd3* into young soldier's brain induce and sustain forager-like activity and scouts for up to 50 days in ant, *Camponotus floridanus*.

RNA interference

RNA interference (RNAi), also known as RNA silencing, refers to a set of molecular processes in which non-coding RNA molecules target and silence the expression of specific nucleic acids (Ha and Kim, 2014). The core components of RNAi pathways are Argonaute proteins, which associate with the sRNAs and silence specific target nucleic acids (Meister, 2013). The Argonaute and sRNA complex is termed the RNA induced silencing complex (RISC).

Non-coding RNAs are transcribed from DNA but, rather than being translated into protein, instead regulate gene expression at both transcriptional and post-translational levels. There are Types of ncRNAs reported in insects that include microRNAs (miRNA), small interfering RNAs (siRNA), PiWi interacting RNAs (piRNA), long noncoding RNAs (lncRNA), architectural RNAs (arcRNA) and circular RNAs (circRNA) (Abu and Jamal, 2016; Beermann *et al.*, 2016; Ng *et al.*, 2016; Chujo *et al.*, 2017; Hanan *et al.*, 2017; Sas-Chen and Schwartz, 2019). The evidence that piRNAs and lncRNAs have epigenetic effects is particularly strong in insects (Chambeyron and Seitz, 2014) (Fig. 3).

P-element Induced Wimpy testis or PiWi interacting RNAs (piRNA)

piRNAs are highly variable, short (21–35 nucleotides), single-stranded ncRNAs that can initiate epigenetic effects within insect genomes. piRNAs were first identified in *D. melanogaster*. piRNAs act to silence TEs and therefore prevent harmful TE-induced mutations. Target repression by piRNAs also comes in two forms: transcriptional gene silencing (TGS) and post-transcriptional gene silencing (PTGS). In Nucleus PIWI proteins are guided by piRNAs to nascent transposon

and generate heterochromatin via DNA or histone methylation, thus silencing transcription. In the cytoplasm, piRNAs elicit post-transcriptional silencing by directing PIWI proteins to slice target transcripts (Ozata *et al.*, 2019).

Autoamplifying biogenesis pathway or ‘ping-pong loop’

piRNAs are produced in additional germ line cells, called ‘nurse cells’ then deposited in the oocyte. Deep-sequencing of *Drosophila* ovarian piRNAs revealed that piRNAs tend to be complementary to each other throughout their first 10 nucleotides. A mature piRNA guides the cleavage of a complementary piRNA precursor, thus contributing to the maturation of another piRNA (Bonasio, 2012; Dowling *et al.*, 2016). piRNA Pathway Genes in *Drosophila melanogaster* involves three Argonaute proteins of the Piwi family (Argonaute3, Piwi, and Aubergine) (Dowling *et al.*, 2016). Argonaute-3 loaded piRNAs frequently have an adenosine at position 10. Aubergine loaded piRNAs tend to have a uridine at their 50 -most position, while Argonaute-3 loaded piRNAs are usually in the sense orientation. Aubergine loaded piRNAs are usually antisense to the transposon sequence (Chambeyron and Seitz, 2014).

Micro RNA

The first miRNA, lin-4 from *Caenorhabditis elegans*, was discovered by Ambros and coworkers in 1993 as an endogenous regulator of genes that control developmental timing (Ambros, 2003). miRNA Pathway Genes - Argonaute1, Dicer1, Loquacious, Drosha, and Pasha (Obbard *et al.*, 2009). In fruit fly, *Drosophila* Dicer-1 is required for miRNA biogenesis, whereas Dicer-2 is devoted mostly to the siRNA pathway (Tomari and Zamore, 2005).

The molecular evidence that miRNAs influence chromatin or passed down through cell divisions in a truly epigenetic manner is still lacking in insects (Lim and Brunet, 2013; Chambeyron and Seitz, 2014).

Small interfering RNA

The siRNA pathway is found throughout insects (Dowling *et al.*, 2016). siRNAs may be associated with the transmission of epigenetic information in insects. siRNAs are loaded into the RNA-induced transcriptional silencing complex (RITS). The RITS then binds to the specific genomic target which results in heterochromatin formation (Castel and Martienssen, 2013). siRNAs may affect X chromosome inactivation in *Drosophila* (Koya and Meller, 2015).

Long non-coding RNAs

lncRNAs represent a broad category of RNAs that are over 200 nucleotides long and not

translated into proteins (Bonasio and Shiekhhattar, 2014). lncRNAs can bind to specific targets and recruit chromatin-modifying enzymes, initiating the formation of a silent or active chromatin state (Fatica and Bozzoni, 2014).

Applications

RNAi plays an important role in regulating gene expression in eukaryotes. Genetically modified Arabidopsis and tobacco plants expressing double standard RNA were tend to resist bollworms. The expression of dsRNA in cotton plants is targeted at P450 gene, CYP6AE14 in the bollworm (*Helicoverpa armigera*). Boll worms reared on the plants containing dsRNA showed retarded growth due to toxification of gossypol. dsRNA treated rice varieties TN1 and PTB33 were observed with low population of brown plant hopper, *Nilaparvata lugens* when comparing untreated plants.

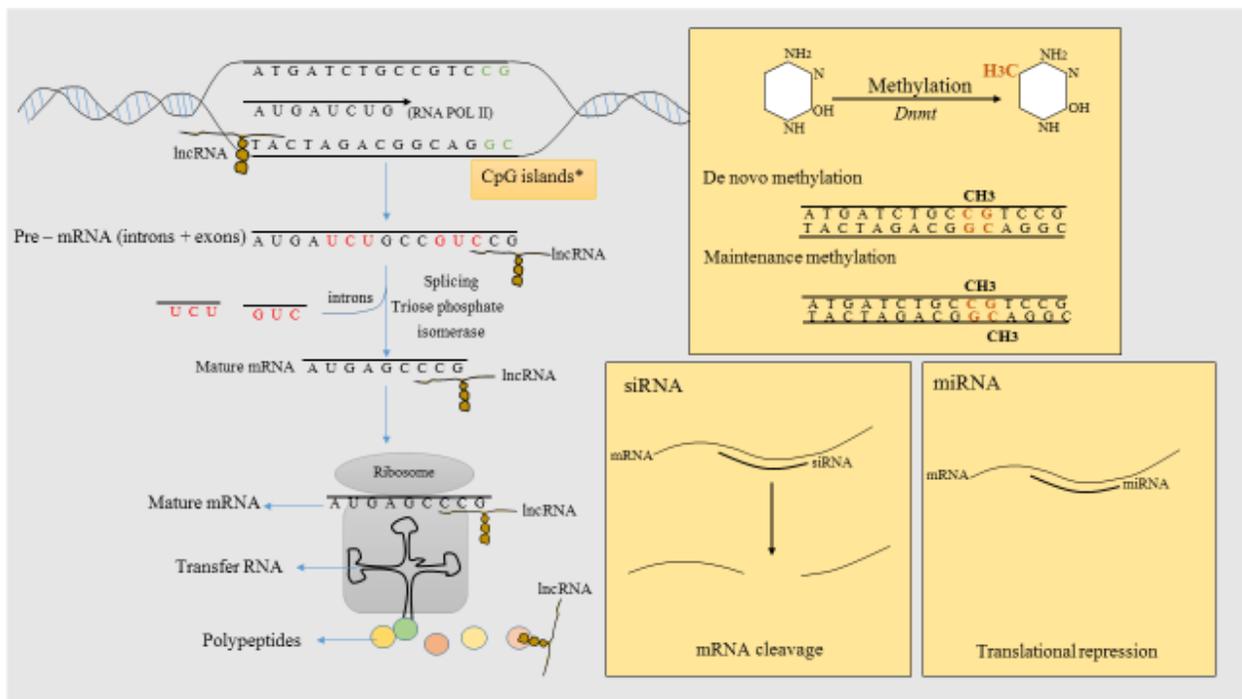


Fig.1 DNA methylation at CpG sites, functions of long non coding RNA, Role of siRNA and miRNA

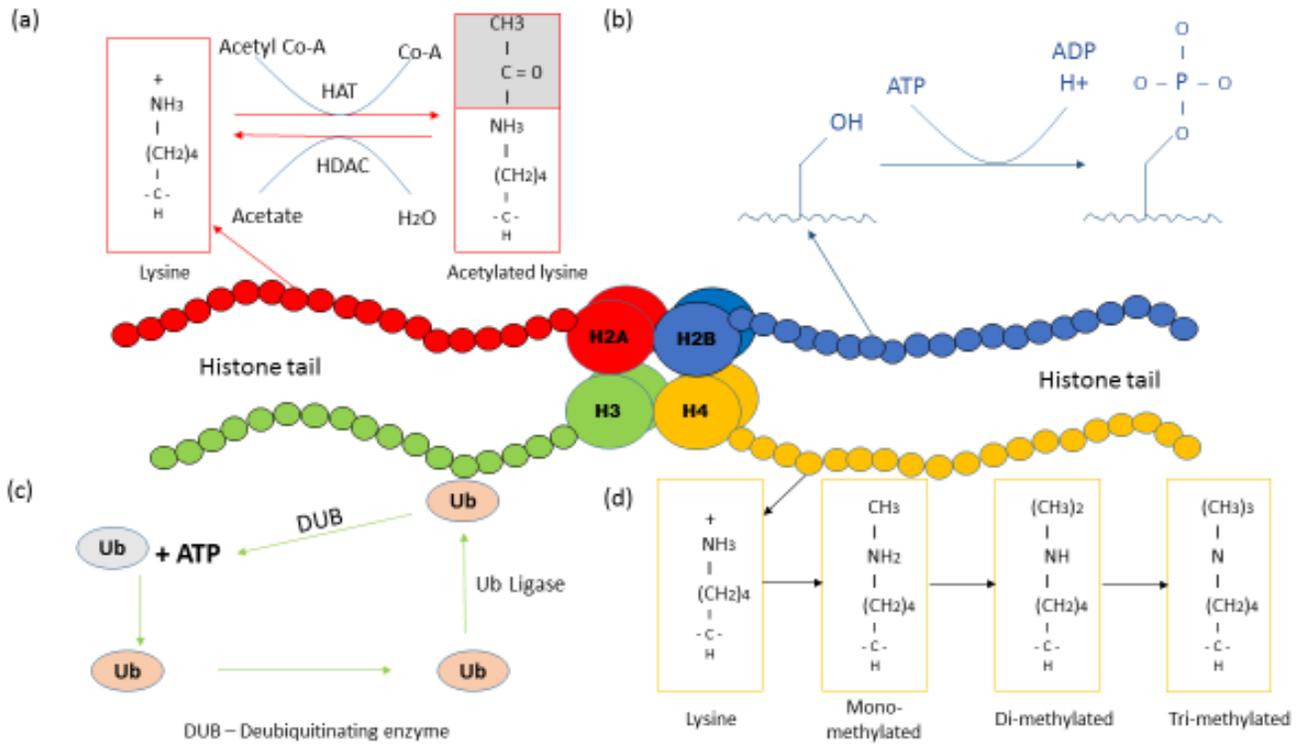


Fig.2 (a) Histone acetylation (b) Histone phosphorylation (c) Histone ubiquitination (d) Histone methylation

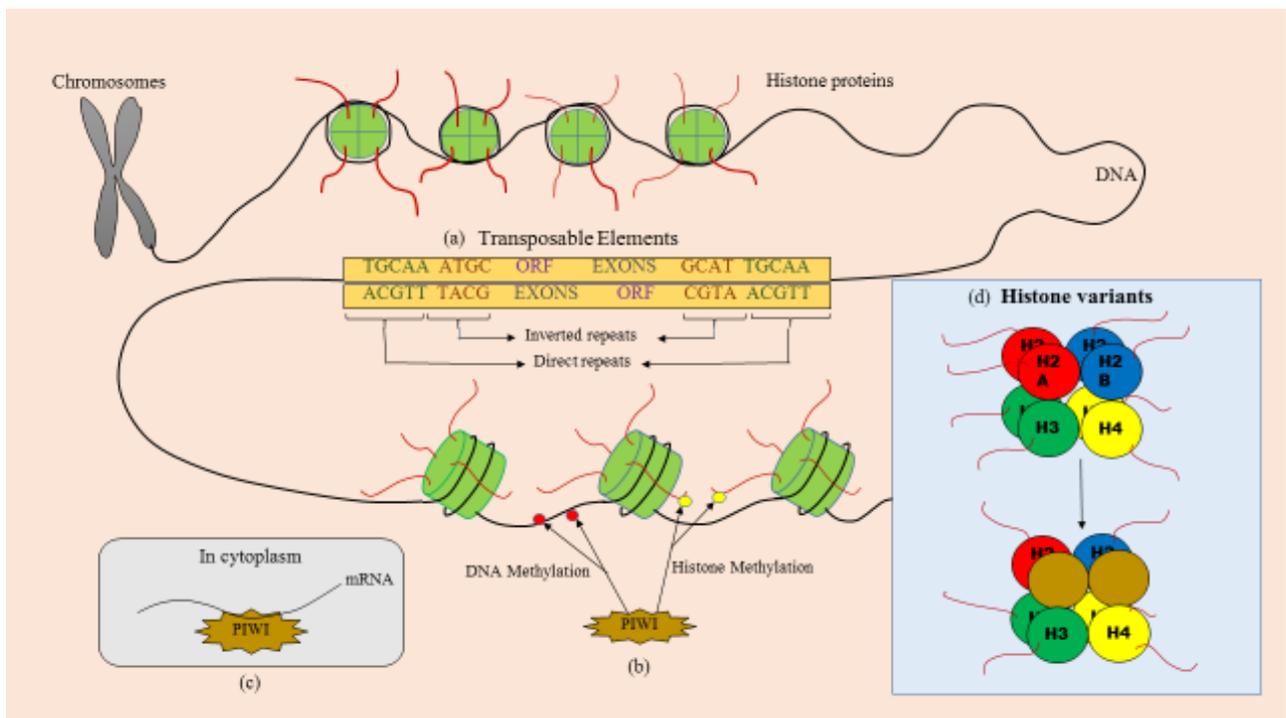


Fig.3 (a) Structure of jumping genes (b) PIWI interacting RNA induced DNA methylation and Histone methylation (c) PIWI interaction with mRNA in cytoplasm (d) Histone variation

Epigenetic studies opens up a new path to walk faraway from our imaginations. Managing insect population without affecting natural environment is a crucial factor in agriculture. Imparting the knowledge on epigenetic to pest management will provide new management tactics. Management of major pests like BPH in rice, *H. armigera* in cotton are some of the proven examples. From our ancient historic periods, humans started domesticating animals, rearing insects for their purpose. There are types of methods for queen rearing but still development of queens form larvae of honey bees through epigenetics are astonishing. Studying epigenetics in insects gives knowledge on rearing/domesticating them, changing their phenotypic diversity as well as in their management. A clear understanding of epigenetics is still wanted for the human life to fulfill the next generation requirements.

Acknowledgement

We acknowledge all coted authors in this particular new science and their reference works were cited in this article. Most of the cited references are review papers instead of original report due to the broad nature of the topic. We thank our Institute Dean, ADACRI, TNAU, Trichy, India for his encouragement to prepare the manuscript.

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How to cite this article:

Pirithiraj, U., R. P. Soundararajan and Gailce Leo Justin, C. 2020. Epigenetics Mechanisms in Insects: A Review. *Int.J.Curr.Microbiol.App.Sci*. 9(05): 2961-2971.
doi: <https://doi.org/10.20546/ijcmas.2020.905.339>