



## REVELATIONS FROM COMPARATIVE MITOCHONDRIAL GENOME ANALYSIS IN FOUR ORDERS OF CLASS INSECTA

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### ABSTRACT

The largest and most diverse group of organisms in the animal kingdom are insects. Molecular markers are powerful tools that can tackle a wide range of insect ecological research issues. These provide a more effective way to study the massive unexplored genetic diversity and gene pool of insects. Recent trends of use of DNA marker techniques in varied domains of insect ecological studies demonstrate that mitochondrial DNA has made a significant contribution towards advancing our knowledge of genetic basis of insect diversity. To shed light on various aspects such as genome organization, base composition, gene rearrangements, and other features, we integrated 165 mitochondrial genomes (mitogenomes) consisting of 37 genes and a noncoding control region, from four major insect orders (Diptera, Lepidoptera, Orthoptera and Hemiptera) for comparative genomic analysis. The same 37 genes were found in the majority of mitochondrial genomes, however the order of genes was found disturbed in a few mitochondrial genomes. The nucleotide composition was found strongly biased towards AT content. Usually, protein-coding genes prefer ATA, ATT and ATG as a canonical start codon. However, inconsistency was observed for few PCGs particularly for COI. The loss of DHU arm was found specific to trnS1 gene. In *Zeugodacus tau* (Pumpkin fruit fly), trnF gene lacked the TΨC arm. Majority of the mismatches (G-U (most common), U-U, U-C, A-A, A-C, A-G and T-T) were found within the acceptor arm, DHU arm and anticodon stem of tRNA genes but few in TΨC stem. Interestingly, a unique gene rearrangement from trnW (W codes for Tryptophan) to trnU (U codes for Selenocysteine) in the mitochondrial genome of *Boettcherisca peregrine* (Flesh fly) was observed. AT-rich control region remains highly variable among most of the insects. The review is aimed to draw conclusions for better interpretations of mitochondrial DNA evolution.

**Key words:** Mitochondrial genome, insects, gene order, nucleotide composition, PCGs, tRNAs, RNA secondary structures, A+T-rich region, gene rearrangement, AT-skew, GC-skew, Diptera, Lepidoptera, Orthoptera, Hemiptera

With a global distribution and a complex evolutionary history, insects are a taxonomically diverse group that appeared date back more than 450 million years (Tihelka et al., 2021; Truman 2019). Most of them are considered as pests of many crops, vectors of many diseases, pollinators of crop plants, parasites of other insects (parasitoids) and biological indicators of climatic changes (Piacenza et al., 2021; Evans and Shao 2022; Chowdhury et al., 2023; Fei et al., 2023; Manikandan et al., 2023). Mitochondrion is a membrane-bound cell organelle that presents in nearly all eukaryotic cells. It actively contributes to the cellular process of generating energy for cell and also involved in processes like cell differentiation, apoptosis and control of cell growth and cell cycle. It contains its own genetic material and carry genetic information that is independent of nuclear genes. Mitochondrial genome (mitogenome) has proved its utility in the different fields of science which includes animal health, molecular evolution, population

genetics and also in comparative evolutionary studies. The choice for the use of mitochondrial genome in populations, biogeographic and phylogenetic studies is well reasonable (a) because of ease of its amplification from a wide variety of taxa (b) haploid in nature (no need of cloning in order to obtain sequence) (c) partially fast evolutionary rate (d) strictly follow maternal inheritance (e) share ancestral pattern of gene arrangement (f) lack of extensive recombination and (g) high copy number. Since after publication of first mitochondrial genome in 1982 (Clary et al., 1982) the list is ever expanding. In the past 20 years, mitochondrial genetic data has been extensively employed in various insect groups for species identification, phylogenetic, biogeographic and molecular evolution investigations (Du et al., 2019; Elyasigorji et al., 2023; Elameen et al., 2024). It is now possible to draw conclusions about the patterns and trends in the genomic evolution of insects from the abundant mitogenome data available from

insects. Cameron (2014) cited the need of comparative mitochondrial DNA analyses for molecular systematics as available mitochondrial genomes in databases exist in good numbers. No comprehensive review involving species from four major orders of class insecta have been made in recent. In the current review, we collected and analysed 165 mitochondrial genome sequences from four major orders of class insecta (Table 1).

Genomic organization of mitochondria in insects, it is a closed circular double-stranded small molecule, size by the range of 14kb to 28kb. So far, the smallest mitochondrial genome of size 14,032 bp was sequenced from *Mitjaevia protuberanta* (Leafhopper) (accession number MN627216) from order Hemiptera (Yuan et al., 2020) and the largest mitochondrial genome of 28,021 bp was sequenced from *Dynastes tityus* (Eastern Hercules

Table 1. Summary of mitogenomes used

Organism	Accession number	References
Diptera		
<i>Sylvicola fenestralis</i>	NC_016176.1	Beckenbach (2012)
<i>Calliphora chinghaiensis</i>	KT936147	Chen et al. (2016 b)
<i>Chrysomya phaonis</i>	KX500359	Chen et al. (2016 a)
<i>C. chloropyga</i>	AF352790	Junqueira et al. (2004)
<i>Cochliomyia hominivorax</i>	AF260826	Lessinger et al. (2000)
<i>Rhopalomyia pomum</i>	NC_013063.1	Beckenbach and Joy (2009)
<i>Mayetiola destructor</i>	NC_013066.1	Beckenbach and Joy (2009)
<i>Culicoides arakawae</i>	AB361004.1	Matsumoto et al. (2009)
<i>Anopheles darlingi</i>	GQ918272	Moreno et al. (2010)
<i>An. sinensis</i>	MF322628	Ding et al. (2018)
<i>An. aquasalis</i>		Martinez-Villegas et al., (2019)
<i>An. anthropophagus</i>	MW279150	Liu et al. (2022)
<i>An. peditaeniatus</i>	MT822295	Guo et al. (2021)
<i>An. nitidus</i>	MW401801	Guo et al. (2021)
<i>An. minimus</i>	KT895423	Hua et al. (2016)
<i>Culex pallens pallens</i>	KT851543	Luo et al. (2016)
<i>Cx. tritaeniorhynchus</i>	KT851544	Luo et al. (2016)
<i>Cx. pipiens pipiens Turkey</i>	HQ724616	Unpublished
<i>Cx. quinquefasciatus</i>	GU188856	Behura et al. (2011)
<i>Aedes notoscriptus</i>	KM676219	Hardy et al. (2016)
<i>Ae. Aegypti</i>	EU352212	Behura et al. (2011)
<i>Drosophila virilis</i>	BK006340	Andrianov et al. (2010)
<i>D. mercatorum</i>	MK575470	Wang et al. (2019)
<i>D. littoralis</i>	NC_011596.1	Andrianov et al. (2010)
<i>D. mauritiana</i>	NC_005779.1	Ballard (2000)
<i>D. melanogaster</i>	NC_001709.1	Lewis et al. (1995)
<i>Hydrotaea spinigera</i>	MH540747	Ma and Huang (2018)
<i>Hypoderma lineatum</i>	GU584123	Weigl et al. (2010)
<i>Cramptonomyia spenceri</i>	NC_016203.1	Beckenbach (2012)
<i>Boettcherisca peregrine</i>	KF921296	Zhong et al. (2016)
<i>Ravinia pernix</i>	KM676414	Guo et al. (2016)
<i>Sarcophaga africa</i>	KM881633	Fu et al. (2016)
<i>S. antilope</i>	MH540748	Huang and Ma (2018)
<i>S. dux</i>	MH540745	Huang and Ma (2018)
<i>Parasarcophaga portschinskyi</i>	KM287570	Shi et al. (2016)
<i>P. similis</i>	KM287431	Yan et al. (2016)
<i>Ferdinandeia cuprea</i>		Le and Gang (2020)
<i>Lathyrophthalmus quinquestriatus</i>	MT834869	Zhou et al. (2021)
<i>Atylotus miser</i>	KT225291	Wang et al. (2016)
<i>Elodia flavipalpis</i>	NC_018118	Zhao et al. (2013)
<i>Janthicuomyia sp.</i>	MK644822	Hou et al. (2019)
<i>Protoplasia fitchii</i>	JN861746	Beckenbach (2012)
<i>Zeugodacus tau</i>	MF966383	Yong et al. (2017)
<i>Bactrocera ritsemai</i>	MF668132	Song et al. (2018)
<i>B. carambolae</i>	MN104219	Drosopoulou et al. (2019)
<i>Dacus longicornis</i>	KX345846	Jiang et al. (2016)

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Lepidoptera		
<i>Hyphantria cunea</i>	GU592049	Liao et al. (2010)
<i>Bomby mori strain Dazao</i>		Liu et al. (2013 b)
<i>B. mori strain H9</i>		Dai et al. (2013)
<i>B. mandarina</i>	AY301620	Pan et al. (2008)
<i>Deroca hyaline</i>	OP379733	Cheng et al. (2022)
<i>Laelia suffusa</i>	MN908152	Li et al. (2021)
<i>Hydrillodes repugnalis</i>	MH013484	Yang et al. (2019)
<i>Asota tortuosa</i>	OP379737	Cheng et al. (2022)
<i>Numenes albofascia</i>	OP379740	Cheng et al. (2022)
<i>Spilosoma lubricipedum</i>	MT591568	Bian et al. (2020)
<i>Euproctis similis</i>	KT258910	Liu et al. (2017)
<i>Mesophleps albilinella</i>	KU366707	Park et al. (2016)
<i>Dichomeris ustalella</i>	KU366706	Park et al. (2016)
<i>Phthonandria atrilineata</i>	EU569764	Yang et al. (2009)
<i>Hyalinetta circumflexa</i>	OP379730	Cheng et al. (2022)
<i>Lassaba albidaria</i>	OP379735	Cheng et al. (2022)
<i>Psyra falcipennis</i>	OP379739	Cheng et al. (2022)
<i>Ampittia virgata</i>	MW288057	Hao et al. (2021)
<i>Halpe Nephele</i>	MW288058	Hao et al. (2021)
<i>Onryza maga</i>	MW288059	Hao et al. (2021)
<i>Ctenoptilum vasava</i>	JF713818	Hao et al. (2012)
<i>Paralebeda femorata</i>	OP379743	Cheng et al. (2022)
<i>Coreana raphaelis</i>	DQ102703	Kim et al. (2006)
<i>Leucoma salicis</i>	NC_063089.1	Sun et al. (2016)
<i>Sphragifera sigillata</i>	OP379736	Cheng et al. (2022)
<i>Zaranga tukuringra</i>	OP379731	Cheng et al. (2022)
<i>Gazalina chrysolopha</i>	OP379732	Cheng et al. (2022)
<i>Ochrogaster lunifer</i>	AM946601	Salvato et al. (2008)
<i>Neptis thisbe</i>	OK393687	Liu et al. (2021)
<i>N. obscurior</i>	OK393686	Liu et al. (2021)
<i>Athyma zeroca</i>	OK393685	Liu et al. (2021)
<i>Aldania raddei</i>	OK393684	Liu et al. (2021)
<i>Parantica sita sita</i>	MG571524	Hu and Wang (2019)
<i>Parnassius apollo</i>	KF746065	Chen et al. (2014)
<i>Sericinus montela Gray</i>	HQ259122	Ji et al. (2012)
<i>Artogeia melete</i>	EU597124	Hong et al. (2009)
<i>Orthaga olivacea Warre</i>	MN078362	Yang et al. (2020)
<i>Eriogyna pyretorum</i>	FJ685653	Jiang et al. (2009)
<i>Caligula boisduvalii</i>	EF622227	Hong et al. (2008)
<i>Antheraea yamamai</i>	EU726630	Kim et al. (2009)
<i>Manduca sexta</i>	EU286785	Cameron and Whiting (2008)
<i>Dolbina paraexacta</i>	OP379729	Cheng et al. (2022)
<i>D. in sexta</i>	OP379742	Cheng et al. (2022)
<i>Rhagastis albomarginatus</i>	OP379741	Cheng et al. (2022)
<i>Adoxophyes honmai</i>	DQ073916	Lee et al. (2006)
Orthoptera		
<i>Euchorthippus fusigeniculatus</i>	HM583652	Zhao et al. (2010)
<i>Acrida cinerea</i>	GU344100	Liu and Huang (2010)
<i>Ceraocris fasciata</i>	KP872953	Gao et al. (2018)
<i>Oxya japonica japonica</i>	MF125299	Li et al. (2020 b)
<i>O. hainanensis</i>	MH718848	Li et al. (2020 b)
<i>O. agavisa robusta</i>	MH718849	Li et al. (2020 b)
<i>O. chinensis</i>	EF437157	Unpublished
<i>O. intricate</i>	KP313875	Dong et al. (2016)
<i>Gastrimargus marmoratus</i>	EU513373	Ma et al. (2009)
<i>Oedaleus asiaticus</i>	EU513374	Ma et al. (2009)
<i>Traulia nigrifibialis</i>	MK059456	Li et al. (2019)
<i>T. szetschuanensis</i>	EU914849	Direct submission

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<i>T. minuta</i>	MF113247	Unpublished
<i>Choroedocus capensis</i>	MK059458	Li et al. (2019)
<i>C. violaceipes</i>	KY236113	Unpublished
<i>Stenocatantops splendens</i>	MK059457	Li et al. (2019)
<i>Xenocatantops brachycerus</i>	KC542806.1	Unpublished
<i>Ceracris versicolor</i>	KJ188251	Xu et al. (2016)
<i>Ruspolia dubia</i>	EF583824	Zhou et al. (2007)
<i>Velarifictorus hemelytrus</i>	KU562918	Yang et al. (2016 a)
<i>Loxoblemmus equestris</i>	KU562919	Yang et al. (2016 a)
<i>Teleogryllus emma</i>	KU562917	Yang et al. (2016 a)
<i>Locusta Migratoria migratoria</i>	EU287446	Ye et al. (2012)
<i>Asiotmethis zacharjini</i>	JX468876	Zhang et al. (2013 a)
<i>Filchnerella helanshanensis</i>	JX468877	Zhang et al. (2013 a)
<i>Pseudomethis rubimarginis</i>	JX468878	Zhang et al. (2013 a)
<i>Thrinchus schrenkii</i>	GU181288	Zhang et al. (2011)
<i>Atractomorpha sagittaris</i>	MK352100	Li et al. (2020 a)
<i>Mekongiana xiangchengensis</i>	HM583653	Zhao et al. (2010)
<i>Mekongiella xizangensis</i>	HM583654	Zhao et al. (2010)
<i>Sinochlora longifissa</i>	KC467055	Liu et al. (2013 a)
<i>Phyllomimus detersus</i>	KT345949	Yang et al. (2016 b)
<i>Anabrus simplex</i>	NC_009967	Fenn et al. (2007)
<i>Xizicus fascipes</i>	JQ326212	Yang et al. (2012)
Hemiptera		
<i>Riptortus pedestris</i>	NC_012462	Hua et al. (2008)
<i>Tetraphleps aterrimus</i>	NC_042679	Zhang et al. (2019)
<i>Cervaphis quercus</i>	KF254841	Wang et al. (2014)
<i>Cavariella salicicola</i>	KC332935	Wang et al. (2013)
<i>Schizaphis graminum</i>	NC_006158	Thao et al. (2004)
<i>Acyrtosiphon pisum</i>	NC_011594	Unpublished
<i>Phymatostetha huangshanensis</i>	MG878381	Su and Liang (2018)
<i>Japanagallia spinosa</i>	KY123687	Wang et al. (2017 a)
<i>Durgades nigropicta</i>	KY123686	Wang et al. (2017 a)
<i>Nacolus tuberculatus</i>	MW218663	Tang et al. (2020)
<i>Hylca paradoxa</i>	MW218660	Tang et al. (2020)
<i>Balala fujiana</i>	MW218661	Tang et al. (2020)
<i>Kalasha nativa</i>	MW218662	Tang et al. (2020)
<i>Bothrogonia ferruginea</i>	KU_167550	Unpublished
<i>Taharana fasciana</i>	KY886913	Wang et al. (2017 b)
<i>Drabescoides nuchalis</i>	KR349344	Wu et al. (2016)
<i>Nephotettix cincticeps</i>	NC_026977	Unpublished
<i>Idioscopus nitidulus</i>	NC_029203	Unpublished
<i>Hydaropsis longirostris</i>	NC_012456	Hua et al. (2008)
<i>Ugyops sp.</i>	MH352481	Yu and Liang (2018)
<i>Stenopirates sp.</i>	JN100019	Li et al. (2012 b)
<i>Geisha distinctissima</i>	FJ230961	Song and Liang (2009)
<i>Physopelta gutta</i>	NC_012432	Hua et al. (2008)
<i>Chauliops fallax</i>	JX839706	Li et al. (2013)
<i>Alloeorhynchus bakeri</i>	HM_235722	Li et al. (2012 a)
<i>Pentatoma rufipes</i>	MT861131	Zhao et al. (2021)
<i>Dinorhynchus dybowskyi</i>	MG450552	Zhao et al. (2018)
<i>Dolycoris baccarum</i>	KC460537	Zhang et al. (2013 b)
<i>Eurydema gebleri</i>	KP207595	Yuan et al. (2015 a)
<i>Eusthenes cupreus</i>	NC_022449	Song et al. (2013)
<i>Halyomorpha halys</i>	NC_013272	Lee et al. (2009)
<i>Coptosoma bifaria</i>	NC_012449	Hua et al. (2008)
<i>Aeschyntelus notatus</i>	NC_012446	Hua et al. (2008)
<i>Corizus tetraspilus</i>	KM983397	Yuan et al. (2015 b)

beetle) (accession number ON312105) of Coleoptera order (Morgan et al., 2022). It typically consists a densely packed set of thirty-seven genes, comprising thirteen protein-coding genes (PCGs), twenty-two transfer RNA genes (tRNAs) and two ribosomal RNA genes (rRNAs) (Boore 1999). The replication origin of mitogenome is typically located in the highly variable major non-coding AT-rich region (Cameron 2014). This region is referred to as the "control region" because it is responsible for controlling replication and transcription. The gene order of mitochondria can be used for intense level phylogenetic relationships due to its slow pace of evolution and more conserved base sequences and amino acid sequences (Boore and Brown 1998; Rokas and Holland 2000). In insects, two DNA strands of mitogenome are termed as major (J) strand and minor (N) strand based on the number of genes encoded by them (Lu et al., 2023; Yi et al., 2024). All PCGs are found on the major strand except nd5, nd4, nd4l and nd1. Similarly, 14 tRNA genes are situated on major strand except trnQ, trnC, trnY, trnF, trnH, trnP, trnL and trnV. Both rRNAs are present on minor strand (Drosopoulou et al., 2019; Yang et al., 2023; Zhu et al., 2023). Figure 1 depicts the mitochondrial gene order of class insecta. In mitochondrial genome of lepidopteran insects, it starts with tRNA<sup>Met</sup> while in dipteran, orthopteran and hemipteran insects, it starts with tRNA<sup>Ile</sup>.

### Composition of nucleotides in mitochondrial genome

Due to the occurrence of mutations in asymmetrical manner, the mitochondrial genome typically exhibits specific-strand bias in nucleotide composition that is

a common feature in all metazoan insects (Hassanin et al., 2005). Understanding the nature of these mutations is crucial for grasping the information about genomic evolution, demographic population history and accurate phylogenetic relationships. Mitogenome does not strictly follow the Chargaff's second parity rule (Nikolaou and Almirantis 2006). The strand-specific compositional bias is indicated by AT skew, as calculated by  $(A-T)/(A+T)$ , and GC skew, as calculated by  $(G-C)/(G+C)$  (Perna and Kocher 1995). Both AT skew and GC skew showed positive or negative values. If more A content than T, it means the strand compositional bias is positively AT skewed, and more G content than C, means positively GC skewed and vice versa. Basically, insect's mitogenomes exhibit strong nucleotide compositional bias (Pei et al., 2024). In all orders, the nucleotide composition of complete sequences is strongly biased towards AT content. Figure 2 shows the nucleotide composition across various species of Diptera, Orthoptera, Hemiptera and Lepidoptera.

### Protein-coding genes (PCGs)

Among a conserved set of 37 genes, the insect's mitochondrial genome generally consists 13 protein-coding genes (7 NADH dehydrogenase subunits (ND1 to ND6, ND4L), 3 cytochrome oxidase subunits (COI, COII and COIII), 2 ATPases (ATP6 & ATP8), 1 CytB gene). These are widely used in evolutionary studies related to families, genera and species. These genes are better proved beneficial for studying the evolutionary relationships among closely related species because of the occurrence of amino acid substitutions and presence



Fig. 1. Mitochondrial gene order in class insecta (Green for tRNAs, Yellow for PCGs, Blue for rRNAs and Grey colour is used to cite control region)

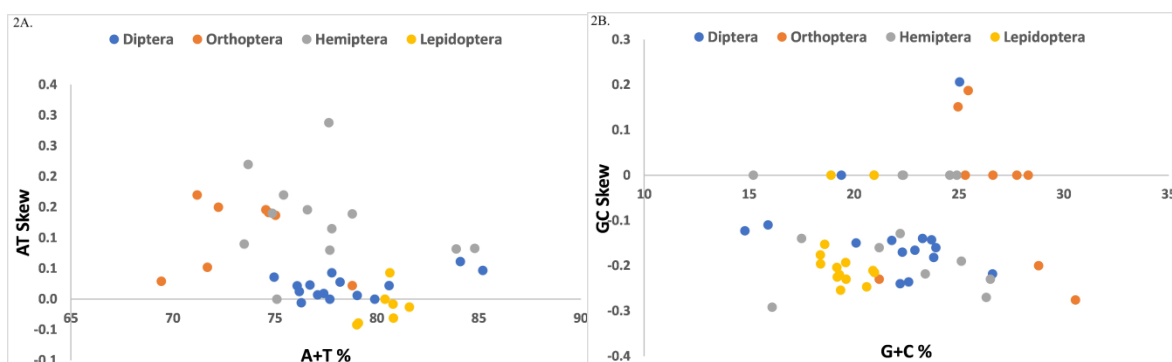


Fig. 2. Nucleotide composition across various species of Diptera, Orthoptera, Hemiptera and Lepidoptera (A) A+T content and AT-skew (B) G+C content and GC-skew

of unconstrained sites (at the third codon position). These genes show faster evolutionary rate as compared to ribosomal RNA genes. Among all the protein-coding genes, COI and COII genes are proved to be the best molecular markers for phylogenetic studies. In most cases, the start codons of PCGs follow the general ATN rule except COI (here N stands for any nucleotide) (Li et al., 2020 b; Milian-Garcia et al., 2022). Three canonical start codons (ATA, ATT and ATG) are typically preferred by most of the PCGs. However, inconsistency in ATN rule was observed for few PCGs. For example, the use of TCG for COI (many times), ND5 and CytB, TTA for COIII, ND5, ND4, ND4L and ND1, GTG for ATP8 and CytB, CAA and CCG for COI, TTG and CTA for ND1, GAA for ND6, TAT for ND4, TAA for ND5 and TTT for COI and ND4L was observed in dipterans, the use of CGA (many times) and TTG for COI, GTG for COII and ND1, GTT for ND4 and ND4L, CTA for COII and TTAG for COI was observed in lepidopterans, the use of CCG, TTA, CTG, ACT, TCT and AAA for COI, CCG for COII, GCU for ND5 and TTG and GTG for ND6 was observed in orthopterans and the use of TTG for COI, ND2, ND5, ATP8 and ATP6, CTG for COI and GTG for ATP6, ND1, ND5 and ND6 was observed in hemipterans.

The incomplete (T), truncated (TA) and fully complete (TAA) termination codons for nearly all the PCGs have been considered a common feature in all metazoan insects (Wolstenholme 1992). By the process of post-transcriptional modifications, these incomplete and truncated stop codons become full stop codons (TAA) (Lu et al., 2023; Stewart and Beckenbach 2009). However, inconsistency was observed in stop codons for some PCGs. For example, the use of TAG for ND2, COIII, ND4, CytB and ND1, CAT for ND4, ND4L, ND5 and ND6, TAT for ATP6, ND5, ND4, CytB and ND1, AGT for CytB, TTA for COIII, ND3 and ND4, ATT for COII and CytB, TTT for ND2, CAC for ND5 and CTT for COII was found in dipterans, the use of TAG for ND2, ATP6, ND3, ND5, ND4, ND4L, CytB and ND1 and AAT for ND3 was found in lepidopterans, the use of TAG for ND2, COI, COIII, ND3, ND5, ND4, CytB and ND1 was found in orthopterans and the use of TAG for ND2, ATP8, ND3, ND5, ND4 and ND4L and CytB was found in hemipterans. Beside these, the use of T-tRNA for COI, COII, ND5, ND6 and CytB, TA-tRNA for ND4, TA-COIII for ATP6, TA-ND4 for ND4L and TA-CytB for ND6 was detected in case of lepidopterans, the use of T-trnW for ND2, T-trnD for COII, TA-trnF for ND5, T-trnL for COI, T-trnPhe for ND5 and T-trnLys for COII in case of orthopterans and

the use of T-tRNA for COI, COII and ND4 and T-COIII for ATP6 in case of hemipterans.

### Transfer RNA (tRNA) and ribosomal RNA (rRNA) genes

Transfer RNA genes are necessary to translate the PCGs. The size differences within tRNAs come from the varied length of TΨC arm and DHU loop. These have all the components of oxidative phosphorylation process. For phylogenetic analyses, ribosomal RNA genes are frequently employed. The *rrnS* is highly conserved than *rrnL*. It is widely used to explore the genetic diversity of phyla. However, investigations at the low and intermediate levels, such as families or genera, frequently use the large subunit of ribosomal RNA (*rrnL*). All tRNA genes exhibit clover-leaf secondary structure except *trnS* gene (Zhao et al., 2010; Zhao et al., 2013; Wang et al., 2014; Jiang et al., 2016; Park et al., 2016; Yang et al., 2016 b; Ding et al., 2018; Liu et al., 2017; Ma and Huang 2018; Martinez et al., 2019; Li et al., 2020 a; Guo et al., 2021; Hao et al., 2021; Li et al., 2021). All metazoan insects have the loss of the DHU arm in the *trnS* (AGN) (Zhang et al., 2011; Wang et al., 2014; Yuan et al., 2015 b; Xu et al., 2016; Yang et al., 2019; Bian et al., 2020) and it was evolved primitively at the time of Metazoa evolution (Garey and Wolstenholme 1989). Even after the DHU arm is absent, this tRNA functions normally (Stewart and Beckenbach 2003). The whole sequence variability within the tRNA genes of lepidopteran insects was found less as compared to dipteran insects. The occurrence of variations is the result of instability within the non-paired sites of DHU and TΨC loops. The loss of TΨC-loop in *trnF* was found in *Z. tau* (Pumpkin Fruit Fly) belonging to Tephritidae family of Diptera. When mRNA is translated into proteins, the tRNA's TΨC-loop and DHU-loop both serve as specific recognition sites. In metazoan insects, aberrant tRNA genes commonly possess mismatched base pairs such as G-U, U-U, U-C, A-A, A-C, A-G, T-T, G-C and single C (Wolstenholme 1992). Among these, G-U pair is the most common mismatch. In dipteran insects, G-U mismatch was reported in two mosquito species i.e. *Anopheles sinensis* and *An. minimus*, T-T in *Drosophila melanogaster* (Vinegar fly), G-U and U-U in *D. mercatorum* (Fruit fly), G-U, U-U and U-C in *Dacus longicornis*, G-U, U-U, A-A and A-C in *Atylotus miser* and G-U, U-U, C-U and A-A in *Elodia flavipalpis*. In lepidopteran insects, G-U and U-U mismatches were reported in *Eriogyna pyretorum* (Giant silkworm moth), *Leucoma salicis* (White satin moth) and *Hydrillodes repugnalis* (Litter moth), U-U, A-C, U-C and G-A in *Parnassius apollo*

(Apollo butterfly) and U-U, A-C, U-C, A-A, and A-G in *Ampittia virgate* (Striped bush hopper), *Halpe nephele* (skipper) and *Onryza maga* (skipper). In orthopteran insects, G-U and U-U mismatches were reported in *Anabrus simplex* (Mormon cricket), G-U and A-G in *Oxya* species, G-U, A-A and U-U in *Gastrimargus marmoratus* (Band-winged grasshopper) and *Oedaleus asiaticus*, (Band-winged grasshopper) G-U, U-U, A-A and C-A in *Xizicus fascipes* (Quiet-calling katydids), G-U, U-U and A-G in *Atractomorpha sagittaris*, G-U, A-A, A-G and U-U in three species of grasshoppers i.e. *Asiotmethis zacharjini*, *Filchnerella helanshanensis* and *Pseudotmethis rubimarginis*, G-U, U-U, A-C, A-A and A-G in *Thrinchus schrenkii* and G-U, A-C, A-G, U-U and U-C in *Ruspolia dubia* (Bush cricket). In hemipteran insects, G-U, U-U, A-A, A-G and A-C were reported in *Phymatostetha huangshanensis*, *Nacolus tuberculatus*, *Hylica paradoxa*, *Balala fujiana*, *Kalasha nativa* (Leafhopper) and *Geisha distinctissima* (Asiatic green flatid), G-U and U-U in *Chauliops fallax* (Stalk-eyed bug), G-U, A-A, A-C, C-U and U-U in *Alloeorhynchus bakeri* (Damsel bug), G-U, U-U and A-C in *Eusthenes cupreus* (Tessaratomid bug), U-U, C-U and G-U in *Corizus tetraspilus* and G-U, A-U, G-C, U-U and U-C in *Pentatoma rufipes* (Forest bug). Most of the mismatches were found within the acceptor arm, DHU arm and anticodon stem of tRNA genes but few in TΨC stem. These non-Watson-Crick pairs greatly influence the thermodynamic stability (Varani and McClain 2000) and could be rectified during posttranscriptional modifications of RNA (Masta and Boore 2004).

Both the ribosomal RNA genes (*rrnS* and *rrnL*) are encoded by minority strand (L-strand). The *rrnL* gene is flanked by *trnL1* and *trnV* while *rrnS* gene is flanked by *tRNAVal* and the control region (Beckenbach 2012; Liu et al., 2013 b; Wang et al., 2013; Zhang et al., 2013 a, Wang et al., 2014; Jiang et al., 2016; Yang et al., 2016 b; Yong et al., 2017; Huang and Ma 2018; Yang et al., 2019; Li et al., 2020 b; Guo et al., 2021; Hao et al., 2021; Zhou et al., 2021; Cheng et al., 2022). The secondary structure of *rrnL* gene is made up of 6 domains marked as I, II, III (not present in mitogenome of arthropods), IV, V and VI, each separated by a single stranded region (Cannone et al., 2002; Pons et al., 2014). Most of the studies related to structure-based phylogeny, pay greatly attention on the 3'-portion of the *rrnL* gene due to the presence of more conservative domains IV and V whereas the rest of the domains are rarely used because of high sequence variations (Flook and Rowell 1997; Buckley et al., 2000). Likewise, the secondary

structure of *rrnS* gene is made up of 4 domains marked as I, II, III, and IV (Hickson et al., 1996). Among these, the more conservative domains III and IV of *rrnS* gene are widely used as molecular markers in studies related to insect's systematics.

### Control region

Control region has a high level of variability as compared to other functional genes due to frequently occurrence of nucleotide substitutions and remarkable differences in its fragment length (Zhang and Hewitt 1997). The variability may also occur due to the motif alterations and copies of tandem repeated regions (Zhang et al., 1995). These differences create major difficulties during the examination of its pattern of structural organization. The appearance of different numbers of tandem repeated regions may be essential to infer the population's genetic structures among the closely related species (Mancini et al., 2008). This region has faster evolutionary rate as compared to other mitochondrial genes. It is typically used as an authentic marker for phylogenetic studies related to intraspecific or closely related species. More importantly, the control region's varied sequence and high A+T concentration have made it difficult to characterise. That's why limited number of full mitochondrial genome sequences are present in GenBank. The variance in control region length among the various species of four orders described in this review is shown in Fig. 3.

### Mitochondrial genome rearrangements

It's a hot issue to discuss how gene rearrangements have evolved in insect mitogenomes. The fact that most of the gene rearrangements occur in tRNAs as compared to PCGs and rRNAs which demonstrate the selective neutrality of the tRNA position within the mitochondrial genome (Dowton et al., 2009). The gene rearrangements can be characterized by tandem duplication random loss, translocation, inversion, deletion and replacement (Dowton et al., 2002; Cameron 2014). The partial duplication of mtDNA genes is the direct result of errors in replication process. In this review, a unique type of replacement from *trnW* to *trnU* (U codes for 21<sup>st</sup> amino acid Selenocysteine) was found in *B. peregrine* (Flesh fly) belonging to family Sarcophagidae of order Diptera (Table 2).

### CONCLUSIONS

In this review, we identified the remarkable differences in gene organization of insect mitochondrial genome suggesting that it undergoes rearrangements

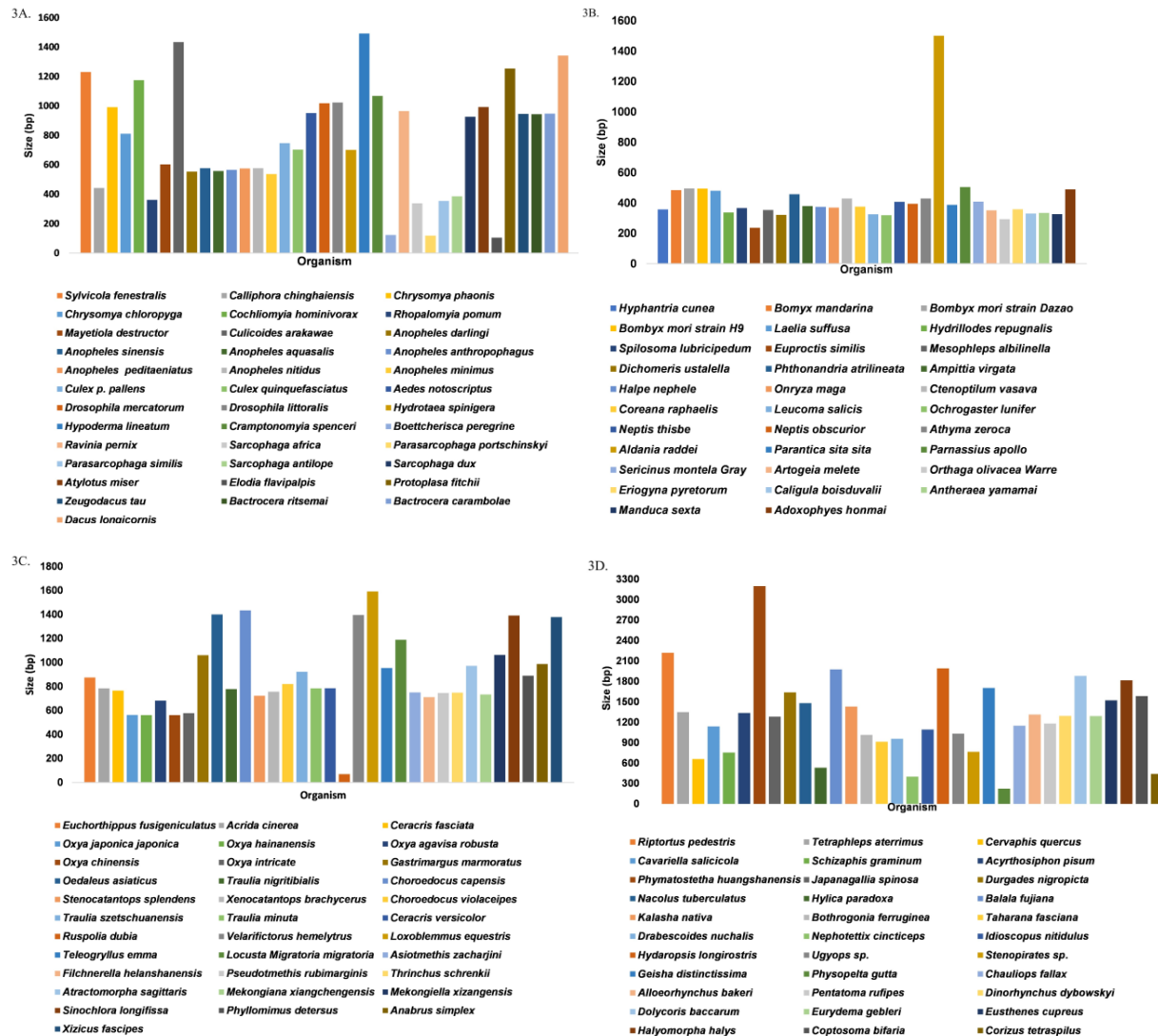


Fig. 3. Variation in Control region length (A) Diptera (B) Lepidoptera (C) Orthoptera (D) Hemiptera

but with conserved genetic makeup. In lepidopteran insects, it starts with tRNA<sup>Met</sup> while in dipteran, orthopteran and hemipteran insects, it starts with tRNA<sup>Ile</sup>. The replacement of trn<sup>W</sup> to trn<sup>U</sup> (U codes for 21<sup>st</sup> amino acid Selenocysteine) was only found in *B. peregrine* (Flesh fly) belonging to family Sarcophagidae of order Diptera. This type of gene rearrangement occurs very rare in insect mitochondrial genome that needs to further exploration. Some species involved inversion, translocation and duplication type of gene re-arrangements. The nucleotide composition is strongly biased towards AT content which makes the mitogenome less stable and more susceptible to alterations. Three canonical start codons (ATA, ATT and ATG) are typically preferred by the majority of PCGs. However, inconsistency was observed for few PCGs

particularly for the gene COI. Several mismatched base pairs such as G-U, U-U, U-C, A-A, A-C, A-G and T-T were detected in transfer RNA genes. Majority of the mismatches were found within the acceptor arm, DHU arm and anticodon stem of tRNA genes but few in TΨC stem. These non-Watson-Crick pairings have a significant effect on thermodynamic stability and could be rectified during post-transcriptional modifications of RNA. Control region, which has a high AT content and is changeable in size and nucleotide sequence, is the main non-coding part of the insect mitogenome. A comparative mitogenome analysis of a large number of insect orders and numerous insect species will be used in future studies to give evidence for evolutionary links between taxa at various taxonomic levels, whether high or low.



Table 2. Gene rearrangements in various families of Diptera, Lepidoptera, Orthoptera and Hemiptera

Order	Species	Type of gene rearrangement	
Diptera	<i>An. darlingi</i>	Inversion of trnA-trnR	
	<i>An. sinensis</i>		
	<i>An. aquasalis</i>		
	<i>An. anthropophagus</i>		
	<i>An. peditaeniatus</i>		
	<i>An. nitidus</i>		
	<i>An. minimus</i>		
	<i>Culex p. pallens</i>		
	<i>Cx. tritaeniorhynchus</i>		
	<i>Cx. pipiens pipiens Turkey</i>		
	<i>Cx. quinquefasciatus</i>		
	<i>Ae. notoscriptus</i>		
	<i>Ae. aegypti</i>		Inversion of trnA-trnR, Translocation of trnI and trnQ downstream to control region
	<i>B. peregrine</i>		Replacement of trnW to trnU
<i>C. phanois</i>	Inversion of trnA-trnR, Insertion of duplicated trnI downstream to control region		
<i>M. destructor</i>	Translocation of trnN, trnI and trnY		
<i>R. pomum</i>	Translocation of trnN, trnI and trnS, Insertion of duplicated trnY downstream to the translocated trnS		
Lepidoptera	<i>A. tortuosa,</i>	Translocation of control region upstream to trnM	
	<i>N. albofascia,</i>		
	<i>H. circumflexa,</i>		
	<i>L. albidaria,</i>		
	<i>P. falcipennis,</i>		
	<i>P. femorata,</i>		
	<i>Z. tukuringra,</i>		
	<i>G. chrysolopha,</i>		
	<i>D. paraexacta</i>		
	<i>D. inexacta</i>		
<i>R. albomarginatus</i>			
<i>S. sigillata</i>	Insertion of duplicated control region upstream to trnV		
<i>B. mandarina</i>	Insertion of duplicated trnS downstream to control region and trnI upstream to nd2, Translocation of trnM to atp6 downstream to the translocated trnS		
Orthoptera	<i>V. hemelytrus</i>	Inversion of trnD- trnK	
	<i>L. equestris</i>		
	<i>T. emma</i>		
	<i>P. detersus</i>		
	<i>S. longifissa</i>		Inversion of trnI-trnQ-trnM and trnD-trnK Translocation of trnQ upstream to trnW and control region downstream to nd2, Inversion of trnD-trnK
Hemiptera	<i>Stenopirates</i> sp.	Translocation of control region upstream to rrnL and nd1-trnL downstream to rrnS, Insertion of duplicated and inverted trnT-trnP-nd6 downstream to translocated nd1-trnL	
	<i>C. quercus</i>		
	<i>C. salicicola</i>		Translocation of trnI –trnM-nd2 upstream to control region and trnW-trnC-trnY downstream to the translocated trnQ
	<i>S. graminum</i>		Insertion of duplicated trnQ downstream to control region, Translocation of trnI to trnY downstream to duplicated trnQ, deletion of trnS downstream to trnN
	<i>A. pisum</i>		Insertion of duplicated trnM upstream and translocation of trnI to trnY downstream to control region, deletion of trnS downstream to trnN

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## AUTHOR CONTRIBUTION STATEMENT

In this review, every author pays full attention to the previous scientific literature. After thoroughly reviewing by all the authors, the corresponding author compiled the data and managed it and submitted the manuscript.

## CONFLICT OF INTEREST

No conflict of interest.

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