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Complete mitochondrial genome sequence of fruit-piercing moth *Eudocima phalonia* (Linnaeus, 1763) (Lepidoptera: Noctuoidea)

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ABSTRACT

The complete mitochondrial genome of the fruit piercing moth *Eudocima phalonia* (Linnaeus, 1763) (Lepidoptera: Noctuoidea) was sequenced and characterized (Genbank Accession No: KY196412). The complete mitogenome is a circular molecule of 15,575 bp length, consisting of 13 protein-coding genes (PCGs), two ribosomal RNA genes (*rrnS* and *rrnL*), 22 transfer RNA (tRNA) genes and an A + T-rich region (D-loop). The nucleotide composition of the genome is highly A + T biased, accounting for 80.67% of nucleotides. All tRNAs have putative secondary structures that are characteristic of mitochondrial tRNA. Most of the PCGs were initiated by typical ATN codons. Five genes were initiated by unusual codons. *Cox1* gene was initiated by an unusual CGA codon and terminated by the typical stop codon GAA. Six genes ended with a single T. The A + T-rich region of 336 bp consisted of repetitive sequences, including two ATAGA motifs, a 19 bp poly-T stretch and three microsatellite-like regions ($(TA)_4$, $(TA)_6$ and two $(TA)_7$). Moreover, three large tandem (one 40 bp and two 25 bp) repeated elements were identified in A + T-rich region. Phylogenetic analysis using PCGs revealed that Superfamily Noctuoidea is a monophyletic group.

1. Introduction

The genomes and genes of mitochondria have been widely used as informative molecular markers in studies of comparative and evolutionary genomics, reconstruction of phylogenetic relationships, population genetics and evolutionary biology [1–5].

Insect mitochondrial genome (mtDNA) is a circular molecule, ranging from 14 to 19 kb in length which encodes 37 genes including 13 protein-coding genes (PCGs), 2 ribosomal RNA (rRNA) genes and 22 transfer RNA (tRNA) genes. In addition, it contains a control region known as the adenine (A) + thymine (T)-rich region which is common in all insect mtDNA. This region is involved in the initiation of both transcription and replication [6].

The order Lepidoptera (butterflies and moths) is one of the largest groups of insects, accounting for > 157,424 described species. It represents one of the evolutionarily most successful lineages of phytophagous insects [7]. The superfamily Noctuoidea within the order Lepidoptera comprises 43,000 described species [8]. Besides, this order includes a number of biological model organisms, many severe pest species, and many best known and most popular invertebrates, giving emphasis to the fact that studies of lepidopteran phylogeny and evolution are of both scientific and public interest.

Despite the huge taxonomic diversity, the current information on the lepidopteran mitogenome is very limited. Only a few reports are available for the characterization of the mitogenomes of Lepidoptera species [9]. Only 57 lepidopteran mitogenomes have been sequenced so far, including 27 butterflies and nearly 30 moths; only 27 are from superfamily Noctuoidea. Sequencing and characterization of mitogenome of more species in Noctuoidea will provide further insight into the deep level evolutionary relationships among these agriculturally important insects.

In this study, we present the complete mitogenome sequence of *Eudocima phalonia* (Linnaeus, 1763) (Genbank Accession No: KY196412) and compare it with those of other Noctuoidea species. *E. phalonia*, commonly known as the fruit-piercing moth, is an important pest of citrus, several commercial fruit crops and beverages [10,11]. *E. phalonia* uses its proboscis to perforate the fruits and suck sap to feed. Larval stage has no such necessity because host plants usually vary for larva and adult stages. Caterpillars are predominantly foliage feeders of numerous wild plants, shrubs and vines within the families Menispermaceae and Fabaceae. The adult species have sexual dimorphism, the males with more frequently lineated forewings and the females with

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Table 1
List of the complete mitogenome of the superfamily Noctuoidea reported so far.

Family	Species	Accession	Reference
Notodontidae	*Phalera flavescens*	JF440342	[27]
	Ochrogaster lunifer	AM946601	[28]
Arctiidae	*Hyphantria cunea*	GU592049	[29]
	Amata formosae	KC513737	[25]
Doidae	*Doa* sp.	KJ508058	[20]
Erebidae	*Nyctemera arctata albofasciata*	KM244681	[18]
	Eudocima phalonia	KY196412	This study
	Catocala deuteronympha	KJ432280	[9]
	Asota plana lacteata	KJ173908	[9]
Lymantriidae	*Lymantria dispar*	FJ617240	[23]
	Gynaephora menyuanensis	KC185412	[26]
Noctuidae	*Sesamia inferens*	JN039362	[30]
	Ctenoplusia agnata	KC414791	[22]
	Ctenoplusia limbirena	KM244665	[18] unpublished
	Spodoptera exigua	JX316220	[36]
	Spodoptera litura	KF543065	[34]
	Agrotis ipsilon	KF163965	[37]
	Agrotis segetum	KC894725	[24]
	Helicoverpa punctigera	KF977797	[35]
	Helicoverpa armigera	GU188273	[19]
	Helicoverpa zea	KJ930516	[43]
	Noctua pronuba	KJ508057	[20]
	Acronicta psi	KJ508060	[20]
	Striacosta albicosta	KM488268	Coates B.S. & Abel C.A., unpublished
	Mythimna separata	KM099034	[21]
	Risoba prominens	KJ396197	[9]
Euteliidae	*Eutelia adulatricoides*	KJ185131	[9]
Coleoptera	*Tribolium casteneum*	AJ312413	Friedrich and Muqim [40]
Diptera	*Drosophila yakuba*	X03240	Clary et al. [41]
	Anopheles gambiae	L20934	Beard et al. [42]

more irregularly marked and mottled. This species is distributed in India, Thailand, Myanmar, Vietnam, Nepal, China, Taiwan, Japan, Korea, South of Russian Far East (migrant), Philippines, Indonesia (New Guinea), Micronesia, Australia, New Zealand, Central Africa (Gabon, Zaire, Congo) [12].

2. Materials and methods

2.1. Insect collection and total DNA extraction

Adult *E. phalonia* moths were collected from Kodaikanal (10° 23′ 5367″ N 77° 49′ 2933″ E) Western Ghats, Tamil Nadu, India. The total DNA was isolated from single individual (thoracic region) using DNA extraction Kit (Genotypic Technology Pvt. Ltd. Bangalore, India). The voucher specimen was deposited at Entomology Research Institute, Loyola College, Chennai (Vouchers Number: ERILMC-049).

2.2. Mitogenome sequencing

Whole mitogenome sequencing (WmtGS) libraries were prepared with Illumina-compatible NEXTflex DNA sequencing kit (BIOO Scientific, Austin, Texas, U.S.A.). Briefly, about 100 ng of mitochondrial enriched DNA was sheared using Covaris S2 sonicator (Covaris, Woburn, Massachusetts, USA) to generate approximate fragment size distribution from 200 bp to 400 bp. The fragment size distribution was checked on Agilent 2200 Tape Station with D1000 DNA screen tapes and reagents (Agilent Technologies, Palo Alto, CA, USA) and subsequently purified using HighPrep magnetic beads (Magbio Genomics Inc., USA). The purified fragments were end-repaired, adenylated and ligated to Illumina multiplex barcode adaptors as per NEXT Flex DNA sequencing kit protocol.

The adapters used in the study were Illumina Universal Adapters:

5′AATGATACGGCGACCACCGAGATCTACACTCTTTCCCTACACGACGCTCTTCCGATCT-3′ and

Index Adapter: 5′-GATCGGAAGAGCACACGTCTGAACTCCAGTCAC [INDEX] ATCTCGTATGCCGTCTTCTGCTTG-3′.

Index unique sequence to identify sample-specific sequence was “TCGGCA”. The adapter-ligated DNA was purified with HighPrep beads and then amplified for 10 cycles of PCR using Illumina-compatible primers provided in the NEXTFlex DNA sequencing kit. The final PCR product (sequencing library) was purified with HighPrep beads, followed by library quality control check. The Illumina-compatible sequencing library was initially quantified by Qubit fluorometer (Thermo Fisher Scientific, MA, USA) and its fragment size distribution was analysed on Agilent Tape Station.

2.3. Sequence assembly and gene annotation

The raw sequences were assembled using Denovo Genome assembly (SPAdes assembler). The sequence annotation was executed using MITOS online tool [13]. The PCGs were recognized by sequence resemblance with that of known lepidopteran sequences. The PCG's nucleotide sequences were deciphered on the basis of the invertebrate mitochondrial genetic code. The PCGs alignment of various lepidopteran mitogenome was executed using Clustal Omega [14]. The composition skewness was calculated using the formula: AT skew = [A − T] / [A + T]; similarly GC skew = [G − C] / [G + C] [15]. The tRNA genes and their putative secondary structures were produced using MITOS software and analysed by comparison with the nucleotide sequence of other lepidopteran tRNA sequences. Tandem repeats at the A + T-rich region were identified using the online Tandem Repeats Finder tool (http://tandem.bu.edu/trf/trf.html) [16]. Relative Synonymous Codon Usage (RSCU) of PCGs was determined using codon usage calculator (www.biologicscorp.com/tools/CodonUsageCalculator).

2.4. Phylogenetic analysis

The phylogenetic relationship among the superfamily Noctuoidea was analysed using 13 PCGs and 2 rRNA of mitochondrial genome. PCGs of mitogenomes of 27 species, including one obtained through this study, were used to reconstruct the phylogenetic tree (Table 1). The sequences of remaining 26 mitogenomes were obtained from the Genbank. The mitogenomes of *Drosophila yakuba* (X03240), *Anopheles gambiae* (L20934) and *Tribolium casteneum* (AJ312413) were used as outgroups. The amino acid sequences of 13 mitochondrial PCGs were aligned using ClustalW and concatenated. The concatenated sets of amino acid sequences from the PCGs were used in the reconstruction of phylogenetic tree using the Model based Maximum Likelihood method using the MEGA version 6.0 program [17]. The most appropriate model Jones-Taylor-Thornton (JTT) was used to infer the phylogenetic tree with 1000 bootstrap replicates.

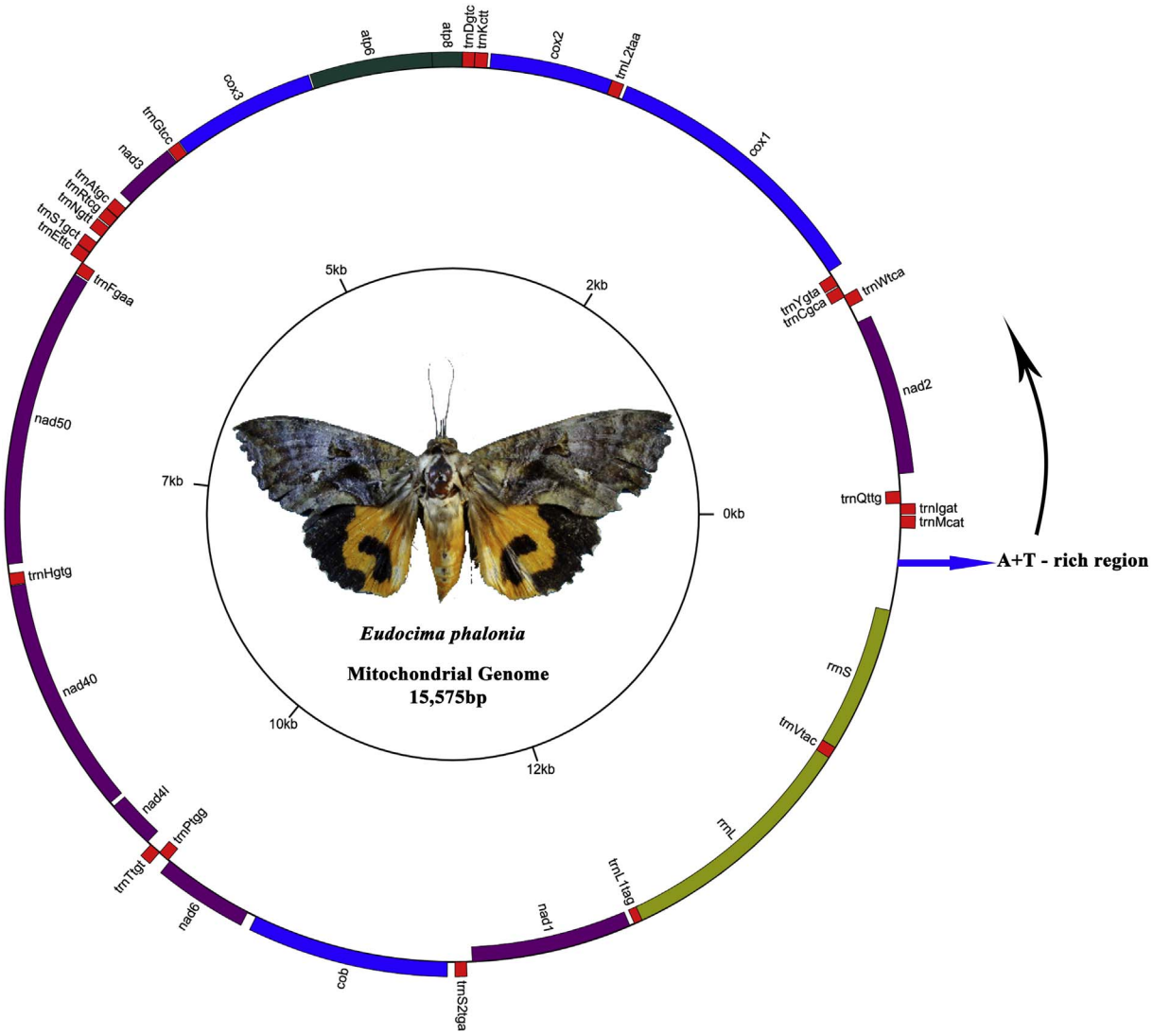


Fig. 1. Map of the complete mitochondrial genome of *Eudocima phalonia* (Lepidoptera: Noctuoidea). The length of this circular genome is 15,575 bp. The sequence starts at A + T-Rich region. The regions corresponding to 13 proteins genes (PCGs), two ribosomal RNA genes and 22 transfer RNA genes are also indicated.

3. Results and discussion

3.1. Genome organization and base composition

The complete mitogenome of *E. phalonia* is a closed circular molecule consisting of 15,575 bp length. The complete mitogenome sequence was submitted to the Genbank (Accession Number: KY196412). The sizes of mitogenomes sequenced so far in superfamily Noctuoidea moths ranged from 15,261 bp in *Ctenoplusia agnata* to 15,671 bp in *Catocala deuteronympha* [9]. The length of *E. phalonia* mitogenome falls within the range of mitogenomes of other Noctuoid moths sequenced. The organization of the *E. phalonia* complete mitogenome is shown in Fig. 1. The *E. phalonia* mitogenome contains 13 PCGs viz. ATPase subunits 6 and 8 (*atp6* and *atp8*), cytochrome *c* oxidase subunits 1–3 (*cox1*, *cox2* and *cox3*), NADH dehydrogenase subunits 1–6 (*nad1*, *nad2*, *nad3*, *nad4*, *nad5* and *nad6*) subunit 4 L of nad (*nad4L*) and cytochrome B (*cob*), 2 ribosomal RNA genes (*rrnS* and *rrnL*), 22 tRNA genes (one each for 18 amino acids and two each for leucine and serine), and a major non-coding region known as the A + T-rich region (Table 2). The order of three tRNA genes of *E. phalonia* mitogenome was *trnM-trnI-trnQ* (Fig. 1), which differed from ancestral order *trnI-trnQ-trnM* [44]. However, the position of the *trnM* of *E. phalonia* (15,500–15,566) was similar to that of other Noctuoidea such as *Nyctemera arctata albofasciata* [18], *Risoba prominens* [9], *Helicoverpa armigera* [19], *Noctua pronuba* [20] and *Eutelia adulatricoides* [9].

3.2. Protein-coding genes (PCGs)

The 13 PCGs of *E. phalonia* mitogenome include *nad1*–6, *nad4L*, three *cox* subunits, two ATPase subunits and one *cob*. The 13 PCGs are 10,809 bp in length and account for 69.39% of the whole mitogenome. Twelve of the PCGs in *E. phalonia* mitochondrial genome were initiated

Table 2
Details on gene organization of the *Eudocima phalonia* mitogenome.

Gene	Direction	Nucleotide no.	Size	IGNc	Anticodon	Start codon	Stop codon
trnI	F	1–57	57	0	GAT		
trnQ	R	60–128	69	2	TTG		
nad2	F	225–1097	873	96		ATT	TAG
trnW	F	1195–1263	69	97	TCA		
trnC	R	1256–1321	66	− 8	GCA		
trnY	R	1330–1395	66	8	GTA		
cox1	F	1421–2935	1515	25		ATG	TAA
trnL2 (UUR)	F	2955–3022	66	19	TAA		
cox2	F	3023–3688	666	0		ATG	TGA
trnK	F	3705–3775	71	16	CTT		
trnD	F	3776–3842	67	0	GTC		
atp8	F	3843–4007	165	0		ATT	TAA
atp6	F	4007–4672	666	0		ATA	TAA
cox3	F	4681–5463	783	8		ATG	TAA
trnG	F	5469–5536	68	5			
nad3	F	5543–5881	339	7		ATA	TAA
trnA	F	5924–5991	68	42	TGC		
trnR	F	5994–6057	64	2	TCG		
trnN	F	6066–6131	66	8	GTT		
trnS1	F	6172–6237	66	40	GCT		
trnE	F	6241–6306	66	3	TTC		
trnF	R	6309–6375	67	2	GAA		
nad5	R	6386–8065	1680	10		ATA	TAA
trnH	R	8117–8183	67	51	GTG		
nad4	R	8188–9522	1335	4		AAA	CAT
nad4L	R	9550–9822	273	27		ATA	TAA
trnT	F	9846–9910	65	23	TGT		
trnP	R	9911–9975	65	0	TGG		
nad6	F	9986–10,501	516	10		ATT	TAA
cob	F	10,554–11,651	1098	52		ATT	TAA
trnS2	F	11,693–11,757	65	41	TGA		
nad1	R	11,789–12,688	900	31		ATT	TAA
trnL1 (CUN)	R	12,716–12,783	68	27	TAG		
rrnL	R	12,763–14,153	1391	− 20			
trnV	R	14,150–14,216	67	− 3	TAC		
rrnS	R	14,217–15,037	821	0			
trnM	F	15,500–15,566	67	0	CAT		
A + T rich region		15,041–15,376	336	0			

by typical ATN codons. One PCG was initiated by an unusual codon. Specifically, 3 PCGs (*cox1*, *cox2* and *cox3*) started with ATG, 4 PCGs (*nad3*, *nad4l*, *nad5* and *atp6*) started with ATA, 5 PCGs (*atp8*, *nad1*, *nad2*, *nad6* and *cob*) started with ATT and one PCG (*nad4*) started with AAA. For the stop codons, ten PCGs (*cox1*, *nad1*, *nad3*, *nad4L*, *nad5*, *nad6*, *cox3*, *atp8*, *atp6* and *cob*) terminated with TAA and 3 PCGs *nad4*, *cox2*, *nad2* terminated with CAT, TGA, TAG respectively (Table 2). The organization of the PCGs was unchanged as seen in the other sequenced lepidopterans. The start codon for *cox1* gene of the lepidopteran insects is not consistent. Change of start codon is common for *cox1* gene in all lepidopterans. The A + T nucleotide composition of 13 PCGs in the mitogenome of *E. phalonia* is 78.39%.

The Relative Synonymous Codon usage (RSCU) of PCGs of the *E. phalonia* was examined and the results are shown in Table 3. In the PCGS of the *E. phalonia* mitogenome, the codons CTG, GCG, CAG and CGG are not represented. The genome-wise A + T bias is also positively correlated in the codon usage of the *E. phalonia*. The six most frequently used codons in the *E. phalonia* mitogenome TTT (Phe), TTA (Leu), ATT (Ile), ATA (Met), TAT (Tyr) and AAT (Asn) accounted for 41.23%. These codons are all composed of A or T nucleotides thus indicating the biased usage of A and T nucleotides in the *E. phalonia* PCGs. Leucine (9.6%), Isoleucine (10.87%), Phenylalanine (7.18%) and serine (11.60%) were the most frequent amino acids in *E. phalonia* mitochondrial protein (39.25%). These amino acids are also the most commonly present in other Noctuoidea moths (Fig. 5).

3.3. Intergenic spacers and overlapping sequences

The mitogenome of *E. phalonia* contains a total of 53 bp overlaps between genes in five locations ranging from 3 to 20 bp in length. The longest 20 bp overlap was found in two locations: *trnG-nad3* and *trnL1-rrnL* (Table 2). The overlapping located between *trnL1-rrnL* was also observed in other Noctuoidea species, such as *E. adulatricoides* (Mell) [9], *Mythimna separata* (Walker) [21], *Ctenoplusia limbirena* (Guenee) [18], *Ctenoplusia agnata* (Staudinger) [22], *Lymantria dispar* (Linnaeus) [23], *Agrotis segetum* (Denis & Schiffermuller) [24], *Amata formosae* [25] and *Doa* sp. [20]. The intergenic spacer sequence of *E. phalonia* mitogenome ranged from 2 to 97 bp, totalling 656 bp in length which was distributed in 26 regions (Table 2.). This intergenic spacers were longer than those of other Noctuoidea moths, including *Doa* sp. (566 bp over 23 regions), *N. arctata albofasciata* (594 bp over 25 regions), *R. prominens* (555 bp over 21 regions), *H. armigera* (618 bp over 25

Table 3
Codon usage of the protein-coding genes in *Eudocima phalonia* mitogenome.[a]

Codon	n	%	RSCU	Codon	n	%	RSCU	Codon	n	%	RSCU
TTT(F)	198	5.53	0.77	CCA(P)	29	0.81	0.25	GAT(D)	35	0.97	0.83
TTC(F)	59	1.64	0.23	CCG(P)	1	0.02	0.01	GAC(D)	7	0.19	0.17
TTA(L)	233	6.51	0.68	ATT(T)	78	2.18	0.40	GAA(E)	44	1.23	0.98
TTG(L)	23	0.64	0.07	ACC(T)	43	1.20	0.22	GAG(E)	1	0.02	0.02
CTT(L)	45	1.26	0.13	ACA(T)	65	1.81	0.33	TGT(C)	20	0.55	0.64
CTC(L)	16	0.45	0.05	ACG(T)	9	0.25	0.05	TGC(C)	11	0.30	0.36
CTA(L)	28	0.78	0.08	GCT(A)	48	1.34	0.61	TGA(W)	80	2.23	0.92
CTG(L)	0	0.0	0.00	GCC(A)	4	0.11	0.05	TGG(W)	7	0.19	0.08
ATT(I)	345	9.64	0.89	GCA(A)	27	0.75	0.34	CGT(R)	8	0.22	0.22
ATC(I)	44	1.23	0.11	GCG(A)	0	0.00	0.00	CGT(R)	1	0.02	0.03
ATA(M)	209	5.84	0.93	TAT(Y)	210	5.87	0.87	CGA(R)	27	0.75	0.75
ATG(M)	16	0.44	0.07	TAC(Y)	31	0.86	0.13	CGG(R)	0	0.00	0.00
GTT(V)	32	0.89	0.39	TAA[b]	214	5.98	0.99	AGT(S)	37	1.03	0.09
GTC(V)	2	0.05	0.02	TAG[b]	3	0.08	0.01	AGC(S)	35	0.97	0.08
GTA(V)	48	1.34	0.58	CAT(H)	60	1.67	0.81	AGA(S)	70	1.95	0.17
GTG(V)	1	0.02	0.01	CAC(H)	14	0.39	0.19	AGG(S)	23	0.64	0.06
TCT(S)	121	3.38	0.29	CAA(Q)	53	1.48	1.00	GGT(G)	31	0.86	0.25
TCC(S)	33	0.92	0.08	CAG(Q)	0	0.00	0.00	GGC(G)	2	0.05	0.02
TCA(S)	88	2.46	0.21	AAT(N)	280	7.82	0.80	GGA(G)	85	2.37	0.69
TCG(S)	8	0.22	0.02	AAC(N)	70	1.95	0.20	GGG(G)	5	0.13	0.04
CCT(P)	53	1.48	0.46	AAA(K)	172	4.80	0.98				
CCC(P)	31	0.86	0.27	AAG(K)	4	0.11	0.02				

[a] A total of 3577 codons were analysed omission of the initiation and terminations codons. RSCU, relative synonymous codon usage.
[b] Stop codon.

regions), *C. limbirena* (599 bp over 24 regions), *C. agnata* (573 bp over 26 regions), *N. pronuba* (624 bp over 26 regions), *E. adulatricoides* (620 bp over 22 region), *A. segetum* (642 bp over 25 regions), *Agrotis ipsilon* (630 bp over 25 regions) and *A. formosae* (583 bp over 23 regions); however they were shorter than *Asota plana* [9] (678 bp over 25 regions), *Gynaephora menyuanensis* [26] (776 bp over 26 regions), *L. dispar* (703 bp over 26 regions), *Acronicta psi* (659 bp over 26 regions), *Catocala deuteronympha* (740 bp over 28 regions), *Phalera flavescens* [27] (747 bp over 26 regions), *Ochrogaster lunifer* [28] (764 bp over 27 regions), *Hyphantria cunea* [29] (705 bp over 26 regions) and *Striacosta albicosta* (762 bp over 25 regions). The longest intergenic spacers of 96 and 97 bp were located between *trnQ-nad2* and *nad2*-trnW respectively in *E. phalonia*. In *Ctenoptilum vasava*, similar intergenic spacer length of 97 bp was found between *nad2* and *trnW* genes [5]. However the first spacer of 96 bp found in *E. phalonia* through this study is not present in other lepidopterans. The 33 bp intergenic spacer region between *trnS2* and *nad1* contained the 'ATACTAA' motif. The 7 bp motif is a common feature among the 17 species selected from superfamily Noctuoidea, showing that this region is conserved and present in maximum of mitogenomes (Fig. 3b).

3.4. Genome composition and skewness

The nucleotide composition of the mitogenome of *E. phalonia* was found to be as follows: A = 6205 (39.83%), T = 6362 (40.84%), G = 1175 (7.54%) and C = 1833 (11.76%). As witnessed in other lepidopterans, the nucleotide composition of the *E. phalonia* mitogenome is heavily biased toward A + T (80.67%) (Table 4.); this was higher than other lepidopterans species such as *O. lunifer* (77.83%) *A. psi* (79.08%), *S. albicosta* (79.32%), *A. formosae* (79.48%) and *N. arctata albofasciata* (79.64%); it was slightly lower than *Gynaephora menyuanensis* (81.47%), *Helicoverpa punctigera* (81.34%), *Agrotis ipsilon* (81.24%), *Spodoptera litura* (81.03%), *C. agnata* (81.08%), *C. limbirena* (81.01%), *N. pronuba* (81.06%), *R. prominens* (81.05), *Catocala deuteronympha* (81.11%) *M. separata* (81.00%) and *Helicoverpa zea* (81.00%). The AT skew and GC skew were calculated for all Noctuoidea mitogenomes; they are presented in Table 4. The AT skew for the *E. phalonia* mitogenome was marginally negative (− 0.012), representing a higher amount of T and A nucleotides. Comparable results were observed in *P. flavescens* (− 0.009), *A. formosae* (− 0.027), *N. arctata albofasciata* (− 0.013), *A. ipsilon* (− 0.005), *A. segetum* (− 0.003), *C. agnata* (− 0.030), *C. limbirena* (− 0.035), *E. adulatricoides* (− 0.005), *Sesamia inferens* [30] (− 0.001), *N. pronuba* (− 0.018), *M. separata* (− 0.011), *R. prominens* (− 0.007) and *Catocala deuteronympha* (− 0.021) for AT skewness. The AT skew of tRNA and rRNA genes in the *E. phalonia* mitogenome were 0.005 and − 0.023 respectively. The AT skew at A + T-rich region of *E. phalonia* mitogenome was − 0.067, showing a partiality for T over A nucleotide. The GC skew values were hostile in all sequenced lepidopteran mitogenomes, showing a higher content of C. The GC skew of *E. phalonia* for 2 rRNA genes was − 0.369, which was higher than that detected for tRNA, PCGs and the A + T-rich regions.

3.5. Transfer RNA genes

The *E. phalonia* mitochondrial genome had 22 tRNA genes that were varied in length from 57 to 68 bp with A + T content of 81.39%. Among these, 21 tRNA genes presented the putative secondary structure detected for mitochondrial tRNAs of other species (Fig. 2); however $tRNA^{Ser1}$ presented unusual secondary structure lacking a dihydrouridine (DHU). This feature has been witnessed in hexapods and metazoan mitogenomes [21,31,32]. A total of 20 mismatched base pairs were observed to occur in 15 of 22 tRNAs genes such as in $tRNA^{Ile}$ [1 U-G], $tRNA^{Gln}$ [1 U-G], $tRNA^{Trp}$ [1 U-G], $tRNA^{Cys}$ [1 U-G], $tRNA^{Leu2}$ [1G-U], $tRNA^{Gly}$ [1 U-G], $tRNA^{Ala}$ [1G-U], $tRNA^{Arg}$ [1 U-U], $tRNA^{Ser}$ [1 U-G], $tRNA^{Gln}$ [1 G-U], $tRNA^{Phe}$ [1 G-U and 1 U-G], $tRNA^{Thr}$ [1 G-U], $tRNA^{Pro}$ [2 G-U], $tRNA^{Leu1}$ [2 U-G and 2 G-U] and $tRNA^{Val}$ [1 G-U]. In these

Table 4
Nucleotide compositions and skewness in superfamily Noctuoidea mitogenomes.

Species	Size (bp)	A %	G%	T%	C%	A + T%	AT skew	GC skew
E. phalonia	15,575	39.83	7.54	40.84	11.76	80.67	− 0.012	− 0.218
P. flavescens	15,659	40.07	7.86	40.80	11.25	80.87	− 0.009	− 0.177
O. lunifer	15,593	40.09	7.43	37.74	14.59	77.83	0.030	− 0.325
H. cunea	15,481	40.57	7.55	39.81	12.05	80.38	0.009	− 0.229
A. formosae	15,463	38.66	7.52	40.82	12.97	79.48	− 0.027	− 0.0.267
Doa sp.	15,228	40.41	7.76	40.01	11.64	80.42	0.004	− 0.2
N. arctata albofasciata	15,431	39.27	7.34	40.37	11.66	79.64	− 0.013	− 0.227
L. dispar	15,569	40.58	7.57	39.29	12.55	79.87	0.016	− 0.247
G. menyuanensis	15,770	40.87	6.88	40.60	11.75	81.47	0.003	− 0.261
H. armigera	15,347	40.54	7.68	40.43	11.33	80.97	0.001	− 0.192
H. punctigera	15,382	40.69	7.58	40.65	11.06	81.34	0.000	− 0.186
H. zea	15,343	40.59	7.58	40.40	11.41	81.00	0.002	− 0.202
A. ipsilon	15,377	40.38	7.71	40.86	11.03	81.24	− 0.005	− 0.177
A. segetum	15,378	40.20	7.79	40.49	11.50	80.69	− 0.003	− 0.192
S. litura	15,374	41.03	7.60	40.00	11.36	81.03	0.012	− 0.198
S. exigua	15,365	40.87	7.67	40.05	11.38	80.92	0.010	− 0.194
C. agnata	15,261	39.57	7.70	41.51	11.19	81.08	− 0.030	− 0.184
C. limbirena	15,306	39.06	7.84	41.95	11.15	81.01	− 0.035	− 0.174
E. adulatricoides	15,360	40.20	7.80	40.65	11.32	80.85	− 0.005	− 0.184
S. inferens	15,413	40.06	7.61	40.17	12.15	80.23	− 0.001	− 0.229
N. pronuba	15,315	39.79	7.80	41.27	11.00	81.06	− 0.018	− 0.170
A. psi	15,350	40.89	7.82	38.19	12.92	79.08	0.034	− 0.168
Striacosta albicosta	15,553	40.14	7.87	39.18	12.79	79.32	0.012	− 0.238
M. separata	15,329	40.02	7.66	40.98	11.33	81.00	− 0.011	0.193
R. prominens	15,343	40.24	7.80	40.81	11.13	81.05	− 0.007	− 0.175
Catocala deuteronympha	15,671	39.68	7.26	41.43	11.61	81.11	− 0.021	− 0.230
Asota plana	15,416	40.08	7.49	40.26	12.16	80.34	− 0.002	− 0.237
PCGs								
E. phalonia	10,809	38.90	8.55	39.49	13.04	78.39	− 0.007	− 0.207
P. flavescens	11,211	33.73	10.95	45.23	10.08	78.07	− 0.146	− 0.041
O. lunifer	11,266	32.47	12.08	43.26	12.19	75.73	− 0.142	− 0.004
H. cunea	11,205	33.59	8.10	45.00	10.42	79.59	− 0.145	0.027
A. formosae	10,782	37.92	8.51	39.39	14.16	77.31	− 0.019	0.249
Doa sp.	10,747	39.70	8.73	38.55	12.60	78.65	0.009	− 0.181
N. arctata albofasciata	10,761	39.07	8.33	39.86	12.72	78.93	− 0.010	− 0.208
L. dispar	11,236	33.22	11.26	44.62	10.90	77.84	− 0.146	0.016
G. menyuanensis	11,228	34.63	10.18	45.15	10.04	79.78	− 0.132	0.007
H. armigera	10,791	39.79	8.64	39.20	12.38	78.95	0.006	0.177
H. punctigera	10,788	39.84	8.53	39.58	12.04	79.42	0.003	0.170
H. zea	10,887	39.84	8.47	39.23	12.43	79.08	0.007	− 0.189
A. ipsilon	10,822	39.53	8.66	39.86	11.93	79.39	− 0.004	− 0.158
A. segetum	10,785	39.29	8.87	39.25	12.57	78.54	0.0004	0.172
S. litura	11,206	40.30	8.38	39.26	12.06	79.56	0.012	− 0.180
S. exigua	10,766	40.08	8.69	38.92	12.28	79.00	0.0146	− 0.171
C. agnata	10,782	38.81	8.58	40.60	11.99	79.41	− 0.022	− 0.165
C. limbirena	10,764	38.19	8.83	40.90	12.06	79.09	− 0.034	− 0.154
E. adulatricoides	10,800	39.25	8.82	39.74	12.18	78.99	− 0.006	− 0.159
S. inferens	10,905	39.35	8.50	38.96	13.17	78.31	0.005	− 0.215
N. pronuba	10,744	39.08	8.78	40.28	11.84	79.36	− 0.015	− 0.148
A. psi	10,725	40.22	8.86	36.69	14.20	76.91	0.045	− 0.231
Striacosta albicosta	11,210	39.46	8.79	37.99	13.76	77.46	0.019	− 0.220
M. separata	11,211	39.43	8.38	40.17	12.03	79.59	− 0.009	− 0.179
R. prominens	10,506	38.97	8.84	40.15	12.02	79.12	− 0.102	− 0.152
Catocala deuteronympha	10,884	38.80	8.23	40.28	12.66	79.08	− 0.187	− 0.212
Asota plana	10,626	39.18	8.59	38.78	13.43	77.96	0.005	− 0.219
tRNA								
E. phalonia	1462	40.90	8.27	40.49	10.32	81.39	0.005	− 0.110
P. flavescens	1485	41.62	7.81	40.61	9.97	82.22	0.012	− 0.121
O. lunifer	1666	41.78	7.33	39.86	11.04	81.63	0.023	− 0.202
H. cunea	1474	41.86	7.87	39.89	10.38	81.75	0.024	− 0.138
A. formosae	1466	40.45	7.98	40.24	11.32	80.69	0.002	− 0.173
Doa sp.	1456	41.55	8.17	39.62	10.64	81.18	0.023	− 0.131
N. arctata albofasciata	1440	40.90	8.05	40.48	10.55	81.38	0.005	− 0.134
L. dispar	1469	41.66	7.96	39.35	11.03	81.01	0.029	− 0.162
G. menyuanensis	1504	41.29	7.38	41.76	9.57	83.05	− 0.006	− 0.129
H. armigera	1471	41.40	8.15	40.38	10.06	81.78	0.012	− 0.104
H. punctigera	1478	41.67	8.18	40.18	9.94	81.85	0.018	− 0.097
H. zea	1475	41.49	8.13	40.20	10.16	81.69	0.015	− 0.111
A. ipsilon	1475	41.15	8.13	40.47	10.23	81.62	0.008	− 0.114
A. segetum	1471	40.72	8.22	40.85	10.19	81.57	− 0.001	− 0.107
S. litura	1473	42.23	7.94	39.58	10.25	81.81	0.032	− 0.127
S. exigua	1468	41.62	8.03	40.05	10.28	81.67	0.019	− 0.122
C. agnata	1472	41.10	8.22	40.28	10.39	81.38	0.010	− 0.116

(*continued on next page*)

Table 4 (*continued*)

Species	Size (bp)	A %	G%	T%	C%	A + T%	AT skew	GC skew
C. limbirena	1466	40.38	8.18	41.33	10.09	81.71	− 0.011	− 0.104
E. adulatricoides	1475	41.35	8.06	40.47	10.10	81.82	0.010	− 0.111
S. inferens	1478	40.86	8.25	40.66	10.21	81.52	0.002	− 0.106
N. pronuba	1468	40.53	8.51	40.66	10.28	81.19	0.001	− 0.094
A. psi	1402	42.22	7.98	39.37	8.27	81.59	0.034	− 0.131
Striacosta albicosta	1486	40.58	8.48	40.44	10.50	81.02	0.002	− 0.106
M. separata	1473	41.07	8.15	40.73	10.05	81.81	0.004	− 0.104
R. prominens	1464	40.77	8.26	41.12	9.83	81.89	− 0.004	− 0.086
Catocala deuteronympha	1478	41.27	7.84	40.52	10.35	81.79	0.009	− 0.137
Asota plana	1457	40.28	8.23	40.70	10.77	80.98	− 0.005	− 0.133
rRNA								
E. phalonia	2212	41.50	4.74	43.49	10.26	84.99	− 0.023	− 0.367
P. flavescens	2198	41.31	4.73	44.04	9.92	85.35	− 0.032	− 0.354
O. lunifer	2157	41.96	4.82	40.19	13.03	82.15	0.022	− 0.460
H. cunea	2234	42.08	4.92	42.75	10.25	84.83	− 0.008	− 0.351
A. formosae	2163	38.93	4.72	44.85	11.51	83.77	− 0.071	− 0.418
Doa sp.	2146	41.61	4.98	42.54	10.85	84.15	− 0.01	− 0.370
N. arctata albofasciata	2058	40.91	4.81	43.34	10.93	84.25	− 0.028	− 0.388
L. dispar	2150	42.79	4.79	41.81	10.60	84.60	0.012	− 0.377
G. menyuanensis	2311	4189	4.28	42.84	10.99	84.73	− 0.011	− 0.439
H. armigera	2155	41.62	4.91	43.34	10.11	84.96	− 0.020	− 0.345
H. punctigera	2161	41.87	4.81	43.35	9.94	85.22	− 0.017	− 0.347
H. zea	2184	41.57	4.85	43.77	9.79	85.34	− 0.025	− 0.337
A. ipsilon	2133	41.49	5.06	43.45	9.98	84.94	− 0.023	− 0.327
A. segetum	2155	41.48	4.91	43.57	10.02	85.05	− 0.024	− 0.341
S. litura	2218	42.65	4.73	42.34	10.28	84.99	0.004	− 0.370
S. exigua	2165	42.35	4.66	42.63	10.34	84.98	− 0.003	− 0.378
C. agnata	2156	39.93	5.10	44.57	10.38	84.50	− 0.054	− 0.341
C. limbirena	2089	39.39	5.12	45.28	10.19	84.67	− 0.069	− 0.331
E. adulatricoides	2169	41.53	4.97	42.87	10.60	84.40	− 0.015	− 0.360
S. inferens	2146	41.51	4.75	42.45	11.27	83.96	− 0.011	0.406
N. pronuba	2144	40.95	4.89	44.12	10.02	85.07	− 0.037	− 0.347
A. psi	2143	41.62	4.99	41.90	11.47	83.52	− 0.003	− 0.393
Striacosta albicosta	2147	42.06	4.84	41.92	11.18	83.98	0.002	− 0.396
M. separata	2198	41.31	4.73	44.04	9.92	85.35	− 0032	− 0.354
R. prominens	2178	42.51	4.77	42.88	9.82	85.39	− 0.004	− 0.345
Catocala deuteronympha	2193	40.08	4.69	44.64	10.57	84.72	− 0.053	− 0.385
Asota plana	2172	41.43	4.83	43.18	10.54	84.61	− 0.020	− 0.371
A + T-rich region								
E. phalonia	336	43.45	2.97	49.70	3.86	93.15	− 0.067	− 0.130
P. flavescens	541	42.14	2.22	49.72	5.91	91.86	− 0.083	− 0.454
O. lunifer	319	44.50	1.60	48.90	5.00	93.40	− 0.047	− 0.524
H. cunea	357	45.66	1.12	49.30	3.92	94.96	− 0.038	− 0.556
A. formosae	484	42.97	2.89	49.79	4.33	92.76	− 0.073	− 0.2
Doa sp.	332	43.07	0.60	53.61	2.71	96.68	− 0.109	− 0.636
N. arctata albofasciata	401	43.39	1.99	50.37	4.23	93.76	− 0.074	− 0.36
L. dispar	435	45.29	1.61	50.80	2.30	96.09	− 0.057	− 0.176
G. menyuanensis	449	43.65	2.45	49.67	4.23	93.32	− 0.065	− 0.266
H. armigera	329	44.37	1.21	50.75	3.64	95.12	− 0.067	− 0.5
H. punctigera	328	45.12	1.21	51.21	2.43	96.33	− 0.063	− 0.333
H. zea	329	45.28	1.21	51.06	2.43	96.35	− 0.059	− 0.033
A. ipsilon	344	46.22	1.45	48.83	3.48	95.05	− 0.027	0.411
A. segetum	345	46.08	0.86	48.40	4.63	94.48	− 0.024	− 0.684
S. litura	326	46.63	2.15	47.24	3.99	93.87	− 0.006	− 0.300
S. exigua	335	42.98	2.68	50.44	3.88	93.42	− 0.079	− 0.181
C. agnata	334	46.70	1.49	46.70	5.08	93.4	0	− 0.545
C. limbirena	422	46.91	2.36	46.20	4.50	93.11	0.007	− 0.473
E. adulatricoides	341	46.04	2.63	46.62	4.69	92.66	− 0.006	− 0.28
S. inferens	314	43.31	1.27	52.54	2.86	95.85	− 0.095	− 0.384
N. pronuba	330	44.24	2.12	49.09	4.54	93.33	− 0.051	− 0.363
A. psi	354	44.63	2.54	47.74	5.08	92.37	− 0.033	− 0.333
Striacosta albicosta	385	43.12	1.30	49.87	5.71	92.99	− 0.073	− 0.629
M. separata	372	44.62	2.42	49.73	3.23	94.35	− 0.054	− 0.143
R. prominens	343	44.02	2.33	49.59	1.11	93.58	− 0.059	0.333
Catocala deuteronympha	390	42.30	2.82	47.94	6.92	90.24	− 0.062	− 0.421
Asota plana	331	45.61	1.20	48.94	4.22	94.55	− 0.035	− 0.55

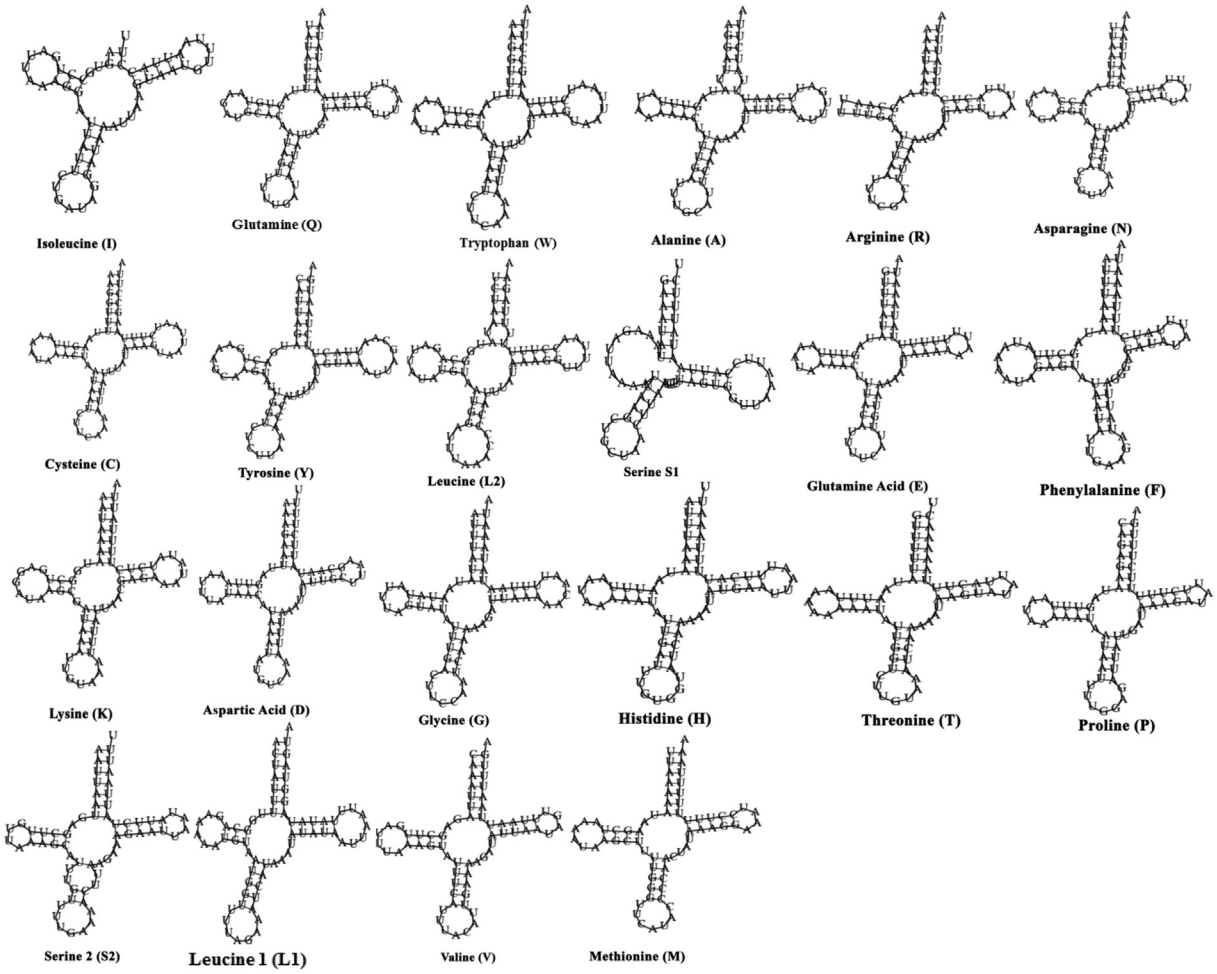


Fig. 2. Putative secondary structures of 22 tRNAs found in mitochondrial genome of *Eudocima phalonia*. The putative secondary structures were produced using MITOS online tool.

mismatches, 9 were U-G and 10 were G-U pairs, which formed a weak bond. The $tRNA^{Arg}$ gene contained a U-U mismatch. The mismatches were commonly located in the acceptor, DHU and anticodon arms, but $tRNA^{Ser1}$ gene showed the U-G mismatch on the TψC stem.

3.6. Ribosomal RNA genes

As in other insect mitogenomes, two rRNA genes (*rrnS* and *rrnL*) were found in *E. phalonia*. The *rrnL* was located between positions 12,673 and 14,153 with a total of 1391 bp in length. The total A + T content of the 2 rRNA genes was 84.39% as analysed in this study. The *rrnS* gene was located between positions 14,217 and 15,037 with 821 bp in length. The A + T content of the rrnS gene was 85.99%.

3.7. The A + T-rich region

The A + T-rich region of *E. phalonia* had 336 bp (position 15,041–15,376) with 93.15% AT and was positioned in the middle of the *rrnS* and *trnM* genes. The length of A + T-rich region of *E. phalonia* was higher than that of *H. zea* (329 bp), *H. punctigera* (326), *H. armigera* (327 bp), *C. agnata* (333 bp), *S. exigua* (335 bp), *S. litura* (325 bp), *A. segetum* (331 bp); it was shorter than that of *Thitarodes renzhiensis* (1366 bp), *Thitarodes yunnanensis* (977 bp), *Bombyx mandarina* (494), *A. pernyi* (552), and *B. mori* (496) *Catocala deuteronympha* (424 bp), *N. arctata albofasciata* (400 bp), *E. adulatricoides* (341 bp) and *M. separata* (372 bp). The A + T-rich region consisted of highest A + T content (93.15%) of the entire mitogenome of *E. phalonia*, which was within the range reported for other lepidopteran insects (Table 4). The A + T-rich region is commonly known to regulate transcription and replication in both vertebrate and invertebrate mitochondrial genomes [33]. Sequence analysis of the *E. phalonia* A + T-rich region revealed the presence of several conserved regions including two "ATAGA" motifs and a 19-bp poly-T stretch (from 15,065 bp to 15,083 bp) at the downstream of the *rrnS* gene. The poly-T stretch is commonly conserved in ditrysian lepidopteran mitochondrial genomes [20] and, has been represented as the origin of minority or light strand DNA replication [6]. Moreover, we have found microsatellite-like $(TA)_4$, $(TA)_6$ and two $(TA)_7$ elements within the A + T-rich region of the *E. phalonia* mitochondrial genome. The occurrence of multiple tandem repeat elements is a distinctive feature of the insect A + T-rich region. We have discovered three large, 40 bp tandem repeat and two 25 bp repeat elements in *E. phalonia* mitochondrial genome (Fig. 3). Similar observations were also reported

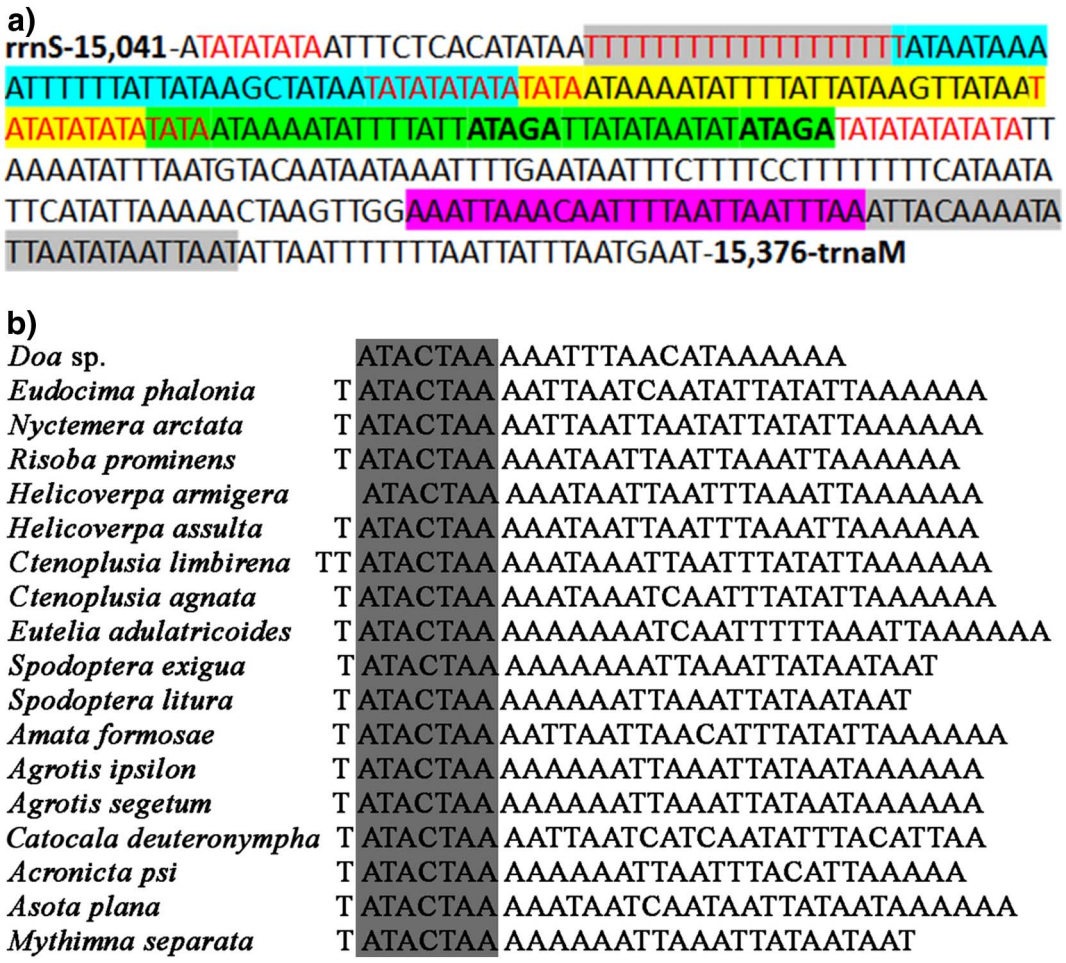


Fig. 3. a) Motifs and tandem repeats found in the A + T-rich region of *Eudocima phalonia* mitochondrial genome. These are indicated by specific colours and highlights. Two motifs (ATAGA) are shown in bold with green highlights. A 19 bp poly stretch (poly T) is shown in red colour with grey highlight. Microsatellites $((TA)_4$, $(TA)_6$, two $(TA)_7)$ are shown in red. Three 40 bp tandem repeats are shown in blue, yellow and green highlights. Two 25 bp tandem repeats are shown in violet and grey highlights.
b) Sequence alignment of the intergenic spacer region between *trnS2* (*TGA*) and *ND1* of 17 Noctuoidea moth species. The aligned nucleotides indicate the conserved motif 'ATACTAA'.

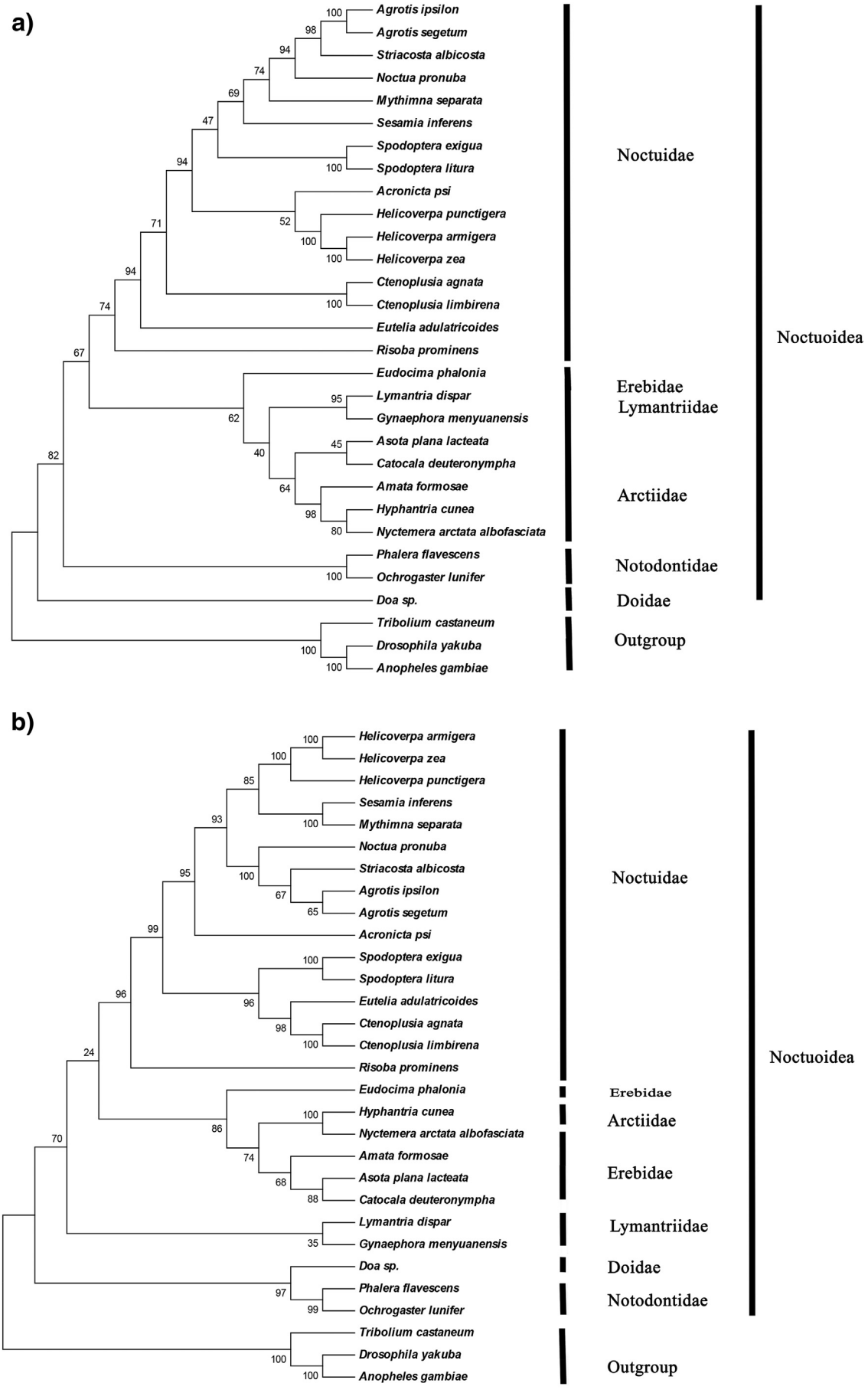
(Supplementary file 1) in other lepidopterans, even though the function of this region remains to be validated.

3.8. Phylogenetic analysis

A total of 27 moth species, representing seven Noctuoidea families (Notodontidae, Arctiidae, Doidae, Lymantriidae, Erebidae, Noctuidae and Euteliidae) were included for phylogenetic analysis. In this study, the phylogenetic trees were reconstructed using two datasets with maximum likelihood method (Fig. 4a, b). The results showed three major evolutionary groups; the first evolutionary group was family Notodontidae, which is a well-supported branch (BP ≥ 99). This evolutionary group consisted of two genera, *Phalera* and *Ochrogaster*. The second **evolutionary group** consisted of families Erebidae, Lymantriidae and Arctiidae with bootstrap proportion (BP ≥ 80). The third **evolutionary group** (BP ≥ 74) contained family Noctuidae as a pest group (Fig. 4a). This **evolutionary group** contained five subfamilies Noctuinae, Heliothinae, Hadeninae, Acronictinae and Plusiinae. Within the third **evolutionary group** subfamily Acronictinae was separated from subfamily Heliothinae with low bootstrap value (BP ≥ 42). The second and third **evolutionary groups** revealed that the superfamily Noctuoidea is a monophyletic group.

Mitogenomes have been used predominantly to analyse phylogeny and evolution. Not many mitochondrial genome sequences are available just now. At present there are only 27 species from superfamily Noctuoidea moths whose complete mitogenomes have been sequenced and deposited in Genbank.

The complete mitochondrial genome of *E. phalonia* with a circular molecule 15,575 bp was successfully determined; it is longer than those of *H. cunea* (15,481), *A. formosae* (14,463), *N. arctata albofasciata* (15,431), *H. armigera* (15,347), *H. punctigera* (15,382), *A. ipsilon* (15,377), *A. segetum* (15,378), *S. litura* (15,374), *S. exigua* (15,365), *C. agnata* (15,261), *C. limbirena* (15,306), *E. adulatricoides* (15,360), *S. inferens* (15,413), *N. pronuba* (15,315), *A. psi* (15,350), *M. separata* (15,329), *R. prominens* (15,343) and shorter than those of *Catocala deuteronympha* (15,671), *G. menyuanensis* (15,770), *P. flavescens* (15,659) and *O. lunifer* (15,593). The gene order and orientation of the mitochondrial genes of *E. phalonia* were similar to other lepidopteran moths. The position of *trnM* gene was found from 1 bp to 68 bp in other Noctuoid moths [9,19,20,22–29,34–37]. However, in *E. phalonia trnM*



(caption on next page)

Fig. 4. A) Phylogenetic tree of superfamily Noctuoidea moths. The phylogeny was reconstructed using 13 PCGs of the 27 species. B) The phylogeny was reconstructed using 13 PCGs of the 27 species plus 2 rRNAs.

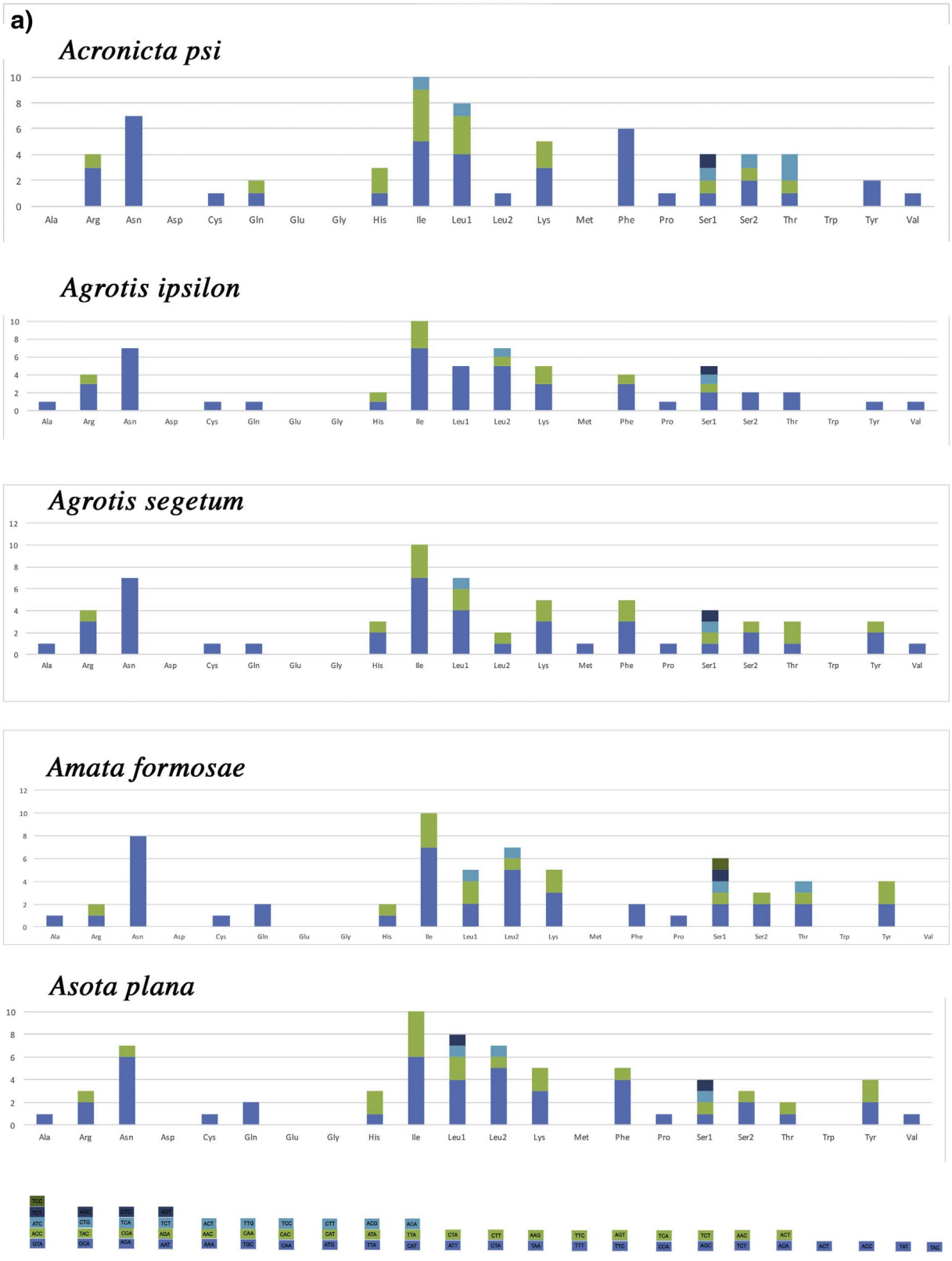


Fig. 5. Relative synonymous codon usage (RSCU) in Noctuoidea mtDNAs. The species name represents the superfamily Noctuoidea.

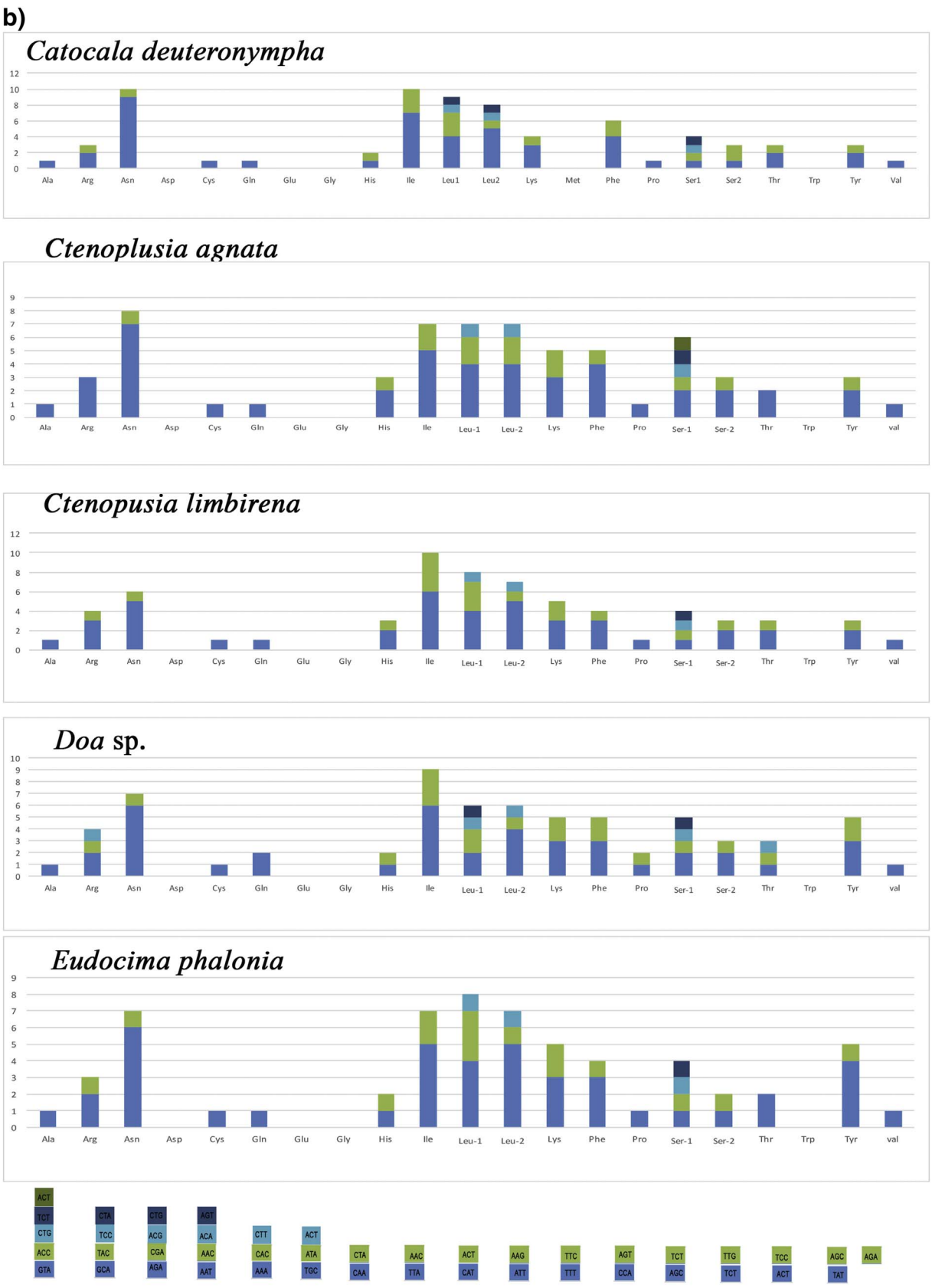


Fig. 5. (*continued*)

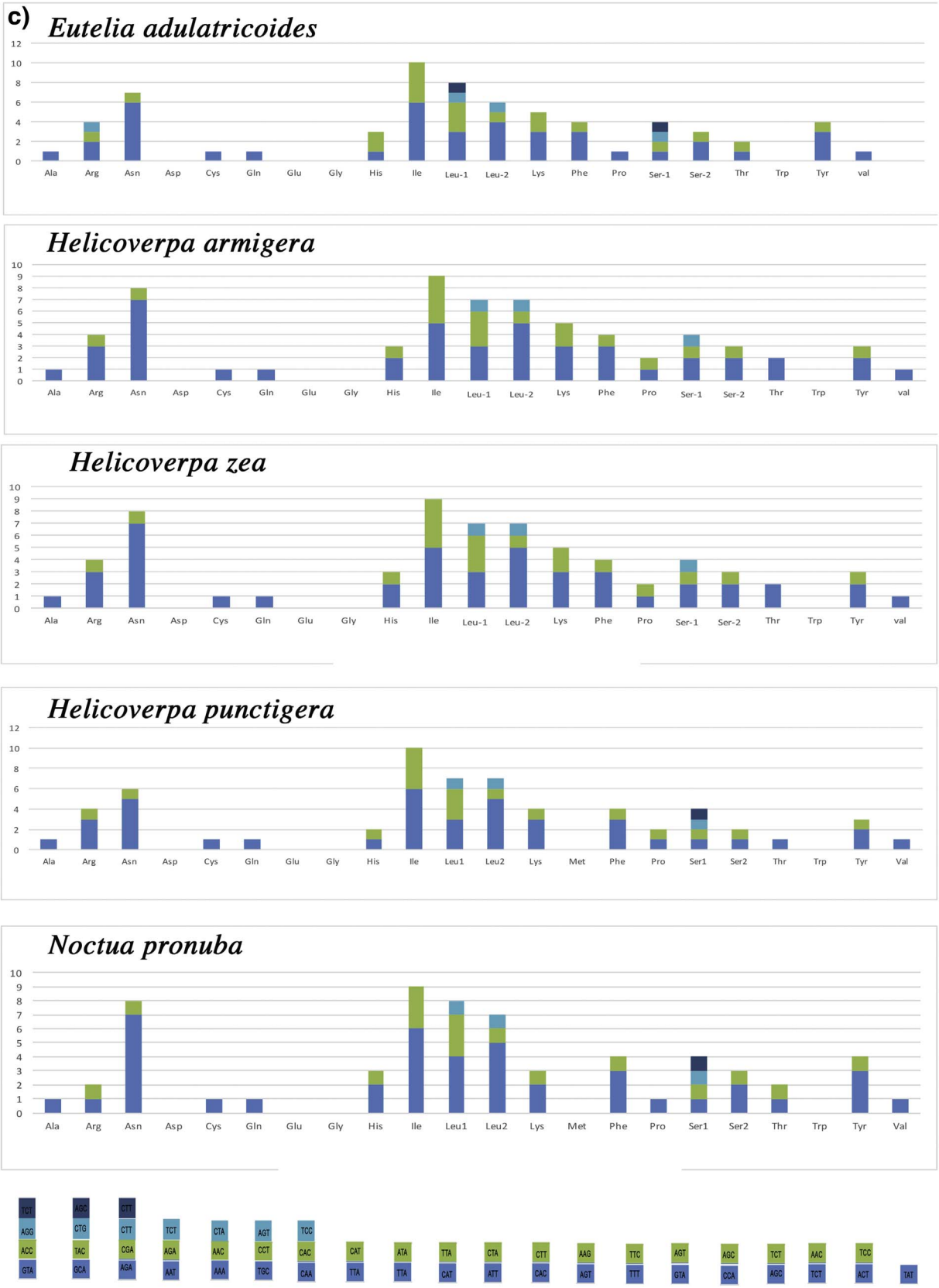


Fig. 5. (*continued*)

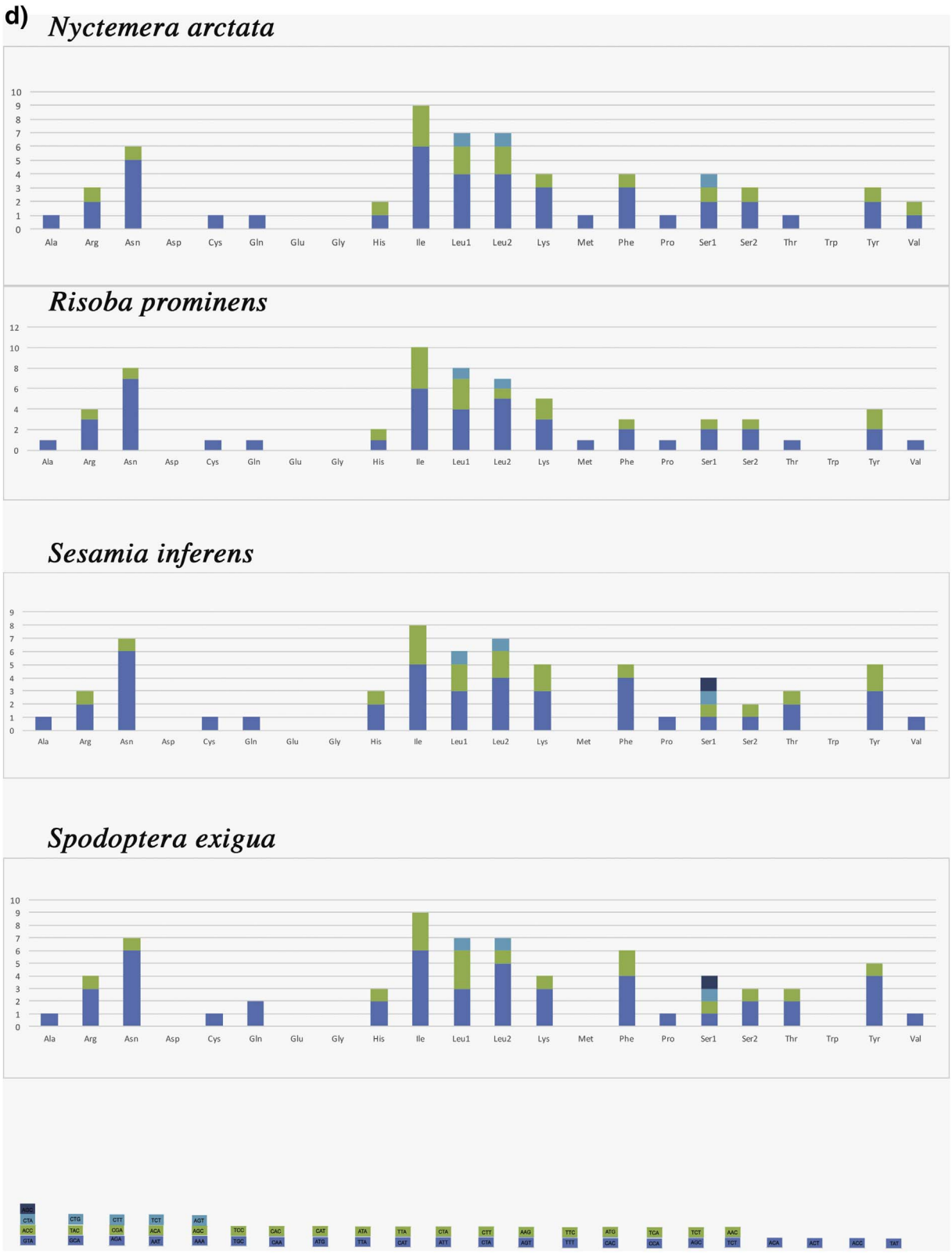


Fig. 5. (*continued*)

gene was found from 15,500 bp to 15,566 bp.

The A + T content of the *E. phalonia* was lower than the other Noctuoidea moths such as *H. punctigera*, *A. ipsilon*, *S. litura*, *C. agnata*, *N. pronuba* and *R. prominens*. These Noctuoid mitogenomes, including *E. phalonia*, present negative AT- and GC skew values.

The incomplete stop codon of a single T has been found in *E. phalonia* two PCG genes. The incomplete stop codon had been commonly found in numerous invertebrate mitochondrial genes [38,45,46]. The relative synonymous codon usage shows wide resemblance with other lepidopteran mitogenomes [28].

Complete mitochondrial genomes are effective markers for deep-level phylogenetic analysis in the Lepidoptera. In this study

Lymantriidae (*L. dispar and G. menyuanensis*), Arctiidae (*H. cunea* and *A. formosae*) and Erebidae (*E. phalonia*, *N. arctata albofasciata* and *Catocala deuteronympha*) were clustered in one node of the phylogenetic tree comprising Lymantriidae, Arctiidae and Quadrifine Noctuidae; these are consistent with the morphological data [39]. Sequencing and characterization of mitogenomes of more Noctuoid moths will help establish the deep level phylogeny of this particular superfamily.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gdata.2017.09.004.

Transparency document

The Transparency document associated with this article can be found, in online version.

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Declaration of interest

The authors declare that there is no conflict of interest.

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