Characterization and Phylogenetic Analysis of the Complete Mitochondrial Genome of *Laelia suffusa* (Lepidoptera: Erebidae, Lymantriinae)

**Jing Li,1,2 Qing Lv,1 Xiao-man Zhang,1 Hui-lin Han,2 and Ai-bing Zhang1,3**

1College of Life Sciences, Capital Normal University, Beijing 100048, P. R. China, 2School of Forestry, Northeast Forestry University, Harbin Heilongjiang 150040, P. R. China, and 3Corresponding author, e-mail: zhangab2008@cnu.edu.cn

Received 10 July 2020; Editorial decision 13 November 2020

**Abstract**

In this study, the complete mitochondrial genome of a white tussock moth, *Laelia suffusa* (Walker, 1855) (Lepidoptera: Erebidae, Lymantriinae), was sequenced and annotated. The genome sequence was 15,502 bp in length and comprised 13 PCGs, 2 rRNAs, 22 tRNAs, and a single noncoding control region (CR). The nucleotide composition of the genome was highly A + T biased, accounting for 79.04% of the whole genome and with a slightly positive AT skewness (0.015). Comparing the gene order with the basal species of Lepidoptera, a typical *trnM* rearrangement was detected in the mitogenome of *L. suffusa*. Besides, the *trnM* rearrangement was found at the head of *trnI* and *trnQ*, rather than at the back. The 13 PCGs used ATN as their start codons, except for the *cox1* which used CGA. Out of the 22 *tRNAs*, only 1 *tRNA* (*trnS1*) failed to fold in a typical cloverleaf secondary structure. The conserved motif ‘ATAGA + poly-T’ was detected at the start of the control region which was similar to other Lepidoptera species. In total, 10 overlapping regions and 19 intergenic spacers were identified, ranging from 1 to 41 and 2 to 73 bp, respectively. Phylogenetic analysis showed that Lymantriinae was a monophyletic group with a high support value and *L. suffusa* was closely related to tribe Orgyiini (Erebidae, Lymantriinae). Moreover, the phylogenetic relationship of Noctuoidea (Lepidoptera) species was reconstructed using two datasets (13 PCGs and 37 genes) and these supported the topology of (Notodontidae + (Erebidae + (Nolidae + (Euteliidae + Noctuidae)))).

**Key words:** *Laelia suffusa*, Lepidoptera, Erebidae, mitogenome, phylogeny

Lepidopteran, including moths and butterflies, are globally distributed phytophagous insects and one of the four largest holometabolous orders (Kristensen et al. 2007). More than 180,000 species of Lepidoptera are described and are only second in the class Insecta to Diptera (Scoble 1992, Pogue 2009, Mullen and Zaspel 2019). More than 180,000 species of Lepidoptera are described and are only second in the class *Insecta* (Kristensen et al. 2007). More than 180,000 species of Lepidoptera are described and are only second in the class *Insecta* (Kristensen et al. 2007). More than 180,000 species of Lepidoptera are described and are only second in the class *Insecta* (Kristensen et al. 2007). More than 180,000 species of Lepidoptera are described and are only second in the class *Insecta* (Kristensen et al. 2007). More than 180,000 species of Lepidoptera are described and are only second in the class *Insecta* (Kristensen et al. 2007).

*Laelia* (Lepidoptera: Erebidae, Lymantriinae) is a genus of tussock moths in the family Erebidae, whose distribution spans throughout Europe and Asia (Chao 1987, 2003). *Laelia suffusa* is a white tussock moth that is mainly distributed in the south and southeast of Asia (Chao 1987, Ahmed et al. 2002). Besides, it is regarded as one of the main pests of rice in Asia, it is important to identify its classification using molecular approaches. This information might provide further understanding of the origin and genetic differentiation with other Lepidoptera pests and a basis for biological pest control. Phylogenetic hypothesis of the superfamily Lepidoptera revealed that there were six strongly supported clades: Noctuidae, Erebidae, Notodontidae, Euteliidae, Nolidae, and Oenosandridae (Zahiri et al. 2011). Previously, Lymantriidae was considered as a family-level classification unit, however, based on morphological and molecular evidence, it was classified as a subfamily of Erebidae (Mitter et al. 2017, Regier et al. 2017). However, the phylogenetic relationships have focused on species diversity (Fox 2013, Ju et al. 2016, Singh and Navkiran 2019, Zhang et al. 2019), pest control (Li and Yan 1991, Armstrong et al. 2003, Yu et al. 2019, Sun et al. 2020), species identification and genetic variations (Singh and Navkiran 2019), and insect physiological adaption (Zapletalová et al. 2016) of *Laelia*. However, very limited research has been conducted on the phylogenetic relationship of genus *Laelia*. Considering that *L. suffusa* is an important pest of rice in Asia, it is important to identify its classification using molecular approaches. This information might provide further understanding of the origin and genetic differentiation with other Lepidoptera pests and a basis for biological pest control.
within Lymantriinae are still under active debate. Initially, it was believed that five tribes were included in the subfamily Lymantriinae: Arctornithini, Lymantriini, Leucomiini, Nygmiiini, and Orgyiini (Zahiri et al. 2011, Zahiri et al. 2012, Wang et al. 2015). However, based on the phylogenetic analysis using several mitochondrial and nuclear genes, the phylogenetic relationship within Lymantriinae could be illustrated as follows: Arctornithini was a sister group to Orgyiini + Nygmiiini together with Lymantriini + Leucomiini (Zahiri et al. 2011, 2012; Wang et al. 2015). However, the phylogenetic relationship based on various molecular markers and taxonomy has often been found to be conflicting, leading to a serious debate on their relative positions (Fibiger and Lafontaine 2005, Mitchell et al. 2006).

Owing to some unique features as maternal inheritance, rapid mutation rate, and limited recombination compared with nuclear genes, mitochondrial DNA markers, and mitogenome have been extensively used in phylogenetic analysis, comparative genomics studies, and species identification (Avise 2009, Cameron, 2014, Qin et al. 2019, Tyagi et al. 2020). The insect mitogenome has a relatively stable structure that encodes 37 genes and a noncoding control region scattered on the circular DNA molecule and with a length of 15,000–18,000. The 37 genes generally include 13 protein-coding genes (PCGs): cytochrome c oxidase genes (cox1, cox2, and cox3), NADH dehydrogenase genes (nad1, nad2, nad3, nad4, nad4L, nad5, and nad6), cytochrome B genes (cytb), ATPase genes (atp6 and atp8), 22 transfer RNA genes (tRNAs), and 2 ribosomal RNA genes (rRNAs, rrlL and rrlS). Besides, a large noncoding region controls replication and transcription (CR region, also named A + T-rich region; Wolstenholme 1992, Ballard and Whirlock 2004, da Fonseca et al. 2008, Cameron 2014). Compared with the single molecular markers from plastids and the nuclear genome, mitogenome can provide information on evolutionary and speciation events required in insect phylogenetic studies (Boore 2006, Qin et al. 2019). Recently, the rapid development of sequencing technologies such as the next-generation sequencing technology has triggered an increase in the available mitochondrial genome data (Cameron 2014).

In this study, the complete mitogenome of *L. suffusa* was sequenced, annotated, and characterized. Using the newly sequenced mitogenome, phylogenetic relationships of Noctuoidea were reconstructed using the 13 PCGs and whole genomes. The mitogenome of *L. suffusa* provided information for future research on species identification, diversity conservation, and population genetics of Erebidae and Noctuoidea.

### Materials and Methods

#### Sampling and DNA Extraction

The specimens of *L. suffusa* were collected from Mt. Luofu, Guangdong Province, P. R. China, and identified based on morphological characteristics. All the collected samples were preserved in 95% ethanol in the field and stored at −20°C. Total genomic DNA was extracted from the leg muscle tissue using the Genomic DNA Extraction Kit (QIAGEN, Hilden, Germany) following the manufacturer’s instructions.

#### Mitogenome Sequencing, Assembly

The purified DNA samples were used to prepare an Illumina TruSeq library and sequenced on the Illumina HiSeq2500 platform. The sequencing platform generated a total of 15-Gb paired-end reads of 150-bp length. Trimmomatic software was used to read trimming the adapters (Fragkostefanakis et al. 2012, Bolger et al. 2014). NGSQC-Toolkit v2.3.336 software and Prinseq were used to conduct rapid quality control of the raw reads. Low quality (ambiguous bases) and short reads (shorter than 95 bp) were filtered during quality control (Schneider and Edwards 2011). Finally, high-quality reads not less than 8 Gb were adopted in the de novo assembly and annotation using MitoZ software (Meng et al. 2019). Sequences from the cox1, cytb and rrlS fragments of *L. suffusa* were used as checkout markers for mitogenome assemblies and they were amplified and sequenced using PCR and Sanger sequencing, respectively.

#### Mitogenome Analysis

MEGA v8.0 was used to analyze the base composition and codon usage of the *L. suffusa* mitogenome (Kumar et al. 2016). Besides, the start and stop codons of the protein-coding genes were identified and validated by comparing with mitogenomes of other Erebidae species. tRNAscan-SE v1.21 software was used to predict the secondary structures of the 22 rRNA genes (Lowe and Chan 2016). The AT and GC asymmetry were represented by the values of AT-skew and GC-skew, calculated as follows: AT-skew = (A−T)/(A+T) and GC skew = (G−C)/(G+C) (Perna and Kocher 1995). The Tandem Repeats Finder program was used to predict the tandem repeats of the control region using the default parameters (Benson 1999).

#### Phylogenetic Analysis

The phylogenetic tree of 52 lepidopteran species (25 species of Erebidae, 19 species of Noctuidae, 2 species of Nolidae, 3 species of Notodontidae, single species of Euteliidae, and 2 outgroups) was reconstructed to confirm the phylogenetic position of the genus *Laelia* within the superfamily Noctuoidea (Table 1). We aligned nucleotide sequences of the 13 PCGs with MAFFT. The nonprotein coding regions were aligned using MUSCLE and default parameters were used (Edgar 2004). SequenceMatrix was used to concatenate the separated genes and partitions (Vaidya et al. 2011). The concatenated sets of nucleotides were organized into two datasets: one dataset included the 13 PCGs while the other represented all the 37 genes (13 PCGs, 22 rRNAs, and 2 rRNA). DAMBE was used to examine the substitution saturations of the two datasets (Xia and Xie 2001). Both datasets were used to perform phylogenetic analyses using maximum likelihood (ML) and Bayesian inference (BI) (Ronquist and Huelsenbeck 2003). ML and BI analyses were performed using RAxML v7.9.6 and MrBayes v 3.2.2, respectively (Stamatakis 2006, Ronquist et al. 2012). The GTR+G+I model was selected in the two datasets and 1,000 bootstrap replicates were used (Rambaut 2014).

#### Result

### Genome Organization and Base Composition

The *L. suffusa* mitogenome was a typical circular DNA molecule of 15,502 bp in length (GenBank MN908152; Table 1; Fig. 1). The newly sequenced mitogenome coded the 37 genes, 13 PCGs, 22 tRNAs, and 2 rRNAs (small ribosomal RNA [rrnS] and large ribosomal RNA [rrnL]), and the A+T-rich noncoding region (Table 2). In total, 23 genes (9 PCGs and 14 tRNAs) were transcribed on the major strand (J-strand) and the remaining 14 genes were transcribed on the minor strand (N-strand). There were 9 genes overlapping...
Table 1. Taxonomy, GenBank accession numbers, mitogenome sizes, and related information of 52 moths mitochondrial genomes used for the phylogenetic analysis

| Superfamily | Family     | Subfamily     | Species                          | GBAN         | Length | A+T% | AT-skew | GC-skew |
|------------|------------|---------------|---------------------------------|--------------|--------|------|---------|---------|
| Noctuoidea | Erebidae   | Lymantriinae  | Noctuoidea Erebidae Lymantriinae |              |        |      |         |         |
|            |            |               | Noctuidae Noctuinae              |              |        |      |         |         |
|            |            |               | Heliothinae                      |              |        |      |         |         |
|            |            |               | Plusinae                         |              |        |      |         |         |
|            |            |               | Acroctinae                       |              |        |      |         |         |
|            |            |               | Euteliidae                       |              |        |      |         |         |
|            |            |               | Nolidae Chlophorinidae           |              |        |      |         |         |
|            |            |               | Notodontidae Pygaerinae Phalerinae |              |        |      |         |         |
|            |            |               | Thaumetiopoeinae                 |              |        |      |         |         |
|            |            |               | Pyraloidea Crambidae Torricoidae |              |        |      |         |         |
|            |            |               |                                  |              |        |      |         |         |

Note: Nyctemera arctica albofasciata was used in sequence of KJ173908, which was modified to Nyctemera albofasciata according to subsequent revision of species list. Similarly, Heliothis subflexa of KT98688 was amended to Chloridea subflexa, and Lachana alpheraki was modified to Dasorgia alpheraki. The species in bold was first sequenced in this study.

regions and 19 noncoding regions in the mitogenome of *L. suffusa*. Besides the control region, the largest noncoding region was located between gene *trnQ* and *nad2*, which was 73 bp in length (Table 2). The gene order of the genome was identical to that previously published of Lymantriidae mitogenome sequences (Fig. 2).

The nucleotide composition of the *L. suffusa* sequence was highly A + T biased: A = 6,218 (40.11%), G = 1,147 (7.40%), T = 6,035 (38.93%), and C = 2,102 (13.56%) (Table 3). Furthermore, the mitogenome showed a slightly positive AT-skew (0.015), illustrating there were more As than Ts. The GC-skew was negative.
(−0.294), declaring a higher frequency of base C than G when compared with other species of Noctuoidea (Table 1).

Gene rearrangement was detected in *L. suffusa* mitogenome compared with species from Hepialoidea and Nepticuloidea. In *L. suffusa* mitogenome, the control region gene order was trnM, trnI, and trnQ, which was different from the basal lepidopteran species (such as *Stigmella roborella*, *Abamus yunnanensis*, and *Thitarodes gonggaensis*) (Fig. 2).

Protein-Coding Genes and Codon Usage

The 13 PCGs were 11,295 bp in length, accounting for 72.86% of the complete *L. suffusa* mitogenome. Nine out of the 13 PCGs (*cox1*, *cox2*, *cox3*, *nad2*, *nad3*, *nad6*, *atp6*, *atp8*, and *cytb*) were scattered on the major strand, whereas four genes (*nad1*, *nad4*, *nad4l*, and *nad5*) were on the minor strand. The start and stop codons of all PCGs are shown in Table 2. The standard ATN start codon was used for most of the PCGs such as ATT for *nad1*, *nad2*, ATG for *cox3*, *nad4*, *nad4l*, *nad6*, *atp6*, *cytb*, and ATA for *cox2*, *nad3*, *nad5*, *atp8*. The only exception was in *cox1* which had CGA (arginine). Three out of the 13 PCGs used incomplete stop codons (T for *cox1*, *cox2*, and TA for *nad4*), and only *nad4* used incomplete termination codon (TA), whereas others used the typical stop codon (TAA).

The average A + T content of the 13 PCGs was 76.88%, and the AT-skew was negative (−0.139), indicating more Ts than As (Table 3). The relative synonymous codon usage of *L. suffusa* was tested based on the 3,605 codons in 13 PCGs, and only codons ACG, UAA, and UAG were not presented (Table 4). The codon usage analysis demonstrated that isoleucine (I; Ile; 11.26%), leucine 2 (L; Leu2; 11.15%), phenylalanine (F; Phe; 8.21%), methionine (M; Met; 6.77%), and asparagine (N; Asn; 5.46%) were the
### Table 2. Annotation and gene organization of the *Laelia suffusa* mitogenome

| Gene       | Strand | Nucleotide number | Size (bp) | Intergenic nucleotides | Anticodon | Start codon | Stop codon |
|------------|--------|-------------------|----------|------------------------|-----------|-------------|------------|
| trnM       | J      | 1–67              | 67       | 4                      | CAU       | –           | –          |
| trnI       | J      | 72–137            | 66       | –3                     | GAU       | –           | –          |
| trnQ       | N      | 135–203           | 69       | 73                     | UUG       | –           | –          |
| nad2       | J      | 277–1,290         | 1014     | ±2                     | –         | ATT         | TAA        |
| trnW       | J      | 1,289–1,354       | 66       | –8                     | UCA       | –           | –          |
| trnC       | N      | 1,347–1,411       | 65       | 6                      | GCA       | –           | –          |
| trnY       | N      | 1,418–1,482       | 65       | –11                    | GUA       | –           | –          |
| cox1       | J      | 1,442–3,020       | 1579     | –                      | –         | CGA         | T          |
| trnL2(UUR) | J      | 3,016–3,082       | 702      | 16                     | UAA       | –           | –          |
| cox2       | J      | 3,083–3,748       | 702      | –                      | UAA       | –           | –          |
| trnK       | J      | 3,765–3,835       | 71       | –1                     | CUU       | –           | –          |
| trnD       | J      | 3,835–3,902       | 68       | 0                      | GUC       | –           | –          |
| atp8       | J      | 3,903–4,067       | 165      | –7                     | –         | ATA         | TAA        |
| atp6       | J      | 4,061–4,738       | 678      | 4                      | –         | ATG         | TAA        |
| cox3       | J      | 4,743–5,531       | 799      | 2                      | ATG       | –           | TAA        |
| trnG       | J      | 5,534–5,601       | 68       | 0                      | UCC       | –           | –          |
| nad3       | J      | 5,602–5,955       | 354      | 14                     | –         | UAA         | TAA        |
| trnA       | J      | 5,970–6,035       | 66       | 12                     | UGC       | –           | –          |
| trnR       | J      | 6,048–6,112       | 65       | 5                      | UGC       | –           | TAA        |
| trnN       | J      | 6,118–6,182       | 65       | 10                     | GUU       | –           | TAA        |
| trnS1(AGN) | J      | 6,193–6,259       | 65       | 5                      | GCU       | –           | TAA        |
| trnE       | J      | 6,265–6,333       | 69       | 6                      | UUC       | –           | TAA        |
| trnF       | N      | 6,340–6,406       | 67       | –20                    | GAA       | –           | TAA        |
| nad5       | N      | 6,387–8,147       | 1761     | 0                      | ATA       | –           | TAA        |
| trnH       | N      | 8,148–8,215       | 68       | –1                     | GUG       | –           | TAA        |
| nad4       | N      | 8,215–9,557       | 1343     | 14                     | –         | ATG         | TA         |
| nad4l      | N      | 9,572–9,859       | 288      | 6                      | –         | ATG         | TAA        |
| trnT       | J      | 9,866–9,929       | 64       | 0                      | UGU       | –           | TAA        |
| trnP       | N      | 9,930–9,994       | 65       | 4                      | UGG       | –           | TAA        |
| nad6       | J      | 9,999–10,529      | 531      | 7                      | ATG       | –           | TAA        |
| cytB       | J      | 10,537–11,688     | 1152     | 7                      | ATG       | –           | TAA        |
| trnS2(UCN) | J      | 11,696–11,760     | 65       | 19                     | UGA       | –           | TAA        |
| nad1       | N      | 11,780–12,718     | 939      | 0                      | ATT       | –           | TAA        |
| trnL1(CUN) | N      | 12,719–12,787     | 69       | –21                    | UAG       | –           | TAA        |
| rrsL       | N      | 12,767–14,157     | 1391     | 0                      | UAC       | –           | TAA        |
| trnV       | N      | 14,158–14,225     | 68       | –1                     | UAC       | –           | TAA        |
| trnS       | N      | 14,225–15,022     | 798      | 0                      | UAC       | –           | TAA        |
| A + T-rich |        | 15,023–15,502     | 480      |                        |           |             |            |

Strand of the genes is presented as J for majority and N for minority strand. IN, negative numbers indicate that adjacent genes overlap, positive numbers indicate intergenic sequences.

---

**Fig. 2.** The gene order of *Laelia suffusa* mitogenome and other 13 lepidopteran species.
most frequently used, whereas cysteine (C; Cys; 0.78%) was the least used (Figs. 3 and 4, Table 4). Codon distribution was consistent with other lepidopteran insects mitogenome.

Transfer RNAs and ribosomal RNAs
The L. suffusa mitogenome contained 22 tRNA genes that were scattered throughout the entire genome. The tRNA length varied from 64 bp (trnT) to 71 bp (trnK), and this was consistent with previously reported Lepidoptera mitogenomes. In total, 14 tRNAs were encoded on the major chain and the rests were on the minor chain. The combined sequence of the 22 tRNAs was 1,470 bp, and the A + T content was 81.43% with a positive AT-skew and negative GC-skew. The A + T content of the two rRNAs genes was slightly higher than that in tRNAs, accounting for 83.69% of the total 2,189-bp sequence (Table 3).

In total, 3,605 codons were analyzed. RSCU stands for relative synonymous codon usage. * stands for termination codon. The codons in bold were the most commonly used in the mitogenome of L. suffusa.

Table 3. Base composition and skewness of the Laelia suffusa mitogenome

|                | Size (bp) | A (bp) | G (bp) | T (bp) | C (bp) | A%  | G%  | T%  | C%  | A+T% | AT-Skew | GC-Skew |
|----------------|-----------|--------|--------|--------|--------|-----|-----|-----|-----|------|---------|---------|
| Whole genome   | 15,502    | 6,218  | 1,147  | 6,035  | 2,102  | 40.11| 7.40| 38.93| 13.56| 79.04| 0.015   | −0.294  |
| PCGs           | 11,295    | 3,739  | 1,307  | 4,945  | 1,304  | 33.10| 10.57| 43.78| 11.54| 76.88| −0.139  | 0.001   |
| tRNA genes     | 1,470     | 612    | 160    | 585    | 113    | 41.63| 10.88| 39.80| 7.69 | 81.43| 0.023   | 0.172   |
| rRNA genes     | 2,189     | 912    | 254    | 920    | 103    | 41.66| 11.60| 42.03| 4.71 | 83.69| −0.004  | 0.422   |
| Control region | 480       | 203    | 17     | 223    | 37     | 42.29| 3.54| 46.46| 7.71 | 88.75| −0.047  | −0.370  |

Table 4. Codon usage of the protein-coding genes in Laelia suffusa

| Codon (aa) | n   | %    | RSCU | Codon (aa) | n   | %    | RSCU |
|------------|-----|------|------|------------|-----|------|------|
| UUU (F)    | 296 | 8.21 | 1.75 | UAU (Y)    | 155 | 4.30 | 1.72 |
| UUC (F)    | 47  | 1.30 | 0.83 | CAU (H)    | 45  | 1.25 | 1.30 |
| UUA (L)    | 402 | 11.15| 4.56 | CUA (L)    | 33  | 0.92 | 0.37 |
| UUG (L)    | 36  | 1.00 | 0.41 | CUG (L)    | 3   | 0.08 | 0.03 |
| CUU (L)    | 47  | 1.30 | 0.53 | CAG (Q)    | 5   | 0.14 | 0.17 |
| CUC (L)    | 8   | 0.22 | 0.09 | CAA (Q)    | 54  | 1.50 | 1.83 |
| CUA (L)    | 33  | 0.92 | 0.37 | CAG (Q)    | 5   | 0.14 | 0.17 |
| CUG (L)    | 3   | 0.08 | 0.03 | CAG (Q)    | 5   | 0.14 | 0.17 |
| AUU (I)    | 406 | 11.26| 1.77 | AAU (N)    | 197 | 5.46 | 1.63 |
| AUC (I)    | 39  | 1.08 | 0.17 | AAC (N)    | 45  | 1.25 | 0.37 |
| AUA (M)    | 244 | 6.77 | 1.06 | AAA (K)    | 78  | 2.16 | 1.70 |
| AUG (M)    | 74  | 2.05 | 1.89 | GUA (D)    | 58  | 1.64 | 1.84 |
| GUU (V)    | 69  | 1.91 | 1.76 | GAA (E)    | 60  | 1.66 | 1.64 |
| GUG (V)    | 12  | 0.33 | 0.31 | GAG (E)    | 13  | 0.36 | 0.36 |
| UCU (S)    | 91  | 2.52 | 2.37 | UGU (C)    | 24  | 0.67 | 1.71 |
| UCC (S)    | 17  | 0.47 | 0.44 | UGC (C)    | 4   | 0.11 | 0.29 |
| UCA (S)    | 83  | 2.30 | 2.17 | UGA (W)    | 85  | 2.36 | 3.00 |
| UCG (S)    | 2   | 0.06 | 0.05 | UGG (W)    | 9   | 0.25 | 1.00 |
| CCU (P)    | 63  | 1.75 | 2.03 | CGU (R)    | 16  | 0.44 | 0.71 |
| CCC (P)    | 26  | 0.72 | 0.84 | CGC (R)    | 2   | 0.06 | 0.09 |
| CCA (P)    | 33  | 0.92 | 1.06 | CGA (R)    | 32  | 0.89 | 1.41 |
| CCG (P)    | 2   | 0.06 | 0.06 | CGG (R)    | 2   | 0.06 | 0.09 |
| ACU (T)    | 77  | 2.14 | 2.04 | AGU (S)    | 36  | 1.00 | 0.94 |
| ACC (T)    | 20  | 0.55 | 0.53 | AGC (S)    | 1   | 0.03 | 0.03 |
| ACA (T)    | 54  | 1.50 | 1.43 | AGA (S)    | 83  | 2.30 | 3.66 |
| ACG (T)    | 0   | 0.00 | 0.00 | AAG (S)    | 1   | 0.03 | 0.04 |
| GCC (A)    | 72  | 2.00 | 2.34 | GGU (G)    | 49  | 1.36 | 0.97 |
| GGC (A)    | 11  | 0.31 | 0.36 | GGC (G)    | 5   | 0.14 | 0.10 |
| GCA (A)    | 36  | 1.00 | 1.47 | GGA (G)    | 110 | 3.05 | 2.17 |
| GCG (A)    | 4   | 0.11 | 0.13 | GGG (G)    | 39  | 1.08 | 0.77 |

Almost all of the 22 tRNAs formed the typical clover-leaf secondary structures, except for the trnS1(AGN) (Fig. 5). The dihydouridine (DHU) arm of trnS1 formed a loop instead of a couple of paired bases. The amino acid acceptor (AA) arm length of the tRNAs was unified (7 bp). Almost all the 22 tRNAs formed the typical clover-leaf secondary structures, except for the trnS1(AGN) (Fig. 5). The dihydouridine (DHU) arm of trnS1 formed a loop instead of a couple of paired bases. The amino acid acceptor (AA) arm length of the tRNAs was unified (7 bp). Several anticodons (AC) loops comprised of six nucleotides except for five tRNAs (trnC, trnl, trnk, trnR, and trnN) whose AA stem was 7 bp, as well as trnS1(AGN) with eight nucleotides. The TΨC (T) length and its arm ranged from 2 to 9 bp and 4 to 5 bp, respectively. The DHU stem length varied from 3 to 4 bp except in trnS1(AGN) with 2 to 8 bp. The AC arms were all 5 bp except for trnL2(UUR) whose AC stem was 4 bp.

Both rRNA genes were encoded on the N strand. The large ribosomal RNA (rrnL), with a length of 1,391 bp was located between trnL1 and trnV, whereas the small ribosomal RNA (rrnS), with a
Fig. 3. The relative synonymous codon usage in the mitogenome of *Laelia suffusa*. Codon families are provided on the X-axis.

Fig. 4. Codon distribution in *Laelia suffusa* mitogenome. Numbers to the left refer to the total number of the codon. Codon families are provided on the X-axis.
length of 798 bp, was located between trnV and the control region (Table 2). The rrnL and rrnS showed significant high A+T content (83.03 and 84.84%, respectively) bias; however, the AT-skew was different (−0.020 and 0.022).

Overlapping and Noncoding Regions
In total, 10 overlapping regions were detected in the L. suffusa mitogenome which varied between 1 and 41 bp. The longest overlapping region was 41 bp, located between the trnY and cox1 (Table 2). There were 19 intergenic spacers scattered throughout the L. suffusa mitogenome and ranging from 2 to 73 bp. The longest spacer region was detected to be located between gene trnQ and nad2, which was an A + T-rich region.

The control region (A + T-rich region) of L. suffusa located between the rrnS and trnM genes was the longest noncoding region (480 bp) in the entire mitogenome (Fig. 1, Table 2). This highest AT content (88.75%) was also found in this region, with a negative AT-skew (−0.047) and GC-skew (−0.370). In the L. suffusa mitogenome, an ATAGA motif close to gene rrnS was also detected and found to be a conserved feature of lepidopteran’s mitogenomes.
An 18-bp poly-T stretch following the ATAGA motif and a 12-bp poly-A string followed by trnM were reported. Three microsatellite-like repetitive elements were also found (Fig. 6).

Phylogenetic Analyses
The phylogenetic relationships among the 52 Lepidoptera species (Table 1) were reconstructed based on the two nucleotide sequences (13 PCGs and 37 genes) datasets using the Maximum Likelihood (ML) and Bayesian Inference (BI) approaches. Besides, Chilo suppressalis and Adoxophyes homnai, which belong to Pyraloidea and Tortricoidea, respectively, were used as outgroups. All the other 50 species were from Noctuoidea. Phylogenetic analysis based on different algorithms (ML and BI analysis) showed approximately identical topologies. Phylogenetic relationships based on the two nucleotide datasets are shown in Figs. 7 and 8. Noctuoidea species were clustered into five families (Erebidae, Noctuidae, Euteliidae, Nolidae, and Notodontidae). The monophyly of Erebidae was well supported based on the topology of the phylogenetic tree. Within the Erebidae, the subfamilies Lymantriinae, Arctinae, and Erebidinae were also monophyletic (Figs. 7 and 8). The phylogenetic relationships obtained were based on the two datasets (13 PCGs and 37 genes) and they were found to be consistent within the Noctuidae. All of the four families (Plusiinae, Heliothinae, Noctuinae, and Acronictinae) in Noctuidae were all monophyletic clades.

Besides the phylogenetic relationships among the Noctuoidea families were reconstructed, the results revealed three main clades in Lymantriinae: Nygmiini + (Lymantriini + Orgyiini). Laelia suffusa, Dasorgyia alpakensis, and seven species of Gynaephora clustered in one lineage, which supported that L. suffusa belongs to Orgyiini. Moreover, there was no clear threshold between Gynaephora and Dasorgyia due to the mixture of the two genera. Within the Lymantriinae, Orgyiini was the most closely related to Lymantriini, and Nygmiini was a sister group. Further, among these subfamilies, Hypeninae was closely related to Lymantriinae even though the support was not very strong.

Discussion
Among the 13 species of the Lymantriinae subfamily, the L. suffusa mitogenome length (15,502 bp) was slightly smaller than the others, except for E. pseudoconspersa (15,461 bp) and E. similis (15,437 bp). The difference was attributed to the variable sequences in the noncoding regions and the control region (CR) (Rand 1993, McKnight and Shafer 1997). Moreover, the positive AT-skew (0.015) was associated with a higher frequency of guanine compared with thymine, which is a common phenomenon in Noctuoidea mitogenomes.

Gene rearrangement was also detected in L. suffusa when compared with the basal taxon of Lepidoptera, such as Hepialoidea and Nepticuloidea (Fig. 2). In lepidopteran mitogenomes, gene rearrangement mainly occurred in three tRNA genes: trnM, trnI, trnQ (Timmermans and Vogler 2012), as identified in the L. suffusa mitogenome. Only two mitogenomes from Nepticuloidea were chosen for the gene rearrangement analysis, and the results were

![Fig. 6. Features present in the AT-rich region of the Laelia suffusa mitogenome. Colored nucleotides indicate the ATATA motif (yellow), the poly-T stretch (green) and microsatellite AT repeat sequences were underlined. Three tandem repeats are indicated in different colors.](image)

![Fig. 7. Phylogenetic tree inferred from nucleotide sequences of 13 PCGs of using the ML and BI analysis. Numbers on the branches are ML bootstrap support and BI posterior probability.](image)
inconsistent. Astrotischeria sp. showed a similar pattern of L. suffusa. However, Thitarodes gonggaensis (The other species chosen from Nepticuloidea) shared similar gene order with Hepialoidea, which was considered to be the ancestral pattern (CR-trnI-trnQ-trnM) (Fig. 2; Zhu et al. 2017, Yang et al. 2019). Based on the phylogenetic results of Mitter et al. (2017), this gene rearrangement likely occurred after the diverging of Hepialoidea superfamily from other lepidopteran lineages. Many models and hypotheses have been used to explain the mitogenome gene rearrangement, such as the tandem duplication-random loss (TDRL) model (Boore 2000), the duplication-nonrandom loss model (Lavrov et al. 2002), and the recombination (Cantatore et al. 1987) and illicit priming of replication by tRNA genes (Dowton et al. 2009). The gene rearrangement of L. suffusa mitogenome can be well explained by a combination of the TDRL model and recombination.

The AT-skew value of the 13 PCGs was −0.139 in the L. suffusa mitogenome was lower than that reported in previously sequenced Lymantriinae mitogenomes. Meanwhile, the slightly positive GC-skew of 0.001 was also higher than that reported in other species. The gene cox1 had a different start codon (CGA) compared with the other 12 protein-coding genes and this is similar to other Lymantriinae insects (Yuan et al. 2018). The incomplete stop codons were observed in Lepidoptera mitogenomes (Ronquist and Huelsenbeck 2003, Stamatakis 2006, Ronquist et al. 2012, Yuan et al. 2018). In the newly sequenced mitogenome, three genes were associated with the incomplete stop codons. For example, cox1 and cox2 used single T and nad4 used TA. The common interpretation for the high frequency of the TAA stop codon is that the TAA terminator is created via post-transcriptional polyadenylation (Ojala et al. 1981). All tRNA genes were predicted to have formed the typical clover-leaf structure, except for trnS1, whose dihydrouridine (DHU) arm formed a loop instead of a couple of paired bases. This is a universal phenomenon occurring in insect mitogenomes and metazoan mitogenomes (Wolstenholme 1992, Ronquist and Huelsenbeck 2003, Stamatakis 2006, Ronquist et al. 2012, Tang et al. 2017). Furthermore, the intergenic spacer located between atp6 and atp8 contained a conserved seven-nucleotide structure (ATGATAA), which is also reported in other lepidopteran mitogenomes. This implies a stable evolutionary structure and potential molecular marker for Lepidoptera of mitogenome (Stamatakis 2006, Ronquist et al. 2012). Noctuoidea is the largest in the Lepidoptera superfamily and includes 4,200 genera and up to 42,400 species (Kitching and Rawlins 1998). Currently, it was widely believed that there were six families in Noctuoidea: Oenosandridae (include 4 genera), Notodontidae (704 genera), Erebidae (1,760 genera), Euteliidae (29 genera), Nolidae (186 genera), and Noctuidae (704 genera) (Kitching and Rawlins 1998; Zahiri et al. 2011, 2012). However, a change in the molecular markers or sampling taxon might lead to different phylogenetic structures. The phylogenetic relationship among the families within Noctuoidea has been debated for a long time (Liu et al. 2016). The monophyly of Noctuidae was confirmed based on the morphological characteristics of the adult and larva; however, the relationships among subfamilies and genera showed poor resolutions (Speidel et al. 1996, Fibiger et al. 2005, Zahiri et al. 2011). Zahiri et al. (2011) revealed that the phylogenetic relationship of Noctuidae was as follows: (Notodontidae + (Euteliidae + (Noctuidae + (Nolidae + (Erebidae + Euteliidae)))) (Mitchell et al. 2006); (Notodontidae + (Nolidae + (Noctuidae + (Erebidae + Euteliidae)))) (Fibiger et al. 2005); (Notodontidae + (Erebidae + (Noctuidae + (Euteliidae + Nolidae)))) (Regier et al. 2017).

In this study, the robust phylogenetic relationships obtained based on the two datasets were similar. The relationships of
Noctuoidea were described as (Notodontidae + (Erebidae + (Nolidae + (Noctuidae + Euteliidae))). These results were consistent with those reported recently, suggesting that Noctuoidea and Euteliidae were the closest taxa, and the Notodontidae was the ancestral family in Noctuoidea (Zahiri et al. 2011, Yang et al. 2019).

The concatenated nucleotide sequences of the 13 PCGs and 37 genes using ML and BI methods provided a well-supported outline of Erebidae. The 25 species of Erebidae were divided into two groups: Erebinae + Calpinae + Aganainae +Arctiinae, which were clustered as one group, and the other two subfamilies Lyantranriinae and Hypeninae clustered in the other group and these findings are similar to those reported in previous studies (Zahiri et al. 2011, 2012; Wang et al. 2015). Initially, L. suffusa was classified into the family Lyantranriidae, which later became Erebidae, and subfamily Lyantranriinae (Mitter et al. 2017, Regier et al. 2017). These findings provide strong evidence for the classification of L. suffusa, which belongs to the Orgyini of Lyantranriinae. All the 13 species of Lyantranriinae clustered into a stable monophyletic group which was supported with strong evidence (PP = 1.0, BS = 100). There were three sister clades included in this group: the first one included L. suffusa as a sister group of the Dasorgyia alpherakii and the genus Gynaephora, which was well supported (PP = 1.0, BS = 100) by ML and BI analysis; and in the second clade, Exproctis similis was at the basal position and a sister to Lymantria dispar + Lymantria umbrosa; in the last clade, a single species Exproctis pseudoconspersa, was the basal taxa of Lyantranriinae. However, the evolutionary history and phylogenetic relationship of Erebidae and Lyantranriinae have attracted great attention and remained unclear (Kitching and Rawlins 1998, Mitter et al. 2017, Regier et al. 2017). Therefore, more advanced studies using larger sample sizes and genetic information are imperative to solve the phylogenetic relationship of Noctuoidea.

Acknowledgments
This work was sponsored by the Natural Science Foundation of China (31772501 and 31400191), China National Funds for Distinguished Young Scientists (31425023), Program of Ministry of Science and Technology of China (2018FY100403), Academy for Multidisciplinary Studies, Capital Normal University to Ai-bing ZHANG, Capacity Building for Sci-Tech Innovation- Fundamental Scientific Research Funds (No. 20530290051), Joint Fund of the Beijing Municipal Natural Science Foundation and Beijing Municipal Education Commission (KZ 201810028046), Beijing Municipal Natural Science Foundation (517200).

Author Contributions
AB Zhang and JL conceived the original idea. QL carried out the experiment. JL wrote the manuscript with support from HLH and ABZ. XMZ offered great in data analysis.

References Cited
Ahmed, N., M. Z. Hasan, and Z. Islam. 2002. Rice Hairy Caterpillar, Laelia suffusa Walker (Lepidoptera: Lyantranriidae), a new recorded rice defoliator in Bangladesh. SAIC Newsletter. 12: 9.
Armstrong, K. F., P. McHugh, W. Chinn, E. R. Frampton, and P. J. Walsh. 2003. Tussock moth species arriving on imported used vehicles determined by DNA analysis. New Zealand Plant Protect. 56: 16–20.
Avise, J. C. 2009. Phylogeography: retrospective and prospect. J. Biogeogr. 36: 3–15.
Ballard, J. W., and M. C. Whitlock. 2004. The incomplete natural history of mitochondria. Mol. Ecol. 13: 729–744.
Benson, G. 1999. Tandem repeats finder: a program to analyze DNA sequences. Nucleic Acids Res. 27: 573–580.
Bolger, A. M., M. Lohse, and B. Usadel. 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinformatics. 30: 2114–2120.
Boore, J. L. 2000. The duplication/random loss model for gene rearrangements exemplified by mitochondrial genomes of deuterostome animals. Comp. Genomics. 12: 133–147.
Boore, J. L. 2006. The use of genome-level characters for phylogenetic reconstruction. Trends Ecol. Evol. 21: 439–446.
Cameron, S. L. 2014. Insect mitochondrial genomics: implications for evolution and phylogeny. Annu. Rev. Entomol. 59: 95–117.
Cameron, S. L., and M. F. Whiting. 2008. The complete mitochondrial genome of the tobacco hornworm, Manduca sexta, (Insecta: Lepidoptera: Sphingidae), and an examination of mitochondrial gene variability within butterflies and moths. Gene. 408: 112–123.
Cantatore, P., M. N. Gadaleta, M. Roberti, C. Saccone, and A. C. Wilson. 1987. Duplication and remolding of tRNA genes during the evolution of rearrangement of mitochondrial genomes. Nature. 329: 853–855.
Chao, C. L. 1987. Economic insect fauna of China (in Chinese). Science Press, Beijing, China.
Chao, C. L. 2003. Fauna sinica insect (in Chinese), Beijing. Science Press, Beijing, China.
Dowton, M., S. L. Cameron, J. I. Dowavic, A. D. Austin, and M. F. Whiting. 2009. Characterization of 67 mitochondrial tRNA gene rearrangements in the Hymenoptera suggests that mitochondrial tRNA gene position is selectively neutral. Mol. Biol. Evol. 26: 1607–1617.
Dubois, N. R., and D. H. Dean. 1995. Synergism between cryia insecticidal crystal proteins and spores of bacillus thuringiensis, other bacterial spores, and vegetative cells against Lymantria dispar (Lepidoptera: Lyantranriidae). Larvae. Environ. Entomol. 24: 1741–1747.
Edgar, R. C. 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. BMC Bioinformatics. 5: 113.
Fibiger, M., and J. D. Lafontaine. 2005. A review of the higher classification of the Noctuoidea (Lepidoptera) with special reference to the Holarctic fauna. Esperiana. 11: 7–92.
da Fonseca, R. R., W. E. Johnson, S. J. O’Brien, M. J. Ramos, and A. Antunes. 2008. The adaptive evolution of the mammalian mitochondrial genome. BMC Genomics. 9: 119.
Fox, R. 2013. The decline of moths in Great Britain: a review of possible causes. Insect. Conserv. Div. 6: 5–19.
Fragkostefanakis, S., F. Dandachi, and P. Kalaitzis. 2012. Expression of arabinogalactan proteins during tomato fruit ripening and in response to mechanical wounding, hypoxia and anaoxia. Plant Physiol. Biochem. 52: 112–118.
Ju, R. T., Y. Y. Chen, L. Gao, and B. Li. 2016. The extended phenotype of Spartinia invasion alters a native herbivorous insect’s abundance and diet in a Chinese salt marsh. Biol. Invasions. 18: 2229–2236.
Kitching, I. J., and J. E. Rawlins. 1998. The Noctuoidea. Walter de Gruyter, New York.
Kristensen, N. P., M. J. Scoble, and O. Karsholt. 2007. Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. Zootaxa. 1668: 699–747.
Kumar, S., G. Stecher, and K. Tamura. 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Mol. Biol. Evol. 33: 1870–1874.
Lavrov, D. V., J. L. Boone, and W. M. Brown. 2002. Complete mtDNA sequences of two millipedes suggest a new model for mitochondrial gene rearrangements: duplication and nonrandom loss. Mol. Biol. Evol. 19: 163–169.
Li, H. K., and J. Y. Yan. 1991. A study of Paeziclonomyia farinosus on Laelia coenosaz. Nat. Enem. Insects. 13: 51–53.
Liu, Q. N., X. Y. Chai, D. B. Bian, B. M. De, C. L. Zhou, and B. P. Tang. 2016. The complete mitochondrial genome of fall armyworm Spodoptera frugiperda (Lepidoptera: Noctuiidae). Genes. Genomics 38: 205–216.
Lowe, T. M., and P. P. Chan. 2016. tRNAscan-SE On-line: search and contextural analysis of transfer RNA genes. Nucleic. Acids. Res. 44: 54–57.
McKnight, M. L., and H. B. Shaffer. 1997. Large, rapidly evolving intergenic spacers in the mitochondrial DNA of the salamander family Ambystomatidae (Amphibia: Caudata). Mol. Biol. Evol. 14: 1167–1176.

Meng, G., Y. Li, C. Yang, and S. Liu. 2019. MitoZ: a toolkit for animal mitochondrial genome assembly, annotation and visualization. Nucleic Acids Res. 47: e63.

Mitchell, A., C. Mitter, and J. C. Regier. 2006. Systematics and evolution of the cutworm moths (Lepidoptera: Noctidae): evidence from two protein-coding nuclear genes. Syst. Entomol. 31:21–46.

Mitter, C., D. R. Davis, and M. P. Cummings. 2017. Phylogeny and evolution of Lepidoptera. Annu. Rev. Entomol. 62: 265–283.

Mullen, G. R., and J. M. Zaspel. 2019. Phylogeny and evolution of Lepidoptera. Annu. Rev. Entomol. 62: 265–283.

Pogue, M. G. 2009. *Lepidoptera biodiversity*. Blackwell Science Publishing, Oxford, United Kingdom.

Qin, J., J. Li, Q. Gao, J. J. Wilson, and A. B. Zhang. 2019. Mitochondrial phylogeny and comparative metigenomics of closely related pine moth pests (Lepidoptera: Dendrolimina). PeerJ. 7: e7317.

Rand, D. M. 2009. Endotherms, ectotherms, and mitochondrial genome size variation. J. Mol. Evol. 37: 281–295.

Regier, J. C., C. Mitter, K. Mitter, M. P. Cummings, A. L. Bazinet, W. Hallwachs, D. H. Janzen, and A. Zwick. 2017. Further progress on the phylogeny of Noctuoidea (Insecta: Lepidoptera) using an expanded gene sample. Syst. Entomol. 42: 82–93.

Ronquist, F., and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics. 19: 1372–1374.

Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huelsenbeck. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61: 539–542.

Schmieder, R., and R. Edwards. 2011. Quality control and preprocessing of metagenomic datasets. Bioinformatics. 27: 863–864.

Schole, M. J. 1992. The Lepidoptera: form, function and diversity. Oxford University Press, Oxford, United Kingdom.

Singh, K. A., and K. Nakvran. 2019. Studies on internal genital features of two species of genus *Laelia* Stephens (Lamiantriadeae: Lepidoptera) from India. J. Hered. Res. 43: 387–390.

Speidel, W., H. Fanger, and C. M. Naumann. 1996. The phylogeny of the Noctuidae (Lepidoptera). Syst. Entomol. 21: 219–231.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics. 22: 2688–2690.

Sun, K. K., W. S. Yu, J. J. Jiang, C. Richards, S. Evan, J. Ma, B. Li, and R. T. Ju. 2020. Mismatches between the resources for adult herbivores and their offspring suggest invasive *Spartina alterniflora* is an ecological trap. J. Ecol. 108:719–732.

Tang, B. P., Z. Z. Xin, Y. Liu, D. Z. Zhang, Z. P. Wang, H. B. Zhang, X. Y. Chai, C. L. Zhou, and Q. N. Liu. 2017. The complete mitochondrial genome of *Sesarmops sinensis* reveals gene rearrangements and phylogenetic relationships in Brachyura. PLoS One. 12: e0179800.

Timmermans, M. J., and A. P. Vogler. 2012. Phylogenetically informative rearrangements in mitochondrial genomes of Coleoptera, and monophyly of aquatic elateriform beetles (Dryopoidea). Mol. Phylogenet. Evol. 63: 299–304.

Tyagi, K., R. Chakraborty, S. L. Cameron, A. D. Sweet, K. Chandra, and V. Kumar. 2020. Rearrangement and evolution of mitochondrial genomes in Thysanoptera (Insecta); Sci. Rep. 10: 695.

Vaidya, G., D. J. Lohman, and R. Metier. 2011. SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. Cladistics. 27: 171–180.

Wang, H. S., N. Wahlberg, J. D. Holloway, J. Bergsten, X. L. Fan, D. H. Janzen, W. Hallwachs, L. J. Wen, W. Fang, and S. Nylin. 2015. Molecular phylogeny of Lymnantrinae (Lepidoptera, Noctuoidea, Erebidae) inferred from eight gene regions. Cladistics. 31: 579–592.

Wolstenholme, D. R. 1992. Animal mitochondrial DNA: structure and evolution. Int. Rev. Cytol. 141: 171–216.

Xia, X., and Z. Xie. 2001. DAMBE: software package for data analysis in molecular biology and evolution. J. Hered. 92: 371–373.

Yanar, O., S. Gömeç, E. F. Topkara, G. Solmaz, and I. Demir. 2017. The effect of plant quality on survival of *Lymnaea dispar* larvae infected by *Bacillus thuringiensis*. Appl. Ecol. Env. Res. 15: 837–847.

Yang, Z. H., T. T. Yang, Y. Liu, H. B. Zhang, B. P. Tang, Q. N. Liu, and Y. F. Ma. 2019. The complete mitochondrial genome of *Sinma extrema* (Lepidoptera; Nolidae) and its implications for the phylogenetic relationships of Noctuoidea species. Int. J. Biol. Macromol. 137: 317–326.

Yu, W. S., X. L. Guo, K. K. Jiang, K. K. Sun, and R. T. Ju. 2019. Comparison of the life history of a native insect *Laeda coenos* with a native plant *Phragmites australis* and an invasive plant *Spartina alterniflora*. Biodivers. Sci. 27: 433–438.

Yuan, M. L., Q. L. Zhang, L. Zhang, C. L. Jia, X. P. Li, X. Z. Yang, and R. Q. Feng. 2018. Mitochondrial phylogeny, divergence history and high-altitude adaptation of grassland caterpillars (Lepidoptera: Lymnantrinae: Gynaephora) inhabiting the Tibetan Plateau. Mol. Phylogenet. Evol. 122: 116–124.

Zahiri, R., I. J. Kitching, J. D. Lafontaine, M. Mutanen, L. Kaila, J. D. Holloway, and N. Wahlberg. 2011. A new molecular phylogeny offers hope for a stable family level classification of the Noctuoidea (Lepidoptera). Zoo. Sci. 40: 138–173.

Zahiri, R., J. D. Holloway, I. J. Kitching, J. D. Lafontaine, M. Mutanen, and N. Wahlberg. 2012. Molecular phylogenetics of Erebidae (Lepidoptera, Noctuoidea). Syst. Entomol. 37: 102–124.

Zapletalová, V., L. Zapletal, and M. Konvička. 2016. Habitat impact on ultraviolet reflectance in moths. Environ. Entomol. 12: 1–6.

Zhang, J., R. Ju, H. Pan, S. F. Pan, and J. Wu. 2019. Enemy-free space is important in driving the host expansion of a generalist herbivore to an inferior exotic plant in a wetland of Yangtze Estuary. Biol. Invasions. 21: 547–559.

Zhu, X. Y., Z. Z. Xin, Y. Wang, H. B. Zhang, D. Z. Zhang, Z. F. Wang, C. L. Zhou, B. P. Tang, and Q. N. Liu. 2017. The complete mitochondrial genome of *Clostera anchoretia* (Lepidoptera: Notodontidae) and phylogenetic implications for Noctuoidea species. Genomics. 109: 221–226.