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Mitochondrial phylogeny, divergence history and high-altitude adaptation of grassland caterpillars (Lepidoptera: Lymantriinae: *Gynaephora*) inhabiting the Tibetan Plateau

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ABSTRACT

Grassland caterpillars (Lepidoptera: Lymantriinae: *Gynaephora*) are the most important pests in alpine meadows of the Tibetan Plateau (TP) and have well adapted to high-altitude environments. To further understand the evolutionary history and their adaptation to the TP, we newly determined seven complete TP *Gynaephora* mitogenomes. Compared to single genes, whole mitogenomes provided the best phylogenetic signals and obtained robust results, supporting the monophyly of the TP *Gynaephora* species and a phylogeny of Arctiinae + (Aganainae + Lymantriinae). Incongruent phylogenetic signals were found among single mitochondrial genes, none of which recovered the same phylogeny as the whole mitogenome. We identified six best-performing single genes using Shimodaira-Hasegawa tests and found that the combinations of *rrnS* and either *cox1* or *cox3* generated the same phylogeny as the whole mitogenome, indicating the phylogenetic potential of these three genes for future evolutionary studies of *Gynaephora*. The TP *Gynaephora* species were estimated to radiate on the TP during the Pliocene and Quaternary, supporting an association of the diversification and speciation of the TP *Gynaephora* species with the TP uplifts and associated climate changes during this time. Selection analyses revealed accelerated evolutionary rates of the mitochondrial protein-coding genes in the TP *Gynaephora* species, suggesting that they accumulated more nonsynonymous substitutions that may benefit their adaptation to high altitudes. Furthermore, signals of positive selection were detected in *nad5* of two *Gynaephora* species with the highest altitude-distributions, indicating that this gene may contribute to *Gynaephora*'s adaptation to divergent altitudes. This study adds to the understanding of the TP *Gynaephora* evolutionary relationships and suggests a link between mitogenome evolution and ecological adaptation to high-altitude environments in grassland caterpillars.

1. Introduction

The *Gynaephora* (Lepidoptera: Erebidae: Lymantriinae) is a small genus with 15 nominated species in the world, among which eight are endemic to the Tibetan Plateau (TP). The TP *Gynaephora* species are major pests in alpine meadows and seriously damage forages, showing well adaptation to the high-altitude environments (Yuan et al., 2015c; Zhang, 2014; Zhang and Yuan, 2013; Zhang et al., 2017). The initial diversification of the TP *Gynaephora* species began during the late Miocene/Pliocene and was potentially associated with the TP uplift and climate changes during this time (Yuan et al., 2015c). Currently, almost all of the TP *Gynaephora* species have altitude specific distributions, with *G. alpherakii* in the highest altitudes (~5000 m above sea level (masl)) and *G. menyuanensis* in the lowest (~3000 masl). Molecular phylogenetic analyses based on multiple loci supported the monophyly of the TP *Gynaephora* species, but species status and phylogenetic relationships of three *Gynaephora* species (*aureata*, *rouergensis* and *minora*) inhabiting the Southeastern TP were ambiguous (Yuan et al., 2015c). Low levels of interspecific divergences are typical features of the TP *Gynaephora* species, but extremely low genetic interspecific distances

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and relatively high intraspecific divergences were found among these three species. This may be due to the limited phylogenetic signals of the genes used and further analyses are needed by using the larger datasets (e.g. mitochondrial genomes).

The insect mitogenome is a typically closed-circular DNA molecule of ~15–18 kb in size and generally encodes 13 protein-coding genes (PCGs) which are directly involved in oxidation phosphorylation (OXPHOS) (Ballard and Whitlock, 2004; da Fonseca et al., 2008). In addition, it contains 2 ribosomal RNA genes (rRNAs), 22 transfer RNA genes (tRNAs), and a large non-coding region that may control its replication and transcription (Boore, 1999; Cameron, 2014; Wolstenholme, 1992). Due to its haploid nature, lack of recombination, maternal inheritance, and rapid evolutionary rate compared to those of the nuclear DNA, animal mitochondrial DNA has been widely used in population genetics, phylogeographics, species identification and molecular phylogenetics (Avise, 2009; Cameron, 2014; Osigus et al., 2013; Simon et al., 2006; Toews and Brelsford, 2012). Given the linkage of mitochondrial genes within the same DNA molecule, it is expected that the same genealogy should be shared by different mitochondrial genes. However, incongruent phylogenetic results have frequently been observed among mitochondrial genes which included different phylogenetic signals (Duchêne et al., 2011; Havird and Santos, 2014; Nadimi et al., 2016; Wang et al., 2017). Although single or a few concatenated genes could serve as a proxy for the entire mitogenomes, the performance of the best genes or regions is highly taxa-dependent (Duchêne et al., 2011; Havird and Santos, 2014; Nadimi et al., 2016; Wang et al., 2017).

The mitogenome has historically been assumed to evolve neutrally, however, mitochondrial genes are expected to have experienced natural selection due to their functional importance in OXPHOS (Blier et al., 2001; da Fonseca et al., 2008; Manoli et al., 2007). During past decades, positively selective signals of mitochondrial genes have been detected in various taxa (da Fonseca et al., 2008; Luo et al., 2013; Scott et al., 2011; Wang et al., 2016; Zhang et al., 2013; Zhou et al., 2014). Mitochondrial genes have become an essential target for investigating the genetic basis of organismal adaptation to various harsh environments (Hassanin et al., 2009; Luo et al., 2013; Wang et al., 2016; Yu et al., 2011; Zhang et al., 2017; Zhou et al., 2014), such as high-altitude environments which are characterized by hypoxia, severe cold and strong ultraviolet radiation. Numerous studies have presented evidence of non-neutral changes in the mitogenomes of organisms living on the TP (Luo et al., 2013), such as birds (Gu et al., 2016; Zhou et al., 2014), mammals (Luo et al., 2012; Peng et al., 2012; Yu et al., 2011), and fish (Li et al., 2013; Wang et al., 2016). However, most of these studies focused on vertebrates, whereas few reports examined adaptive evolution of insect mitogenomes to high-altitude environments (Zhang et al., 2013; Zhang et al., 2017). Recently, we showed the adaptive divergence of mitochondrial genes between two *Gynaephora* species inhabiting the highest and lowest high altitudes (Zhang et al., 2017). However, only two species were included in the previous study and a further analysis by including other six TP *Gynaephora* species is needed to investigate the adaptive evolution of the TP *Gynaephora* species to high-altitude environments from a mitogenomic perspective.

In this study, we newly sequenced and annotated seven complete mitogenomes of *Gynaephora* collected from alpine meadows of the TP. Combined with two *Gynaephora* mitogenomes sequenced in our previous studies (Yuan and Zhang, 2013; Yuan et al., 2016a), we performed a comparative mitogenomics analysis for all the eight TP *Gynaephora* species, in order to: (1) reconstruct a robust mitochondrial phylogeny of the TP *Gynaephora* species that could be used as framework for further evolutionary studies; (2) assess the phylogenetic signals of single mitochondrial genes; (3) estimate divergence times of main lineages within *Gynaephora*; and (4) detect positively selective signals of the mitochondrial genes in the TP *Gynaephora* species during their adaptation to high-altitude environments.

2. Materials and methods

2.1. Sample collection and DNA extraction

We collected *Gynaephora* samples from seven localities in the alpine meadows of the TP. Detailed sampling information is provided in Table S1. All samples were initially preserved in 100% ethanol in the field, and transferred to −80 °C until used for DNA extraction. For each *Gynaephora* species, total genomic DNA was extracted from the thorax muscle of a single specimen using a DNeasy Tissue Kit (Qiagen) according to the manufacturer's protocols.

2.2. PCR amplification and sequencing

For each *Gynaephora* species, whole mitogenome was amplified in overlapping fragments by 15 *Gynaephora*-specific primers designed from mitogenomic sequences of *G. alpherakii* and *G. menyuanensis* (Yuan and Zhang, 2013; Yuan et al., 2016a). Sequences of the primers used in this study are provided in Table S2. PCR and sequencing reactions were conducted as described previously (Yuan et al., 2015a,b).

2.3. Sequence annotation and bioinformatics analysis

Sequence annotation, including the determination of PCGs, tRNAs and rRNAs, and the prediction of the secondary structures of tRNAs, was conducted as described previously (Yuan et al., 2015a,b). All the complete mitogenome sequences of *Gynaephora* newly sequenced in the present study have been deposited in GenBank (accession numbers NC_029162–NC_029164, KY688083–KY688086). Nucleotide composition, codon usage and K2P genetic distance were analyzed with MEGA 6.06 (Tamura et al., 2013). Strand asymmetry was calculated using the formulas: AT-skew = [A − T]/[A + T] and GC-skew = [G − C]/[G + C] (Perna and Kocher, 1995).

2.4. Phylogenetic analysis

Nineteen mitogenomic sequences from Erebidae were used for phylogenetic analyses (Table 1). Two Noctuidae species (*Sesamia inferens* and *Agrotis ipsilon*) were used as outgroups. Each PCG was aligned individually with codon-based multiple alignments using MUSCLE as implemented in MEGA 6.06 (Tamura et al., 2013). The rRNAs and tRNAs were aligned with MAFFT (http://mafft.cbrc.jp/alignment/server/) and MEGA 6.06 (Tamura et al., 2013), respectively, as described previously (Yuan et al., 2015b). To determine if sequence saturation existed in our alignments, we performed a test of substitution saturation using DABME 6.4.20 (Xia, 2013). No substitution saturation was found for 13 PCGs, *rrnL*, *rrnS* and 22 tRNAs, even in the third positions of 13 PCGs (Table S3). Therefore, all sites of 37 mitochondrial genes were used in phylogenetic analyses. Alignments of individual genes were concatenated as the "supergene" dataset (PCGRT) containing 14,712 nucleotides. The best partitioning schemes and corresponding nucleotide substitution models for the PCGRT dataset were selected by PartitionFinder 1.1.1 (Lanfear et al., 2012), as described previously (Yuan et al., 2016b). The best-fit partitioning schemes and corresponding evolutionary models (Table S4) determined by PartitionFinder were implemented in the following phylogenetic analyses.

Phylogenetic analyses were conducted for each dataset on the CIPRES Science Gateway 3.3 (Miller et al., 2010). ML analysis was performed with RAxML-HPC2 on XSEDE 8.0.24 (Stamatakis, 2014) using the GTRGAMMA model and the node reliability was evaluated by 1000 bootstraps (BS). Bayesian analysis was carried out using MrBayes 3.2.2 (Ronquist et al., 2012). Two independent runs with four chains (three heated and one cold) were conducted simultaneously for 20,000,000 generations, with sampling every 2,000 generations. Stationarity is considered to be reached when ESS (estimated sample size) value is above 100 and PSRF (potential scale reduction factor) approach

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