Zootaxa 3985 (1): 125–141
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3985.1.7
http://zoobank.org/urn:lsid:zoobank.org:pub:439DC3AC-E11F-47F4-876B-DA30848F4F13

Molecular phylogeny of the butterfly tribe Satyrini (Nymphalidae: Satyrinae) with emphasis on the utility of ribosomal mitochondrial genes *16s rDNA* and nuclear *28s rDNA*

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Abstract

The tribe Satyrini is one of the most diverse groups of butterflies, but no robust phylogenetic hypothesis for this group has been achieved. Two rarely used *16s* and *28s* ribosomal and another seven protein-coding genes were used to reconstruct the phylogeny of the Satyrini, with further aim to evaluate the informativeness of the ribosomal genes. Our maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) analyses consistently recovered three well-supported clades for the eleven sampled subtribes of Satyrini: clade I includes Eritina and Coenonymphina, being sister to the clade II + clade III; clade II contains Parargina, Mycalesina and Lethina, and the other six subtribes constitute clade III. The placements of the taxonomically unstable *Davidina* Oberthür and geographically restricted *Paroeneis* Moore in Satyrina are confirmed for the first time based on molecular evidence. The close relationships of *Callerebia* Butler, *Loxerebia* Watkins and *Argestina* Riley are well-supported. We suggest that *Rhaphicera* Butler belongs to Lethina. The partitioned Bremer support (PBS) values of MP analysis show that the *16s rDNA* contributes well to the nodes representing all the taxa from subtribe to species levels, and the *28s rDNA* is informative at the subtribe level. Furthermore, our ML analyses show that the ribosomal genes *16s rDNA* and *28s rDNA* are informative, because most node support values are lower in the ML tree after the removal of them than that in ML tree constructed based on the full nine-gene dataset. This indicates that some other ribosomal genes should be tentatively used through combining with traditionally used protein-coding genes in further analysis on phylogeny of Satyrini, providing that proper representatives are sampled.

Key words: molecular systematics, rapid radiation, Satyrina, MAFFT, partitioned Bremer support

Introduction

The butterfly tribe Satyrini, belonging to Satyrinae of the family Nymphalidae of Lepidoptera, comprises approximately 2200 described extant species and can be found nearly worldwide (Ackery *et al.* 1999; Peña *et al.* 2011). Due to its high diversity, many members of the Satyrini have been designated as model organisms in various research fields such as ecology (e.g., Schmitt & Haubrich, 2008), developmental biology (e.g., Oliver *et al.,* 2012), and conservation biology (e.g., Slamova *et al.,* 2012). According to the results of recent systematic studies (Kodandaramaiah *et al*., 2010a; Penz, 2007; Peña *et al.,* 2006; Peña & Wahlberg, 2008; Peña *et al,.* 2011; Wahlberg *et al.,* 2009), 13 subtribes are currently defined from the Satyrini (Marín *et al.,* 2011). However, phylogenetic relationships among them remain largely unresolved (Marín *et al.,* 2011; Peña *et al.,* 2011). Based on the hitherto largest sample density and five genetic markers (*COI*, *EF-1α*, *GAPDH*, *RpS5* and *wingless*), Peña *et al.* (2011) conducted a comprehensive phylogenetic study on Satyrini, recognizing that the topologies showing the relationships of different subtribes were generally incongruent, and moreover, the basal nodes were most weakly supported.

Selecting suitable genetic markers is of great importance in studies of molecular systematics. The protein-coding genes (e.g., *COI*, *EF-1α*, *wingless*), possibly being easily alignable and without secondary structure, have been used in various higher phylogenetic studies on satyrines (e.g., Kodandaramaiah *et al.,* 2010b; Peña *et al.,* 2010; Price *et al.,* 2011). After comparing with the phylogenetic performances between insect nuclear ribosomal

Accepted by C. Prieto: 12 Jun. 2015; published: 9 Jul. 2015