



# Characterization and comparative analysis of six complete mitochondrial genomes from ectomycorrhizal fungi of the *Lactarius* genus and phylogenetic analysis of the *Agaricomycetes*

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## ABSTRACT

*Lactarius* is one of the most prominent genera of mushroom-forming fungi in the world. In the present study, complete mitochondrial genomes (mitogenomes) from six *Lactarius* species were sequenced and assembled. The six mitogenomes were all composed of circular DNA molecules, with total lengths ranging from 38,445 bp to 60,843 bp. The GC contents, GC skews, and AT skews of the mitogenomes varied among the six species. Mitogenomic synteny analysis revealed the presence of gene rearrangements among the mitogenomes. Among the 15 core protein coding genes (PCGs) within the mitogenomes, *nad4L* exhibited the least genetic distance among species, indicating a high degree of conservation. In addition, the Ka/Ks values for all 15 core PCGs were <1, suggesting that they were subject to purifying selection. Comparative analyses indicated that the increase of intron numbers and sizes contributed to the expansion of mitogenomes in *Lactarius*. Phylogenetic analyses based on three combined gene datasets yielded identical and well-supported (BPP ≥ 0.83) topologies, dividing the six *Lactarius* species into two groups. This study provides the first report of mitogenomes from *Lactarius* and promotes further understanding of the genetics, evolution, and phylogenetic relationships of this important ectomycorrhizal fungal genus.

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## 1. Introduction

Mitochondria host genomes distinct from nuclear genomes in eukaryotes, and they also contain important genetic information that is useful for understanding eukaryotic evolution and genetics [1,2]. Mitochondrial genomes exhibit many characteristics that contribute to their usefulness in phylogenetic and evolutionary studies including maternal inheritance, conservative gene sequences, numerous molecular markers, and low recombination rates [3–5]. The rapid development of next generation sequencing technology has resulted in increasing numbers of available mitochondrial genomes [6,7], leading to considerable recent research interest of these genomes. Mutations in the mitochondrial genome are thought to be closely related to aging of animals and the emergence of many diseases [8]. Compared to animals or plants, the mitochondrial genomes of fungi have been significantly less studied [9]. This is particularly true for the *Basidiomycetes*, and these knowledge-gaps limit our understanding of genetic variation and evolution of these important fungal genomes. The rate of mutation in fungal

mitochondrial genomes (mitogenomes) is thought to fall between that of animals which exhibit the highest rates among eukaryotes, and that of plants which exhibit the lowest rates [10]. However, the size, gene arrangement, and structure of fungal mitogenomes varies greatly, even among species of the same genus [7,11,12]. Elucidating the characterization and organization of fungal mitogenomes, including the variation of these characteristics among different species, will enable a fuller understanding of the phylogenetic and evolutionary relationships of fungi [7,13–15].

*Lactarius* fungi belong to the *Russulaceae* family within the *Basidiomycetes* and are characterized by milky fluids (“latex”) that they exude when cut or damaged [16]. *Lactarius* is one of the most prominent genus of mushroom-forming fungi in the Northern hemisphere [17,18], but are also native to Africa, Australia, and elsewhere [16,19]. A variety of biological activities have been reported for these organisms including antimicrobial, anticancer, antinociceptive, and antioxidant activities [20–22]. These activities are thought to result from their bioactive metabolites that include sesquiterpenoids, oligosaccharides, terpenoids, sterols, and polysaccharides [23–25]. In addition to its medicinal value, *Lactarius* has a unique taste, and consequently has become one of the most popular and highly valued mushrooms in the northern hemisphere [23,26].

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*Lactarius* are ectomycorrhizal fungi (ECMF) that occur in a variety of habitats, including boreal forests, arctic tundra, tropical oak forests, and tropical rain forests [27–29]. In forest ecosystems, ECMF play an important role in carbon and nitrogen cycling [30,31]. ECMF provide water and mineral elements for the host plants, and in return, the host plants provide carbon nutrients for the fungi [32]. Numerous ECMF genes have evolved in response to the adaptation of a symbiotic lifestyle [33,34]. However, the mitochondrial genomes of ECMF have been little studied [35,36], limiting a complete understanding of the genetic characteristics and evolutionary histories of ECMF. Further, *Lactarius* is a large fungal genus with hundreds of described species, but only limited morphological characteristics that can be used for taxonomic classification, thereby leading to species classification problems [19]. In contrast, the mitochondrial genome is a reliable tool for phylogenetic analysis, and has been used in taxonomic and phylogenetic analyses of many species [37,38]. However, no mitogenomes of *Lactarius* have been previously reported.

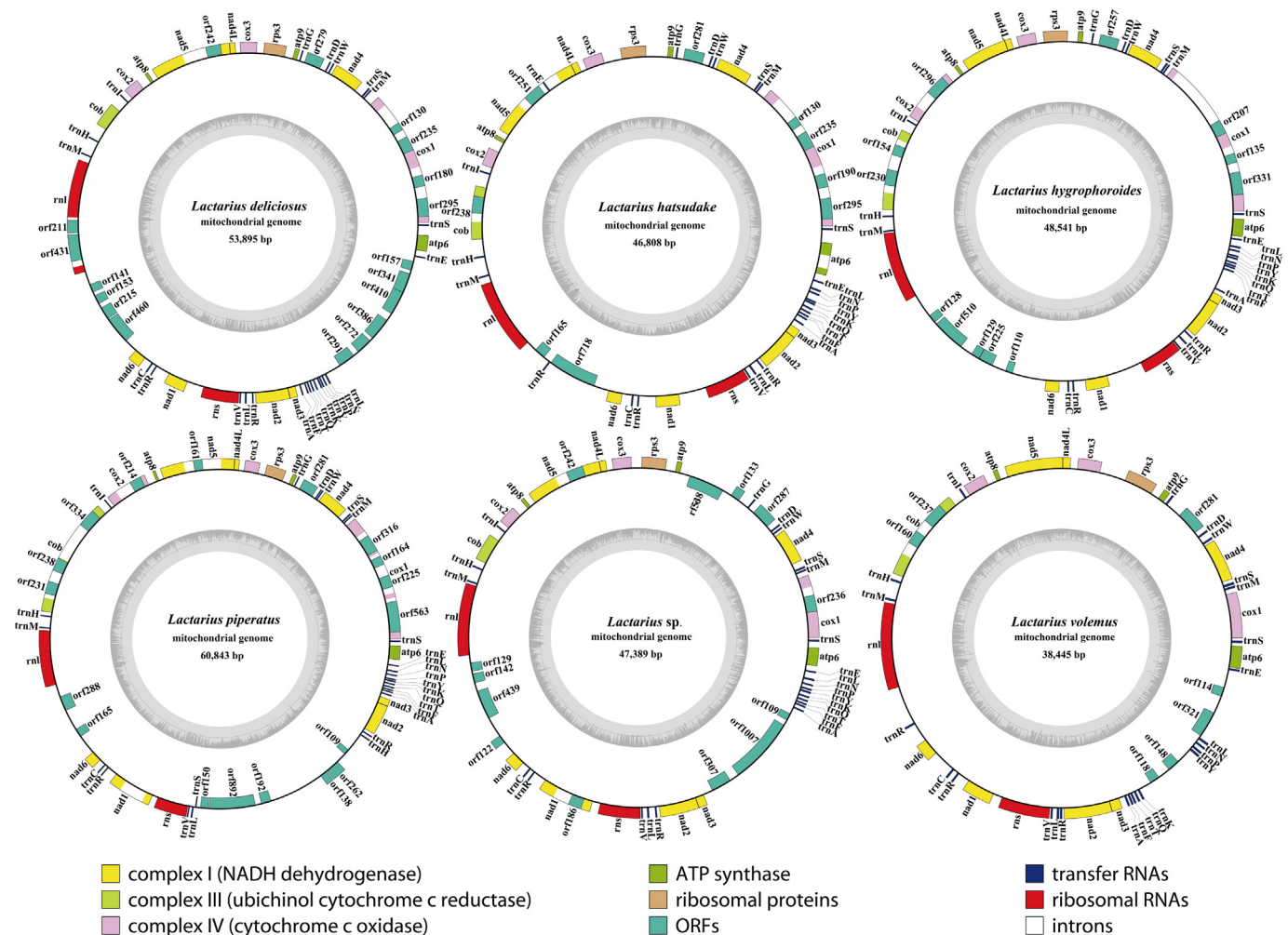
In the present study, the complete mitogenomes of six *Lactarius* species (*L. deliciosus* s9, *L. hatsudake* s20, *L. hygrophoroides* s19, *L. piperatus* s49, *Lactarius* sp. s50, and *L. volemus* s8) were sequenced and assembled. Variation in gene contents, gene orders, repeat events, and genome structures, were compared among the annotated genomes to assess conservation and divergence of these characteristics. Further, whole genome datasets and single mitochondrial genes were assessed as potential molecular markers to delineate phylogenetic relationships among

*Agaricomycetes*. To our knowledge, this is the first report of mitogenomes from *Lactarius*, and thus provides an important foundation for the future study of *Lactarius* taxonomy, genetics, and evolutionary biology, in addition to the study of these properties of ectomycorrhizal fungi, in general.

## 2. Materials and methods

### 2.1. Sample collection and DNA extraction

Six *Lactarius* fruiting bodies were collected from the Liangshan Yi Autonomous Prefecture of Sichuan, China, in September 2016. Soil and leaves were first cleared from the surface of the collected fruiting bodies. The fruiting bodies were then placed on ice and brought to the laboratory for preservation at 4 °C prior to further use. The fruiting bodies were identified based on morphological characteristics and molecular analyses [39,40]. The six specimens were deposited as vouchers in the collection center of the Biotechnology and Nuclear Technology Research Institute under the following accession numbers: *L. deliciosus*: s9; *L. hatsudake*: s20; *L. hygrophoroides*: s19; *L. piperatus*: s49; *Lactarius* sp.: s50; and *L. volemus*: s8. Genomic DNA was extracted from the caps of the fruiting bodies using a fungal DNA extraction kit (Cat. #D3390-00, Omega Bio-Tek, Norcross, GA, USA), following the manufacturer's instructions.



**Fig. 1.** Circular maps of six newly sequenced mitochondrial genomes from different *Lactarius* species. Genes are represented by different colored blocks, as indicated in the legend below the maps. Colored blocks outside of each ring indicate that the genes are on the direct strand while colored blocks within the rings indicate that the genes are located on the reverse strand.

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