

Molecular phylogeography and population structure of a mid-elevation montane frog *Leptobrachium ailaonicum* in a fragmented habitat of southwest China

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ABSTRACT

Leptobrachium ailaonicum is a vulnerable anuran restricted to a patchy distribution associated with small mountain streams surrounded by forested slopes at mid-elevations (approximately 2000–2600 m) in the subtropical Mount Wuliang and Mount Ailao ranges in southwest China (Yunnan Province) and northern Vietnam. Given high habitat specificity and lack of suitable habitat in lower elevations between these ranges, we hypothesized limited gene flow between populations throughout its range. We used two mitochondrial genes to construct a phylogeographic pattern within this species in order to test our hypothesis. We also examined whether this phylogeographic pattern is a response to past geological events and/or climatic oscillations. A total of 1989 base pairs were obtained from 81 individuals of nine populations yielding 51 unique haplotypes. Both Bayesian and maximum parsimony phylogenetic analyses revealed four deeply divergent and reciprocally monophyletic mtDNA lineages that approximately correspond to four geographical regions separated by deep river valleys. These results suggest a long history of allopatric separation by vicariance. The distinct geographic distributions of four major clades and the estimated divergence time suggest spatial and temporal separations that coincide with climatic and paleogeographic changes following the orogeny and uplift of Mount Ailao during the late Miocene to mid Pliocene in southwest China. At the southern distribution, the presence of two sympatric yet differentiated clades in two areas are interpreted as a result of secondary contact between previously allopatric populations during cooler Pleistocene glacial cycles. Analysis of molecular variance indicates that most of the observed genetic variation occurs among the four regions implying long-term interruption of maternal gene flow, suggesting that *L. ailaonicum* may represent more than one distinct species and should at least be separated into four management units corresponding to these four geographic lineages for conservation.

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1. Introduction

Past geologic events and climatic fluctuations have had profound impacts on the phylogeographic structure and genetic patterns of species in southwest China (Liu et al., 2007; Yuan et al., 2008). These influences have resulted in a high number of species in the temperate, subtropical and tropical mountains of this region, which are the major components of the South-Central China and Indo-Burman biodiversity hotspots (Myers et al., 2000; Wikramanayake et al., 2001; CEPF, 2005; CI, 2007). Two hypotheses have been proposed to explain the production of such high diversity in this region. One hypothesis is that extreme topographic variation

of deep river valleys between recently uplifted mountains associated with the collision of the Indian subcontinent and the mainland of Asia created climatic conditions that are complex and diverse both altitudinally and latitudinally resulting in a high abundance of species (Yang, 1991; Zhao, 1999). The Hengduan Mountains, beginning at the southeast corner of the Tibetan Plateau, are north to south ranges of high mountains with alternating deep river valleys, which formed and now accommodate the main stems of some of the largest rivers in China and Southeast Asia (i.e., Irrawaddy, Mekong, Red, Salween, and Yangtze; Li et al., 1995; Brookfield, 1998). At the southern subsection of the Hengduan mountain chain are the Wuliang and Ailao mountains, which stretch across central-south Yunnan from northwest to the southeast (Fig. 1). The Ailao and Wuliang mountains are considered part of the Indo-Burman Hotspot, as they are located at the convergence of the Central and South Asian tropical zones (Myers et al., 2000; CI, 2007).

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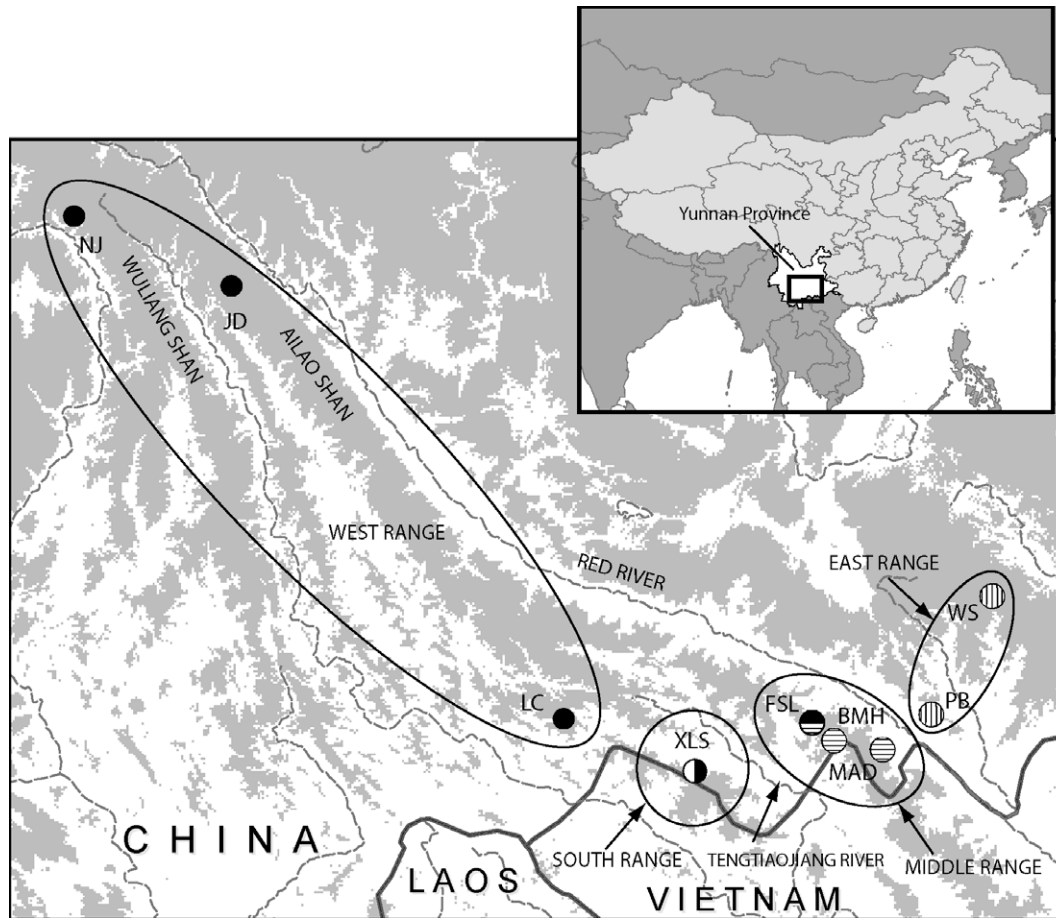


Fig. 1. The geographic distribution of *Leptobrachium ailaonicum* sampled in this study. WS, Wenshan; PB, Pingbian; MAD, Maandi; BMH, Baimahe; FSL, Fenshuijing; XLS, Xilongshan; LC, Luchun; JD, Jingdong; NJ, Nanjian. Solid black dots indicate the presence of haplotypes from Lineage A, white dots from Lineage B, dots with horizontal hatching from Lineage C, and dots with vertical hatching from Lineage D. The two dots at XLS and FSL indicate that haplotypes of Lineage A are present at those localities with individuals of Lineage B and C, respectively. Grey shading signifies elevations of 1500 m and above.

The other hypothesis put forth to explain the high diversity of this region is that the southern temperate and tropical regions in China were refugia for various animals and plants during Pleistocene glacial periods (Wu, 1980, 1987; Wang and Liu, 1994; Li et al., 2005; Long et al., 2006). Though most of China has never been covered by ice sheets, it, together with neighboring areas in eastern Asia, has experienced a development of cooler and drier climates within the last 15-million year period (Axelrod et al., 1996). The tremendous climatic changes during this period, particularly Quaternary glaciations, have led to many extinctions and influenced the distribution and evolution of many plants and animals in China and its neighboring areas (Wang and Ge, 2006). However, to date there is little to no information on the phylogeographic patterns of most of the species from subtropical and tropical mountain regions of Asia (Hewitt, 2000). Thus, we wanted to test whether historical changes in geography (such as orogenesis) or Quaternary climatic oscillations affected the phylogeographic patterns of the mustache toad (*Leptobrachium ailaonicum*) in Yunnan.

Leptobrachium ailaonicum is a medium size toad belonging to an unusual group restricted to southern China and Vietnam in which the males possess external cornified spines on the maxillary region and are larger than the females (reverse sexual size dimorphism). Based on these characters, this small group of toads was separated into its own genus *Vibrissaphora* (Liu, 1945). *Leptobrachium ailaonicum* was first described by Yang et al. (1983) with recent taxonomic changes by Rao and Wilkinson (2008), who synonymized

the genus *Vibrissaphora* into *Leptobrachium* and retained the species within *Leptobrachium*, and Zheng et al. (2008), who synonymized *L. echinatum* from Vietnam into *L. ailaonicum*. Until recently this species was known only from localities in the northern parts of the Mount Wuliang and Mount Ailao ranges in central Yunnan Province, China (Yang et al., 1983; Chen et al., 1984; Zhao, 1998; Fei, 1999; Fei et al., 2005; Yang and Rao, 2008) and the Fan Si Pan Mountains of northern Vietnam (Dubois and Ohler, 1998; Ho et al., 1999). However, our fieldwork has considerably extended the known range of this species by the discovery of several populations between these known localities, and two localities east of the Red River (Fig. 1). We failed to find new localities to the west of the Mekong River and along the Mount Ailao range between the northern and southern localities even though we searched over the past decade in suitable habitat.

This species is uncommon and highly adaptive to montane environments, inhabiting moist evergreen broad-leaf primary forests at elevations between 2000 and 2600 m above sea level but absent below 1500 m (Zhao, 1998; Fei, 1999; personal field observations). This species only breeds in moderately broad forested mid to high elevation mountain streams that have a relatively slow flow of cold clear water at an average depth of about 10 cm (Chen et al., 1984; Ho et al., 1999; personal field observations). We postulate that the extensive low-elevation “sea” surrounding the higher elevation montane “islands” acts as a strong dispersal barrier that isolates local populations resulting in strong genetic subdivision of the species due to its specialized ecological requirements.

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