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Partitioned Bayesian analyses, dispersal–vicariance analysis, and the biogeography of Chinese toad-headed lizards (Agamidae: *Phrynocephalus*): A re-evaluation

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Abstract

The toad-headed lizards of genus *Phrynocephalus* are distributed from northwestern China to Turkey and are one of the major components of the central Asian desert fauna. To date, published morphological and molecular phylogenetic hypotheses of *Phrynocephalus* are only partially congruent, and the relationships within the genus are still far from clear. We re-analyzed published mitochondrial gene sequence data (*12S*, *16S*, *cyt b*, *ND4-tRNA*^{Leu}) by employing partition-specific modeling in a combined DNA analysis to clarify existing gaps in the phylogeny of Chinese *Phrynocephalus*. Using this phylogenetic framework, we inferred the genus' historical biogeography by using weighted ancestral-area analysis and dispersal–vicariance analysis in combination with a Bayesian relaxed molecular-clock approach and paleogeographical data. The partitioned Bayesian analyses support the monophyly of *Phrynocephalus* and its sister-group relationship with *Laudakia*. An earlier finding demonstrating the monophyly of the viviparous group is corroborated. However, our hypothesis of internal relationships of the oviparous group differs from a previous hypothesis as our results do not support monophyly of the oviparous taxa. Instead, the viviparous taxa form a clade with many oviparous taxa exclusive of *P. helioscopus* and *P. mystaceus*. Our results also suggest that: (1) *P. putjatia* is a valid species, comprising populations from Guide, Qinghai Province and Tianzhu, Gansu Province; (2) *P. hongyuanensis* is not a valid species, synonymized instead with *P. vlangalii*; (3) *P. zetangensis* is not a valid species and should be included in *P. theobaldi*; (4) the population occurring in Kuytun, Xinjiang Uygur Autonomous Region is recognized as *P. guttatus* instead of *P. versicolor*; and (5) the Lanzhou population of *P. frontalis* is part of *P. przewalskii*. Congruent with previous hypotheses, the uplift of the Tibetan Plateau played a fundamental role in the diversification of *Phrynocephalus*. An evolutionary scenario combining aspects of vicariance and dispersal is necessary to explain the distribution of *Phrynocephalus*. Bayesian divergence-time estimation suggests that *Phrynocephalus* originated at the Middle–Late Miocene boundary (15.16–10.4 Ma), and diversified from Late Miocene to Pleistocene from a center of origin in Central Asia, Tarim Basin, and Junggar Basin temperate desert, followed by several rapid speciation events in a relatively short time. The proposed biogeographic scenarios also indicate that the Tarim Basin desert may be the secondary diversification center, followed by Junggar Basin temperate desert and Alashan Plateau temperate desert. In the viviparous group, the allopatric speciation of *P. theobaldi* and *P. vlangalii* may have been caused by the uplifting of Tanggula Mountain Ranges. In addition, the results of this study make an important contribution to understanding the uplift of the Tibetan Plateau and Tian Shan Mountains and the biogeography of the entire region.

Keywords: *Phrynocephalus*; Mitochondrial DNA; Partitioned Bayesian inference; Biogeography; Tibetan Plateau; Tian Shan

1. Introduction

The agamid lizard genus *Phrynocephalus*, i.e., toad-headed lizards, comprise over 40 distinct species that inhabit arid regions from northwestern China to the western side of the Caspian Sea, across the Tibetan Plateau, and

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southwest Asia to the Arabian Peninsula. They constitute one of the major components of the central Asian desert fauna and are highly adapted to sand dunes and desert environments. The reproductive biology of *Phrynocephalus* is notable in that there exist two reproductive modes: viviparity and oviparity. All six viviparous species (subspecies) are endemic to China and mainly restricted to high elevations in the Tibetan Plateau. Its special distribution and phylogenetic history would be helpful in deducing the origination, diversification and dispersion of agamid lizards, and testing the link between speciation, adaptation, and historical changes in their biogeography.

Despite considerable previous morphological, allozyme, karyological, osteological, and ethological work, the phylogenetic and taxonomic relationships within the toad-headed lizards remain controversial and largely unresolved (e.g., Arnold, 1999; Dunayev, 1996; Golubev, 1993; Macey et al., 1993, and references therein), especially those among the approximately 18 Chinese species (Zhao and Alder, 1993; Pang et al., 2003). Members of the genus are characterized by similar morphological characters that contribute to the current problematic taxonomy of the group. Whiteman (1978) first pursued the evolutionary history of 23 *Phrynocephalus* species based on cladistic analysis of 16 osteological characteristics, which is, so far, the phylogenetic study with the most complete taxon sampling. Although an almost fully resolved tree was presented, many of the relationships should be considered tentative because of inappropriate outgroup taxa and misidentification of specimens. Arnold (1999) presented another phylogeny of the genus using 46 morphological data of 25 species. The analysis also left several unresolved nodes and the results were highly contradictory to those of Whiteman (1978). Recent morphological studies have raised further questions concerning the taxonomy and evolutionary relationships of Chinese toad-headed lizards (Wang and Jiang, 1992; Wang et al., 1996, 1999, 2002). A recent study by Pang et al. (2003) using mitochondrial DNA sequence data shed more light on the relationships of the Chinese *Phrynocephalus* and corroborated the monophyly of the viviparous group for the first time and identified two major clades representing the Chinese *Phrynocephalus* species: the viviparous group and the oviparous group (Clade A and Clade B in Fig. 1, respectively). However, all analyses (ML, MP, and unpartitioned Bayesian analyses) by Pang et al. (2003) could not resolve many of the interrelationships among the oviparous species, and this fact could be attributed to rapid radiation of the clades. More recent evidence from mtDNA *ND2* fragments has provided additional information about the taxonomy of *Phrynocephalus* (Wang and Fu, 2004), most notably for the *P. versicolor* species complex (*P. versicolor*, *P. frontalis*, and *P. przewalskii*), although the fundamental and broader evolutionary and biogeographic questions are still unclear.

The broad distribution of the genus *Phrynocephalus* has been explained by several different hypotheses. Ananjeva and Tuniyev (1992) speculated that there were two original centers for the *Phrynocephalus* species: Central Asia (a northern Tethys origin) and Middle Asia (a southern Tethys origin). Through a phylogenetic analysis of allozymes, Macey et al. (1993) suggested that *Phrynocephalus* represents an old radiation that has been evolving in response to the Indian collision with Eurasia 35 Ma, and a clade in the former Soviet Union may have diverged as a result of internal Eurasian block movements in Afghanistan caused by the indenting Indian continent. Later, Arnold (1999) proposed that *Phrynocephalus* originated in the Arabia-NW India area rather than in Central Asia, and achieved its current distribution by dispersal. However, Wang and Macey (1993) initially considered the origin of the viviparous species group as a result of a vicariance event associated with the uplifting of the Tibetan Plateau, which was subsequently supported by Zeng et al. (1997) and Pang et al. (2003). Meanwhile, Pang et al. (2003) hypothesized that the oviparous group achieved their current distribution by dispersal, based on low genetic divergences among its members and the geological hypothesis proposed by Xia and Hu (1993), who hypothesized 23.8–1.8 Ma for the formation of the Chinese desert. They also suggested that the close geographic proximity of the current deserts in northern China permitted dispersal of the oviparous species. However, Wang and Fu (2004), on the basis of *ND2*, proposed that the current distribution patterns of the *P. versicolor* species complex resulted from vicariance due to historical desert fragmentation rather than the traditional west-to-east dispersal hypothesis. As a consequence, there is yet to be a good evolutionary picture of how *Phrynocephalus* evolved as a whole, further testing the roles of vicariance and dispersal in speciation.

This study takes advantage of recent advances in phylogenetic methodology. Bayesian analysis is an attractive alternative to other model-based methods because prior knowledge can be quantified and current implementations estimate parameters (including trees) using posterior distributions, rather than optimization (Yang and Rannala, 1997; Larget and Simon, 1999). In addition, Bayesian analysis permits use of complex, parameter-rich stochastic models within a statistical framework, facilitating combined data analysis recognizing among-partition heterogeneity in data source and in properties of the evolutionary process. Moreover, the use of partitioned Bayesian analyses has facilitated the exploration of partition-specific evolutionary models and should reduce systematic error, thus providing more accurate posterior probability estimates (e.g., Nylander et al., 2004; Brandley et al., 2005). One potential shortcoming of the model-based analyses of Pang et al. (2003) was the assumption of a homogeneous substitution model (i.e., GTR + G) and parameter values across all gene regions.

Thus, as an extension of the molecular phylogenetics and biogeography of the Chinese *Phrynocephalus*, we reanalyzed the published multiple mitochondrial gene sequences of Pang et al. (2003) by employing partition-specific modeling in a combined analysis, i.e., partitioned