



Aridification driven diversification of fan-throated lizards from the Indian subcontinent

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ABSTRACT

The establishment of monsoon climate and the consequent aridification has been one of the most important climate change episodes in the Indian subcontinent. However, little is known about how these events might have shaped the diversification patterns among the widely distributed taxa. Fan-throated lizards (FTL) (Genus: *Sitana*, *Sarada*) are widespread, diurnal and restricted to the semi-arid zones of the Indian subcontinent. We sampled FTL in 107 localities across its range. We used molecular species delimitation method and delineated 15 species including six putative species. Thirteen of them were distinguishable based on morphology but two sister species were indistinguishable and have minor overlaps in distribution. Five fossils were used to calibrate and date the phylogeny. Diversification of fan-throated lizards lineage started ~18 mya and higher lineage diversification was observed after 11 my. The initial diversification corresponds to the time when monsoon climate was established and the latter was a period of intensification of monsoon and initiation of aridification. Thirteen out of the fifteen FTL species delimited are from Peninsular India; this is probably due to the landscape heterogeneity in this region. The species poor sister genus *Otocryptis* is paraphyletic and probably represents relict lineages which are now confined to forested areas. Thus, the seasonality led changes in habitat, from forests to open habitats appear to have driven diversification of fan-throated lizards.

1. Introduction

The Asian climate has been largely shaped by the uplift of the Himalayas, the rise of Tibetan plateau and glaciation in the Northern hemisphere (Zhisheng et al., 2001; Ali and Aitchison, 2008; Patnaik et al., 2012; Harrison et al., 1992). The establishment of monsoon climate was perhaps one of the most important outcomes of these events. The earliest evidence for the monsoon season in South Asia is during early Eocene (~55–52 mya) (Shukla et al., 2014) around the time the Indian plate collided with the Asian plate. Other studies suggest that monsoon-like pattern occurred much later around ~40 mya (Licht et al., 2014; Liu et al., 2017). While some authors construe that the origin of South Asian monsoon season is due to the uplift of Tibetan plateau (Kutzbach et al., 1993), others argue that it is also due to the changes in the land-sea distribution (Ramstein et al., 1997). The most recent hypothesis is that the establishment of South Asian monsoon is not related to the uplift of the Tibetan plateau but rather it is due to movement of the Indian plate into the tropical Northern Hemisphere from the tropical Southern Hemisphere (Liu et al., 2017). When the monsoon formed in South Asia (after Eocene) it was followed by

pronounced seasonality. First there was a cooling and drying phase around the Eocene-Oligocene boundary (~35 mya: Licht et al., 2014). This was followed by increased seasonality linked with the uplift of the Himalayas and Tibetan plateau (~23 mya: Clift et al., 2008) and an accelerated aridification from late Miocene onwards (~10 mya: Nelson, 2007; Molnar et al., 1993; Dettman et al., 2001). The Indian and Asian monsoons strengthened around 9–8 mya (Zhisheng et al., 2001) and there was drastic drop in ocean temperatures around 5 mya (Zachos et al., 2001). The global climate change during the Miocene and the aridification which followed may have influenced the diversification of several biotas of the Indian subcontinent. Past studies have highlighted the expansion of C4 grasses in many parts of the world including Asia during late Miocene 8–6 mya (Quade et al., 1989; Cerling et al., 1997; Retallack, 2001; Edwards et al., 2010; Stromberg, 2011; Agarwal and Ramakrishnan, 2017). The first grazing mammals started appearing in the subcontinent around 10 mya and there is evidence of long-term climatic influence on the vegetation structure and mammalian ecological diversity in this region (Barry et al., 2002; Badgley et al., 2008). Patnaik (2003) compared extant and fossil murids from Siwaliks, India and reported that abundance and distribution of murids from the

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Table 1
Primers used for DNA amplification and sequencing.

Primers	Sequence (5'-3')	Size (bp)	Reference
<i>ND2</i> L4437b H5540	AAGCAGTTGGGCCCATACC TTTAGGGCTTGAAGGC	~1026	Macey et al. (1997 and 2000)
<i>RAG1</i> RAG13F RAG18R	TCTGAATGGAAATTCAGCTGTT GATGCTGCCTCGGTGGCCACCTTT	~1005	Groth and Barrowclough (1999)
<i>R35</i> R35 F R35 R	GACTGTGGAYGAYCTGATCAGTGTGGTGCC GCCAAAATGAGSGAGAARCGCTTCTGAGC	~665	Leaché (2009)
<i>PDC</i> PHO F2 PHO R1	AGATGAGCATGCAGGAGTATGA TCCACATCCACAGCAAAAACTCCT	~424	Bauer et al. (2007)

Pliocene tend to overlap with the present. Patnaik (2003) suggests this is an indication of the establishment of monsoon climate similar to present during the early Pliocene. Furthermore, he also reports the appearance of hypsodonty and grazing components in murid molars in the late Miocene when there was a shift from C3-C4 plants (Patnaik, 2003).

The role of monsoon climate in shaping the current diversity and distributions of Indian biota remains unclear. Miocene aridification has shown to have influenced diversification in three groups of lizards (*Cyrtopodion*, *Cyrtodactylus* & *Ophisops*) in the Indian subcontinent (Agarwal et al., 2014; Agarwal and Karanth, 2015; Agarwal and Ramakrishnan, 2017). However, information is scarce on the groups that started diversifying more recently during the late Miocene and Pliocene.

In this regard, the fan-throated lizards (*Sitana* Cuvier, 1827) a widespread genus of small, terrestrial lizards is of much interest (Smith, 1935; Deepak et al., 2016a). They are inhabitants of open areas in the arid and semi-arid regions of India (Deepak et al., 2016a). They are distributed over much of India and in the plains and coasts of Sri Lanka. Until recently fan-throated lizards were thought to be a monotypic genus (Das, 1997). In the turn of this century three species were described from Nepal (Anders and Kästle, 2002; Schleich and Kästle, 1998; Schleich et al., 1998). In the past two years, six new species were described from India and Sri Lanka and the species diversity in *Sitana* increased from four to ten (Amarasinghe et al., 2015; Deepak et al., 2016a, 2016b). Additionally, a new genus of fan-throated lizard, *Sarada* Deepak, Giri and Karanth, 2016, with three species (Deepak et al., 2016a), was recently described. Thus, currently, the *Sarada-Sitana* complex consists of 13 species. The genus *Otocryptis*, a wet zone limited taxa distributed in Southwest India and Sri Lanka, has been shown to be the immediate sister of *Sarada-Sitana* complex (Macey et al., 2000; Grismer et al., 2016). Recent studies have shown the split between *Sitana* and *Otocryptis* is ~28 mya and this lineage originated from the wet zones in SE Asia (Grismer et al., 2016).

Given that the fan-throated lizards are widespread, semi-arid zone adapted and have multiple species distributed in a heterogeneous landscape with complex geological and climatic history, they are an ideal group for investigating speciation and biogeographic patterns, particularly with respect to the recently established arid zone. In the current study, we sampled fan-throated lizards from across their range covering different landscapes. We used multilocus genetic data to understand its phylogenetic relationship and diversification patterns. Additionally, species-delimitation tools based on gene trees and species trees were also implemented to characterize cryptic diversity in this group. We also compared morphological data to check if the delimited species are morphologically different. We wanted to address three main questions in this study 1. When did *Sarada + Sitana* start diversifying? And do their diversification dates correspond to the time when arid and semi-arid zones were getting established? 2. How many putative species

of *Sitana* and *Sarada* are found in India? 3. What are the potential biogeographic barriers governing the current distribution of different *Sarada + Sitana* species?

2. Materials and methods

2.1. Taxon sampling, DNA sequencing, and sequence alignment

We generated 257 sequences from 109 individuals collected in 107 localities across the distributional range of *Sitana* and *Sarada* (Supplementary material, Table S1; Fig. S1). Type localities and other likely habitats were targeted and lizards were hand collected during various field trips between 2011 and 2016. In areas under the jurisdiction of forest department collections were made with permits from respective state forest departments. Genomic DNA was extracted from liver and tail tip tissue samples that were stored in 99.9% ethanol and refrigerated at -20°C . DNeasy (Qiagen™) blood and tissue kit were used to extract DNA. The entire gene sequences for NADH dehydrogenase subunit 2 (ND2: ~1026 bp) mitochondrial gene and partial sequences of three nuclear genes: Recombination activating gene 1 (RAG1: ~1026), RNA fingerprint protein 35 (R35: 655 bp), and Phosducin (PDC: ~424 bp) were amplified by polymerase chain reaction (PCR) and sequenced. Primer sequences for these loci are listed in Table 1. The PCR cycles were same as in previous studies (Macey et al., 1997; Macey et al., 2000; Groth and Barrowclough, 1999; Bauer et al., 2007; Leaché, 2009).

2.2. Phylogenetic analysis

We reconstructed the molecular phylogeny of fan-throated lizards using the concatenated dataset with maximum likelihood (ML) and Bayesian methods (BI). *Otocryptis* was used as outgroup based on the findings by Macey et al. (2000). ND2 sequences for *Otocryptis wiegmanni* and other published sequences of *Sitana* were downloaded from GenBank (Supplementary material, Table S1). We were not able to get samples of three species of *Sitana* (*S. schleichi* Anders and Kästle, 2002, *S. fusca* Schleich and Kästle, 1998 and *S. devakai*, Amarsinghe, Ineich and Karunarathna, 2015) and one *Otocryptis* (*O. nigristigma* Bahir and Silva, 2005). Sequences were aligned using ClustalW and uncorrected genetic distances were calculated using MEGA 5 (Tamura et al., 2011). The program PartitionFinder v1.1.1 (Lanfear et al., 2012) was used to find the best partition scheme and model of sequence evolution for each partition. The optimal partitioning scheme included seven partitions (Supplementary material, Table S2). Likelihood analysis was undertaken in the program RAxML 1.3.1 (Stamatakis et al., 2005). This program employs only one model of sequence evolution, therefore we used GTR+G for all seven partitions. RAxML GUI (Silvestro and Michalak, 2012) was used to conduct a maximum likelihood analysis. We used the ML+ rapid bootstrap method to search for best scoring

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