Paleoclimate determines diversification patterns in the fossorial snake family Uropeltidae Cuvier, 1829

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ABSTRACT

Understanding how and why diversification rates vary across evolutionary time is central to understanding how biodiversity is generated and maintained. Recent mathematical models that allow estimation of diversification rates across time from reconstructed phylogenies have enabled us to make inferences on how biodiversity copes with environmental change. Here, we explore patterns of temporal diversification in Uropeltidae, a diverse fossorial snake family. We generate a time-calibrated phylogenetic hypothesis for Uropeltidae and show a significant correlation between diversification rate and paleotemperature during the Cenozoic. We show that the temporal diversification pattern of this group is punctuated by one rate shift event with a decrease in diversification and turnover rate between ca. 11 Ma to present, but there is no strong support for mass extinction events. The analysis indicates higher turnover during periods of drastic climatic fluctuations and reduced diversification rates associated with contraction and fragmentation of forest habitats during the late Miocene. Our study highlights the influence of environmental fluctuations on diversification rates in fossorial taxa such as uropeltids, and raises conservation concerns related to present rate of climate change.

1. Introduction

Environmental factors play a key role in mediating diversification processes by driving microevolutionary change and shaping phenotypic evolution. Until recently, researchers had to rely on the paleontological record to understand how biotic and abiotic factors have influenced spatio-temporal diversification patterns (Barnosky, 2001; Benton, 2009; Vermeij, 1994, 1987). Fossil data are, however, incomplete, unevenly distributed in space and time and are not available for many taxa, limiting inferences on diversification processes to certain taxa (Benton et al., 2000; Valentine et al., 2006). Recently, the advent of mathematical models and analytical tools to estimate speciation and extinction rates from reconstructed phylogenies (Etienne et al., 2012; Morlon et al., 2011; Nee et al., 1994b; Rabosky, 2014, 2006; Stadler, 2011) have revolutionized the study of historical diversification patterns. These methods have allowed more precise inferences on the underlying evolutionary mechanisms and the factors that influence diversification rates.

Although fossil evidence suggests that the environment has had a strong influence on speciation and extinction dynamics (Ezard et al., 2011), the potential role of paleoclimatic fluctuations in influencing diversification rates in different taxa has not been explored in great

detail. Climatic fluctuations can trigger shifts in species ranges (Barry et al., 1995; Thomas and Lennon, 1999) and thereby influence lineage diversification (Hou et al., 2011; Kolář et al., 2016; Pepper et al., 2011). Climate is also a driver of mass extinctions (Ivany et al., 2000; Lewis et al., 2008; Thomas, 1990), which not only prune branches off the tree of life (Green et al., 2011), but also influence lineages that survive by increasing ecological opportunity and thus enhancing diversification (Krug et al., 2009). A few empirical studies employing recently developed analytical tools to estimate diversification rates from molecular phylogenies suggest that paleoclimatic fluctuations have had a pronounced effect on diversification rates in several taxa (e.g. Birds – Claramunt and Cracraft, 2015; Jetz et al., 2012; Insects – Condamine et al., 2016; Spiny-rayed fish – Near et al., 2012; Amphibians – Roelants et al., 2007; Mammals – Stadler, 2011). Other studies have highlighted the pivotal role of mass extinctions in diversification rate variation (Krug et al., 2009; Longrich et al., 2012). Such studies, however, have been predominantly on aquatic and above ground terrestrial taxa. Fossorial taxa (i.e. those that are predominantly subterranean and burrow into the ground) have been largely ignored. The subterranean environment is structurally simple and thought to be relatively stable compared to above ground in terms of environmental fluctuations, and thus thought to persist relatively unchanged for millions of years

(Gibert and Deharveng, 2002). However, how environmental factors influence temporal diversification in fossorial taxa and the macroevolutionary implications of fossoriality remain unexplored.

We here investigate temporal diversification patterns of the snake family Uropeltidae, a lineage of highly specialized fossorial snakes found predominantly in the moist forests in peninsular India and Sri Lanka. Phylogenetically, Uropeltidae is within the major clade Alethinophidia. Morphology and molecular based phylogenies of snakes have consistently placed Uropeltidae sister to Cylindrophidae (Hsiang et al., 2015; Pyron et al., 2013a; Slowinski and Lawson, 2002; Streicher and Wiens, 2016; Vidal and Hedges, 2002; Wiens et al., 2008), although a few studies place Anomochilidae as the sister group to Uropeltidae (Hsiang et al., 2015; Lee et al., 2007; Lee and Scanlon, 2002 (Hsiang et al., 2015; Lee et al., 2007; Lee and Scanlon, 2002). Together, the clade comprising Uropeltidae, Cylindrophidae and Anomochilidae is generally referred to as Asian anilioids.

Presently the family Uropeltidae is represented by ca. 55 species within nine genera – *Melanophidium*, *Platyplectrurus*, *Teretrurus*, *Brachyophidium*, *Plectrurus*, *Pseudoplectrurus*, *Rhinophis*, *Pseudotyphlops* and *Uropeltis* (Wallach et al., 2014) with some authors considering *Pseudoplectrurus* as a synonym of *Rhinophis* (Pyron et al., 2016). The relationships among these genera have remained largely unknown, and morphology and molecular based phylogenetic analyses have resulted in unresolved polytomies (Bossuyt et al., 2004; Olori and Bell, 2012; Rieppel and Zaher, 2002). Here we present a robust genus level phylogenetic hypothesis along with divergence time estimates. We show that the temporal diversification pattern was influenced by a single diversification rate shift correlated with paleoclimatic events during the Cenozoic.

2. Materials and methods

2.1. Sampling

Sampling was carried out at multiple sites within the state of Kerala, Southern India. Collected samples were photographed, euthanized, fixed and preserved in ethanol, following which heart or liver tissues were collected and stored for DNA extraction. Additional tissue samples were obtained from ethanol preserved specimens deposited at the Zoological Survey of India – Western Ghat Regional Center (ZSI-WGRC).

2.2. DNA sequencing

Total genomic DNA was extracted using the standard Phenol-chloroform protocol (Bilton and Jaarola, 1996). One nuclear (c-mos) and three mitochondrial genes (12s rRNA, 16s rRNA and ND4) were amplified with the standard 3-step PCR protocol (Palumbi, 1996). We used hybrid primers with universal primer tails – T7 promoter (F) and T3 (R) attached to forward and reverse primers for PCR amplification (Appendix, Table A.1). PCR products were checked on an agarose gel, purified with ExoFastAP (Thermo Scientific™) and Sanger sequenced by Macrogen Inc, South Korea.

2.3. Phylogenetic analyses

A total of 71 taxa representing ~45 Operational Taxonomic Units (OTU's) (Uropeltidae + outgroups) were used for the analyses. Sequences of some uropeltids and their outgroups were obtained from Genbank (Appendix, Table A.3). Sequences of all the taxa for each gene were aligned separately using the MUSCLE algorithm (Edgar, 2004) implemented in MEGA6 (Tamura et al., 2013). Gaps were removed using Gap Strip/squeeze v2.1.0 (http://www.hiv.lanl.gov) with a gap tolerance of 75%, which deletes only columns that contain 75% gaps. Each gene dataset was checked for substitution saturation using DAMBE5 (Xia, 2013). The final multi-gene dataset containing 2121bp

was concatenated using SequenceMatrix v1.8 (Vaidya et al., 2011). The dataset was partitioned by codon position and PartitionFinder v1.1.1 (Lanfear et al., 2012) was used to find the best fit models of nucleotide substitution (Appendix, Table A.4). A Maximum Likelihood analysis was carried out in RAxML GUI v1.3 (Silvestro and Michalak, 2012) with 1000 bootstrap replicates using default parameters. Bootstrap support was summarized as a 50% majority rule tree using Summtrees v4.0.0 (Sukumaran and Holder, 2015) implemented in the python library DendroPy v4.0.3 (Sukumaran and Holder, 2010). Clades with bootstrap values > 90 were considered as strongly supported, while those with values between 70 and 90 were considered as moderately supported. Bayesian inference of phylogeny was carried out in Mr. Bayes v3.2.0 (Ronquist et al., 2012) for the combined dataset with default priors using Markov chain Monte Carlo (MCMC) with two independent runs performed for 12.97 million generations, when the standard deviation of the split frequency fell below 0.01. MCMC chains were checked for convergence using Tracer v1.6 (Rambaut et al., 2014) and summarized as a 50% majority rule tree after discarding the first 25% of the samples as burn-in. Clades with posterior probabilities greater than 0.95 were considered as strongly supported.

2.4. Divergence dating

For the divergence dating analyses we obtained representative sequences for the four gene regions of all major lineages within Alethinophidia from Genbank to derive a dataset of 2133 bp with 116 taxa. We included additional taxa that were not part of the analyses in Section 2.3. These additions were needed because there was no reliable calibration source within the smaller dataset. We did not use this larger dataset for the RAxML and MrBayes analyses, because it has been shown that outgroup choice may affect tree topology within the ingroup (Kodandaramaiah et al., 2010; Wheeler, 1990).

Divergence times were estimated through Bayesian Inference implemented in BEAST v2.3.0 (Bouckaert et al., 2014). The combined dataset was partitioned into three bins as determined by TIGER v1.02 (Cummins and McInerney, 2011) and the best fit models were determined by PartitionFinder v1.1.1 (Appendix, Table A.4). We constrained the monophyly of three major clades and calibrated the tree by temporally constraining four nodes based on available fossil data (Appendix, Table A.5). Two independent analyses were run for 100 million generations sampling every 1000 generations. A relaxed uncorrelated lognormal clock model was used with a birth-death speciation prior. Other priors were set to their default values. The two runs were checked for convergence in Tracer v1.6 and the first 25% of each run was discarded as burn-in. We combined the two runs using Log-Combiner v2.3.0 and constructed a maximum clade credibility tree using TreeAnnotator v2.3.0 in the BEAST2 package.

2.5. Diversification analyses

We pruned taxa from the ultrametric tree obtained from the divergence dating analyses to represent only the Asian anilioids, which included two species of Cylindrophidae, one species of Anomochilidae and 42 Operational Taxonomic Units within Uropeltidae (Appendix, Table A.6). We conducted all diversification analyses on three separate increasingly less inclusive trees pruned to represent the stem Asian anilioids, crown Asian anilioids and stem Uropeltidae to investigate the robustness of the temporal diversification pattern and rate estimates. The pruned datasets included 63% of the Asian anilioids which are presently represented by ca. 70 species and 75% of Uropeltidae which is represented by ca. 55 species.

We first plotted a Lineage through time (LTT) plot for the three trees. A visual inspection of the LTT plot of the stem Asian anilioids indicated an initial plateau ending at around 55 Ma and a smaller plateau around 34 Ma. Such plateaus in the LTT plots are often suggestive of relatively high background extinction or mass extinction

events (Crisp and Cook, 2009; Harvey et al., 1994). To further test the possibility that the temporal diversification pattern of Asian anilioids was punctuated by mass extinction events, we simulated 100 trees under different diversification models based on parameters estimated by LASER v2.4.1 (Rabosky, 2006), with and without mass extinction events incorporating incomplete taxon sampling and a diversified sampling strategy, and compared the resulting LTT plots with that of the empirical LTT plot. Since our phylogeny represents all genera within the Asian anilioids, we used a diversified sampling strategy that selects tips to maximize diversity by specifying higher probability of sampling older nodes. We simulated two mass extinction events at 55 Ma and 34 Ma for the stem Asian anilioids and one mass extinction event at 34 Ma for the crown Asian anilioids and the stem Uropeltidae. We modeled the intensity of the two mass extinctions by varying the probability of a lineage surviving the mass extinction event from 0.50% to 0.02% and visually compared the LTT plots. To account for the possibility of cryptic species and the unresolved taxonomy of uropeltids, we conducted the same analyses by reducing the sampling fraction by arbitrarily increasing the total number of taxa within the clade by 10 and 20 species to represent a total of 80 and 90 species for the stem and crown Asian anilioid tree, and a total of 65 and 75 taxa for the stem Uropeltidae tree. All simulations were conducted in the R package TESS v2.1.0 (Höhna et al., 2015) (downloaded from https://github.com/hoehna/TESS on 03.03.2017).

We performed a second series of analyses under the CPP on Mass Extinction Times (CoMET) model (May et al., 2016) implemented in TESS to estimate the timing of mass extinction events. CoMET explicitly models the timing of mass extinction events by considering speciation rate shifts, extinction rate shifts and mass extinction events as a compound Poisson process. The prior probability of surviving the mass extinction event was specified using a beta prior with shape parameters $\alpha = 5.26$ and $\beta = 100$ for the stem Asian anilioids, which specifies a 95% loss in the total number of species, and $\alpha = 33.33$ and $\beta = 100$ for the crown Asian anilioids and stem Uropeltidae trees, which specifies a 75% loss in the total number of species. We performed the analyses under a uniform sampling strategy using empirical Bayesian hyperpriors, which automatically specifies suitable hyperparameter values for the prior distribution of the speciation and extinction rate parameters by running an initial Bayesian MCMC analysis under a constant birth-death model (Höhna et al., 2015). We used a range of priors specifying the mass extinction rate where $\lambda_M = 0.1$, ln2, 2 and 5. We estimated the posterior probability density for each of the parameters by running the two independent MCMC chain for two million generations each. We discarded 25% of the samples as burn-in and assumed convergence when the estimated ESS values were above 300.

We further investigated if the temporal diversification pattern was influenced by episodic rate shifts. We used the birth-death-shift (BDS) model implemented in the R package TreePar v3.3 (Stadler, 2011) to estimate the maximum likelihood diversification and turnover rates along with timing of rate shift events accounting for incomplete taxon sampling. We analyzed the three pruned trees for zero, one, two, three, four and five rate shift events and estimated parameters for each 0.1 million year time interval. We performed likelihood ratio tests on pairs of models differing by one rate shift to select the best model. Since the sampling strategy is known to influence diversification rate estimates (Höhna et al., 2011), and the BDS model assumes uniform sampling, we used a stepping-stone algorithm to estimate marginal likelihoods for the different diversification models with both a uniform and diversified sampling strategy implemented in TESS. We estimated marginal likelihoods for a set of 18 models which included a yule model, constant birth-death model, exponentially decreasing speciation rates, exponentially increasing extinction rates and four rate shifts models with and without mass extinction events incorporating rate shift times estimated by the BDS analysis. We specified two mass extinction events at 55 Ma and 34 Ma for the stem Asian anilioids and one mass extinction event at 34 Ma for the crown Asian anilioids and stem Uropeltidae, as

was done in the LTT plot simulations and the CoMET analysis. We evaluated these candidate models using pair-wise Bayes factor (BF) comparisons and interpreted the values obtained using the scale provided by Jeffries (1961), wherein a BF greater than 3.2 is considered substantial and BF greater than 10 is considered as strong support for model M_0 over M_1. To account for cryptic species within Uropeltidae, we conducted two similar analyses estimating the marginal likelihoods and evaluating candidate models on each of the three trees, reducing the sampling fraction by arbitrarily increasing the total number of species within the clade by 10 and 20, as in the case of the simulated LTT plots. We further estimated the diversification and turnover rate parameters for the best model by running MCMC simulations using the tess.mcmc function in TESS.

We also used a paleoenvironment dependent birth-death model (Condamine et al., 2013), implemented in the R package RPANDA v 1.0 (Morlon et al., 2016), to test for the dependency of speciation and extinction rates on paleotemperature using the crown Asian anilioid and stem Uropeltidae trees. We used deep sea benthic foraminiferal oxygen isotope record, a proxy for Cenozoic global temperature (Zachos et al., 2008) inbuilt in RPANDA. We then estimated speciation and extinction rates as a function of paleotemperature with a linear and exponential dependency for a set of four paleotemperature dependant models – (1) speciation rate varying with paleotemperature and no extinction (2) speciation varying with paleotemperature and constant extinction rate (3) constant speciation rate and extinction varying with paleotemperature, and (4) both speciation and extinction varying with paleotemperature. We compared the fit of these models using the second derivative of Akaike's Information Criterion (AIC) scores.

3. Results

3.1. Phylogenetic relationships

Maximum likelihood (RAxML) and Bayesian analyses (MrBayes and BEAST) consistently recovered four major clades – clade I: comprising the three species of *Melanophidium*; clade II: comprising *Platyplectrurus*, *Teretrurus* and *Brachyophidium*; clade III: comprising *Pseudoplectrurus*, *Plectrurus*, Indian and Sri Lankan *Rhinophis*, *Pseudotyphlops* and Sri Lankan *Uropeltis*; Clade IV: comprising the Indian *Uropeltis*. The topologies obtained from the Maximum likelihood and Bayesian inference on the combined dataset were similar, with deeper nodes being resolved with high support (supplementary material, Fig. S1). *Melanophidium* was recovered as sister to all other uropeltids. *Platyplectrurus* was sister to *Teretrurus* while *Brachyophidium* was nested within *Teretrurus*. *Pseudoplectrurus* was sister to *Plectrurus,* and the two genera were together sister to the Indian *Rhinophis* + all Sri Lankan uropeltids. The Indian *Rhinophis* was recovered as monophyletic, sister to the Sri Lankan uropeltids in the ML and MrBayes analysis while the Sri Lankan uropeltids were nested within the Indian *Rhinophis* in the BEAST analysis. The Sri Lankan uropeltids (Sri Lankan *Rhinophis* + Sri Lankan *Uropeltis* + *Pseudotyphlops*) were also recovered as monophyletic with moderate support although relationships within this clade were not resolved. The Indian *Uropeltis* formed a well supported monophyletic group sister to the clade comprising *Pseudoplectrurus* + *Plectrurus* + (Indian *Rhinophis* + Sri Lankan uropeltids). Overall, the phylogenetic hypothesis for relationships among genera is well supported except for relationships among the Sri Lankan uropeltids.

3.2. Divergence dating

The BEAST MCMC analyses produced a topology consistent with the topology obtained from the MrBayes analyses (Fig. 1). The posterior mean estimates of the divergence times for the calibrated nodes were comparable to that of the prior node ages except for the estimates obtained for stem Colubroidea (mean = 65.14 Ma), which was much older than the prior (mean = 51.78 Ma). Our analysis indicates that
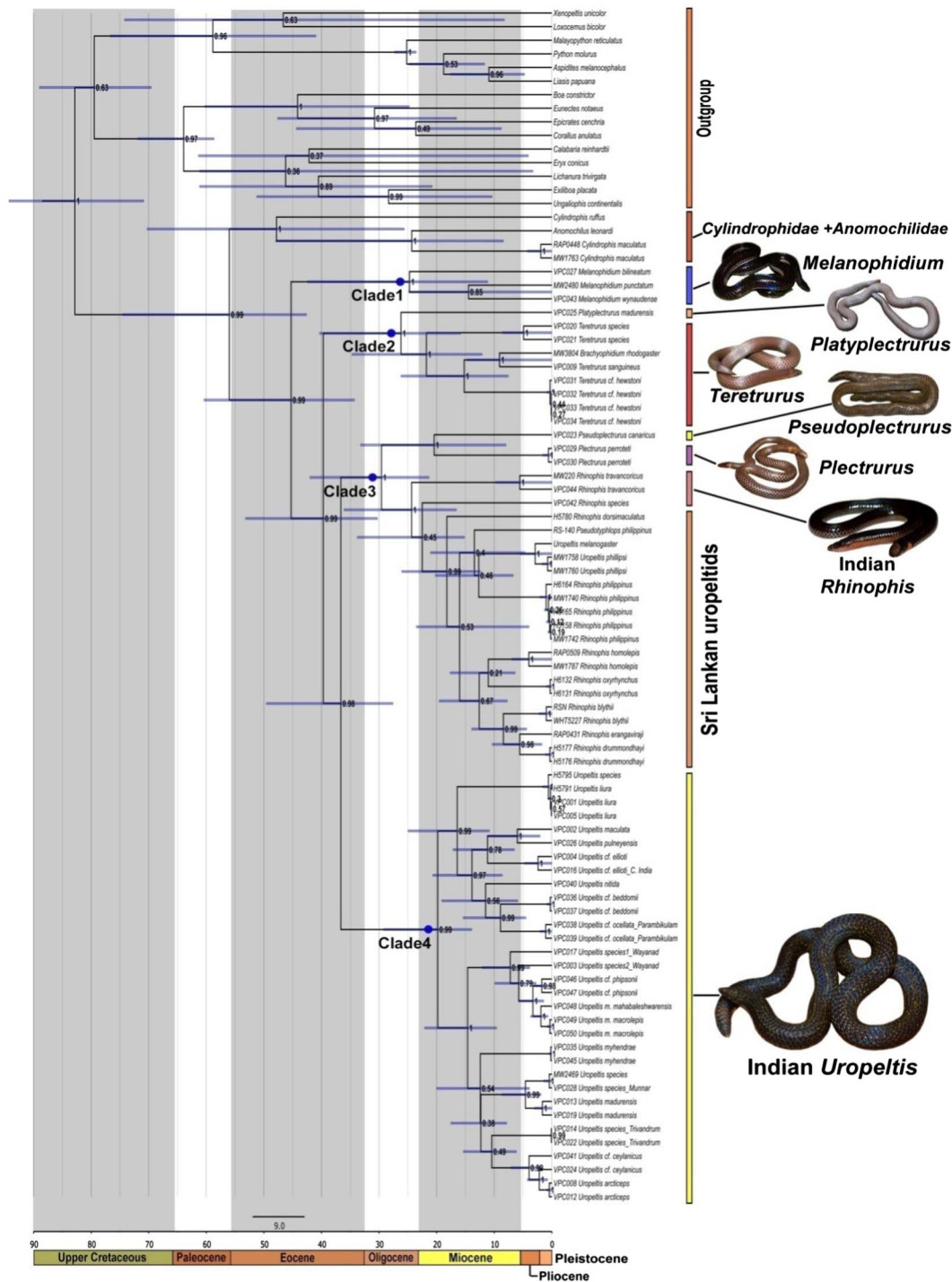
Fig. 1. Ultrametric tree of the Asian anilioids (Uropeltidae, Cylindrophidae and Anomochilidae) and outgroups, with divergence time estimates obtained from the combined dataset in BEAST. Nodal values indicate posterior probabilities and bars at the node indicate the 95% confidence intervals. The four major clades recovered from the MrBayes analysis are indicated at the node by a blue circle. The shaded grey and white regions of the image indicate adjacent geological time periods. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Uropeltidae forms a well supported monophyletic group. The dating estimates (Fig. 1) indicate that the divergence between the Asian anilioids ((Cylindrophidae + Anomochilidae) + Uropeltidae) and the rest of the Henophidia occurred during the upper Cretaceous (mean age = 82.83 Ma, CI = 94.28–70.87 Ma). Uropeltidae split from its sister Cylindrophidae + Anomochilidae during the Paleocene – Eocene boundary (mean age = 56.02 Ma, CI = 74.57–42.59 Ma). Basal divergences corresponding to the four major clades – I, II, III and IV occurred during the Eocene (between 55.8 and 33.9 Ma). The split

between the Indian *Rhinophis* and the Sri Lankan uropeltids occurred ca. 22 Ma (CI = 33.77–15.13 Ma) at the Oligocene-Miocene boundary. The divergence time estimates indicate a long temporal gap (ca. 26 Ma) between the stem and crown age of the Asian anilioids.

3.3. Diversification analyses

The LTT plot of the empirical stem Asian anilioid chronogram shows an initial plateaued region (i.e. no diversification events) starting at ca.
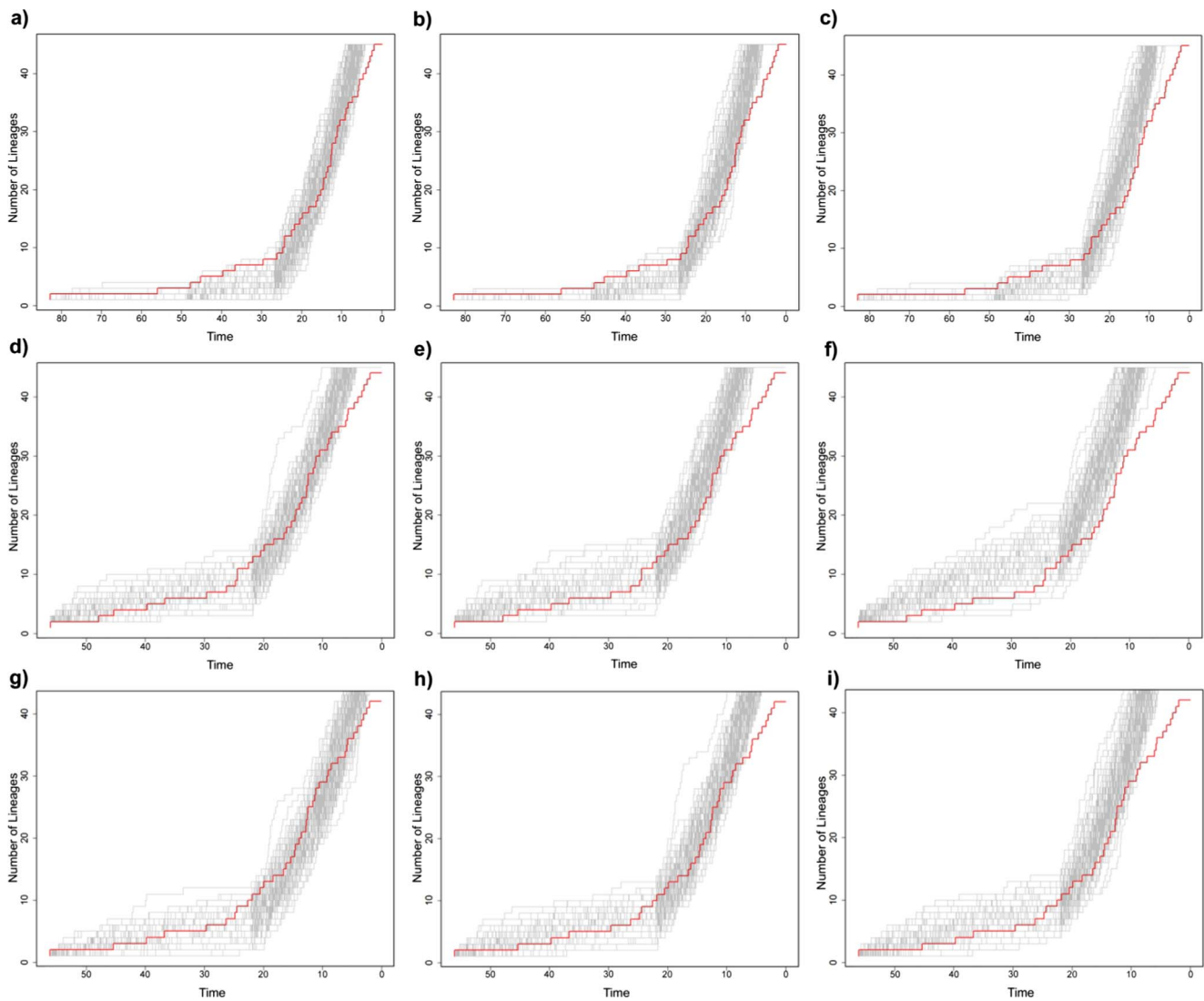
Fig. 2. Lineage through time plots for the 100 simulated trees modeled for a 2:1 birth-death process with one and two mass extinction events for different sampling fractions. The red line represents the empirical LTT plot while the gray lines represent the simulated LTT plots. (a), (b), (c) LTT plots for the stem Asian anilioids with 0.64, 0.56 and 0.50 sampling fraction respectively (d), (e), (f) LTT plots for the crown Asian anilioids with 0.64, 0.56 and 0.50 (g), (h), (i) LTT plots for the stem Uropeltidae with 0.76, 0.64 and 0.56 sampling fraction respectively.

83 Ma and ending at ca. 56 Ma, with a subsequent increase in lineage accumulation rate until ca. 26 Ma followed by a sharp increase in diversification events and a final decrease at ca. 10 Ma (Fig. 2). The LTT plot obtained for the crown Asian anilioids and stem Uropeltidae chronograms show an initial slow phase of lineage accumulation and an increase in diversification events after ca. 26 Ma and a final decrease at 10 Ma (Fig. 2). LTT plots generated by the simulations indicate that a 2:1 constant birth-death process (speciation rate estimated from a constant Yule process and extinction rate half the speciation rate) with two mass extinction events at 55 Ma and 34 Ma with a survival probability of 0.05 and 0.10 respectively, overlaps with the LTT plot of the empirical stem Asian anilioid chronogram. The simulated LTT plot incorporating a single mass extinction event at 34 Ma with survival probability of 0.10 closely matches the LTT plot for the empirical crown Asian anilioids and stem Uropeltidae (Fig. 2).

Analyses under the CoMET model to estimate the timing of mass extinction events identified one potential mass extinction event at ca. 57 Ma for the stem Asian anilioids and two potential, mass extinction events between ca. 56–49 Ma and ca. 31–27 Ma for the crown Asian anilioids and the stem Uropeltidae when assuming $\lambda_M = 2$ (Fig. 3). All mass extinction events identified by CoMET under the four mass

extinction rate priors recovered positive but non-significant support ($2lnBF > 2 < 6$) (Appendix, Fig. A.2).

Likelihood Ratio Tests of the pairs of rate shift models estimated using the BDS model indicated a 2-rate model with a rate shift at around 11 Ma to be the best fit model for the stem Asian anilioids and the stem Uropeltidae while a constant rate model best explained the crown Asian anilioids (Table 1; Appendix, Table A.8, A.9, A.10). This pattern was also consistent when reducing the sampling frequency by adding 10 taxa to the clade, but a constant rate model was the best model for the stem Uropeltidae when 20 taxa were added (Appendix, Table A.14). The diversification and turnover rate estimates from the BDS model suggested a marginal increase in diversification rate and a sharp decrease in turnover rates from ca. 11 Ma to present for both the stem Asian anilioids and stem Uropeltidae (Table 1). Pair-wise Bayes Factor comparisons of the different rate shift models incorporating both uniform and diversified sampling strategy suggested the two-rates model with a diversified sampling strategy to be the best model for the stem Asian anilioids, crown Asian anilioids and stem Uropeltidae across different sampling fractions (Table 1; Appendix, Table A.11, A.12, A.13). MCMC parameter estimates for the best model for all three trees indicated an initial moderate rate of diversification and high turnover
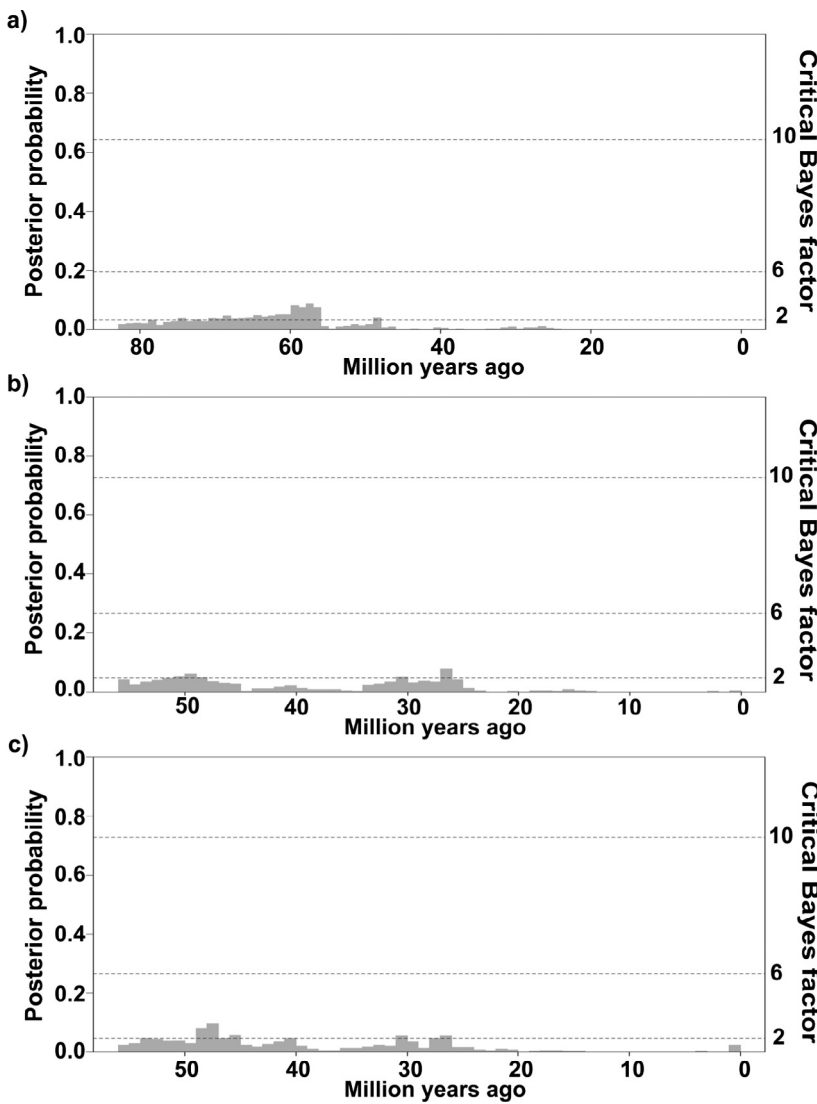
Fig. 3. Plots showing the posterior probability of the timing of mass extinction events for the CoMET model assuming $\lambda_M = 2$ (a) Timing of mass extinction events for stem Asian anilioids; (b). Timing of mass extinction events for stem Uropeltidae (c) Timing of mass extinction events for stem Uropeltidae. A critical Bayes factor (2lnBF) greater than two is considered as positive support for a potential mass extinction event.

with a marked drop in diversification rate and turnover rates at ca. 11 Ma (Table 1).

Evaluation of the influence of paleotemperature on diversification in the crown Asian anilioid and stem Uropeltidae trees using the paleoenvironment dependent birth-death model suggested a strong correlation between paleotemperature and diversification rates. The best supported model for both the pruned trees suggested a strong linear positive dependency of speciation and extinction rates on temperature (Table 2; Appendix, A.15). For the stem Uropeltidae, the analysis also indicates that the rate of change in extinction rates with temperature

was higher compared to the rate of change in speciation rate with temperature (Table 2).

4. Discussion

4.1. Phylogenetic relationships and biogeography

The two largest genera – *Uropeltis* and *Rhinophis* – were not recovered monophyletic. The Indian *Uropeltis* species formed a clade with high support. All three Sri Lankan *Uropeltis* formed a clade, which,

Table 1
Parameter estimates for the best model using the birth-death-shift (BDS) model with diversification rate per million years and rate shift times in million years.

	Stem Asian anilioids		Crown Asian anilioids		Stem Uropeltidae	
Best model:	2-rate model-uniform sampling		Constant birth-death model-uniform sampling		2-rate model-uniform sampling	
Parameter estimate (TreePar)	Diversification rate/Turnover rate	Rate shift time	Diversification rate/Turnover rate	Rate shift time	Diversification rate/Turnover rate	Rate shift time
	0.03097/0.08253		0.068554/0.000001	–	0.03360/0.07655	
	0.01433/0.92994	10.93		–	0.02900/0.85558	11.02
Best model:	2-rate model-diversified sampling		2-rate model- diversified sampling		2-rate model- diversified sampling	
Parameter estimates (TESS)	Mean Diversification/Extinction rate	Rate shift time	Mean Diversification/Extinction rate	Rate shift time	Mean Diversification/Extinction rate	Rate shift time
	0.03412/0.03587		0.03950/0.03202		0.04636/0.02711	
	0.62548/1.12187	10.93	0.59239/0.80209	11.02	0.41041/1.29649	11.02

Table 2
Parameter estimates of the eight paleoenvironment-dependant models and two rate constant models for the stem Uropeltidae. λ and μ are initial speciation and extinction rates respectively when temperature is 0 while α and β are the rate of change of speciation and extinction rates respectively.

Stem Uropeltidae

Model	Parameters	Dependency	logLik	AICc	ΔAICc	λ	α	μ	β
Yule	Speciation	Constant	−154.34	310.79	2.70	0.066	–	–	–
	Extinction	0							
const BD	Speciation	Constant	−154.34	313.00	4.91	0.066	–	3.7E−08	–
	Extinction	Constant							
1	Speciation	Linear	−153.28	310.88	2.79	0.022	0.006	–	–
	Extinction	0							
2	Speciation	Linear	−153.28	313.20	5.11	0.022	0.006	0.001	–
	Extinction	Constant							
3	Speciation	Constant	−154.18	314.99	6.90	0.074		0.044	−0.007
	Extinction	Linear							
4	Speciation	Linear	−149.50	308.09	0	−0.03	0.028	−0.34	0.06
	Extinction	Linear							
5	Speciation	Exponential	−153.77	311.86	3.77	0.046	0.052	–	–
	Extinction	0							
6	Speciation	Exponential	−153.77	314.18	6.09	0.046	0.054	2.004e−07	–
	Extinction	Constant							
7	Speciation	Constant	−154.34	315.32	7.23	0.066		1.247e−07	−0.03
	Extinction	Exponential							
8	Speciation	Exponential	−153.31	315.71	7.62	0.059	0.026	−0.009	0.065
	Extinction	Exponential							

grouped together with the Sri Lankan *Rhinophis* and the monotypic Sri Lankan endemic *Pseudotyphlops*. Pyron et al. (2016) in their recent phylogeny of Uropeltidae recovered the Sri Lankan uropeltids (*Rhinophis*, *Uropeltis* and *Pseudotyphlops*) as a single clade with the Indian *Rhinophis travancoricus* nested within it, which warranted them to move the Sri Lankan *Uropeltis* and *Pseudotyphlops* to *Rhinophis*. Contrastingly, our results suggest all Sri Lankan uropeltids were together monophyletic, and this larger clade was either sister to the Indian *Rhinophis* (MrBayes analysis; supplementary material, Fig. S1) or nested within the Indian *Rhinophis* (BEAST analysis; Fig. 1). We note that Pyron et al. (2016) did not sample all genera and had a poor representation of Indian taxa, whereas we have included all genera and an extensive sampling of Indian species. The nested pattern of Sri Lankan elements within Indian clades has been previously reported in many groups such as freshwater fish, freshwater crabs and caecilians (Bossuyt et al., 2004). Such patterns have also been discussed previously in uropeltid snakes (Bossuyt et al., 2004; Cadle et al., 1990; Pyron et al., 2013b), but, these results have not been conclusive due to the low representation of Indian taxa in their analysis. Our study, which comprises the most comprehensive analysis of Uropeltidae, clearly indicate the Sri Lankan uropeltids to be nested within Indian species of clade III (Fig. 1) and provides further evidence for the *in-situ* diversification of Sri Lankan uropeltids following a dispersal event from India.

Brachyophidium was nested within *Teretrurus* with high support, and we therefore suggest that the former should be synonymized with the latter, as in Smith (1943) and several other works (Cadle et al., 1990; Rieppel and Zaher, 2002). However, we note that the taxonomic history of the two genera has been complex (McDiarmid et al., 1999), and a detailed taxonomic reassessment may be required to stabilize the two names.

Our dating estimates for the Alethinophidia dataset with 116 taxa were similar to those of Zheng and Wiens (2016) except for the stem Alethinophidia and for the dates within Henophidia. These differences are likely because Zheng and Wiens (2016) did not calibrate any node within Henophidia. Divergence times for the stem Asian anilioids and the crown Asian anilioids were similar to those in Pyron and Burbrink (2012) and Hsiang et al. (2015).

Previous biogeographic analyses suggest that boas (Boidea) started evolving in Madagascar + Africa (Noonan and Chippindale, 2006; Reynolds et al., 2014). Boas are sister to the clade comprising Bolyeriidae, Xenopeltidae, Loxocemidae and Pythonidae. Within the latter clade, Bolyeriidae (endemic to Mauritius) is sister to the rest (Streicher and Wiens, 2016). Recent geophysical data suggest that Mauritius separated from Madagascar between 83.5 and 70 Ma (Torsvik et al., 2013), suggesting a likely Malagasy origin for the entire clade. Our analyses suggest that the stem Asian anilioids split from the rest of the Henophidia (Boidea + Bolyeriidae, Xenopeltidae, Loxocemidae and Pythonidae) ca. 82 Ma, which closely corresponds to the breakup of the Indian subcontinent from Madagascar. Therefore, we surmise that the Asian anilioids may have originated in India as a result of vicariance between India and Madagascar.

The split between Uropeltidae and Cylindrophidae + Anomochilidae is estimated at ca. 56 Ma (Fig. 1), corresponding to a time period (50–57 Ma) when biotic interchange was prevalent between India and mainland Asia (Aitchison et al., 2007; Grismer et al., 2016; Klaus et al., 2010; Li et al., 2013). This suggests an initial dispersal of the Asian anilioids into mainland Asia and subsequent divergence into Uropeltidae in India and Cylindrophidae + Anomochilidae in south-east Asia.

4.2. Temporal diversification pattern

Model evaluation for the different BDS models for the stem Asian anilioids and stem Uropeltidae supported a 2-rate model with increase in diversification rate and decrease in turnover rates between ca. 11 Ma to present. However, parameter estimates from the MCMC simulations after incorporating diversified sampling indicated a decrease in diversification rates and turnover rates at around 11 Ma. This pattern of decreased diversification at ca. 11 Ma was consistent even after reducing sampling fraction (Appendix, Table A.14). This incongruence between diversification rate parameters could be because TreePar assumes a uniform sampling strategy that specifies equal probability for each node to be sampled regardless of node age. Model evaluation of the rate shift models under a uniform and diversified sampling strategy indicates strong support for diversified sampling strategy. It has been shown that the sampling strategy can influence diversification rate estimates (Höhna et al., 2011). Specifically, extinction rates are drastically underestimated when a diversified sample is treated as random or uniform, leading to biased estimates for diversification rates (Höhna et al., 2011). To summarize, the two methods – BDS and TESS – both indicate a shift in diversification rates ca. 11 Ma with the parameter estimates in TESS under diversified sampling indicating a decrease in

the diversification and turnover rates.

The overall decrease in diversification and turnover rates at ca. 11 Ma closely coincides with a period of gradual cooling and contraction of forests in the Late Miocene, which started ca. 10 Ma (Osborne, 2008; Zachos et al., 2008). The Cenozoic climate is characterized by pronounced climatic fluctuations with an initial extremely warm period during the Paleocene-Eocene Thermal Maxima (PETM) around 55 Ma and the Early Eocene Climatic Optimum (EECO) at ca. 50 Ma proceeding with a gradual prolonged cooling with few intermittent warm periods such as the Late Oligocene warming and Mid Miocene Climatic Optima (MMCO) (Mudelsee et al., 2014; Zachos et al., 2001, 2008). The Miocene Climatic Optimum (~17.5–15 Ma) characterized by an increase in temperature, high precipitation and expansion of rain forests (Keeley and Rundel, 2005; Osborne, 2008), was soon followed by a rapid cooling between 14.7 and 12.7 Ma (Lear et al., 2010) and a gradual prolonged cooling until 6 Ma (Zachos et al., 2001) which has been associated with the expansion of grasslands and fragmentation of forests (Cerling et al., 1997; Osborne, 2008). Phytographic reconstructions of the Cenozoic vegetation from different locations in India also reflect global paleoclimatic patterns (Behrensmeyer et al., 2007; Mandaokar and Mukherjee, 2012; Prasad et al., 2009; Quade et al., 1995; Samanta et al., 2013; Shukla and Mehrotra, 2014). There is palynological evidence for a tropical to sub-tropical warm humid climate in India during the early Miocene (Kern et al., 2013; Mandaokar and Mukherjee, 2012). Stable isotope variation in Indian paleosols and pollen fossils from the later Miocene also indicate replacement of forests with C4 grasslands between ca. 11 and 5 Ma associated with global cooling (Quade et al., 1995; Zhang et al., 2012). Range contraction and reduced niche availability associated with fragmentation of forests and grassland expansion could lead to decrease in diversification rate (Cardillo et al., 2003; Rolland and Salamin, 2016), as also indicated in our dataset at ca. 11 Ma. Similar patterns of decreased diversification in many groups of terrestrial taxa such as insects, mammals and reptiles have been linked to biome turnover in the cooler late Miocene (Brennan and Oliver, 2017; Condamine et al., 2016; Condamine and Hines, 2015; Finarelli and Badgley, 2010; Stadler, 2011; Toussaint et al., 2014).

Our paleotemperature-dependant analysis in RPANDA shows a positive dependence of speciation and extinction with temperature for both the crown Asian anilioid and stem Uropeltidae trees. Turnover rates were higher during warmer periods (Table 1) and the rate of change in extinction rate with temperature was much higher compared to the rate of change of speciation rate with temperature, suggesting that uropeltid snakes are highly sensitive to climatic fluctuations. This is consistent with our diversification rate estimates which indicate high rates of turnover prior to 11 Ma, influenced by frequent warming events. The close concordance between diversification rate shifts and global paleoclimatic fluctuations corroborates the paleotemperature dependant analysis, and the results together highlight the influence of paleoenvironmental changes on diversification rates. We acknowledge that extinction rates are very difficult to accurately estimate (see for e.g. Nee et al., 1994a; Rabosky, 2010). However, some studies have reported that extinction rates can be estimated with reasonable accuracy under certain conditions (Etienne et al., 2012; Morlon et al., 2011). Therefore, further simulation studies are needed to understand under what scenarios extinction rates are reliable. Here, instead of basing our inferences on absolute extinction rates, we instead use relative extinction rates which we believe are more informative.

The LTT plot simulations indicate a major mass extinction event at the root of the tree and a subsequent minor mass extinction after ca 18 Ma. However, the long plateau at the base of the stem Asian anilioid tree cannot be confidently attributed to a mass extinction because such a pattern could just be an artifact of branch lengths and branching pattern, and inclusion of the outgroup. The CoMET analysis also renders positive but low support (2lnBF < 6) for two mass extinction events. The power of the CoMET model is limited by its inability to detect sequentially close mass extinction events and mass extinctions events at

the root of the tree (May et al., 2016). Although not statistically significant, the timings of mass extinctions supported by the CoMET analysis between 56–49 Ma and 31–27 Ma, are both consistent with major paleoclimatic events associated with the extremely warm PETM and EECO (Sluijs et al., 2014; Wright and Schaller, 2013) and the cold Eocene-Oligocene transition (EOT) (Bosboom et al., 2014; Sun and Windley, 2015; Wang et al., 2016). Both these time periods have been associated with high rates of extinctions in marine invertebrates, amphibians, reptiles and land mammals (Ezard et al., 2011; Haasl and Hansen, 1996; Hooker et al., 2004; Ivany et al., 2000; Prothero, 1994; Thomas, 1990). While there is no strong support for mass extinction events in our trees, the simulated LTT plots and CoMET analysis are suggestive of higher extinction rates during the time period between the Paleocene to Oligocene, which is also supported by higher turnover rates estimated by TESS prior to ca. 11 Ma. These analyses together suggest a dominant role of Cenozoic climatic fluctuations in influencing temporal patterns in diversification of these snakes.

Several paleontological and neontological studies have supported the view that paleoenvironmental changes have been a prominent driver of macroevolutionary dynamics (Claramunt and Cracraft, 2015; Condamine et al., 2013; Ezard et al., 2011; Hannisdal and Peters, 2011; Lagomarsino et al., 2016). There is also ample paleontological evidence for diversification rate increase following mass extinctions (Ezard et al., 2011; Krug et al., 2009; Krug and Jablonski, 2012; Sibert and Norris, 2015). However, some recent rate estimates based on molecular phylogenies indicate no such pattern following mass extinctions (Meredith et al., 2011; Near et al., 2013; Stadler, 2011). Our analysis could not detect strong evidence for mass extinction events but show that the temporal diversification dynamics of the fossorial uropeltid snakes have been influenced by paleoclimatic fluctuations during the Cenozoic.

Our study suggests that the diversification dynamics of uropeltid snakes were influenced by above ground temperature fluctuations and that increase in temperature has a greater effect on extinction rates than on speciation rates. Studies on subterranean rodent burrows suggest that microclimate in burrows are influenced by prevailing above ground environmental conditions such as temperature, precipitation and vegetation (Burda et al., 2007) and are thus sensitive to above ground environmental fluctuations. Habitat specialization is thought to increase extinction risk (Colles et al., 2009). Like many other fossorial vertebrates, uropeltid snakes are highly specialized to their fossorial environments (Gans and Baic, 1977; Gans et al., 1978; Olori and Bell, 2012), and may not be able to cope with rapid environmental fluctuations, as suggested by high turnover rates during periods of rapid fluctuating temperatures.

Given the present rate of global temperature rise and species extinction crisis (Barnosky, 2001), understanding how biodiversity has coped with environmental fluctuations in the past is vital for assessing extinction risks of species and effective conservation management (Barnosky, 2001; Purvis, 2008; Purvis et al., 2000). Studies assessing extinction risk in mammals have consistently suggested fossorial species to have lower risks (Davidson et al., 2009; Liow et al., 2009). However, these inferences cannot be generalized to other fossorial vertebrates and further studies are required to understand how ecology and physical environment mediate the macroevolutionary dynamics of species living underground and how this in turn influences the extinction risk of species to rapid human mediated environmental change.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2017.08.017.

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