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Phylogenetic relationships of xenodermid snakes (Squamata: Serpentes: Xenodermidae), with the description of a new genus

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Abstract

Xenodermidae is a generally poorly known lineage of caenophidian snakes found in South, East and Southeast Asia. We report molecular phylogenetic analyses for a multilocus data set comprising all five currently recognised genera and including new mitochondrial and nuclear gene sequence data for the recently described *Stoliczkia vanhnuailianai*. Our phylogenetic results provide very strong support for the non-monophyly of *Stoliczkia,* as presently constituted, with *S. borneensis* being more closely related to *Xenodermus* than to the Northeast Indian *S. vanhnuailianai*. Based on phylogenetic relationships and morphological distinctiveness, we transfer *Stoliczkia borneensis* to a new monotypic genus endemic to Borneo, *Paraxenodermus* **gen. nov.** We also present new morphological data for *P. borneensis*.

Key words

Borneo, endemic, morphology, *Paraxenodermus* gen. nov., phylogeny, taxonomy

Introduction

The caenophidian snake family Xenodermidae Gray, 1849 includes five currently recognised genera, namely *Achalinus* Peters, 1869, *Fimbrios* Smith, 1921, *Parafimbrios* Teynié, David, Lottier, Le, Vidal & Nguyen, 2015, *Xenodermus* Reinhardt, 1836 and *Stoliczkia* Jerdon, 1870. *Achalinus* is the most speciose of these genera, with 19 currently recognised species, 10 of which were described in the past five years (Uetz et al. 2021). *Achalinus* spp. are distributed from north of 20° latitude in Vietnam, across south-east China and into central Japan (Fig. 1). *Fimbrios* comprises two species (Smith 1921; Ziegler et al. 2008), distributed in southern and central Laos and Vietnam,

with a record from southern Cambodia (Fig. 1). The two species of the recently described *Parafimbrios* are thus far recorded only from northern Vietnam, Laos and Thailand (Fig. 1). The monotypic *Xenodermus* may be the most widespread xenodermid species, occurring in southernmost Myanmar, Thailand, peninsular Malaysia, Borneo, Sumatra and Java (Fig.1). The genus *Stoliczkia* currently includes three poorly known species with a particularly disjunct distribution, two occurring in Northeast India (*S. khasiensis* Jerdon, 1870 and *S. vanhnuailianai* Lalronunga, Lalhmangaiha, Zosangliana, Lalhmingliani, Gower, Das & Deepak, 2021) and one in northern and western Borneo (*S. borneensis*) (Das 2021; Stuebing et al. 2014) (Fig.1). Previously, molecular data were available only for *S. borneensis* (Vidal and Hedges 2002), and few morphological data for the <10 reported specimens of *Stoliczkia* (sensu lato) had been published (Lalronunga et al. 2021). In this paper, we report the first molecular data for Northeast Indian *Stoliczkia* and new morphological data for *S. borneensis*. We test the monophyly of *Stoliczkia*, and describe a new genus for the Bornean species.

Materials and Methods

DNA extraction and amplification

We collected a liver sample from the holotype (and only reported specimen of) *Stoliczkia vanhnuailianai,* preserved it in 99% ethanol and stored in –20°C freezer. We extracted genomic DNA using the DNeasy (Qiagen) blood and tissue kit and amplified partial sequences of four mitochondrial (mt) and two nuclear (nu) genes. The mt genes are 16S rRNA (*16S*, 528 base pairs [bp]), 12S rRNA (*12S*, 317 bp), cytochrome *b* (*cytb,* 654 bp) and cytochrome oxidase subunit 1 (*co1*, 710 bp); and the nu markers are oocyte maturation factor (*cmos*, 449 bp) and neurotrophin-3 (*nt3*, 507 bp*)*. PCR conditions followed previously reported protocols (*16S*, primers 16Sar-L and 16Sbr-H: Palumbi et al. 1991; *12S*, primers 12Sa-L and 12Sb-H: Palumbi et al.1991; *cytb*, primers GluDG L: Palumbi 1996 and H16064: Burbrink et al. 2000; *co1,* primers LCO 1490 (F) and HCO 2198 (R): Folmer et al. 1994; *cmos*, primers S77 and S78: Lawson et al. 2005; *nt3,* primers nt3f and nt3r: Townsend et al. 2008). Sanger sequencing was carried out using the same primers. We assembled contigs from bidirectional sequence chromatograms and edited them in SnapGene Viewer (http://www.snapgene.com/products/snapgene_viewer).

Phylogeny

We aligned the new sequences for *Stoliczkia vanhnuailianai* with eight other xenodermids, and an outgroup, the non-xenodermid caenophidian *Acrochordus granulatus*. We checked for stop codons in unexpected regions by translating nucleotide alignments to amino acids for protein-coding genes (*cytb, co1, cmos, nt3*) using MEGA 7 (Kumar et al. 2016). We aligned sequences using ClustalW (Thompson et al.1994) in MEGA 7 (Kumar et al. 2016) with default settings (alignments online from the Natural History Museum data portal: https://doi.org/10.5519/gbzyjuli).

First, we built individual gene trees using Maximum Likelihood (ML). Based on availability of sequence data, we selected one species per xenodermid genus (though included both *S. borneensis* and *S. vanhnuailianai* for *Stoliczkia*) and the outgroup. We then aligned and concatenated the six gene sequences into a single dataset (3122 basepairs in length) with ten tips, including the outgroup (Table 1).

We used PartitionFinder2 (Lanfear et al. 2017) to identify the best-fit partition scheme for the concatenated dataset and the best-fit model of sequence evolution for each partition as determined by the Bayesian Information Criterion (BIC), using the default greedy algorithm linked to branch lengths (Lanfear et al. 2012). The best-fit scheme for the concatenated dataset comprises six partitions, by gene and by codon position (Table 2). We performed Maximum Likelihood (ML; Felsenstein 1981) phylogenetic analyses with RAxML GUI Ver. 2.0 (Edler et al. 2021), using the GTRGAMMA model of sequence evolution, which is recommended over GTR+G+I because the 25 rate categories account for potentially invariant sites (Stamatakis 2006). For Bayesian (BI) phylogenetic analyses we used MrBayes 3.2.6 (Ronquist et al. 2012) via the XSEDE portal CIPRES Science Gateway v3.3 (Miller et al. 2010), with default prior settings and with all six partitions assigned their best-fit model as determined by PartitionFinder (Table 2). We set up two separate runs with four Markov chains each, initiated from random trees and allowed to run for one million generations, sampling every 100 generations and discarding the first 25% of trees as "burn-in". We terminated the analyses when the standard deviation of split frequencies was less than 0.005, and then constructed majority rule consensus trees. We checked for effective sample size (ESS) values using Tracer 1.7 (Rambaut et al. 2014), all parameter values had ESS values >200. We quantified support for internal branches in ML and BI trees using bootstrap (500 replicates) and posterior probability, respectively. We assessed levels of support for relationships incompatible with optimal trees by inspecting bipartition tables of ML bootstrap or BI posterior probability trees using PAUP* 4.0a 169 (X86) (Swofford 2003). We rooted the trees with *Acrochordus granulatus* because it is a non-xenodermid caenophidian snake (Figueroa et al. 2016; Deepak et al. 2018; Zaher et al. 2019).

Molecular dating

We aligned a larger dataset with 68 tips including two scolecophidians (*Gerrhopilus mirus* and *Liotyphlops albirostris*) and representatives of all subfamilies of Alethinophidia, including nine xenodermids (sampling all five currently recognised genera). We aligned this dataset

Table 1. GenBank accession numbers and voucher numbers for the sequences used in this study. Sequences used in the ML and BI concatenated phylogeny are indicated with an asterisk. Accession codes for sequences newly generated in this study are in bold text.

Species	**Family**	***12S***	***16S***	***cytb***	***cmos***	***nt3***	***co1***
*Acrochordus granulatus**	Acrochordidae	AF544738	AF544786	AF217841	HM234057	FJ434082	MH273113
Acrochordus javanicus	Acrochordidae	KX694587	AF512745	KX694897	HM234058	KX694991	LC533890
Agkistrodon contortrix	Viperidae (Crotalinae)	AF156587	AF156566	EU483383	—	—	MN135583
Ahaetulla pulverulenta	Colubridae (Ahaetuliinae)	KC347304	KC347339	KC347454	KC347378	—	—
Anilius scytale	Aniliidae	AF544753	FJ755180	U69738	AF544722	FJ434066	—
Anomochilus leonardi	Cylindrophiidae + Anomochiliidae	AY953430	AY953431	—	—	—	—
Aparallactus capensis	Atractaspididae (Aparallactinae)	FJ404129	AY188045	AY188006	AY187967	—	—
Aplopeltura boa	Pareidae (Pareinae)	AF544761	AF544787	JF827673	JF827696	FJ434085	—
Asthenodipsas laevis	Pareidae (Pareinae)	—	KX660197	KX660469	KX660336	—	—
Azemiops feae	Viperidae (Azemiopinae)	KX694579	AF057234	AY352747	AF544695	KX694977	KP403570
Bitis nasicornis	Viperidae (Viperinae)	DQ305411	AY188048	DQ305457	AY187970	—	MH273549
Boa constrictor	Boidae	AF512744	AB177354	AB177354	AF544676	—	MH140079
Boaedon fuliginosus	Lamprophiidae (Lamprophiinae)	FJ404169	AY188079	AF471060	FJ404270	FJ434094	AY122663
Bothrolycus ater	Lamprophiidae (Lamprophiinae)	FJ404144	AY611859	AY612041	FJ404347	—	MH273562
Buhoma depressiceps	Lamprophiidae incertae sedis	FJ404147	AY611860	AY612042	AY611951	—	—
Buhoma procterae	Lamprophiidae incertae sedis	FJ404148	AY611818	AY612001	AY611910	—	—
Bungarus fasciatus	Elapidae	EU547135	EU579523	EU579523	AY058924	KX694998	KY769767
Calabaria reinhardtii	Calabariidae	KF576842	Z46494	AY099985	AF544682	—	MH273568
Calamaria pavimentata	Colubridae (Calamariinae)	MH445959	KX694624	AF471081	AF471103	KX694999	MK064858
Candoia carinata	Candoiidae	AF544741	EU419850	AY099984	AY099961	FJ434077	—
Cantoria violacea	Homalopsidae	EF395873	KX694627	EF395897	—	KX695001	—
Casarea dussumieri	Bolyeridae	AF544754	AF544827	U69755	AF544731	FJ434069	—
Charina bottae	Charinidae (Charininae)	AF544743	AF544816	AY099986	AY099971	FJ434079	—
Chilabothrus striatus	Boidae	—	—	KC329933	KC329991	DQ465554	—
Contia tenuis	Colubridae (Dipsadinae)	AY577021	AY577030	GU112384	AF471134	—	KU986070
Corallus annulatus	Boidae	JX244286	—	KC750012	KC750007	—	MH140107
Cylindrophis ruffus	Cylindrophiidae+Anomochilidae	MK065683	AB179619	AB179619	AF471133		MK064906
Daboia russelii	Viperidae (Viperinae)	DQ305413	EU913478	EU913478	AF471156	—	GQ225661
Ditypophis vivax	Lamprophiidae	FJ404150	AY188052	AY188013	—	—	KU567322
Epicrates cenchria	Boidae	AF368059	—	HQ399501	KC330008	JX576186	—
Eryx colubrinus	Erycidae	AF544747	AF544819	U69811	AF544716	DQ465569	—
Eryx conicus	Erycidae	GQ225680	AF512743	GQ225658	—	—	—
Eunectes notaeus	Boidae	AF368057	AM236347	HQ399499	HQ399536	—	—
Gerrhopilus mirus	Gerrhopilidae	AM236345	AM236345	AM236345		GU902566	AM236345
Grayia ornata	Colubridae (Grayiinae)	AF158434	AY611866	AY612048	AF544684	KX695019	MH274058

Species	Family	*12S*	*16S*	*cytb*	*cmos*	*nt3*	*co1*
Hologerrhum philippinum	Lamprophiidae (Cyclocorinae)		—	MG458758	MG458766	—	—
Homoroselaps lacteus	Lamprophiidae (Atractaspidinae)	KX694590	AY611809	AY611992	AY611901	KX695021	—
Liasis mackloti	Pythonidae	EF545024	EF545051	U69839	AF544726	FJ434075	—
Liopholidophis sexlineatus	Lamprophiidae (Pseudoxyrhophiinae)	FJ404174	AY188063	DQ979985	AY187985	—	JQ909421
Liotyphlops albirostris	Anomalepididae	AF366693	AF366762	AF544672	AF544727		MH140260
Loxocemus bicolor	Loxocemidae	AF512737	AF544828	AY099993	AY444035	FJ434072	—
Micrelaps bicoloratus	Lamprophiidae (Aparallactinae)		—	DQ486349	DQ486173	—	—
Mimophis mahfalensis	Lamprophiidae (Psammophiinae)	KX694543	AY188070	DQ486461	AY187992	KX695030	JQ909482
Naja (Afronaja) mossambica	Elapidae	GQ359658	AY611813	AY611996	AY611905	—	—
Naja (Boulengerina) melanoleuca	Elapidae	U96801	AY611812	AY611995	AY611904	—	MH274485
Oxyrhabdium leporinum	Lamprophiidae (Cyclocorinae)	—	—	AF471029	DQ112081	—	—
Oxyuranus scutellatus	Elapidae	EU547100	EU547149	EU547051	EU546916	—	—
Pareas carinatus	Pareidae (Pareinae)	AF544773	AF544802	JF827677	JF827702	FJ434086	—
Prosymna janii	Lamprophiidae (Prosymninae)	FJ404193	FJ404222	FJ404319	FJ404293	—	—
Pseudaspis cana	Lamprophiidae (Pseudaspidinae)	FJ404187	AY611898	AY612080	DQ486167	—	—
Pseudoxenodon karlschmidti	Colubridae (Pseudoxenodontinae)	KX694578	JF697330	AF471080	AF471102	KX695042	MK064781
Python bivittatus	Pythonidae	KF010492	KF010492	JX401131	AF435016		KF010492
Rhinophis drummondhayi	Uropeltidae	AY700997	AY701028	AF544673	AF544719	FJ434071	—
Sanzinia madagascariensis	Sanziniidae	EU403571	AY336066	U69866	EU403580	—	MH274606
Tropidophis feicki	Tropidophiidae	AF512733	AF512733	KF811124	KF811110	—	—
Ungaliophis continentalis	Charinidae (Ungaliophiinae)	AF512741	AF544833	U69870	AF544724	FJ434081	—
Xenopeltis unicolor	Xenopeltidae	AF512735	AB179620	AB179620	AF544689	FJ434073	MK064839
Xenophidion schaeferi	Xenophidiidae		—	AY574279	MK070320	MK070322	—
Xylophis perroteti	Pareidae (Xylophiinae)	—	MK340908	MN970042	MK344193	—	—
*Achalinus rufescens**	Xenodermidae	KX694570	KX694613	KX694895	—	KX694990	
*Achalinus spinalis**	Xenodermidae	MK065581	MK194153	MK201476	—	—	MK064822
*Achalinus zugorum**	Xenodermidae		MT503100	MT513238	—	—	MT502775
*Fimbrios klossi**	Xenodermidae		—	KX694894	—	—	KP410745
*Parafimbrios lao**	Xenodermidae		—	—	—	—	KP410746
*Parafimbrios vietnamensis**	Xenodermidae		—	—	—	—	MH884515
*"Stoliczkia" borneensis**	Xenodermidae	AF544779	AF544808	—	AF544721	FJ434083	
*Stoliczkia vanhnuailianai**	Xenodermidae	**OL352693**	**OL352694**	**OL422473**	**OL422475**	**OL422474**	**OL422476**
*Xenodermus javanicus**	Xenodermidae	AF544781	AF544810	AF544810	AF544711	—	—

Table 2. Partitions and models of sequence evolution used in the ML and BI phylogenetic analyses for the concatenated dataset. 1st, 2nd and 3rd refer to the codon position.

Partitions	Sites	BI	ML
1	*co1*[1st], *nt3*[1st]	K80+I	GTR+G
2	*cytb*[2nd], *co1*[2nd]	HKY+I	GTR+G
3	*cytb*[3rd], *co1*[3rd]	HKY+G	GTR+G
4	*12S, 16S, cytb*[1st]	GTR+G	GTR+G
5	*cmos*[1st], *cmos*[2nd], *nt3*[1st], *nt3*[2nd]	K80+I	GTR+G
6	*cmos*[3rd]	HKY	GTR+G

separately using the same methods outlined above (alignments available at: https://doi.org/10.5519/gbzyjuli). We applied seven fossil calibrations (Table 3), largely those recommended by Head (2015) and Head et al. (2016) as recently utilized by Deepak et al. (2021). Additionally, we set the root of the tree at a maximum age of 128 Ma and a minimum age of 123 Ma (i.e., Early Cretaceous, to correspond to the approximate age of the Serpentes root (based on point or mean values from Zheng and Wiens, 2016; Miralles et al. 2018; Burbrink et al. 2020). The best-fitting partition scheme and model(s) of sequence evolution identified using PartitionFinder had ten partitions (Appendix 1). Initially we carried out divergence dating by analysing this dataset and partition scheme with BEAST version 2.5 (Bouckaert et al. 2019) using XSEDE in the CIPRES Science Gateway v3.3 (Miller et al. 2010) under a Yule tree process. We assigned a relaxed log-normal clock for each partition of the concatenated BEAST analysis. We set up two independent runs, each employing the Markov Chain Monte Carlo (MCMC) for 100,000,000 generations, sampling every 5,000 trees. We obtained effective sample size (ESS) values using Tracer 1.7 (Rambaut et al. 2014). ESS values were below 100 for the priors and posteriors employing the best-fit model identified using PartitionFinder. We also repeated the analysis implementing the less-complex HKY model for the partitions but otherwise using the same settings. However, in this second analysis, we recovered ESS values above 200 for all the priors and posteriors for the two independent runs.

Morphology

We provide here morphological and meristic data for two specimens of *Stoliczkia borneensis* (BMNH 1946. 1.15.58 and UNIMAS 8002) and additional published information on unspecified specimens from Stuebing et al. (2014). Total length, snout-vent length and tail length were measured with thread and a ruler to the nearest 1 mm. Other dimensions were recorded with dial calipers, to the nearest 0.1 mm. Bilateral scale counts separated by a comma are reported in left, right order. Ventral scales were counted following Dowling (1951). Length and width of head scales were measured at the longest and the widest points of the respective scale(s). Eye diameter was measured horizontally.

Museum abbreviations

UNIMAS—Universiti Malaysia Sarawak; **NHMUK**—Natural History Museum, London (specimen numbers have a BMNH prefix); **ZSIK**—Zoological Survey of India, Kolkata, and **ZRC**—Herpetofauna and fish fauna collection at Lee Kong Chian Natural History Museum, Singapore.

Results

Phylogeny

The single-gene ML trees are shown in Fig. 2. Depending on taxon sampling (limited by availability of sequence data), generally *S. borneensis* and *S. vanhnuailianai* show close affinities with *Xenodermus* and with *Achalinus,* respectively. Although ML bootstrap support for many relationships are not strong (<90), support for *Stoliczkia* monophyly in the four gene trees for which both species were sampled is negligible, being only 25 for *16S* and 0–0.2 for *12S, cmos* and *nt3*. The ML and BI trees derived from the concatenated dataset agree in the set of relationships depicted (Fig. 1), with generally moderate (70–90 ML bootstrap; 0.80–0.90 BI posterior probability) to high support (>90 ML; >0.95 BI). Importantly, there is zero bootstrap or posterior probability support for *Stoliczkia* monophyly in these latter trees. Instead, the best-supported relationships that are incompatible with this optimal set of relationships for *Stoliczkia* spp. are for *Xenodermus javanicus* being more closely related to *Fimbrios and Parafimbrios* (ML bootstrap = 20; BI posterior probability = 0) and for *S. borneensis* being more closely related to *Fimbrios* and *Parafimbrios* (ML bootstrap = 5; BI posterior probability = 9). Thus, we conclude that the available DNA sequence data provide good to strong support for *S. borneensis* being more closely related to *Xenodermus* than to *S. vanhnuailianai*, and for *S. vanhnuailianai* being more closely related to *Achalinus* than to *S. borneensis*, and very strong support for non-monophyly of *Stoliczkia*.

Morphology

Previously, extensive data were available for only a single vouchered specimen (the holotype, BMNH 1946.1.15.58) of *Stoliczkia borneensis* (Lalronunga et al. 2021). Data for an additional specimen (UNIMAS 8002) are presented in Table 4. This specimen agrees with data presented by Lalronunga et al. (2021) corroborating that *S. vanhnuailianai* resembles the type species of the genus, *S. khasiensis* much more closely than either does *S. borneensis*. Notable differences between the Bornean species and the two Northeast Indian species include presence of 4–6 small scales between the frontals and prefrontals in *S. borneensis* which are absent in the Northeast Indian

Table 3. Parameter values for fossil calibrations used in the BEAST divergence dating analysis. Ages in Ma. All maximum ages soft, except hard maximum for calibration 6.

Calibration	Node calibrations	Offset	Maximum age	Mean	Standard deviation
1	Oldest divergence within crown Alethinophidia	93.9	100.5	1.5	1.25
2	Oldest divergence between non-xenodermid colubroids and their closest living relative (Xenodermidae)	50.5	72.1	6.1	1.25
3	Divergence between Boinae and its sister taxon (Erycinae + Candoiinae)	58	64	1.8	1.25
4	Divergence between *Corallus* and (*Chilabothrus* + (*Epicrates* + *Eunectes*))	50.2	64	4	1.25
5	Divergence between Viperinae and Crotalinae	20	23.8	1	1.25
6	Divergence between *Acrochordus javanicus* and (*A. ararfurae* + *A. granulatus*)	18.1	23.1	1.5	1.25
7	Oldest divergence between *Naja* (*Afronaja*) and *Naja* (*Boulengerina*)	17	20	1	1.25

Table 4. Morphometric (in mm) and meristic data for *Paraxenodermus borneensis*. Data for the holotype (*) from Lalronunga et al. (2021). Data for unspecified specimens from Stuebing et al. (2014).

Voucher Number	UNIMAS 8002	BMNH 1946.1.15.58*	Unspecified specimens
Sex	male	male	
Snout-vent length	481	541	
Tail length (Ta)	232	248	
Total length (TL)	713	789	
TaL / TL	0.33	0.31	
Horizontal eye diameter	2.7	2.8	
Head length	9.6	17.9	
Head width	8.0	10.8	
Head height	5.2	5.5	
Dorsal scale rows at one head length behind head	31	31	
Dorsal scale rows at midbody	31	32	31–35
Dorsal scale rows at one head length before vent	25	25	
Ventrals	206	208	205–210 (“females only”)
Subcaudals	128	123	117–124
Anal shields	1	1	
Supralabials	10,10	10,-	10 or 11
Supralabials touching eye	0	0	
Infralabials	14,13	14,-	
Infralabials touching anterior genials	1–2	1–3	
Suboculars	3,3	3,3	
Loreals	1,1 (+ 2 very small scales on both sides close to nasals)	1,1 (+ 2 very small scales on both sides close to nasals)	
Preoculars	2,2	3,3	
Supraoculars	3,3	2,2	
Postoculars	4,4	2,4	
Anterior temporals	0,0	0,0	

species; supralabials not contacting the eye in *S. borneensis* versus contacting the eye *S. vanhnuailianai* and *S. khasiensis*; 10 or 11 supralabials versus 8 or 9 supralabials. Although *S. borneensis* is seemingly most closely related to *Xenodermus* (Fig. 2), the two taxa differ markedly in external morphology—for example, *X. javanicus* lacks large scales on the head other than at the snout tip whereas *S. borneensis* additionally has large parietal and frontal shields. *Xenodermus javanicus* and *S. borneensis* share a derived condition of having more small, irregular head scales than are present in other xenodermids.

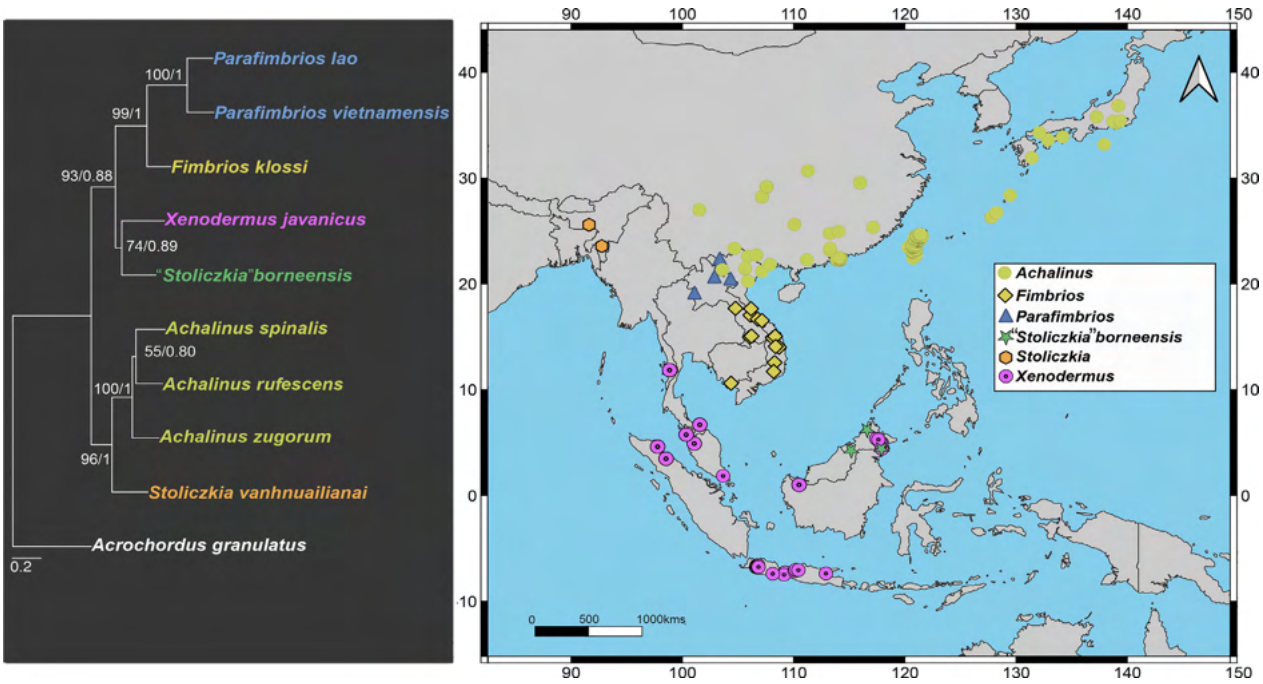

Figure 1. Left panel: Multilocus ML phylogeny showing relationships of xenodermid snakes. Numbers at internal branches are: ML bootstrap support / BI posterior probability support. Right panel: map depicting distribution of all currently recognised xenodermid genera. Source: GBIF, Teynié et al. 2015, Ziegler et al. 2008). Additional localities for *Xenodermus javanicus* from Smith, 1943; Tweedie, 1954; Taylor, 1965; David and Vogel, 1996; Wallach et al. 2014).

Systematics

Stoliczkia — (Jerdon, 1870)

Stoliczkaia — Boulenger, 1890
Stolickaia — Palacky, 1898
Stolickaja — Palacky, 1898
Estoliczkaia — Briceño-Rossi, 1934
Stoliczkaia — Smith, 1943
Stolzickia — Taub, 1967
Stoliczkai — Murthy and Pillai in Majupuria, 1986

Content—*S. khasiensis* (Fig. 3A–B) and *S. vanhnuailianai* (Fig. 3C–D)

Diagnosis. This genus can be diagnosed based on the combination of the following features: (1) maxillary teeth small and subequal, (2) head very distinct from (much wider than) 'neck', with large shields on dorsal aspect, (3) posterior one-third of the head and posterior temporal region covered with small scales like those of the anterior end of the body, (4) 3 small scales between parietal and supralabial shields immediately behind eye (5) 8–9 supralabials, (6) nostril in a large concave nasal, (7) body slender and somewhat laterally compressed, (8) ventrals large, and (9) dark dorsum and pale venter meet along a regular straight line ventrolaterally and subcaudals partially or completely darker than venter.

Distribution. This genus is restricted to Northeast India (Fig. 1). *Stoliczkia khasiensis* is thus far known only from Khasi hills, Meghalaya state, India and the recently described *Stoliczkia vanhnuailianai* is known only from Mizoram state, India.

Etymology. The genus is named after the Moravian-born Ferdinand Stoliczka (1838–1874). A geologist-natural historian, he was appointed as a palaeontologist with the Geological Survey of India in 1863. Stoliczka collected vertebrates and molluscs from northern India, Andaman and Nicobar Islands, Myanmar and the Malay Peninsula. He served as the official Naturalist with the Second Mission to Yarkand, in central Asia. A biography and a list of published works and reports by Stoliczka can be found in Kolmaš (1982).

Paraxenodermus, gen. nov.

http://zoobank.org/A08F93FC-187B-48BD-8AFA-A02-EBA98651B

Type species. *Paraxenodermus borneensis* (Boulenger, 1899).

Type locality. Mount Kinabalu, North Borneo (4,200 ft / 1,280 m); the holotype is deposited in the Natural History Museum, London as BMNH 1946.1.15.58; collected by Richard Hanitsch in March, 1899.

Content—*Paraxenodermus borneensis*

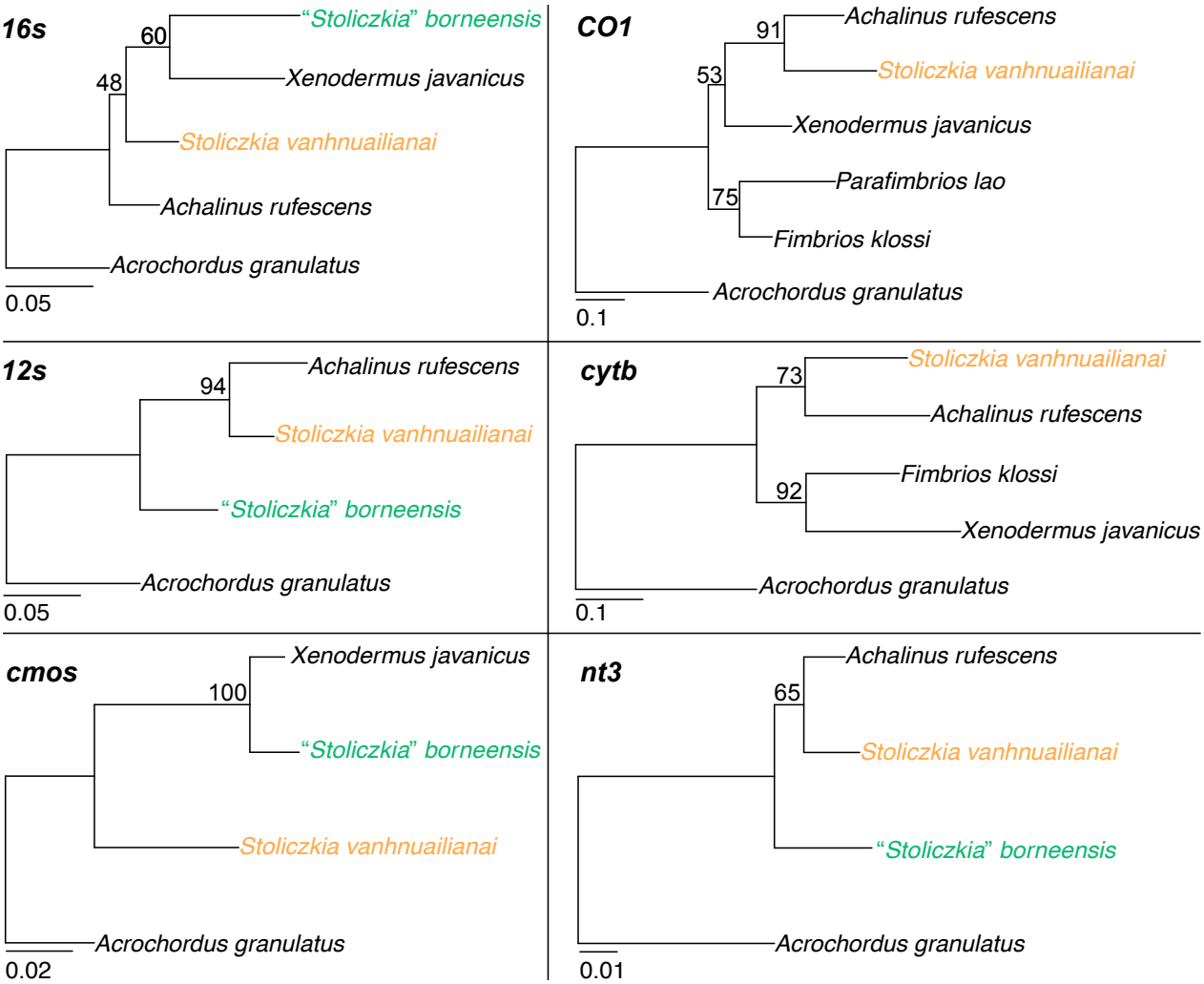

Figure 2. Single-gene ML trees showing inferred phylogenetic relationships of xenodermid snakes, rooted with outgroup *Acrochordus granulatus*. ML bootstrap support is shown at internal branches. Scale bars indicate substitutions per site.

Paraxenodermus borneensis

Figs 3E–F, 4 & 5

Stoliczkaia borneensis Boulenger 1899: 452
Stoliczkaia borneensis — de Rooij 1917: 45
Stoliczkaia borneensis — de Haas 1950: 530
Stoliczkaia borneensis — Haile 1958: 766
Stoliczkaia borneensis — Stuebing: 1991: 329
Stoliczkia borneensis — Manthey and Grossmann 1997: 394
Stoliczkia borneensis — Malkmus et al. 2002
Stoliczkia borneensis — Das 2006a: 9
Stoliczkia borneensis — Das 2006b: 500–501
Stoliczkia borneensis — Das 2012 :153
Stoliczkia borneensis — Das 2018: 151, 169
Stoliczkia borneensis — Stuebing et al. 2014: 79
Stoliczkia borneensis — Wallach et al. 2014: 689
Stoliczkia borneensis — Boundy 2020: 172
Stoliczkia borneensis — Lalronunga et al. 2021: 569–580

Diagnosis. This genus can be diagnosed based on the combination of the following features: (1) maxillary teeth small and subequal, (2) head very distinct from (much wider than) 'neck', with large shields on dorsal aspect, (3) posterior one-third of the head and posterior temporal region covered with small scales like those of the anterior of the body, (4) numerous small scales between parietal and supralabial shields immediately behind eye, (5) a row of 4–6 small scales between the frontal and prefrontal shields, (6) 10–11 supralabials, (7) nostril in a large concave nasal, (8) body slender and somewhat laterally compressed, (9) ventrals large, and (10) dorsum with numerous dorsolateral and middorsal pale blotches, venter pale with brown patches and subcaudals dark grey.

Comparison to other xenodermid genera. Morphologically *Paraxenodermus borneensis* differs from all other xenodermid snakes by a combination of the following characters: presence of head shields (absent in *Xenodermus javanicus*, other than at snout tip), approximately one-third of the head covered with small scales similar to dorsal scales on the anterior of the body (versus head scales distinct from body scales in *Achalinus, Fimbrios* and *Parafimbrios*), head much wider than 'neck' (versus head indistinct from neck in *Fimbrios, Parafimbrios* and *Achalinus*) and presence of a row of small scales between frontal and prefrontal scales (absent in *Stoliczkia*).

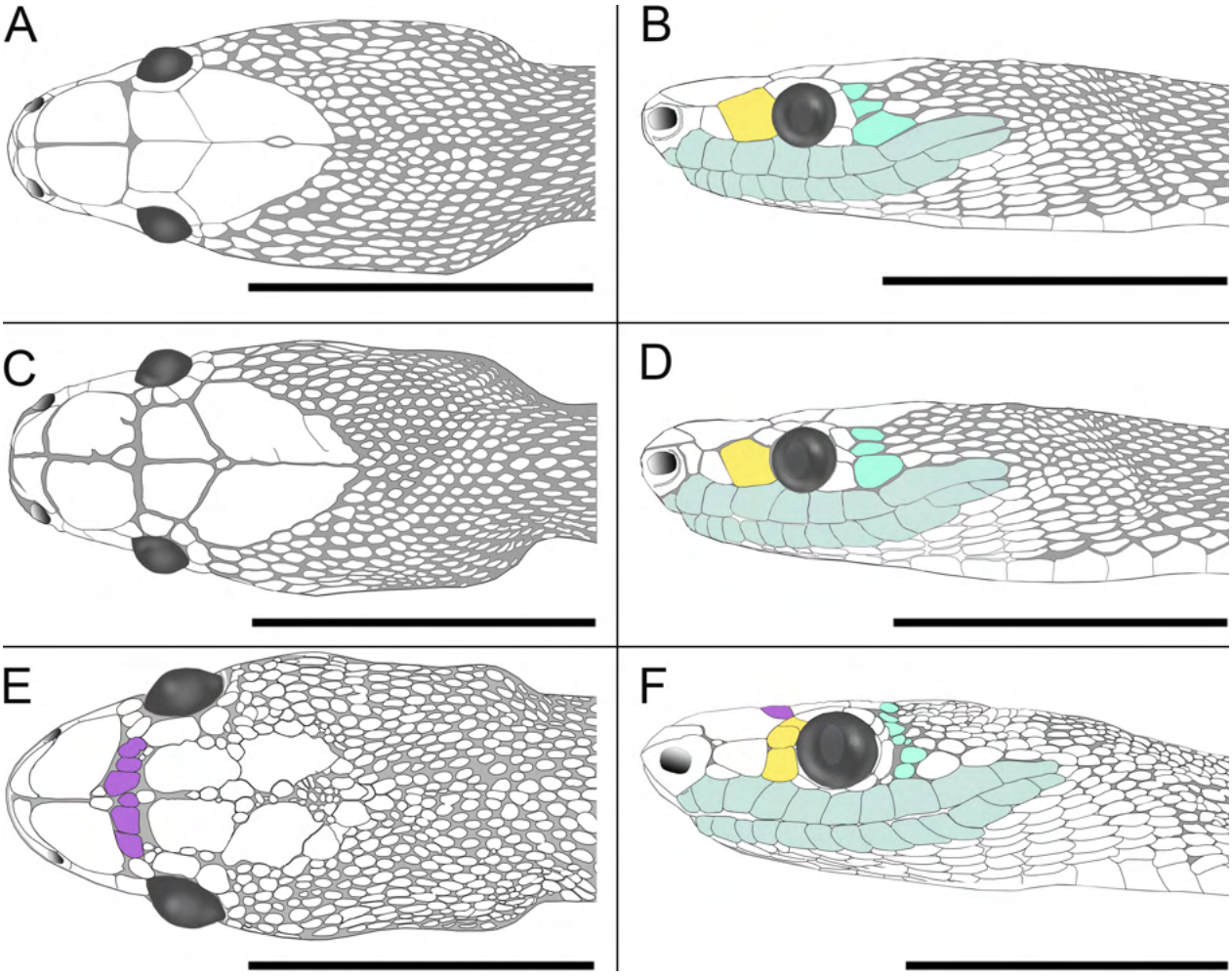

Figure 3. Line drawings of *Stoliczkia khasiensis* (A, B), *Stoliczkia vanhnuailianai* (C, D) and *Paraxenodermus borneensis* (E, F) based on ZSIK 14945, BNHS 3656 and BMNH 1946.1.15.58 respectively. Genus characteristics are highlighted in different colours: 1) some supralabials in contact with eye in *Stoliczkia*, separated by circumorbital scales in *Paraxenodermus*; 2) fewer supra- and infralabials in *Stoliczkia* than in *Paraxenodermus*; 3) single prefrontal in *Stoliczkia* versus 2–3 in *Paraxenodermus*, 4) fewer scales between parietal and supralabials immediately behind eye in *Stoliczkia* than in *Paraxenodermus,* and 5) small row of scales between frontal and prefrontals absent in *Stoliczkia*, present in *Paraxenodermus*. Note small scales behind the temporals are indicative rather than precisely accurate. Pale grey coloured areas are bare skin exposed between scales. Illustrations by V. Deepak and Surya Narayanan. Scale bars = 10 mm.

Distribution. The new genus is restricted to the island of Borneo and so far, reported from the Kinabalu Massif (Boulenger 1899) and the contiguous Crocker Range, both in Sabah, in the northeastern part of Borneo (Das 2006a), as well as in the isolated Gunung Murud (Das 2006b), in Sarawak State. https://www.inaturalist.org/observations?taxon_id=28573). Information is not available for the holotype, but all other reported individuals were found late at night, moving slowly on rocky banks of streams at elevations of 950–2,100 m above sea level (Das 2006a).

Variation. The two examined specimens of *Paraxenodermus borneensis,* the holotype BMNH 1946.1.15.58 and UNIMAS 8002, differ slightly in the number of small scales lying between the frontal and prefrontals, being six and four, respectively. We counted six small scales in this position in images of a live individual on the internet (https://www.inaturalist.org/taxa/28573). UNIMAS 8002 also differs from BMNH 1946.1.15.58 in having a two more ventrals (208 versus 206) and five additional subcaudals (128 versus 123), and in being smaller (713 mm versus 789 mm total length).

Etymology. The generic name *Paraxenodermus* is composed of the modern Latin generic name *Xenodermus* and the Latin adjective par (paris), meaning, among other possibilities, “similar to”.

Discussion

Taken at face value, our phylogenetic results and the distribution of xenodermid genera (Fig. 1) indicate that there are two main radiations within Xenodermidae; one in Northeast India, northern mainland Southeast Asia and Japan (*Stoliczkia* + *Achalinus* sensu stricto) and one in eastern mainland Indochina and southeast Sundaland

Figure 4. Holotype of *Paraxenodermus borneensis* (Boulenger, 1899), BMNH 1946.1.15.58. Photographs by Kevin Webb. Scale bar increments in mm.

Figure 5. *Paraxenodermus borneensis* in life (ZRC 2.5731), from Crocker Range, Sabah, in the north-western Borneo. Sequences for this specimen was published in Vidal and Hedges (2002) and used in this study. Photograph by Indraneil Das.

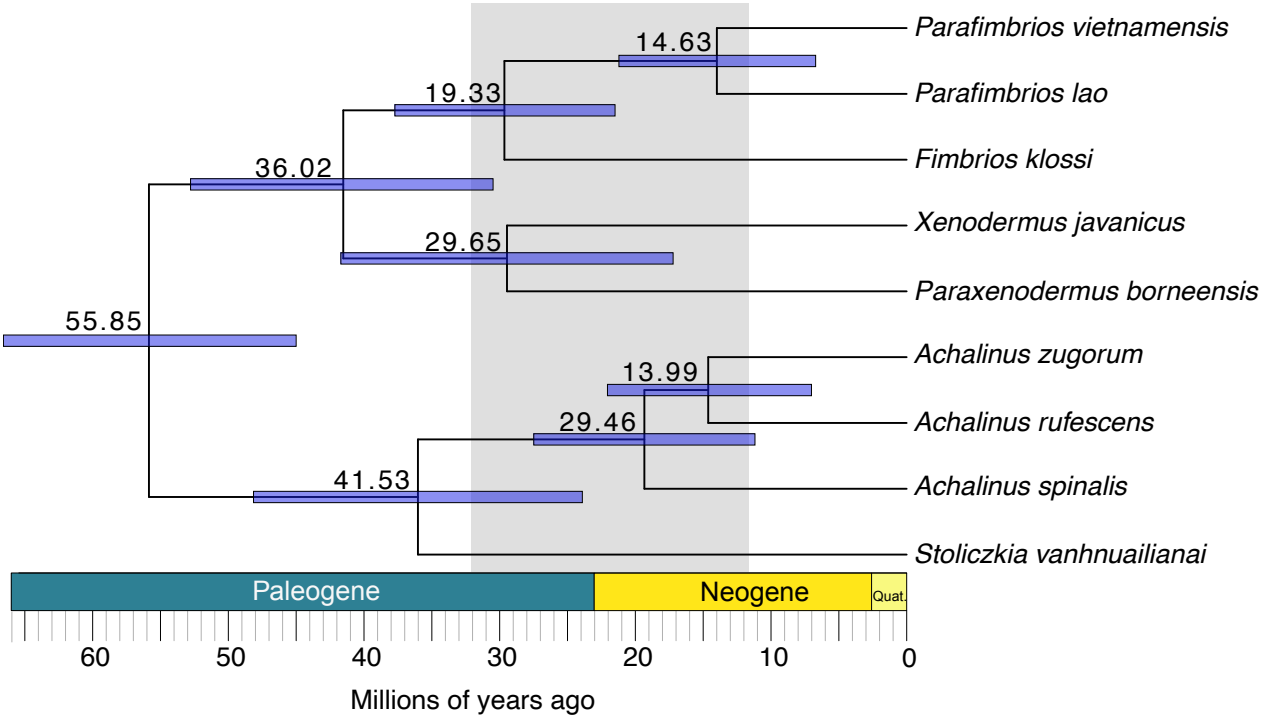

Figure 6. BEAST chronogram showing estimated divergence times for xenodermid snakes inferred from 68 tips for a concatenated mt and nu dataset. Numbers at internal branches indicate mean divergence ages, with blue bars showing 95% highest posterior density intervals. See Appendix 2 for complete dated phylogeny.

(*Fimbrios, Parafimbrios, Paraxenodermus, Xenodermus*). The most parsimonious interpretation is that the most recent common ancestor of these two main xenodermid radiations occurred in mainland Indochina, suggested by our dating analyses to be approximately 66.7–44.6 Ma (Fig. 6). However, this would be better tested in future by undertaking probabilistic biogeographic analyses of a more broadly taxonomically sampled tree.

Establishment of a new genus for *S. borneensis* and a new understanding of phylogenetic relationships removes the exceptional geographic disjunction presented by the previous concept of *Stoliczkia*. These results also strengthen evidence for endemic radiations within both Borneo (e.g. Blackburn et al. 2010; Wood et al. 2012; Hertwig et al. 2013; Fritz et al. 2014) and Northeast India (e.g., Pawar et al. 2007; Kamei et al. 2012).

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Appendix 1

Partitions and models of sequence evolution used in the BEAST analyses for the 68 tips dataset. 1st, 2nd and 3rd refer to the codon position.

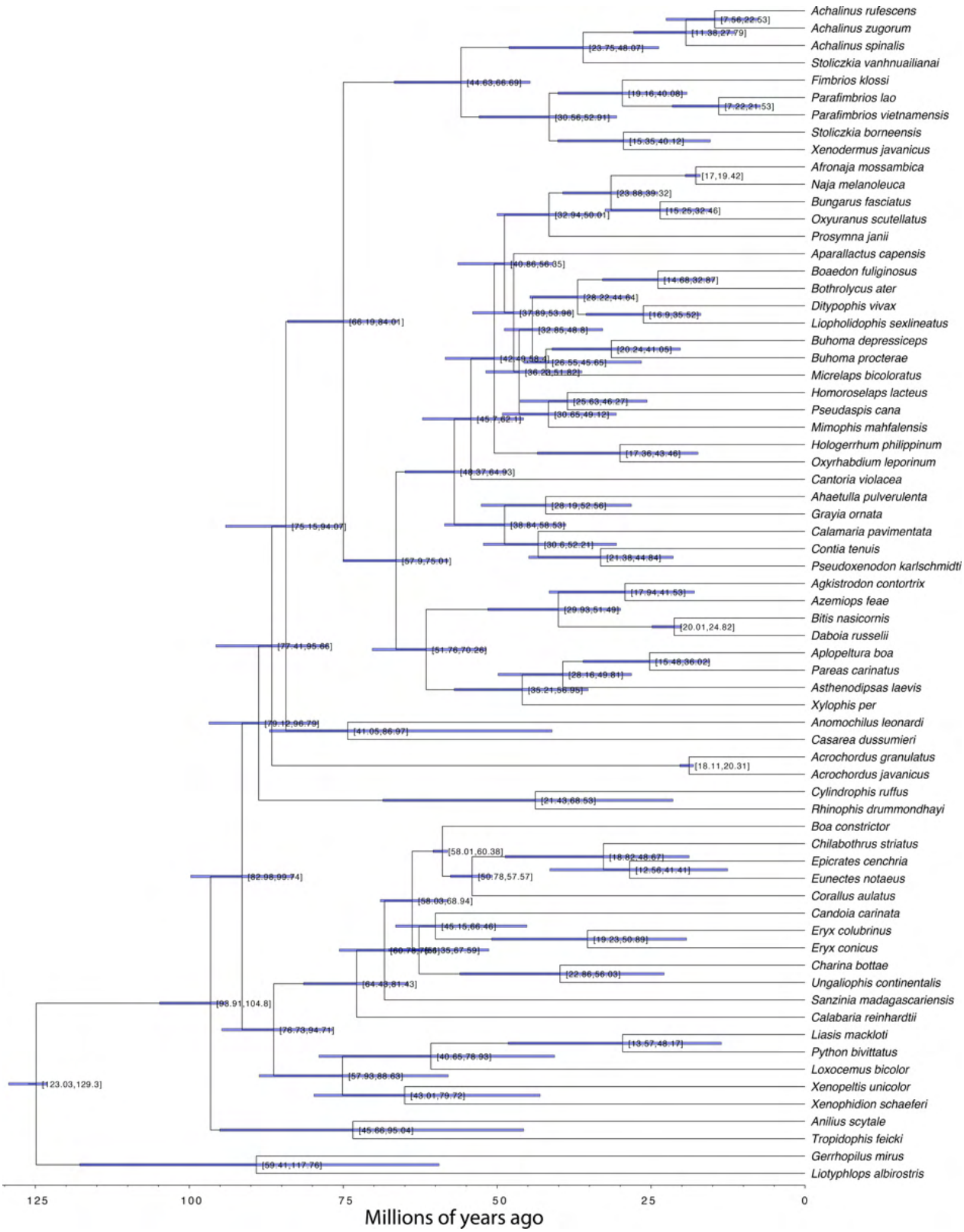
Partitions	Sites	model
1	*12S*	GTR+G
2	*16S, cytb*^{1st}	GTR+I+G
3	*co1*^{1st}, *cytb*^{2nd}	SYM+I+G
4	*cytb*^{3rd}	GTR+I+G
5	*co1*^{2nd}	HKY+G
6	*co1*^{3rd}	GTR+I+G
7	*cmos*^{1st}, *cmos*^{2nd}	K80+G
8	*cmos*^{3rd}	HKY+G
9	*nt3*^{1st},*nt3*^{2nd}	SYM+G
10	*nt3*^{3rd}	HKY+G

Appendix 2

Specimens examined and/or photographed

Achalinus meridianus (holotype) BMNH 1946.1.12.31
Achalinus formosanus (holotype) BMNH 1946.1.7.78
Fimbrios klossi (syntype) BMNH 1946.1.15.87
Xenodermus javanicus (holotype) BMNH 1946.1.15.90
Stoliczkia khasiensis (holotype) BMNH 1946.1.15.67
Stoliczkia khasiensis ZSIK 14945
Stoliczkia borneensis (holotype) BMNH 1946.1.15.58
Stoliczkia borneensis UNIMAS 8002, ZRC 2.5731
Stoliczkia vanhnuailianai (holotype) BNHS 3656

Appendix 3



BEAST chronogram generated using concatenated-gene for representatives of all families and subfamilies of alethinophidian snakes. Error bars and the numbers at internal branches indicate 95% highest posterior densities for node ages.

Appendix 4

Paraxenodermus borneensis (UNIMAS 8002) from near Samling Camp at Ravenscourt, Lawas, Sarawak Malaysia. Photographs by Indraneil Das.