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

V. Deepak1,2,*, Samuel Lalronunga3, Esther Lalhmingliani3, Abhijit Das4, Surya Narayanan5, Indraneil Das6, David J. Gower2

1 Senckenberg Dresden, Königsbrücker Landstraße 159, 01109 Dresden, Germany
2 Department of Life Sciences, The Natural History Museum, London SW7 5BD, UK
3 Systematics and Toxicology Laboratory, Department of Zoology, Mizoram University, Aizawl 796004, Mizoram, India
4 Wildlife Institute of India, Chandrabani, Dehradun 248001, Uttarakhand, India
5 Suri Sehgal Centre for Biodiversity and Conservation, Ashoka Trust for Research in Ecology and the Environment, Royal Enclave, Srirampura, Bangalore, Karnataka 560064, India
6 Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia

http://zoobank.org/386BF265-9338-409A-9A44-15B70C953A53

Corresponding author: V. Deepak (veerappandeepak@gmail.com)

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 Asia (*S. khasiensis* Jerdon, 1870 and *S. vanhnuailianai* Lalronunga, L. Mangaihaia, Zosangliana, L. Manningliani, 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 16 Sar-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 GTR+GAMMA 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* 4.0a169 (X86) (Swofford 2003). We rooted the trees with *Acrochordus granulatus* because it is a non-xenodermid caenophidian snake (Figuerola 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 *Liophyphops albiostris*) 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| MH127311|
| Acrochordus javanicus    | Acrochordidae           | KX694587| KX512745| KX694897| HM234058| KX694991| LC533890|
| Agkistrodon contortrix   | Viperidae (Crotalinae)  | AF156587| AF156566| EU483383| —       | —       | MN135583|
| Ahaetulla pulcherrima    | Colubridae (Ahaetulinae)| KC347304| KC347339| KC347454| KC347378| —       | —      |
| Anilus styale            | Anilidae                | AF544753| FJ551880| U697381 | AF544722| FJ434066| —       |
| Anomochilus leonardi     | Cylindrophilidae + Anomochilidae | AY953430| AY953431| —       | —       | —       | —       |
| Aparallactus capensis    | Atractaspidae (Aparallactinae) | FJ404129| AY188045| AY188066| AY187967| —       | —       |
| Aplopeltura boa          | Pareidae (Pareinae)     | AF544761| AF544787| TF827673| JT827696| FJ434085| —       |
| Asthenodipsas laevis     | Pareidae (Pareinae)     | —       | KX660197| KX660469| KX660363| —       | —       |
| Azemiops ferox           | Viperidae (Azemiopinae) | KX694579| AF057234| AY352747| AF544695| KX694977| KP043570|
| Bitis nascomis           | Viperidae (Viperinae)   | DQ305411| AY188048| DQ305457| AY187970| —       | MH127354|
| Boa constrictor          | Boidae                  | AF512744| AB177354| AB177354| AF544676| —       | MH140079|
| Boidodon fuliginosus     | Lamprophiidae (Lamprophiinae) | FJ404169| AY188079| AF471060| FJ404270| FJ434094| AY128663|
| Bothrops atrox           | Lamprophiidae (Lamprophiinae) | FJ404144| AY611859| AY612041| FJ403474| —       | MH127352|
| Buhoma depressiceps      | Lamprophiidae incertae sedis | FJ404147| AY611860| AY612042| AY611951| —       | —       |
| Buhoma procerae          | Lamprophiidae incertae sedis | FJ404148| AY611818| AY612001| AY611910| —       | —       |
| Bungarus fasciatus       | Elapidae                | EU547135| EU579523| EU579523| AY058924| KX694998| KY769767|
| Calabaria reinhardtii    | Calabaridae             | KF576842| Z464944 | AY099985| AF544682| —       | MH127356|
| Calamaria pavimentata    | Colubridae (Calamariinae) | MH144595| KX694624| AF471081| AF471103| KX694999| MK064858|
| Canoidea carinata        | Candoidea               | AF544741| EU419850| AY099984| AY099961| FJ434077| —       |
| Cantoria violacea        | Homalopsidae            | EF395873| KX694627| EF395897| —       | KX695001| —       |
| Cassarea dussumieri      | Bolyeridae              | AF544754| AF544827| U697551 | AF544731| FJ434069| —       |
| Chironia bottae          | Charinidae (Charininae) | AF544743| AF544816| AY099986| AY099971| FJ434079| —       |
| Chilabothurus striatus   | Boidae                  | —       | —       | —       | KC329933| KC329991| DQ465554|
| Contis teteanus          | Colubridae (Dipsadinae) | AY577021| AY577030| GU112384| AF471134| —       | KU86070|
| Corallus annulatus       | Boidae                  | JX243842| AY750012| AY750007| —       | —       | MH140107|
| Cylindrophis rufus       | Cylindrophilidae + Anomochilidae | MK065683| AB179619| AB179619| AF471133| MK064906| —       |
| Daboia russellii         | Viperidae (Viperinae)   | DQ305413| EU913478| EU913478| AF471106| —       | GQ255661|
| Dryophis vivax           | Lamprophiidae           | FJ404150| AY188052| AY188013| —       | —       | KU567322|
| Epicrates cenchria       | Boidae                  | AF368059| —       | HJ395901| KC33008 | JX56186| —       |
| Eryx colubrinus          | Erycidae                | AF544747| AF544819| U698111 | AF544716| DQ465569| —       |
| Eryx conicus             | Erycidae                | GQ225856| AF312743| GQ225658| —       | —       | —       |
| Euoneutes noteaes        | Boidae                  | AF368057| AM236347| HQ399499| HQ399536| —       | —       |
| Gerehoplus mirus         | Gerehophilidae          | AM236345| AM236345| AM236345| GU902566| AM236345| —       |
| Gravata ornata           | Colubridae (Grayiinae)  | AF158434| AY611866| AY612048| AF544684| KX695019| MH124058|
| Species                      | Family                    | 12S  | 16S  | cytB  | cmos  | nt3  | co1  |
|-----------------------------|---------------------------|------|------|-------|-------|------|------|
| Hologerrhum philippinum     | Lampropodidae (Cyclocorinae) |      |      |       |       |      |      |
| Homoroselaps lacceus        | Lampropodidae (Atractaspidae) |     |      |       |       |      |      |
| Liasis mackloth             | Pythonidae                |     |      |       |       |      |      |
| Liophidophis sexlineatus    | Lampropodidae (Pseudoxyrhophiinae) |     |      |       |       |      |      |
| Liophidophis albirostris    | Anomalepidae              |     |      |       |       |      |      |
| Loxocemus bicolor           | Lampropodidae (Aparallactinae) |     |      |       |       |      |      |
| Micrakps bicolitarus        | Lampropodidae (Aparallactinae) |     |      |       |       |      |      |
| Mimophis mahafelandesi      | Lampropodidae (Psammophiinae) |     |      |       |       |      |      |
| Naja (Afronaja) mossambica  | Elapidae                  |     |      |       |       |      |      |
| Naja (Boulengerina) melanoleuca | Elapidae                  |     |      |       |       |      |      |
| Oxyrhadinium leporinum      | Lampropodidae (Cyclocorinae) |     |      |       |       |      |      |
| Oxyuranus scutellatus       | Elapidae                  |     |      |       |       |      |      |
| Paras carinatus             | Pareidae (Pareinae)       |     |      |       |       |      |      |
| Prosyna janii               | Lampropodidae (Prosyninae) |     |      |       |       |      |      |
| Pseudopsis cana             | Lampropodidae (Psammophiinae) |     |      |       |       |      |      |
| Pseudoxenodon karlsmithi    | Colubridae (Pseudoxenodontinae) |     |      |       |       |      |      |
| Python bivittatus           | Pythonidae                |     |      |       |       |      |      |
| Rhinophis drummondhaysi     | Uropodidae                |     |      |       |       |      |      |
| Sanztia madagascariensis    | Sanztiaidae               |     |      |       |       |      |      |
| Tropidophis fechi           | Tropidophiidae            |     |      |       |       |      |      |
| Ungaliophis continentalis  | Charinidae (Ungaliophiinae) |     |      |       |       |      |      |
| Xenopeltis unicoler         | Xenopeltidae              |     |      |       |       |      |      |
| Xenopeltion scharfei        | Xenopeltidae              |     |      |       |       |      |      |
| Xylophis perroteti         | Pareidae (Xylophiinae)    |     |      |       |       |      |      |
| Achalinus rufescens*        | Xenodermidae              |     |      |       |       |      |      |
| Achalinus spinalis*         | Xenodermidae              |     |      |       |       |      |      |
| Achalinus zugonum*          | Xenodermidae              |     |      |       |       |      |      |
| Fimbrios klossi*            | Xenodermidae              |     |      |       |       |      |      |
| Parafimbrios kao*           | Xenodermidae              |     |      |       |       |      |      |
| Parafimbrios vietnemensis*  | Xenodermidae              |     |      |       |       |      |      |
| "Stoliczkia" bomeensis*     | Xenodermidae              |     |      |       |       |      |      |
| Stoliczkia vanhualamianti*  | Xenodermidae              |     |      |       |       |      |      |
| Xenoderma jwananci*         | Xenodermidae              |     |      |       |       |      |      |
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          | col, m3 | K80+I | GTR+G |
| 2          | ceb, col | HKY+I | GTR+G |
| 3          | cyb, col | HKY+G | GTR+G |
| 4          | 12S, 16S, ceb | GTR+G | GTR+G |
| 5          | cmos, cmos, nt3, nt3 | K80+I | GTR+G |
| 6          | cmos | 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.
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.
Systematics

_Stoliczka_ — (Jerdon, 1870)

*Stoliczkaia* — Boulenagner, 1890
*Stolickaja* — Palacky, 1898
*Stolickajia* — Palacky, 1898
*Estoliczkaia* — Briceño-Rossi, 1934
*Stoliczkaia* — Smith, 1943
*Stolickaia* — Taub, 1967
*Stoliczka* — Murthy and Pillai in Majupuria, 1986

Content — *S. khasiensis* (Fig. 3A–B) and *S. vanhnuaiinanai* (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). *Stoliczkaia khasiensis* is thus far known only from Khasi hills, Meghalaya state, India and the recently described *Stoliczkaia vanhnuaiinanai* 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*
Paraxenodermus borneensis

Figs 3E–F, 4 & 5

Stoliczia borneensis — Boulenger 1899: 452
Stoliczia borneensis — de Rooij 1917: 45
Stoliczia borneensis — de Haas 1950: 530
Stoliczia borneensis — Haile 1958: 766
Stoliczia borneensis — Stuebing: 1991: 329
Stoliczia borneensis — Manthey and Grossmann 1997: 394
Stoliczia borneensis — Malkmus et al. 2002
Stoliczia borneensis — Das 2006a: 9
Stoliczia borneensis — Das 2006b: 500–501
Stoliczia borneensis — Das 2012: 153
Stoliczia borneensis — Das 2018: 151, 169
Stoliczia borneensis — Stuebing et al. 2014: 79
Stoliczia borneensis — Wallach et al. 2014: 689
Stoliczia borneensis — Boundy 2020: 172
Stoliczia 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 Stoliczia).
Vertebrate Zoology 71, 2021, 747–763

**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. 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/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).

**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 (*Stoliczka + 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).

Acknowledgements

We thank K. Lallmangaia and Isaac Zosangliana for their support in the field. Specimen of S. vanhnuailianai was collected under the research and collection permission (A.380115/2011-CWLW/338) issued by the Department of Environment, Forest and Climate Change, Government of Mizoram. AD’s research is supported by SERB-DST (CRG/2018/000790) and Director, Wildlife Institute of India. Special thanks are due to Malawmdawngliana for research assistance. Sabah field work by I. Das was supported by research grant UNIMAS 192/99(4), under research permit from Sabah Parks TS/PTD/5/5 Jld.14(76). UNIMAS 8002 from Sarawak Biodiversity Centre, supported by research grant UNIMAS 192/99(4), under research permit from Sabah Parks TS/PTD/5/5 Jld.14(76). UNIMAS 8002 from Sarawak Biodiversity Centre, supported by research grant UNIMAS 192/99(4), under research permit from Sabah Parks TS/PTD/5/5 Jld.14(76). UNIMAS 8002 from Sarawak Biodiversity Centre, supported by research grant UNIMAS 192/99(4), under research permit from Sabah Parks TS/PTD/5/5 Jld.14(76). UNIMAS 8002 from Sarawak Biodiversity Centre, supported by research grant UNIMAS 192/99(4), under research permit from Sabah Parks TS/PTD/5/5 Jld.14(76). UNIMAS 8002 from Sarawak Biodiversity Centre, supported by research grant UNIMAS 192/99(4), under research permit from Sabah Parks TS/PTD/5/5 Jld.14(76). UNIMAS 8002 from Sarawak Biodiversity Centre, supported by research grant UNIMAS 192/99(4), under research permit from Sabah Parks TS/PTD/5/5 Jld.14(76).

Boundy J (2020) Snakes of the World: a supplement. CRC Press. 273 pp.
Briceno-Rossi AL (1934) El problema del ofidismo en Venezuela. Boletín del Ministerio de Salubridad y de Agricultura y Cria, Caracas 2(14), 1079–1177 & 2(15), 15–103, illus.
Burbick FT, Lawson R, Slowinski JB (2000) Mitochondrial DNA phylogeography of the polytypic north American rat snake (Elaphe obsoleta): A critique of the subspecies concept. Evolution 54(6): 2107–2118. https://doi.org/10.1554/00143820(2000)054[2107:MDPOTJ2.0.CO;2
Burbick FT, Grazziotin FG, Pyron RA, Cundall D, Donnellan S, Irish F, Keogh JS, Kraus F, Murphy RW, Noonan B, Raxworthy CJ, Ruane S, Lemmon AR, Lemmon EM, Zaher H (2020) Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. Systematic Biology 69: 502–520. https://doi.org/10.1093/sysbio/syz062
Das I (2006a) Crocker Range National Park, Sabah, as a refuge for Borneo’s montane herpetofauna. Amphibian and Reptile Conservation 4(1): 3–11. https://doi.org/10.1514/journal.arc.0040015
Das I (2006b) Geographic Distribution. Stoliczkia borneensis (Stoliczka’s Water Snake). Herpetological Review 37(4): 500–501.
Das I (2021) A Naturalist’s Guide to the Snakes of South-East Asia: Malaysia, Singapore, Thailand, Myanmar, Borneo, Sumatra, Java and Bali. Third edition. John Beaufoy Publishing. Oxford, 176 pp.
David P, Vogel G (1996) The snakes of Sumatra. Chimaira, Frankfurt am Main, 200 pp.
Deepak V, Ruane S, Gower DJ (2018) A new subfamily of fossorial colubrid snake from the Western Ghats of peninsular India. Journal of Natural History 52(45–46): 2919–2934. https://doi.org/10.1080/00222939908678228
Deepak V, Maddock ST, Williams R, Nagy ZT, Conradie W, Rocha S, Harris DJ, Perera A, Gvozdič V, Doherty-Bone TM, Kamei RG, Megan M, Labisko J, Morel C, Cooper N, Day JJ, Gower DJ (2021) Molecular phylogenetics of sub-Saharan African natricine snakes, and the biogeographic origins of the Seychelles endemic Lycoglossophis seychellensis. Molecular Phylogenetics and Evolution 161: 107152. https://doi.org/10.1016/j.mpev.2021.107152
de Rooij N (1917) The Reptiles of the Indo-Australian Archipelago. Il. Ophidia. Leiden (E. J. Brill), xiv + 334 pp. https://doi.org/10.5962/bhl.title.5069
Dolwyn HG (1951) A proposed standard system of counting ventrals in snakes. British Journal of Herpetology 1(5): 97–99.
Edler D, Klein J, Antonelli A, Silvestro D (2021) raxmlGUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAxML. Methods in Ecology and Evolution 12: 373–377. https://doi.org/10.1111/2109-036X.13512
Felsenstein J (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. Journal of Molecular Evolution 171: 368–376. https://doi.org/10.1007/BF01734359
Fritz U, Gemel R, Kohlmair C, Vamberger M, Praschag P (2014) Phylogeography of the Asian softshell turtle Amodya cartilaginea (Boddaert, 1770): evidence for a species complex. Vertebrate Zoology 64(2): 229–243.
Figueroa A, McKelvy AD, Grismer LL, Bell CD, Lailvaux SP (2016) A novel species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. PLoS One 11(9): 1–31. https://doi.org/10.1371/journal.pone.0161070
Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome C oxidase subunit
I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.

Hass CPI, De (1950) Checklist of the snakes of Indo-Australian Archipelago. Treubia 20: 511–625

Haile NS (1958) The snakes of Borneo, with a key to the species. Sarawak Museum Journal 8: 743–771.

Head JJ (2015) Fossil calibration dates for molecular phylogenetic analysis of snakes 1: Serpentes, Alethinophidia, Boidae, Pythonidae. Palaeontology Electonica 18: 1–17. https://doi.org/10.26879/487

Head JJ, Mahlow K, Mueller J (2016) Fossil calibration dates for molecular phylogenetic analysis of snakes 2: Caenophidia, Colubroidea, Elapoidae, Colubridae. Palaeontology Electonica 19: 1–21. https://doi.org/10.26879/625

Hertwig ST, Schweizer M, Das I, Haas A (2013) Diversification in a biodiversity hotspot–The evolution of Southeast Asian rhacophorid tree frogs on Borneo (Amphibia: Anura: Rhacophoridae). Molecular Phylogenetics and Evolution 68(3): 567–581. https://doi.org/10.1016/j.ympev.2013.04.001

Jordon TC (1870) Notes on Indian herpetology. Proceedings of the Asiatic Society of Bencoolen 1870: 66–85.

Kamei RG, Mauro DS, Gower DJ, Van Bocxlaer I, Sherratt E, Thomas A, Babu S, Bossuyt F, Wilkinson M, Biju SD (2012) Discovery of a new family of amphibians from northeast India with ancient links to Africa. Proceedings of the Royal Society B: Biological Sciences 279(1737): 2396–2401. https://doi.org/10.1098/rspb.2012.0150

Kolmst J (1982) Ferdinand Stolicka (1838–1874): the life and work of the Czech explorer in India and High Asia. Wiener Studien zur Tibetologie und Buddhis-muskunde. Universität Wien, Vienna. Vol. 9, xi + 58 pp.

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33: 1870–1874. https://doi.org/10.1093/molbev/msw096

Lalrongunga S, Lahlmangaika H, Zosangliana I, Lahlmingliana E, Gower DJ, Das A, Deepak V (2021) A new species of Stolickzia Jerdon, 1870 (Serpentes: Xenodermidae) from Mizoram, India. Zootaxa 4996(3): 569–580. https://doi.org/10.11646/zootaxa.4996.3.9

Lanfear R, Calcott B, Ho SY, Guindon S (2012) PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695–1701. https://doi.org/10.1093/molbev/msq202

Lanfear R, Frandsen PB, Wright AM, Serfeld T, Calcott B (2017) PartitionFinder2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution 34: 772–773. https://doi.org/10.1093/molbev/msw260

Lawson R, Slowinski JB, Crother BL, Burbrink FT (2005) Phylogeny of the Colubroidea (Serpentes): New evidence from mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution 37(2): 581–601. https://doi.org/10.1016/j.ympev.2005.07.016

Malkmus R, Manthey U, Vogel G, Hoffmann P, Kosuch J (2002) Amphibians and reptiles of Mount Kinabalu (North Borneo). A.R.G. Gantner Verlag, Rugell, 404 pp.

Manthey U, Grossmann W (1997) Amphibien & Reptilien Südostasiens. Natur und Tier Verlag (Münster), 512 pp.

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, Louisiana, 14 November 2010, 1–8. https://doi.org/10.1109/GCE.2010.5676129

Miralles A, Marín J, Markus D, Herrel A, Hedges SB, Vidal N (2018) Molecular evidence for the paraphyly of Scelopohidia and its evolutionary implications. Journal of Evolutionary Biology 31(12): 1782–1793. https://doi.org/10.1111/jeb.13781

Murthy TSN, Pillai RS (1986) Snakes. In: Majupuria, T.C. (Ed.), Wild-life wealth of India (resources & management). Tecpress Service, Bangkok, 224–244, illust.

Palacky J (1898) La distribution des ophidiens sur le globe. Mémoires de la Société Zoologique de France 11: 88–125.

Palumbi SR, Martin AP, Romano WL, McMillan WO, Stice L, Grabowski G (1991) The Simple Fool’s Guide to PCR ver. 2. University of Hawaii, Honolulu: 25–28.

Palumbi SR (1996) The polymerase chain reaction. In: Hillis DM, Moritz C, Mable BK (Eds) Molecular systematics. 2nd ed. Massachusetts: Sinauer Associates, 205–247.

Pawar S, Koo MS, Kelley C, Ahmed MF, Chaudhuri S, Sarkar S (2007) Conservation assessment and prioritization of areas in Northeast India: Priorities for amphibians and reptiles. Biological Conservation 136(3): 346–361. https://doi.org/10.1016/j.biocon.2006.12.012

Peters WCH (1869) Über neue Gattungen und neue oder weniger bekannte Arten von Amphibien (Eremias, Dicrodon, Euprepes, Leposoma, Taphilops, Eryx, Rhynchosynch, Elapomorphus, Achalinus, Coronella, Dromicus, Xenopholis, Anoplodipsis, Spilotes, Tropidionos). Monatsberichte der königliche Akademie der Wissenschaften zu Berlin 1869(5): 432–445.

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer. Version 1.6. Available from: http://beast.bio.ed.ac.uk/Tracer (accessed 27 July 2014).

Reinhardt JT (1836) Afhandling om Xenodermus javanicus. Oversigt over det Kongelige Danske videnskabernes selskabs forhandlinger. Kjobenhavn 3: 6–7.

Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Smith MA (1921) New or little-known reptiles and batrachians from southern Annam (Indochina). Proceedings of the Zoological Society of London 1921: 423–440.

Smith MA (1943) The fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese subregion. Reptilia and Amphibia. Vol. III, Serpentes: Typhlops, Eryx, Rhynchosynch, Elapomorphus, Achalinus, Coronella, Dromicus, Xenopholis, Anoplodipsis, Spilotes, Tropidionos). Natur und Tier Verlag (Münster), 512 pp.

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic inference and model choice across the whole of the tree. Bioinformatics 22(21): 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Stuebing RB (1991) A checklist of the snakes of Borneo. Raffles Bulletin of Zoology 39(2): 323–362

Stuebing RB, Inger RF, Tan FL (2014) Field guide to the snakes of Borneo. Raffles Bulletin of Zoology 1870 (Serpentes: Xenodermidae) from Mizoram, India. Zootaxa 4996(3): 569–580. https://doi.org/10.11646/zootaxa.4996.3.9

Thomas A, Babu S, Bossuyt F, Wilkinson M, Biju SD (2012) Molecular phylogenetics and Evolution 37(2): 581–601. https://doi.org/10.1016/j.ympev.2005.07.016

Taub AM (1965) Comparative histological studies on the parotid gland of colubrid snakes. Doctoral Dissertation, State University of New York, Buffalo, 239 pp., 3 Figs, 8 pls.

Taylor EH (1965) The serpents of Thailand and adjacent waters. University of Kansas Science Bulletin 45(9): 609–1096.
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_cyb<sup>1</sup> | GTR+I+G |
| 3          | co<sup>1</sup>, cyb<sup>2</sup> | SYM+I+G |
| 4          | cyb<sup>3</sup> | GTR+I+G |
| 5          | co<sup>1</sup> | HKY+G    |
| 6          | co<sup>1</sup> | GTR+I+G |
| 7          | cmos<sup>1</sup>, cmos<sup>2</sup> | K80+G   |
| 8          | cmos<sup>3</sup> | HKY+G    |
| 9          | mt<sup>1</sup>, mt<sup>2</sup> | SYM+G   |
| 10         | mt<sup>3</sup> | HKY+G    |

Appendix 2

Specimens examined and/or photographed

Achalimus meridianus (holotype) BMNH 1946.1.12.31
Achalimus 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
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.