

A new species of Papuan groundsnake (Squamata: Colubridae: *Lielaphis*) from New Guinea

TIANQI HUANG^{1,*}, CHRISTOPHER C. AUSTIN², JUSTIN M. BERNSTEIN^{3,4}, BULISA IOVA⁵, JACKSON R. ROBERTS⁶, JEFFREY H. FREDERICK⁷ & SARA RUANE¹

¹Life Sciences Section, Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, Illinois, USA

 sruane@fieldmuseum.org;  <https://orcid.org/0000-0002-9543-1297>

²Museum of Natural Sciences and Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana, USA

 ccaustin@lsu.edu;  <https://orcid.org/0000-0003-3890-418X>

³Slippery Rock University, College of Engineering and Science, Department of Biology, Slippery Rock, Pennsylvania USA

⁴Department of Mammalogy, Division of Vertebrate Zoology, American Museum of Natural History, New York, New York, USA

 jbernstein@amnh.org;  <https://orcid.org/0000-0002-5249-3340>

⁵Papua New Guinea National Museum and Art Gallery, P.O. Box 5560, Boroko, National Capital District, Papua New Guinea

 iovabulisa@gmail.com;  <https://orcid.org/0000-0003-4989-1708>

⁶Virginia Museum of Natural History, Martinsville, Virginia, USA

 roberts.jackson265@gmail.com;  <https://orcid.org/0009-0002-7397-7296>

⁷Department of Biology, University of Kentucky, Lexington, Kentucky, USA

 jf frederick2@uky.edu;  <https://orcid.org/0000-0001-5014-2507>

*Corresponding author:  thuanguang@fieldmuseum.org;  <https://orcid.org/0000-0002-5341-6419>

Abstract

The recently resurrected genus *Lielaphis* (Squamata: Colubridae) is comprised of 19 medium-sized, terrestrial snakes collectively regarded as groundsnakes. Although found primarily in New Guinea, a biologically megadiverse region with high conservation priorities, *Lielaphis* remain poorly studied due to their largely homogenous appearance, elusive nocturnal nature, limited records, and complex taxonomic history, leaving high potential for undescribed species still existing within this group. Using high-throughput sequence data of 12 previously described species of *Lielaphis* and representatives of its sister taxon, *Stegonotus*, we apply an integrative approach combining genetic analyses with morphological examinations using vouchered specimens to explore the cryptic diversity of *Lielaphis*. We place particular emphasis on populations occurring on and adjacent to mainland New Guinea. We identify both molecular and morphological evidence for a new species, *Lielaphis slashi* **sp. nov.** from the northeastern lowlands of mainland New Guinea, bringing the number of *Lielaphis* species to 20, along with a potential range extension of *L. aplini*. Despite the recent resurgence of interest in New Guinea's snake diversity, our findings highlight persistent knowledge gaps, emphasizing the need for more comprehensive taxonomic studies of the speciose New Guinea herpetofauna.

Key words: Morphology, phylogenetics, Serpentes, systematics, taxonomy

Introduction

Although long regarded as a biologically diverse region with high conservation priorities (Myers *et al.* 2000; Mittermeier *et al.* 2003; Oliver *et al.* 2013; Oliver *et al.* 2022; Slavenko *et al.* 2023), New Guinea's fauna is still understudied and faces imminent conservation threats from industrial plantations and timber harvesting (Filer *et al.* 2009; Shearman & Bryan 2011; Nelson *et al.* 2014; Gaveau *et al.* 2021; White *et al.* 2021). As such, it is imperative to document its biodiversity and discover undescribed species of New Guinea to inform effective conservation planning and management. In the past decade, the snake diversity of New Guinea has been gaining new attention, and taxonomic work has uncovered a number of endemic species in this region, including in the cryptic Papuan groundsnakes of the genus *Lielaphis* (Kaiser *et al.* 2018; Ruane *et al.* 2018; Kaiser *et al.* 2019; O'Shea & Richards 2021; Bernstein *et al.* 2026).

Lielaphis Günther, 1863 was formerly subsumed under the genus of *Stegonotus* Duméril, Bibron & Duméril, 1854; *Stegonotus sensu lato* is closely related to the more well-known and speciose genus *Lycodon* Fitzinger, 1826 (Kaiser *et al.* 2018; Ruane *et al.* 2018; Bernstein *et al.* 2026). Given the genomic evidence for non-monophyly of *Stegonotus sensu lato* when considering *Lycodon sensu lato*, Bernstein *et al.* (2026) resurrected *Lielaphis*, that consists of taxa found in New Guinea, Australia, and parts of Wallacea, with *L. modestus* (Schlegel, 1837) as the type species. Bernstein *et al.* (2026) included 13 taxa now considered *Lielaphis*—*L. admiraltiensis* (Ruane, Richards, Mcvay, Tjaturadi, Krey & Austin, 2017), *L. aplini* (O’shea & Richards, 2021), *L. australis* (Günther, 1872), *L. derooijae* (Ruane, Richards, Mcvay, Tjaturadi, Krey & Austin, 2017), *L. diehli* (Lindholm, 1905), *L. guentheri* (Boulenger, 1895), *L. heterurus* (Boulenger, 1893), *L. iridis* (Ruane, Richards, Mcvay, Tjaturadi, Krey & Austin, 2017), *L. keyensis* (Doria, 1874), *L. melanolabiatus* (Ruane, Richards, Mcvay, Tjaturadi, Krey & Austin, 2017), *L. modestus* (Schlegel, 1837), *L. nancuro* (Kaiser, Kaiser, Mecke & O’shea, 2021), and *L. reticulatus* (Boulenger, 1895); in addition, there are six species that occur in the same region and likely represent and are assumed here to be *Lielaphis* (*L. aruensis* (Doria, 1875), *L. ayamaru* (Kaiser, O’shea & Kaiser, 2019), *L. cucullatus* (Duméril, Bibron & Duméril, 1854), *L. dorsalis* (Werner, 1924), *L. parvus* (Meyer, 1874), and *L. poechi* (Werner, 1924)) based on the group’s biogeography (Bernstein *et al.* 2026), resulting in a total of 19 known *Lielaphis* species. Derived from an ancestral lineage reaching New Guinea in the late Miocene, *Lielaphis* is the sister taxon to *Stegonotus sensu stricto*, and is now restricted to the Philippines and Moluccas (Bernstein *et al.* 2026). Because of their secretive nature and often nondescript appearance, information about the ecology and natural history of *Lielaphis* is scarce. Previous observations indicate these snakes are nocturnal and that some species and populations specialize primarily on squamate eggs (McDowell 1972; Shine 1991; Trembath *et al.* 2009). Some taxa, such as *L. australis*, also exhibit sexual size dimorphism and sex-biased dispersal (Shine 1994; Dubey *et al.* 2008; Trembath *et al.* 2009). In addition, *Lielaphis* has a complex taxonomic history due to lost and damaged type specimens, erroneous records, and the low accessibility of their native range. Thus, there are likely numerous unrecognized species within *Lielaphis* that have yet to be formally described (Kaiser *et al.* 2018; Ruane *et al.* 2018).

By integrating genomic and morphological data collected from specimens sampled across New Guinea and surrounding regions, the work presented here reveals a cryptic new species of *Lielaphis* dwelling in lowland habitats in northeastern New Guinea. Additionally, we identified a putative new morph of *L. aplini* with potential range extension and recommend further sampling and analyses to determine whether it represents a distinct species. Our findings further elucidate the systematics of *Lielaphis*, serving as an essential step in further quantifying New Guinea’s squamate diversity.

Materials and methods

Sampling and Bioinformatics

We obtained fresh liver and muscle tissues from 90 *Lielaphis* (Table S1). These samples represented 12 previously described taxa, though identity of 14 individuals was initially unclear as to their taxonomic affinity. These individuals were identified in field collection notes as taxa restricted to regions inconsistent with their collection localities and were thus treated as potentially undescribed taxa. Using the phylogeny of Bernstein *et al.* (2026), we also included representatives from the sister taxon, *Stegonotus* (two *S. batjanensis* (Günther, 1865) and six *S. muelleri* (Duméril, Bibron & Duméril, 1854)) and the natricid *Tropidonophis dendrophiops* (Günther, 1883) as outgroup taxa. Tissue samples and morphological data were both obtained from field collection efforts and the following natural history collections and/or field series: Australian Biological Tissue Collection (ABTC), American Museum of Natural History (AMNH), Australian Museum (AMS), Bernice Pauahi Bishop Museum (BPBM), Field Museum of Natural History (FMNH), University of Kansas Biodiversity Institute and Natural History Museum (KU), Louisiana State University Museum of Natural Science Zoology Collections (LSUMZ), Museum of Comparative Zoology (MCZ), Museum of Vertebrate Zoology (MVZ), Museums and Art Galleries of the Northern Territory (NTM), Papua New Guinea National Museum and Art Gallery (PNGNM), Queensland Museum (QM), South Australian Museum (SAMA), and the field series of Benjamin J. Evans (BJE), Christopher C. Austin (CCA), and Rafe M. Brown (RMB). All museum codes were used according to Sabaj (2025).

Genomic DNA was extracted using Qiagen® DNeasy blood and tissue kit protocol for all 99 tissues. We quantified and normalized DNA extracts using a Qubit 3 fluorometer (high sensitivity; Thermo Fisher Scientific:

Invitrogen). The extracts were sent to Daicel Arbor Biosciences (Ann Arbor, Michigan, USA) for DNA sequencing. Samples were enriched using either the UCE Tetrapods 5Kv1 probe set (Faircloth *et al.* 2012), targeting ~5,000 ultraconserved elements (UCEs), or the Squamate Conserved Loci (SqCL) v2 probe set (Singhal *et al.* 2017). Samples were sequenced on the Illumina NovaSeq 6000 platform on a partial S4 PE150 lane (UCEs) or Element Biosciences AVITI partial PE150 high-throughput flowcell (SqCL) to approximately 1 Gbp per library. Sequencing details are described in Bernstein *et al.* (2026).

We processed the raw genomic reads using Phyluce v1.7.3 (Faircloth 2016). We first trimmed the adapter and barcode sequences from the reads with illumiprocessor using default settings (Faircloth 2013; Del Fabbro *et al.* 2013; Bolger *et al.* 2014). Trimmed reads were then assembled using SPAdes (Bankevich *et al.* 2012) with default parameters. We aligned homologous UCE loci and edge-trimmed the alignments. Data matrices were created for each locus that were $\geq 75\%$ of taxa (“75% complete matrices” hereafter) and were subsequently concatenated for downstream analyses. Raw reads can be found in NCBI’s Sequence Read Archive (SRA) under projects accession numbers PRJNA1490688 and PRJNA1337899.

To call variants from the dataset of the 75% complete matrices, we first built a consensus sequence from all ingroup sample alignments (including *Stegonotus*). We then mapped and sorted data of all samples using the consensus through BWA (Li 2013). Next, we performed SNP discovery using tools from the Genome Analysis Toolkit v4.6 (McKenna *et al.* 2010; Van der Auwera *et al.* 2013). We marked duplicate reads by invoking *MarkDuplicates* and then generated per-sample genotype likelihoods in GVCf files using *HaplotypeCaller*. This was followed by combining all GVCf files and variant calling through *CombineGVCfs* and *GenotypeGVCfs* respectively. Variants were subsequently quality-filtered by *VariantFiltration* and *SelectVariants* to remove those with a quality score below 20. To avoid the effect of linkage for downstream analyses, *SelectVariants* was invoked again to keep only the first SNP per locus.

Phylogenetic Estimation

To explore the phylogenetic relationships of the sampled *Lielaphis*, we used the concatenated 75% complete matrix to generate a maximum-likelihood (ML) tree through IQ-TREE v2.4.0 (Nguyen *et al.* 2015; Chernomor *et al.* 2016; Minh *et al.* 2020). To generate the tree, we specified a GTR model of nucleotide substitution and invoked ModelFinder (Kalyaanamoorthy *et al.* 2017) to infer the best type of GTR model. The branch support was assessed using 10,000 ultrafast bootstrap replicates (UFB; Hoang *et al.* 2018) and 1,000 Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-aLRT; Guindon *et al.* 2010) iterations. We considered relationships that had UFB ≥ 95 and SH-aLRT ≥ 80 strongly supported. Accounting for gene tree-species tree discordance, we ran a coalescent analysis in ASTRAL-IV (Zhang *et al.* 2018) to generate a species tree. Specifically, for each locus in the 75% complete matrix, we generated an individual UCE tree using IQ-TREE with ModelFinder (Kalyaanamoorthy *et al.* 2017) and without estimating branch support. We then used the resultant trees and a mapping file indicating the putative species identity of each sample as inputs to create a species tree. We considered relationships in the species tree supported if Bayesian Posterior Probabilities (Bpp) was ≥ 0.95 .

The UCE ML tree was complemented by a mitochondrial cytochrome-b (CytB) tree with 36 samples constructed through IQ-TREE v2.4.0 (Nguyen *et al.* 2015) using the same parameters described above. The CytB sequences were acquired and aligned from the raw reads following the protocol by Bernstein and Ruane (2022). Based on availability, we used two *S. muelleri* samples as the outgroup taxon and multiple samples from 14 *Lielaphis* clusters we uncovered from the UCE ML tree as the ingroup. An additional sample representing the type species, *L. modestus* (Naturalis Biodiversity Center, Leiden: RMNH 43599), was obtained from Bernstein *et al.* (2026) and included in this analysis to verify its placement and affinity with respect to the putative new taxa. The sample was collected from Maluku, Indonesia, within this species’ known range (i.e., “true” *L. modestus* to represent the type species).

Demography and Population Demarcation

We performed a STRUCTURE analysis (Pritchard *et al.* 2000) using one SNP per locus. The final product from the variant calling described above was first converted to STRUCTURE format using R package adegenet v2.1.10 (Jombart 2008; Jombart & Ahmed 2011). As our primary goal was to discover unrecognized diversity in *Lielaphis*,

we only included samples (N = 29) from lineages with unexplored genetic structures indicated by the ML tree. We ran STRUCTURE v2.3.4 with a Markov chain Monte Carlo (MCMC) length of 100,000 generations and a burn-in of 50,000 generations. We ran the analyses for K = 2–9 populations with five iterations each. The optimal number of K was examined using the Evanno's method (Evanno *et al.* 2005) through STRUCTURE HARVESTER (Earl & vonHoldt 2012). We further examined the SNP data to estimate the likely number of populations (i.e., putative species) by performing a discriminate analysis of principal components (DAPC) using R package adegenet v2.1.10 (Jombart *et al.* 2010). We selected SNPs genotyped in at least 75% of individuals and samples with at least 50% of loci genotyped to conduct this analysis. We applied a *de novo* DAPC approach that used k-means clustering to find the number of clusters (Jombart *et al.* 2010). *optim.a.score* was used to find the optimal number of PCs to retain (Jombart *et al.* 2010).

Testing for Lineage Divergence

During analyses, we uncovered a previously undescribed group of individuals sister to *L. heterurus* (Clade A hereafter); the specimens of Clade A were all identified as *L. parvus* in the initial field notes of collectors (e.g., CCA, and see Ruane *et al.* 2018). However, all of these specimens were collected from northeastern mainland New Guinea, whereas *L. parvus* is restricted in range to Yapen, an island not connected to the mainland (Kaiser *et al.* 2018). Due to the unavailability of any Yapen Island samples for genetic analyses, we built ecological niche models using 22 mainland occurrence records (Phillips *et al.* 2006; Warren & Seifert 2011) to help determine if it was possible Clade A actually represents true *L. parvus* from an ecological perspective. Environmental predictors initially comprised the 19 historical bioclimatic variables at 30 arc-second spatial resolution downloaded from WorldClim v2.1 (Fick & Hijmans 2017), supplemented with relevant EarthEnv Global 1-km Consensus Land Cover v1.0 classes (Tuanmu & Jetz 2014) and surface soil variables from the SoilGrids250m v2.0 dataset (Hengl *et al.* 2017), including bulk density, pH, organic carbon density, and clay content, to represent soil properties potentially influencing species distributions. Multicollinearity among predictors was assessed using pairwise Pearson correlation analyses, and variables were further screened for ecological relevance. Based on these criteria, precipitation of the driest month, mean temperature of the coldest quarter, evergreen broadleaf forest cover, and soil pH (0–5 cm depth) were retained for model construction. To reduce model complexity given the limited sample size, only linear and quadratic feature classes were permitted, and the regularization multiplier was set to 1.5 to minimize overfitting (Warren & Seifert 2011; Merow *et al.* 2013; Radosavljevic & Anderson 2014). We evaluated model performance using five-fold cross-validation, and predictor importance was assessed using the jackknife procedure implemented in MaxEnt (Phillips *et al.* 2006; Phillips & Dudík 2008). Then we assessed habitat suitability of Yapen, the range of true *L. parvus*, for the Clade A specimens to determine whether the two groups overlap in ecological niche occupancy, which would support that they could be the same species. Habitat suitability was categorized on a scale from 0 to 1, with values > 0.7 classified as highly suitable.

In addition to Clade A, the *L. iridis* complex, composed here of *L. iridis* and *L. aplini*, contained another group of individuals that could represent a separate taxon (Clade B hereafter, see results below). Specimens of Clade B were all identified as *L. modestus* in the field notes of collectors. To explore whether Clade B is a standalone new species, we also used CytB data to calculate and examine ML pairwise genetic distances within and between the three clades in the *L. iridis* complex through IQ-TREE v2.4.0 (Nguyen *et al.* 2015). Note that this equivalent analysis was not possible with respect to Clade A vs. *L. parvus* due to a lack of genetic sampling for topotypic *L. parvus*.

Morphological Data

While genetic data were not available for all specimens, and voucher specimens were not available for all samples with genetic data, we examined the following morphological characters for all available specimens of interest: snout-vent length, tail length, number of mid body dorsal rows, number of ventral scales, number of subcaudal scales, subcaudal scales divided or undivided, anal plate divided or undivided, number of supralabial scales, number of infralabial scales, presence of a loreal scale, number of pre-ocular scales, number of postocular scales, number of supralabials in contact with eye, genial scales in contact or interrupted by gular scales, and presence/absence of

apical pits on dorsal scales. For newly described species, additional morphological information, such as color and pattern, were also recorded (see Table S2).

Results

Sequencing efforts acquired a total of 4,870 UCEs across 99 samples, and the concatenated 75% complete matrices retained 4,137 UCEs. The topology inferred by the UCE ML tree was largely congruent with prior studies (Bernstein *et al.* 2026). All samples of previously identified species were grouped into their respective monophyletic groups with most nodes strongly supported (Fig. 1). We used the topology of the concatenated ML tree to create a mapping file with 14 described and putative taxa, including the three outgroup species, to generate the species tree, which had most nodes well supported (Fig. S1); the CytB tree was also broadly consistent with the UCE tree (Fig. S2). True *L. modestus* was sister to *L. admiraltiensis*, not Clade B, thus Clade B does not represent *L. modestus*. The ML pairwise genetic distance between Clade B and *L. aplini* ranged from 2.8% to 3.3%, and that between it and *L. iridis* ranged from 6.2% to 7.3%.

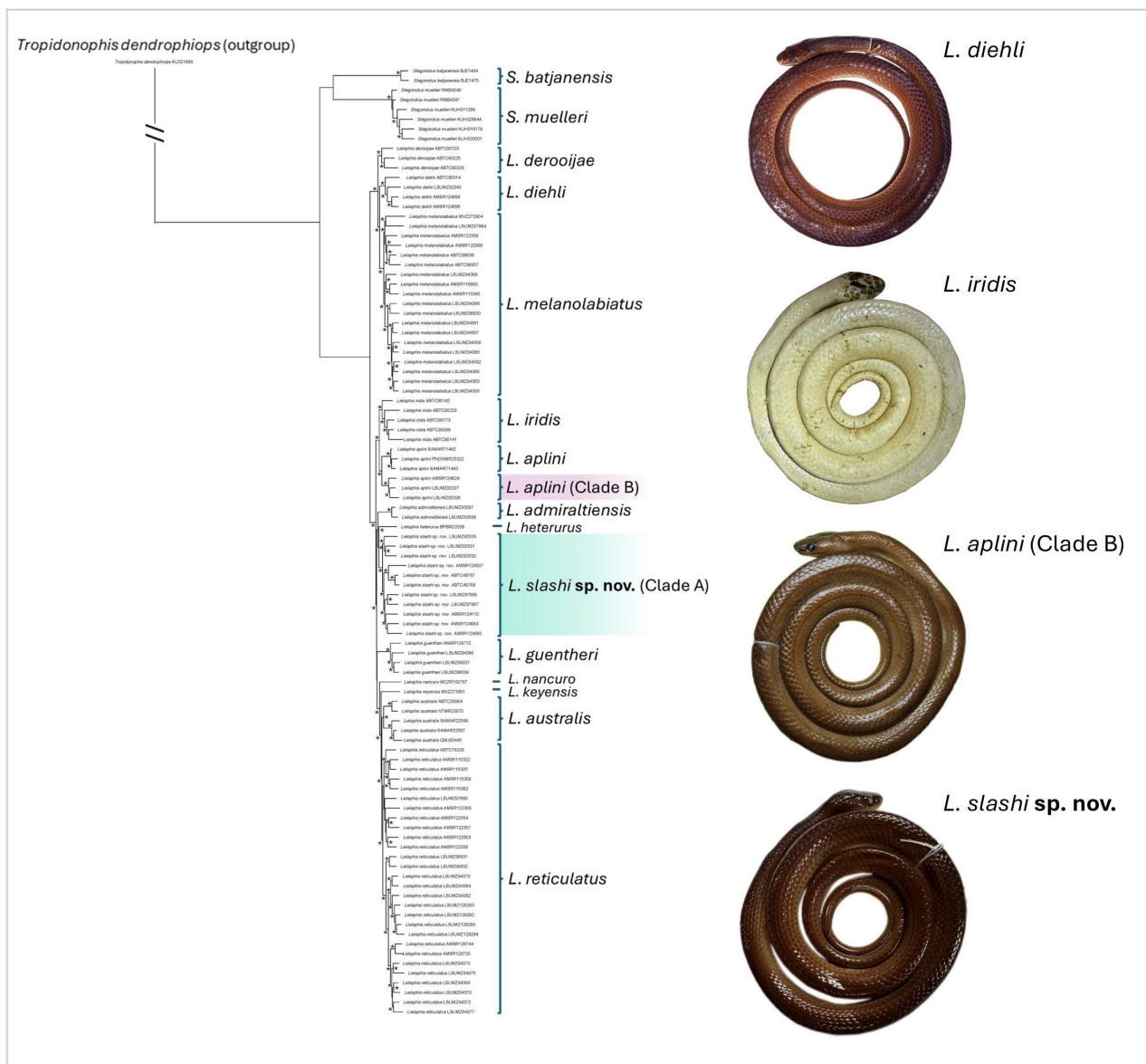


FIGURE 1. Ultraconserved elements maximum-likelihood tree of *Lielaphis* and *Stegonotus* species inferred by IQ-TREE with Clade A (*L. slashi sp. nov.*) and Clade B (putative northern *L. aplini*) highlighted. Photographs of exemplar included taxa on the left: (top to bottom) *L. melanolabiatus*, *L. iridis*, putative northern *L. aplini* (Clade B), and *L. slashi sp. nov.* (Clade A). * indicates UFB ≥ 95 and SH-aLRT ≥ 80 .

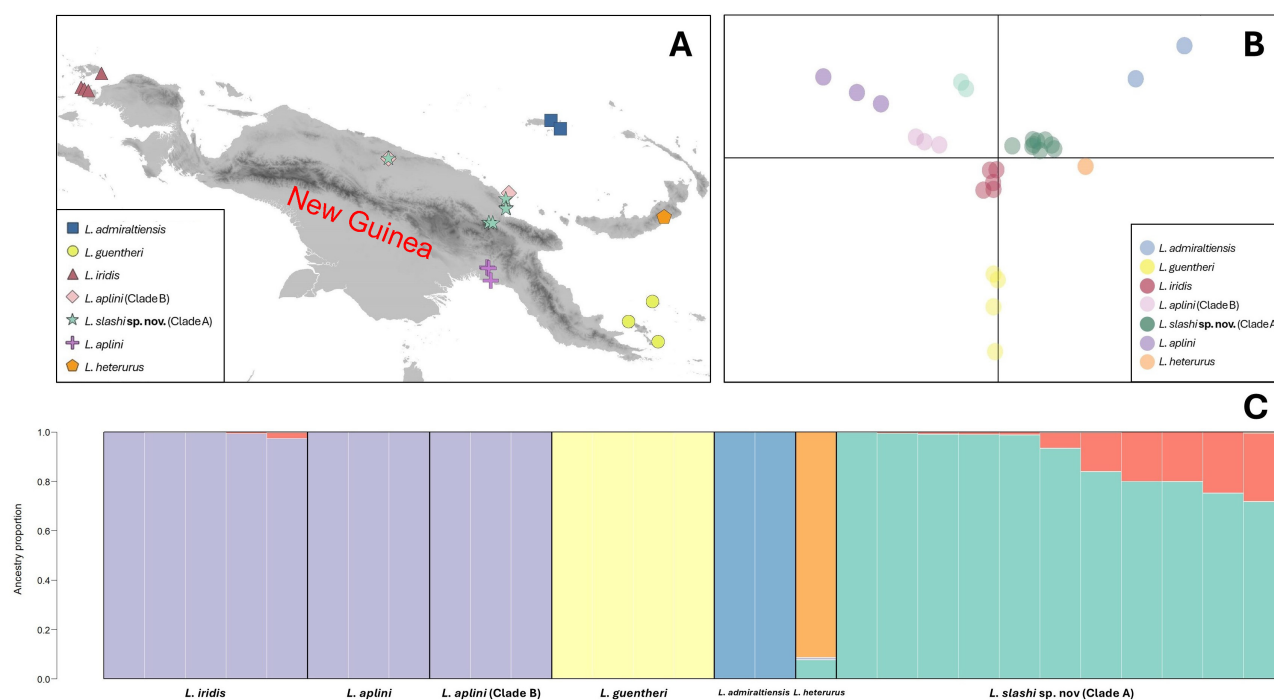


FIGURE 2. (A) Map of sampling localities for *Lielaphis* used in demography and population demarcation analysis; (B) DAPC plot showing the genetic clustering of seven *Lielaphis* taxa; (C) STRUCTURE plot inferring five distinct clusters, indicated by different colors, across seven recognized and putative *Lielaphis* taxa delineated by vertical black lines.

For the STRUCTURE analyses, besides the two clades in question (A and B), we only included *L. admiraltiensis*, *L. aplini*, *L. guentheri*, and *L. heterurus* because they were most closely related to the lineages of interest based on the phylogeny (Fig. 1), with all species coming from mainland New Guinea and adjacent islands (Fig. 2A). The Evanno method indicated a best fit model of $K = 6$, where *L. guentheri*, *L. admiraltiensis*, *L. heterurus*, and Clade A each formed their own distinct population cluster, while *L. iridis*, *L. aplini*, and Clade B could not be clearly distinguished from each other via STRUCTURE (Fig. 2C). This indicated that *L. iridis*, *L. aplini*, and Clade B came from the same, relatively recent ancestral population. The *de novo* DAPC identified eight unique clusters among the seven known and putative species (Fig. 2B). Members of all examined species were unambiguously assigned to their species-specific clusters, while members of Clade A were split into two distinct clusters. Since members of the two Clade A clusters were deeply embedded in other analyses, such subdivision might be an artifact owing to the high sensitivity of DAPC on subtle genetic structures (Jombart *et al.* 2010). Given the limited sample size, MaxEnt performance was moderate with an average test AUC of 0.672 (SD = 0.094), but it was consistent across replicates, and adequately captured known occurrence localities. The MaxEnt results showed that Yapen only contained habitats with low suitability (mean = 0.27) for Clade A, while habitats with very high suitability (> 0.70) for Clade A were primarily located in eastern lowland part of mainland New Guinea (Fig. S3).

Morphological data showed consistent differences between the two potentially new taxa, Clade A and Clade B, their respective sister taxon, and all other relevant *Lielaphis* and *Stegonotus* specimens examined (Table 1; Table S2). Based on both genetic and morphological evidence, we refrain from recognizing Clade B as a species at this time due to the weak support as being distinct in STRUCTURE and the short ML pairwise genetic distances between it and *L. aplini*, and thus consider that it may represent a distinct northern brown morph of *L. aplini*, which, if accurate, would be a substantial range extension. However, the evidence strongly supports the recognition of Clade A as a new species of *Lielaphis*, and thus we describe Clade A as a new species of *Lielaphis* below.

TABLE 1. Morphological characters of Clades A and B, their sister taxa, sympatric taxa, and relevant species *sensu stricto*.

Species	N	Mid-body dorsal rows	Ventrals	Subcaudals	Supralabials	Infralabials
<i>L. slashi</i> sp. nov. (Clade A)	16	17	165–181	83–107	8, 9	8, 9, 10
<i>L. aplini</i> , northern (Clade B)	8	17	196–217	80–89	7, 8	8, 9 , 10
<i>L. aplini</i> ^{1,*}	4	19	229–239	83–95	8,9	8,9
<i>L. heterurus</i> ^{2,Δ}	19	17	179–198	76–93	7	8, 9
<i>L. deihli</i> [#]	11 ⁴	15	162–175	65–85	7	8, 9
<i>L. parvus sensu stricto</i>	2 ³	17	173, 177	87, 100	7	8
<i>L. modestus sensu stricto</i>	18	17	190–206	58–94	7, 8	8, 9, 10

¹Data from O'Shea and Richards 2021.

²Data from Kaiser *et al.* 2018.

³Includes one lost syntype with no infralabial count recorded.

⁴Data of five individuals from Ruane *et al.* 2018.

*Sister taxa of *L. aplini* Clade B.

ΔSister taxa of *L. modestus*.

#Sympatric species of both putative species.

In case of multiple values of scales, the value in bold represents the condition observed in the majority of specimens examined here.

***Lielaphis slashi* sp. nov.**

Slash's groundsnake

(Figs. 3, 4)

Stegonotus parvus Ruane *et al.* 2018

Holotype (Fig. 3). LSUMZ 92332 (field number CCA 3312), adult male. Collected by C. C. Austin on 4 July 2006 from Utai Village in Sanduan Province, Papua New Guinea, elevation 208 m above sea level (3.3961°S, 141.5829°E).

Paratypes (N = 4; Fig. 4). LSUMZ 92331 (field number CCA 3216), juvenile, presumably male (hemipenes not inverted, sex inconclusive without intrusive dissection). Collected by C. C. Austin on 3 July 2006 from Utai Village in Sanduan Province, Papua New Guinea, elevation 208 m above sea level (3.3961°S, 141.5829°E). LSUMZ 92333 (field number CCA 3418), adult, presumably female (hemipenes not inverted, sex inconclusive without intrusive dissection). Collected by C. C. Austin on 6 July 2006 from Utai Village in Sanduan Province, Papua New Guinea, elevation 208 m above sea level (3.3961°S, 141.5829°E). LSUMZ 97666 (field number CCA 16639), juvenile, presumably male (hemipenes not inverted, sex inconclusive without intrusive dissection). Collected by C. C. Austin on 14 July 2012 from Kalibobo Point in Madang Province, Papua New Guinea, elevation 0 m above sea level (5.2097°S, 145.8074°E). LSUMZ97667 (field number CCA16661), juvenile, presumably female (hemipenes not inverted, sex inconclusive without intrusive dissection). Collected by C. C. Austin on 15 July 2012 from Kalibobo Point in Madang Province, Papua New Guinea, elevation 0 m above sea level (5.2097°S, 145.8074°E).

Diagnosis. A new species of *Lielaphis* that can be diagnosed from its congeners by the combination of the following characteristics: a reddish-brown unpatterned dorsum with an unmarked white or cream venter that may be barely darker towards the subcaudal scales, 17 scale rows at midbody, absence of apical pits, 165–181 ventral scales and 83–107 divided subcaudal scales, two preocular scales, two postocular scales, eight to nine (primarily eight) supralabial scales, eight to ten (primarily ten) infralabial scales, supralabial and infralabial scales cream to light tan, supralabials darker, infralabials may be slightly mottled anteriorly.

Description of holotype. Adult male in excellent state of preservation, with hemipenes exposed and five short ventral slits around midbody. Snout–vent length 726 mm with 177 ventral scales, tail length 285 mm with 99 divided subcaudal scales. Anal scale single. Supralabials nine with the fourth and fifth in contact with the eye. Infralabials ten, with first pair in contact behind mental, infralabials one to six in contact with inframaxillaries. Rostral broader than high, a small part visible from above. Circumoculars five: one supraocular, two preoculars, two postoculars,

and no suboculars. Nasal in contact with first supralabial. Single loreal, in contact with nasal, lower preocular, prefrontal, and supralabials two and three. Supralabials four and five in contact with orbit. Anterior temporals two. Dorsal surface of head includes pair of internasals, pair of prefrontals, pair of supraoculars, frontal marginally wider than long, pair of parietals. Two pairs of inframaxillaries, both in contact with each other. Dorsal scale rows 17–17–15 (15th ventral from anterior, midbody, and 15th ventral anterior to cloaca).

Variation. Paratypes similar to the holotype, except for the following differences: All paratypes with eight supralabials instead of nine; LSUMZ 97666 (field number CCA 16639) with light cream to grayish cream labials instead of darker cream to light tan.

Coloration in life. Based on photos of paratype LSUMZ 97666. Dorsal coloration dark brown with no markings and with lighter coloration laterally. Color of iris black. Dorsum of head dark brown. Supralabials light brown to tan and lighter on the lower end, infralabials white with brown to tan pigments; one to three and five having slightly darker pigments than the rest. Ventral and subcaudal scales white and iridescent with some sporadic, irregular dark brown spots.

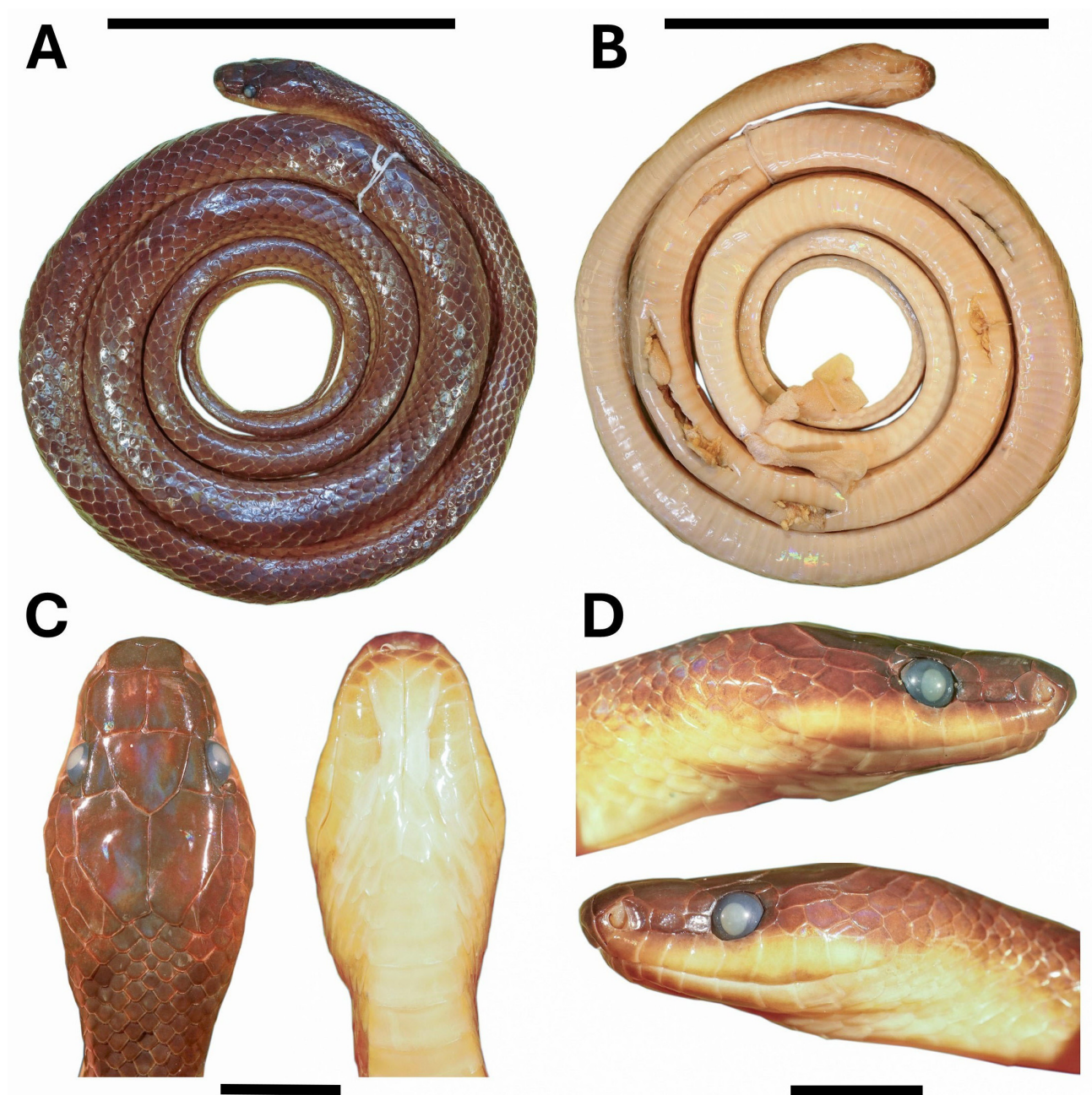


FIGURE 3. Photographs of holotype *Lielaphis slashi* sp. nov. LSUMZ92332 showing dorsum (A), venter (B), ventral and dorsal sides of head (C), and right and left lateral sides of head (D). Black bars equal to 100 mm in (A) and (B), and equal to 10 mm in (C) and (D). Photographs from T. Huang.



FIGURE 4. Life photo of a juvenile *Lielaphis slashi* sp. nov. (LSUMZ 97666, paratype). Photograph from C. C. Austin.

Coloration in preservative. Overall dorsal coloration reddish-brown in preservation with lighter coloration laterally with no patterns present. Color of iris opaque grey in preservation. Dorsum of head dark reddish-brown. Supralabials cream to light tan overall, with one to two having a light reddish-brown wash, and six to eight having a reddish-brown wash infringing the upper half of the scales where they come into contact with the temporals. Ventral scales and subcaudals unmarked white to cream with no pattern, subcaudals slightly darker posteriorly. Ventral scales show slight iridescence under lights.

Etymology. The species epithet is a patronym to honor Mr. Saul Hudson, known popularly and professionally as the musician “Slash,” in recognition for his life-long support of museums and zoos, and especially for his love of snakes. Slash has frequently promoted and acted as an advocate for snakes across various media outlets over many years. Senior author SR also credits much of her scientific writing as having occurred while listening to Slash’s music, including that of Slash’s Snakepit, Guns N’ Roses, and Velvet Revolver.

Natural history and distribution. Information on the natural history of the species is lacking but individuals here were found in largely undisturbed secondary forest. It is currently known from north of the Central Cordillera in Sanduan, East Sepik, and Madang Provinces of Papua New Guinea, and may also occur in the Indonesian province of Papua north of the central mountain ranges.

Comparisons. The known individuals of this species were initially identified as *L. parvus* with respect to field collection notes (see Ruane *et al.* 2018). The species is sympatric with the putative northern brown morph of *L. aplini* and with *L. diehli* and is the sister taxon to *L. heterurus*. It differs from *L. parvus* by having more supralabial scales (eight to nine versus seven in *L. parvus*) and more infralabial scales (primarily ten versus eight in *L. parvus*), and by its range on the New Guinea mainland north of the Central Cordillera while *L. parvus* is known only from Yapen Island, Papua Province, Indonesia. It can be easily distinguished from its sister taxon *L. heterurus* by having divided subcaudal scales (versus undivided in *L. heterurus*) and a darker venter (white to cream versus dark gray in *L. heterurus*). It also differs from the latter by having a combination of fewer ventral scales (165–181 versus 179–198 in *L. heterurus*), more supralabial scales (eight to nine versus seven in *L. heterurus*), and more infralabial

scales (primarily ten versus eight to nine in *L. heterurus*), and by being found on the New Guinea mainland north of the Central Cordillera while *L. heterurus* is known only from the islands of New Britain, New Ireland, and Duke of York, Papua New Guinea. It differs from the sympatric putative northern brown morph of *L. aplini* by having a combination of fewer ventral scales (165–181 versus 196–217 in putative northern *L. aplini*), more supralabial scales (primarily eight versus primarily seven in putative northern *L. aplini*), and more infralabial scales (primarily ten versus primarily eight and nine in putative northern *L. aplini*). It differs from the sympatric *L. diehli* by having a combination of more mid-body dorsal rows (17 versus 15 in *L. diehli*), more subcaudals (83–107 versus 65–85 in *L. diehli*), more supralabials (eight to nine versus seven in *L. diehli*), and more infralabials (primarily ten versus primarily eight in *diehli*).

Discussion

To advance knowledge of cryptic diversity within the genus of *Lielaphis*, we used a combination of genome-wide sequence data and morphology to investigate *Lielaphis* taxonomy, and identified a new species, *Lielaphis slashi*. Currently only known from the north of the Central Cordillera, particularly the lowland habitats in northeast mainland New Guinea, *L. slashi* is sister to *L. heterurus* from the Bismarck Archipelago and exhibits significant morphological differences from its congeners.

We also revealed a lineage of *Lielaphis* sister to *L. aplini*. Though it possesses distinguishable morphological characters, due to the lack of evidence shown by our population demarcation analyses combined with some but not a substantial amount of mtDNA divergence, we do not recognize it as a new species at this time. We consider this population to be a regional variation of *L. aplini* pending further evidence that would warrant species-level status. This would expand the range of *L. aplini* to include both sides of the Central Cordillera, a first for *Lielaphis*. We caution that the northern population may in fact represent a separate taxon, but that additional sampling and evidence is needed to better understand the status of this species, which are currently in progress. As of now, we are confident in stating that it does not represent *L. modestus* despite initial field identifications of the individuals included here.

The rapid late Miocene geological uplift in New Guinea created the Central Cordillera, a mountainous divide that has been shown to explain the high diversity of numerous taxa occurring in the region (Polhemus & Polhemus 1998; Bruxaux *et al.* 2018; Roycroft *et al.* 2022; Ferreira *et al.* 2024). This central mountain range also acts as a biogeographic barrier for the Australasian groundsnake genus of *Lielaphis*, given that *Lielaphis* displays lower habitat suitability and diversity at higher elevations in studies using niche models (Bernstein *et al.* 2026). With growing research interests in snake taxonomy and ecology on this remote yet biologically megadiverse tropical island, recent years have witnessed the description of multiple new snake species on either side of the mountain range (Ruane *et al.* 2018; Kaiser *et al.* 2018; Kaiser *et al.* 2019; Roberts & Austin 2020; O'Shea & Richards 2021; Roberts *et al.* 2022; Bernstein *et al.* 2026). Prior to this study, 12 *Lielaphis* species were presumed to occur on the New Guinea mainland and its closely surrounding islands—*L. aplini*, *L. ayamaru*, *L. cucullatus*, *L. derooijae*, *L. diehli*, *L. dorsalis*, *L. guentheri*, *L. iridis*, *L. melanolabiatus*, *L. parvus*, *L. poechi*, and *L. reticulatus* (Kaiser *et al.* 2018; Kaiser *et al.* 2019; O'Shea & Richards 2021; Bernstein *et al.* 2026). The addition of *L. slashi* here brings up the number of *Lielaphis* species in the region to 13, and the total number of *Lielaphis* species to 20. Even so, the cryptic diversity of this secretive, ground-dwelling group of snakes likely remains significantly underexplored (Ruane *et al.* 2018; Kaiser *et al.* 2018) and future research, especially that using high-resolution genomic data and finer scale sampling coupled with more advanced analytical tools will further clarify the taxonomy of these snakes.

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References

- Bankevich, A., Nurk, S., Antipov, D., Gurevich, A.A., Dvorkin, M., Kulikov, A.S., Lesin, V.M., Nikolenko, S.I., Pham, S., Prjibelski, A.D. & Pyshkin, A.V. (2012) SPAdes: a new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology*, 19 (5), 455–477.
<https://doi.org/10.1089/cmb.2012.0021>
- Bernstein, J.M. & Ruane, S. (2022) Maximizing molecular data from low-quality fluid-preserved specimens in natural history collections. *Frontiers in Ecology and Evolution*, 10, 893088.
<https://doi.org/10.3389/fevo.2022.893088>
- Bernstein, J.M., Austin, C.C., Soto-Centeno, J.A., Huang, T., Roberts, J.R., McGuire, J.A., Iskandar, D., Frederick, J.H., Weinell, J.L., Brown, R.M. & Ruane, S. (2026) Diversification and colonization in the Indo-Australian Archipelago: genomic insights from colubrid snakes. *Journal of Biogeography*, 53 (4), e70202.
<https://doi.org/10.1111/jbi.70202>
- Bolger, A.M., Lohse, M. & Usadel, B. (2014) Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics*, 30 (15), 2114–2120.
<https://doi.org/10.1093/bioinformatics/btu170>
- Boulenger, G.A. (1895) On a collection of reptiles and batrachians from Ferguson Island, D'Entrecasteaux Group, British New Guinea. *The Annals and Magazine of Natural History*, Series 6, 16, 28–32.
<https://doi.org/10.1080/00222939508680222>
- Bruxaux, J., Gabrielli, M., Ashari, H., Prŷs-Jones, R., Joseph, L., Milá, B., Besnard, G. & Thébaud, C. (2018) Recovering the evolutionary history of crowned pigeons (Columbidae: *Goura*): implications for the biogeography and conservation of New Guinean lowland birds. *Molecular Phylogenetics and Evolution*, 120, 248–258.
<https://doi.org/10.1016/j.ympev.2017.11.022>
- Chernomor, O., von Haeseler, A. & Minh, B.Q. (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology*, 65 (6), 997–1008.
<https://doi.org/10.1093/sysbio/syw037>
- Del Fabbro, C., Scalabrin, S., Morgante, M. & Giorgi, F.M. (2013) An extensive evaluation of read trimming effects on Illumina NGS data analysis. *PLoS One*, 8 (12), e85024.
<https://doi.org/10.1371/journal.pone.0085024>
- Doria, G. (1875) Enumerazione dei rettili raccolti dal Dott. O. Beccari in Amboina alle Isole Aru ed alle Isole Kei durante gli anni 1872–73. *Annali del Museo Civico di Storia Naturale di Genova*, 6, 325–357.
- Dubey, S., Brown, G.P., Madsen, T. & Shine, R. (2008) Male-biased dispersal in a tropical Australian snake (*Stegonotus cucullatus*, Colubridae). *Molecular Ecology*, 17 (15), 3506–3514.
<https://doi.org/10.1111/j.1365-294x.2008.03859.x>
- Duméril, A.M.C., Bibron, G. & Duméril, A.H.A. (1854) *Erpétologie générale ou Histoire naturelle complète des reptiles. Vol. 7. Partie I*. Roret, Paris, xvi + 780 pp.
<https://doi.org/10.5962/bhl.title.112278>
- Earl, D.A. & vonHoldt, B.M. (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, 4 (2), 359–361.
<https://doi.org/10.1007/s12686-011-9548-7>
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A. & Li, J. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29 (2), 129–151.
- Evanno, G., Regnaut, S. & Goudet, J. (2005) Detecting the number of clusters of individuals using the software STRUCTURE:

- a simulation study. *Molecular Ecology*, 14 (8), 2611–2620.
<https://doi.org/10.1111/j.1365-294x.2005.02553.x>
- Faircloth, B.C., McCormack, J.E., Crawford, N.G., Harvey, M.G., Brumfield, R.T. & Glenn, T.C. (2012) Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. *Systematic Biology*, 61 (5), 717–726.
<https://doi.org/10.1093/sysbio/sys004>
- Faircloth, B.C. (2013) illumiprocessor: a trimmomatic wrapper for parallel adapter and quality trimming. Available from: <https://doi.org/10.6079/J9ILL> (accessed 10 May 2025)
- Faircloth, B.C. (2016) PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics*, 32 (5), 786–788.
<https://doi.org/10.1093/bioinformatics/btv646>
- Ferreira, F., Oliver, P., Kraus, F., Günther, R., Richards, S., Tjaturadi, B., Arida, E., Hamidy, A., Riyanto, A., Trilaksono, W. & Thébaud, C. (2025) Molecular and acoustic evidence for large-scale underestimation of frog species diversity on New Guinea. *Frontiers of Biogeography*, 18, e137988.
<https://doi.org/10.21425/fob.18.137988>
- Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37 (12), 4302–4315.
<https://doi.org/10.1002/joc.5086>
- Filer, C., Keenan, R.J., Allen, B.J. & McAlpine, J.R. (2009) Deforestation and forest degradation in Papua New Guinea. *Annals of Forest Science*, 66 (8), 813.
<https://doi.org/10.1051/forest/2009067>
- Gaveau, D.L.A., Santos, L., Locatelli, B., Salim, M.A., Husnayaen, H., Meijaard, E., Heatubun, C. & Sheil, D. (2021) Forest loss in Indonesian New Guinea (2001–2019): trends, drivers and outlook. *Biological Conservation*, 261, 109225.
<https://doi.org/10.1016/j.biocon.2021.109225>
- Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Systematic Biology*, 59 (3), 307–321.
<https://doi.org/10.1093/sysbio/syq010>
- Günther, A. (1865) Fourth account of new species of snakes in the collection of the British Museum. *The Annals and Magazine of Natural History*, Series 3, 15, 89–98.
<https://doi.org/10.1080/00222936508681770>
- Günther, A. (1872) Seventh account of new species of snakes in the collection of the British Museum. *The Annals and Magazine of Natural History*, Series 4, 9, 13–37.
<https://doi.org/10.1080/002229372011951771>
- Günther, A. (1883) Description of two snakes from the 'Challenger' collections. *The Annals and Magazine of Natural History*, Series 5, 11, 136–137.
<https://doi.org/10.1080/00222938309459109>
- Hengl, T., Mendes de Jesus, J., Heuvelink, G.B.M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B. & Guevara, M.A. (2017) SoilGrids250m: global gridded soil information based on machine learning. *PLoS One*, 12 (2), e0169748.
<https://doi.org/10.1371/journal.pone.0169748>
- Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2018) UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35 (2), 518–522.
<https://doi.org/10.1093/molbev/msx281>
- Jombart, T. (2008) adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics*, 24 (11), 1403–1405.
<https://doi.org/10.1093/bioinformatics/btn129>
- Jombart, T., Devillard, S. & Balloux, F. (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genetics*, 11 (1), 94.
<https://doi.org/10.1186/1471-2156-11-94>
- Jombart, T. & Ahmed, I. (2011) adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics*, 27 (21), 3070–3071.
<https://doi.org/10.1093/bioinformatics/btr521>
- Kaiser, C.M., Kaiser, H. & O'Shea, M. (2018) The taxonomic history of Indo-Papuan groundsnakes, genus *Stegonotus* Duméril *et al.*, 1854 (Colubridae), with some taxonomic revisions and the designation of a neotype for *S. parvus* (Meyer, 1874). *Zootaxa*, 4512 (1), 1–73.
<https://doi.org/10.11646/zootaxa.4512.1.1>
- Kaiser, C.M., O'Shea, M. & Kaiser, H. (2019) A new species of Indo-Papuan groundsnake, genus *Stegonotus* Duméril *et al.*, 1854 (Serpentes, Colubridae), from the Bird's Head Peninsula of West Papua, Indonesia, with comments on differentiating morphological characters. *Zootaxa*, 4590 (2), 201–230.
<https://doi.org/10.11646/zootaxa.4590.2.1>
- Kaiser, H., Kaiser, C.M., Mecke, S. & O'Shea, M. (2021) A new species of *Stegonotus* (Serpentes: Colubridae) from the remnant

- coastal forests of southern Timor-Leste. *Zootaxa*, 5027 (4), 489–514.
<https://doi.org/10.11646/zootaxa.5027.4.2>
- Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A. & Jermin, L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14 (6), 587–589.
<https://doi.org/10.1038/nmeth.4285>
- Li, H. (2013) Aligning sequence reads, clone sequences and assembly contigs with BWA-MEM. *arXiv preprint*, arXiv:1303.3997.
- Lindholm, W.A. (1905) Ueber einige Eidechsen und Schlangen aus Deutsch-Neuguinea. *Jahrbücher des Nassauischen Vereins für Naturkunde*, 58, 227–240.
- McDowell, S.B. (1972) The species of *Stegonotus* (Serpentes, Colubridae) in Papua New Guinea. *Zoologische Mededelingen*, 47 (2), 6–26.
- McKenna, A., Hanna, M., Banks, E., Sivachenko, A., Cibulskis, K., Kernytsky, A., Garimella, K., Altshuler, D., Gabriel, S., Daly, M. & DePristo, M.A. (2010) The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Research*, 20 (9), 1297–1303.
<https://doi.org/10.1101/gr.107524.110>
- Merow, C., Smith, M.J. & Silander, J.A. Jr (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, 36 (10), 1058–1069.
<https://doi.org/10.1111/j.1600-0587.2013.07872.x>
- Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A. & Lanfear, R. (2020) IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution*, 37 (5), 1530–1534.
<https://doi.org/10.1093/molbev/msaa015>
- Mittermeier, R.A., Mittermeier, C.G., Brooks, T.M., Pilgrim, J.D., Konstant, W.R., Da Fonseca, G.A.B. & Kormos, C. (2003) Wilderness and biodiversity conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 100 (18), 10309–10313.
<https://doi.org/10.1073/pnas.1732458100>
- Meyer, A.B. (1874) Eine Mittheilung von Herrn Dr. Adolf Bernhard Meyer über die von ihm auf Neu-Guinea und den Inseln Jobi, Mysore und Mafoor im Jahre 1873 gesammelten Amphibien. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1874, 128–140.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403 (6772), 853–858.
<https://doi.org/10.1038/35002501>
- Nelson, P.N., Gabriel, J., Filer, C., Banabas, M., Sayer, J.A., Curry, G.N., Koczberski, G. & Venter, O. (2014) Oil palm and deforestation in Papua New Guinea. *Conservation Letters*, 7 (3), 188–195.
<https://doi.org/10.1111/conl.12058>
- Nguyen, L.T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32 (1), 268–274.
<https://doi.org/10.1093/molbev/msu300>
- O'Shea, M. & Richards, S.J. (2021) A striking new species of Papuan groundsnake (*Stegonotus*: Colubridae) from southern Papua New Guinea, with a dichotomous key to the genus in New Guinea. *Zootaxa*, 4926 (1), 26–42.
<https://doi.org/10.11646/zootaxa.4926.1.2>
- Oliver, L.A., Rittmeyer, E.N., Kraus, F., Richards, S.J. & Austin, C.C. (2013) Phylogeny and phylogeography of *Mantophryne* (Anura: Microhylidae) reveals cryptic diversity in New Guinea. *Molecular Phylogenetics and Evolution*, 67 (3), 600–607.
<https://doi.org/10.1016/j.ympev.2013.02.023>
- Oliver, P.M., Bower, D.S., McDonald, P.J., Kraus, F., Luedtke, J., Neam, K., Hobin, L., Chauvenet, A.L.M., Allison, A., Arida, E., Clulow, S., Günther, R., Nagombi, E., Tjaturadi, B., Travers, S.L. & Richards, S.J. (2022) Melanesia holds the world's most diverse and intact insular amphibian fauna. *Communications Biology*, 5 (1), 1182.
<https://doi.org/10.1038/s42003-022-04105-1>
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190 (3–4), 231–259.
<https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Phillips, S.J. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31 (2), 161–175.
<https://doi.org/10.1111/j.0906-7590.2008.5203.x>
- Polhemus, D.A. & Polhemus, J.T. (1998) Assembling New Guinea: 40 million years of island arc accretion as indicated by the distributions of aquatic Heteroptera (Insecta). In: Hall, R. & Holloway, J.D. (Eds.), *Biogeography and Geological Evolution of SE Asia*. Backhuys Publishers, Leiden, pp. 327–340.
- Pritchard, J.K., Stephens, M. & Donnelly, P. (2000) Inference of population structure using multilocus genotype data. *Genetics*, 155 (2), 945–959.
<https://doi.org/10.1093/genetics/155.2.945>
- Roberts, J.R. & Austin, C.C. (2020) A new species of New Guinea Worm-Eating Snake (Elapidae: *Toxicocalamus* Boulenger,

- 1896), with comments on postfrontal bone variation based on micro-computed tomography. *Journal of Herpetology*, 54 (4), 446–459.
<https://doi.org/10.1670/20-043>
- Roberts, J.R., Iova, B. & Austin, C.C. (2022) A new species of New Guinea Worm-Eating Snake (Serpentes, Elapidae, *Toxicocalamus* Boulenger, 1896) from Western Highlands Province, Papua New Guinea. *Zoosystematics and Evolution*, 98 (2), 399–409.
<https://doi.org/10.3897/zse.98.90520>
- Radosavljevic, A. & Anderson, R.P. (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography*, 41 (4), 629–643.
<https://doi.org/10.1111/jbi.12227>
- Roycroft, E., Fabre, P.H., MacDonald, A.J., Moritz, C., Moussalli, A. & Rowe, K.C. (2022) New Guinea uplift opens ecological opportunity across a continent. *Current Biology*, 32 (19), 4215–4224.
<https://doi.org/10.1016/j.cub.2022.08.021>
- Ruane, S., Richards, S.J., McVay, J.D., Tjaturadi, B., Krey, K. & Austin, C.C. (2018) Cryptic and non-cryptic diversity in New Guinea ground snakes of the genus *Stegonotus* Duméril, Bibron and Duméril, 1854: a description of four new species (Squamata: Colubridae). *Journal of Natural History*, 52 (13–16), 917–944.
<https://doi.org/10.1080/00222933.2017.1391959>
- Sabaj, M.H. (2025) Codes for Natural History Collections in Ichthyology and Herpetology (online supplement), Version 9.7 (3 Mar 2025). American Society of Ichthyologists and Herpetologists, Washington, DC. Available from: <https://www.asih.org/resources/standard-symbolic-codes> (accessed 15 January 2026)
- Schlegel, H. (1837) *Essai sur la physionomie des serpents. Partie descriptive*. J. Kips, J.H.Z. & W.P. van Stockum, La Haye, xvi + 606 pp.
<https://doi.org/10.5962/bhl.title.4273>
- Shearman, P. & Bryan, J. (2011) A bioregional analysis of the distribution of rainforest cover, deforestation and degradation in Papua New Guinea. *Austral Ecology*, 36 (1), 9–24.
<https://doi.org/10.1111/j.1442-9993.2010.02111.x>
- Shine, R. (1991) Strangers in a strange land: ecology of the Australian colubrid snakes. *Copeia*, 1991 (1), 120–131.
<https://doi.org/10.2307/1446254>
- Shine, R. (1994) Sexual size dimorphism in snakes revisited. *Copeia*, 1994 (2), 326–346.
<https://doi.org/10.2307/1446982>
- Singhal, S., Grundler, M., Colli, G. & Rabosky, D.L. (2017) Squamate conserved loci (SqCL): a unified set of conserved loci for phylogenomics and population genetics of squamate reptiles. *Molecular Ecology Resources*, 17 (6), e12–e24.
<https://doi.org/10.1111/1755-0998.12681>
- Slavenko, A., Allison, A., Austin, C.C., Bauer, A.M., Brown, R.M., Fisher, R.N., Ineich, I., Iova, B., Karin, B.R., Kraus, F., Mecke, S., Meiri, S., Morrison, C., Oliver, P.M., O’Shea, M., Richmond, J.Q., Shea, G.M., Tallwin, O.J.S. & Chapple, D.G. (2023) Skinks of Oceania, New Guinea, and Eastern Wallacea: an underexplored biodiversity hotspot. *Pacific Conservation Biology*, 29 (6), 526–543.
<https://doi.org/10.1071/pc22034>
- Trembath, D.F., Fearn, S. & Undheim, E.A.B. (2009) Natural history of the slaty grey snake (*Stegonotus cucullatus*) (Serpentes: Colubridae) from tropical north Queensland, Australia. *Australian Journal of Zoology*, 57 (2), 119–124.
<https://doi.org/10.1071/zo08091>
- Tuanmu, M.N. & Jetz, W. (2014) A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*, 23 (9), 1031–1045.
<https://doi.org/10.1111/geb.12182>
- Van der Auwera, G.A., Carneiro, M.O., Hartl, C., Poplin, R., Del Angel, G., Levy-Moonshine, A., Jordan, T., Shakir, K., Roazen, D., Thibault, J. & Banks, E. (2013) From FastQ data to high-confidence variant calls: the Genome Analysis Toolkit best practices pipeline. *Current Protocols in Bioinformatics*, 43 (1), 11.10.1–11.10.33.
<https://doi.org/10.1002/0471250953.bi1110s43>
- Warren, D.L. & Seifert, S.N. (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, 21 (2), 335–342.
<https://doi.org/10.1890/10-1171.1>
- Werner, F. (1924) Neue oder wenig bekannte Schlangen aus dem Naturhistorischen Staatsmuseum in Wien. I. Teil. *Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse, Abteilung I*, 133, 29–56.
- White, T.H. Jr, Bickley, P., Brown, C., Busch, D.E., Dutson, G., Freifeld, H., Krofta, D., Lawlor, S., Polhemus, D. & Rounds, R. (2021) Quantifying threats to biodiversity and prioritizing responses: an example from Papua New Guinea. *Diversity*, 13 (6), 248.
<https://doi.org/10.3390/d13060248>
- Zhang, C., Rabiee, M., Sayyari, E. & Mirarab, S. (2018) ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics*, 19 (Supplement 6), 153.
<https://doi.org/10.1186/s12859-018-2129-y>

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

TABLE S1. List of samples used in the UCE and CytB analyses.

TABLE S2. Morphological data of individual specimens measured in this study.

FIGURE S1. *Lielaphis* and *Stegonotus* species tree inferred by ASTRAL-IV with Clade A (*L. slashi* **sp. nov.**) and Clade B (putative northern *L. aplini*) highlighted; numbers by nodes indicate Bayesian Posterior Probability value for each node.

FIGURE S2. CytB ML tree of *Lielaphis* and *Stegonotus* species inferred by IQ-TREE with Clade A (*L. slashi* **sp. nov.**) and Clade B (putative northern *L. aplini*) highlighted.

FIGURE S3. Distribution of *Lielaphis slashi* **sp. nov.** predicted by MaxEnt with Yapen island highlighted in the green box. Blue dots are occurrence points used to construct the ecological niche models.